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Early hominid evolution and ecological change through the African Plio-Pleistocene

The habitats in which extinct hominids existed has been a key issue in addressing the origin and extinction of early hominids, as well as in understanding various morphological and behavioral adaptations. Many researchers postulated that early hominids lived in an open savanna (Dart, 1925; Robinson, 1963; Howell, 1978). However, Vrba (1985, 1988) has noted that a major global climatic and environmental shift from mesic, closed to xeric, open habitats occurred in the late African Pliocene (approximately 2·5 m.y.a.), thus implying that the earliest hominids existed in these mesic, wooded environs. This climatic shift is also suggested to have contributed to a pulse in speciation events with turnovers of many bovid and possibly hominid species. Previous environmental reconstructions of hominid localities have concentrated on taxonomic identities and taxonomic uniformitarianism to provide habitat reconstructions (e.g., Vrba, 1975; Shipman & Harris, 1988). In addition, relative abundances of species are often used to reconstruct a particular environment, when in fact taphonomic factors could be affecting the proportions of taxa. This study uses the morphological adaptations of mammalian assemblages found with early hominids to reconstruct the habitat based on each species' ecological adaptations, thus minimizing problems introduced by taxonomy and taphonomy. Research presented here compares east and south African Plio-Pleistocene mammalian fossil assemblages with 31 extant mammalian communities from eight different habitat types. All communities are analyzed through ecological diversity methods, that is, each species trophic and locomotor adaptations are used to reconstruct an ecological community and derive its vegetative habitat. Reconstructed habitats show that *Australopithecus* species existed in fairly wooded, well-watered regions. *Paranthropus* species lived in similar environs and also in more open regions, but always in habitats that include wetlands. *Homo* is the first hominid to exist in areas of fairly open, arid grassland. This change from closed to open habitats occurs gradually from about 4 m.y.a. until about 2 m.y.a. when there is a major increase in arid and grazing adapted mammals. Therefore, the appearance of open savannas do not appear to have influenced the origination or adaptations of the earliest hominids, but could have contributed to their demise. As Stanley (1992) hypothesized, *Homo* species appear the first to be adapted to open, arid environments. © 1997 Academic Press Limited

Introduction

Many theories of early hominid evolution invoke environmental change to more open and xeric habitats as the causal agent for both origination and extinction events (Dart, 1925; Robinson, 1963; Howell, 1978; Vrba, 1985, 1988; Stanley, 1992). However, researchers have differences of opinion as to which species of hominids might have been the result of these aridification pressures: *Australopithecus, Paranthropus,* or *Homo*? Therefore, it is not only necessary to arrive at accurate habitat reconstructions for early hominid species, but to examine any alterations in those environments over time and compare those changes to appearances and disappearances of early hominids.

Much paleoecological research has centered on the study of single taxa or taxonomic groups and how the functional morphology of that taxonomic group is related to an animal's ecology, and thus its environment (Robinson, 1963; Vrba, 1974, 1975, 1980, 1988; Kay, 1975, 1978; Grine, 1981; Stern & Susman, 1983; Kappelman, 1988; Benefit & McCrossin, 1990; Ciochon,

1990; Spencer, 1995; Lewis, 1997). Community paleoecological analysis has traditionally concentrated on reconstructing the environment through the study of species organization and composition of the fossil fauna recovered from a locality (Dodd & Stanton, 1990). I use a combination of these two methodologies to reconstruct habitats for a variety of Pliocene hominid localities dating from 3·6 Ma until about 1 m.y.a. This is accomplished by first identifying the major trophic and locomotor adaptation of each fossil species through morphological analysis. These adaptations are then examined through ecological diversity analysis in a community perspective. Each fossil assemblage is thus a representative sample of a community of mammalian adaptations.

However, as with morphological studies that compare fossil animals to living ones, these fossil community assemblages had to be compared with modern analogs. Thus, a variety of modern habitats for which lists of large mammalian species were available were selected for this comparative study. These localities were taken from eight major vegetative habitat types, including forests, closed woodland, woodland–bushland transition, medium density woodland and bushland, open woodlands, shrubland, grasslands or plains, and desert.

Success of these paleoecological analyses is related to methods that minimize the effect of taphonomic processes. Accumulation of a fossil assemblage involves a number of processes that can alter the composition of the assemblage away from the original community. Therefore, I tested these methods on modern "death" assemblages. These assemblages consist of remains of mammals that have either died or been killed and left as surface assemblages or have been amassed by various carnivores and other animals. These death assemblages are all located within the modern vegetative habitats for which the entire community is known. Therefore, the results of the habitat reconstructions produced by the death assemblages are compared directly with the living community to determine if death assemblages reflect the habitat in which they were accumulated.

To address questions regarding hominid evolution and extinction, I use the habitat reconstructions of the Pliocene localities. First, I show how mammalian community composition alters with regard to proposed environmental changes that may have affected early hominids, such as suggested by Vrba (1988) at about 2·5 m.y.a. and at about 1·7 m.y.a. (Cerling, 1992; deMenocal, 1995). I also explore the possibility that particular species of hominids were adapted to specific vegetative habitat. Finally, I trace the ecological evidence provided by these fossil localities over time to see if the pattern of stasis purportedly exhibited in *Australopithecus* (Stanley, 1992) and *Paranthropus* (Wood *et al.*, 1994) corresponds to any climatic stasis.

Methods

Previous fauna-based environmental reconstructions of fossil localities include methods of taxonomic uniformitarianism (e.g., Vrba, 1974), functional or ecological morphology (e.g., Kappelman, 1988; Benefit & McCrossin, 1990), species diversity indices (e.g., Rose, 1981; Avery, 1982), faunal resemblance indices (e.g., Van Couvering & Van Couvering, 1976), and ecological structure analysis (e.g., Andrews *et al.*, 1979; Andrews, 1989). To generate habitat reconstructions in this study, I use a combination of functional morphology and ecological structure analysis to minimize taphonomic overprint, as well as to make these hominid fossil localities more comparable with their modern analogs. Behrensmeyer (1991) has noted that broad-scaled paleoenvironmental reconstructions based on the presence of taxa are likely to be accurate despite the taphonomic history of the assemblage. Andrews *et al.* (1979) designed
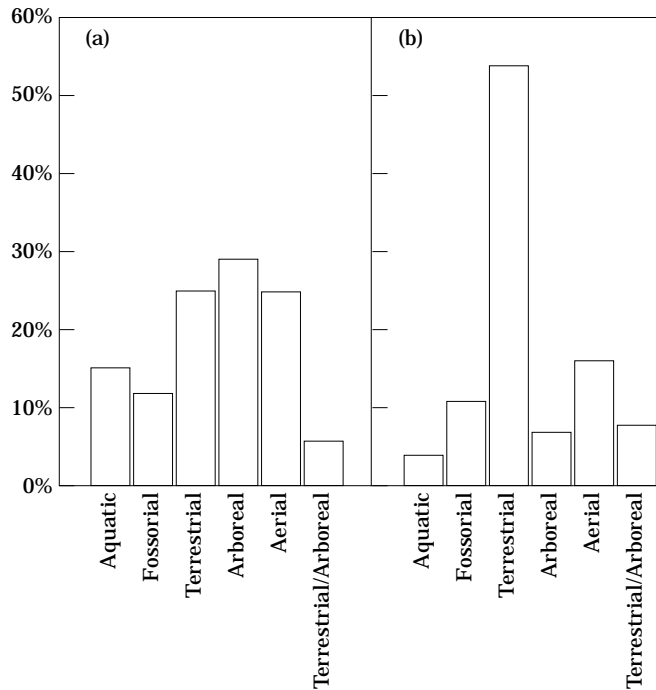
Figure 1. The percentages of locomotor ecovariables compared in two African communities (after Andrews et al., 1979). (a) Nigerian rain forest; (b) Serengeti.

ecological structure analysis to enable comparisons of fossil localities with extant communities across time and geographic regions. In addition, using the complete macromammal community eliminates problems encountered when deriving an environmental reconstruction from just one animal or group of animals, e.g., bovids, and provides an ecological reconstruction of a more complete community.

Ecological structure analysis
Fleming (1973) used this method to examine structural changes in faunal communities across latitudes. Andrews *et al.* (1979) recognized the significance of the method to compare communities across time and geographic regions without regard for taxonomic differences, and thus its usefulness for reconstructing habitats. At the basis of this analysis is the assignment of trophic, locomotor and body size ecological variables (ecovariables) to each mammal from each community. While Andrews *et al.* (1979) compared total spectra between communities (Figure 1), I examine abundance of each ecovariable (e.g., arboreality) from all habitats together (Figure 2). This type of examination shows a different perspective of ecological differences among habitats.

I use two categories of ecovariables for these reconstructions: locomotor and trophic. Preliminary analysis showed that body size was less effective for separating habitats than the trophic and locomotor adaptations (Reed, 1996). While these ecovariables are based on those of Andrews *et al.* (1979), I used additional trophic variables and different combinations of locomotor ecovariables for this study. These ecovariables are fairly broad, and therefore, can be readily identified from morphological analysis of fossil material.
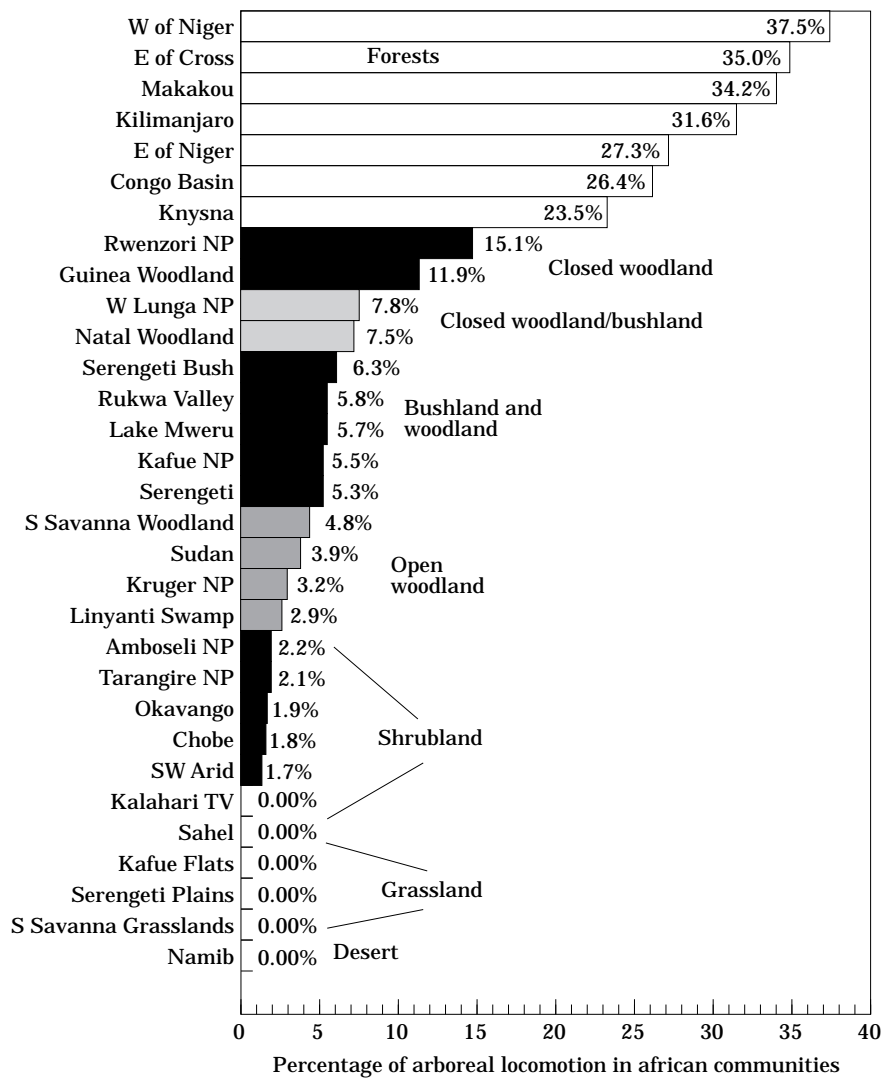
Figure 2. The percentages of arboreal locomotion in vegetative habitats ranging from forests to desert. The percentages of arboreality decline as tree cover declines and tree cover declines as mean annual rainfall decreases (see Table 1).

Locomotor categories include terrestrial, arboreal, aquatic, fossorial, and terrestrial/arboreal locomotion. Terrestrial locomotion refers to an animal that moves from place to place or feeds on the ground, for example, a bovid or a zebra. Arboreal locomotion describes a mammal that moves and feeds in trees at least 90% of the time, for example *Dendrohyrax arboreus*, the tree hyrax. Aquatic locomotion refers to animals that spend a major portion of their time in the water, and thus, water is a necessity. *Hippopotamus amphibius* is in this category. Fossorial locomotion describes an animal that utilizes or makes underground burrows, or uses its forelimbs to dig for food. An example is *Orycteropus afer*, the aardvark. Terrestrial/arboreal

locomotion is a characteristic of animals that use the ground to move from place to place, but often feed or sleep in trees. Examples of mammals that exhibit this type of adaptation are *Panthera pardus*, the leopard, and *Cercopithecus aethiops*, the vervet monkey. Because the assignment of the terrestrial/arboreal locomotion ecovariable from morphological analysis to fossils might have been equivocal, all of the locomotor ecovariables except arboreal loco-motion were combined into total terrestrial locomotion for some analyses, that is, this percentage equals the relative abundances of aquatic, fossorial, terrestrial, and terrestrial/arboreal locomotion together.

There are 12 trophic ecovariables. Browsers are mammals that eat leaves. There are two ecovariables that encompass grazing animals: (1) grazers are mammals that eat relatively dry grass in bulk; and (2) fresh-grass grazers are mammals that eat specific types of grass from edaphic grasslands. (Edaphic grasslands are those in which the grasses grow in water-logged soils, such as might be found in wetlands or swamps.) Mixed feeders are mammals that eat both dicot and monocot leaves (browse and grass) in varying proportions. There are two ecovariables for frugivorous mammals: fruit–leaf eaters and fruit–insect eaters. Because these ecovariables had to be reconstructed through morphological analysis of fossil material, however, these two adaptations were collapsed into one ecovariable (total frugivory). Insectivores are mammals that eat only insects (irrespective of their taxonomic classification, e.g., the canid, *Otocyon megalotis*, is a carnivore that eats only insects). There are three meat-eating ecovariables: (1) meat-eaters are mammals that eat only meat; (2) meat/bone eaters include animals that ingest the bone as well as meat; and (3) meat/nonvertebrate eaters are mammals that eat both meat and insects, crustaceans, etc. Root and bulb eaters consume roots and tubers, e.g., the porcupine. Finally, an omnivore is an animal whose diet contains food from at least three of the other trophic categories without preference. *Mellivora capensis*, the honey badger, is an example of a mammal in this category.

Description and collection of data sets

Modern African habitats. The first part of this study entailed collecting data on biotic and abiotic factors from published accounts of African national parks, game reserves, etc. to create a comparative sample of diverse modern habitat types (Table 1). These modern habitat types are broadly characterized, for example, the "forest" category includes lowland rain, tropical temperate, and montane forests. Fossil assemblages are more likely to yield reconstructions of broadly defined biozones rather than by microhabitats contained within each habitat type. Categories of vegetative habitats include forests, closed woodlands, woodland–bushland transition, medium density woodland and bushland areas, open woodlands, shrublands (including scrub woodlands), grasslands and plains, and deserts (Figure 3). In general, these modern habitats provide an ecological gradient from areas that are well-watered throughout the year (forests) to those that are extremely dry or quite seasonal (shrubland and deserts). Between these two extremes, the structure of the vegetation shows a decreasing density of trees with decreasing rainfall. However, the topological features of the landscape and the impact of fires, herbivores, and humans influence the plant life so that this gradient is not completely linear (Bourliere & Hadley, 1983).

I compiled lists of species from these habitats ranging in geographical breadth from western to eastern and southern African national parks, game reserves and specific vegetative regimes (Swynnerton, 1958; Lamprey, 1962; Child, 1964; Vesey-Fitzgerald, 1964; Sheppe & Osborne, 1971; Lind & Morrison, 1974; Kingdon, 1974a,b, 1977, 1979, 1982a,b; Ansell, 1978; Rautenbach, 1978; Smithers, 1978; Behrensmeyer *et al.*, 1979; Perera, 1982; Bremen & de

Table 1 Modern African habitat localities

| Locality	Rainfall	Category	Species	Arboreal	Aquatic	Frugivory	Terrestrial	Meat/bone	Fress grass	Grass
W of River Niger, Nigeria	1600	Forest	33	37·50%	12·50%	40·63%	62·50%	0·00%	6·25%	0·09%
E of Cross River, Nigeria	1550	Forest	40	35·00%	17·50%	47·50%	65·00%	0·00%	5·00%	0·00%
Makakous, Gabon	1800	Forest	41	34·15%	7·32%	56·10%	65·85%	0·00%	7·32%	0·00%
Kilimanjaro, Tanzania	1050	Forest (montane)	19	31·58%	0·00%	42·11%	68·42%	0·00%	0·00%	0·00%
E of River Niger, Nigeria	1596	Forest	32	27·27%	15·15%	36·36%	72·73%	0·00%	9·09%	0·00%
Congo Basin, Zaire	1800	Forest	53	26·42%	13·21%	43·40%	73·58%	0·00%	1·89%	0·00%
Knysna Forests, South Africa	1016	Forest (some montane)	17	23·53%	5·88%	41·18%	76·47%	0·00%	0·00%	0·00%
Rwenzori NP, Uganda	900	Closed woodland	51	15·09%	9·43%	26·42%	81·13%	3·77%	11·32%	3·77%
Guinea Woodland, Nigeria	1000	Closed woodland	59	11·86%	8·47%	20·34%	88·14%	3·39%	11·86%	5·08%
W Lunga NP, Zambia	825	Closed woodland/bushland transition	44	6·67%	11·11%	17·78%	93·33%	2·22%	6·67%	11·11%
Natal Woodland, South Africa	875	Closed woodland/bushland transition	40	7·50%	7·50%	22·50%	92·50%	3·77%	9·43%	9·43%
Serengeti Bushland, Tanzania	803	Bushland	64	6·25%	4·69%	17·19%	93·75%	4·69%	4·69%	12·50%
Rukwa Valley, Tanzania	700	Bushland/woodland	52	5·77%	7·69%	19·23%	94·23%	3·85%	9·62%	9·62%
Lake Mweru, Zambia	850	Bushland/woodland/edaphic grasslands	35	5·71%	8·57%	22·86%	94·29%	5·71%	14·29%	11·43%
Kafue NP, Zambia	821	Medium density woodland	55	5·45%	10·91%	12·73%	94·55%	3·64%	12·73%	10·91%
Serengeti NP, Tanzania	750	Bushland/woodland	75	5·33%	8·00%	17·33%	94·67%	4·00%	6·67%	10·67%
S Savanna Woodland, South Africa	650	Open woodland	83	4·82%	6·02%	13·25%	95·18%	3·61%	6·02%	16·87%
Sudan Savanna, Nigeria	689	Open woodland	51	3·92%	5·88%	11·76%	96·08%	5·88%	7·84%	7·84%
Kruger NP, South Africa	675	Open woodland	63	3·17%	7·94%	12·70%	96·83%	4·76%	6·35%	12·70%
Linyanti Swamp, Botswana	650	Open woodland/swamp	35	2·86%	14·29%	11·43%	97·14%	2·86%	17·14%	17·14%
Amboseli NP, Kenya	600	Open/scrub woodland	46	2·17%	4·35%	8·70%	97·83%	4·35%	6·52%	15·22%
Tarangire NP, Tanzania	600	Open/scrub woodland	48	2·08%	2·08%	8·33%	97·92%	6·25%	4·17%	12·50%
Okavango Delta, Botswana	600	Shrubland with flood plain	54	1·85%	11·11%	7·41%	98·15%	3·70%	9·26%	16·67%
Chobe NP, Botswana	650	Scrub woodland with river	56	1·79%	8·93%	7·14%	98·21%	3·57%	10·71%	16·07%
SW Arid Region, South Africa	400	Shrubland	60	1·67%	6·67%	8·33%	98·33%	5·00%	3·33%	23·33%
Kalahari Thornveld, South Africa	450	Shrubland	15	0·00%	0·00%	6·67%	100·00%	6·67%	0·00%	13·33%
Sahel Savanna, Nigeria	450	Shrubland/grassland/edaphic grassland	31	0·00%	9·68%	6·45%	100·00%	3·23%	9·68%	6·45%
Serengeti Plains, Tanzania	500	Grasslands	19	0·00%	0·00%	0·00%	100·00%	15·79%	0·00%	26·32%
S Savanna Grasslands, South Africa	500	Grasslands	41	0·00%	9·76%	4·88%	100·00%	4·88%	2·44%	24·39%
Kafue Flats, Zambia	821	Edaphic grasslands	36	0·00%	14·29%	5·71%	100·00%	5·71%	14·29%	17·14%
Namib Desert, Namibia	125	Desert	18	0·00%	0·00%	11·11%	100·00%	11·11%	0·00%	11·11%
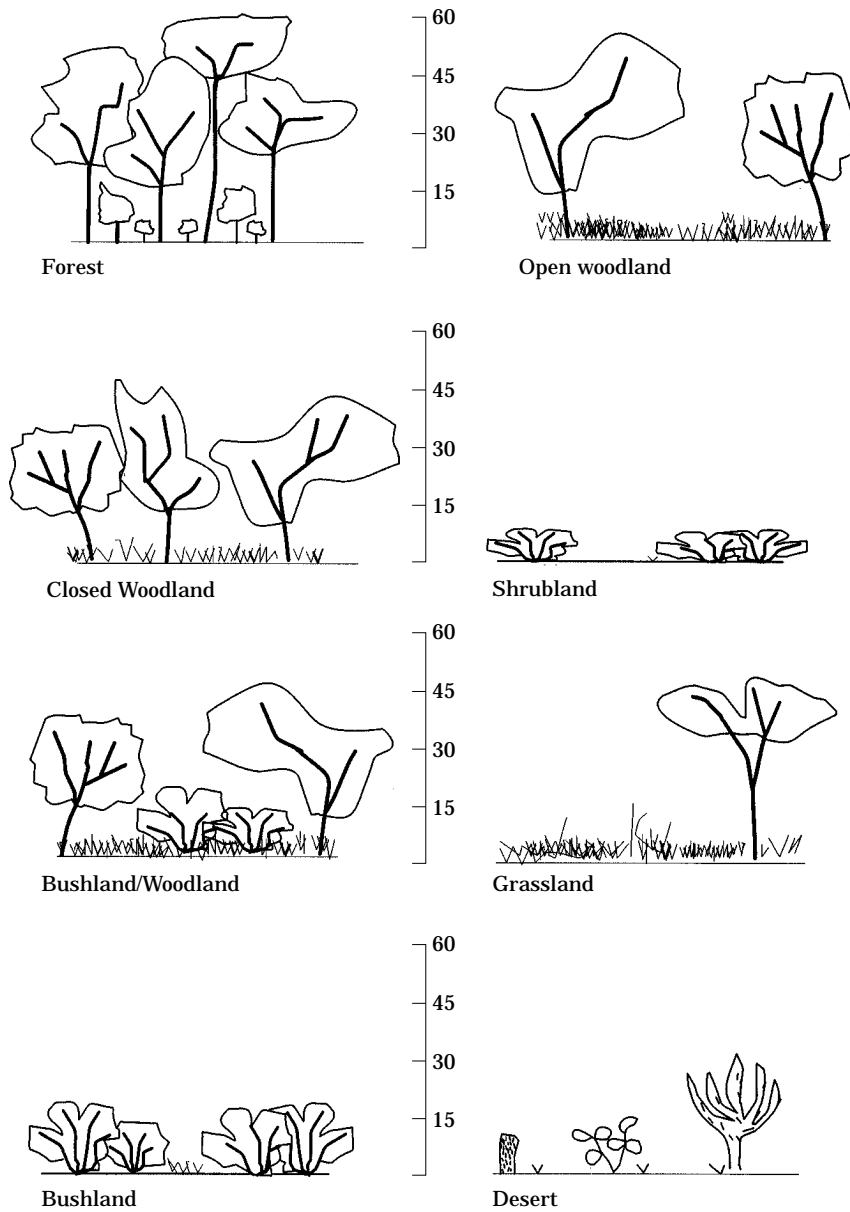
Figure 3. Examples of eight habitat types used in this study. Scale in feet.

Wit, 1983; Emmons *et al.*, 1983; White, 1983; Lanjouw, 1987; Happold, 1989; Skinner & Smithers, 1990). Areas in which species had been introduced, or habitats that were extremely altered by humans were not used. However, it should be noted that most African habitats have

been altered by human intervention to some degree. Data on rainfall, vegetative cover, temperature and seasonality were also collected.

After preliminary investigations using both micro- and macromammals, I restricted the analysis to macromammals (Reed, 1996). At fossil sites, micromammals are often accumulated separately from macromammals and are sometimes poorly represented. Therefore, I avoided potential taphonomic problems by using only large mammalian taxa, i.e., those weighing greater than 500 g. Mammals from modern communities were assigned ecovariables based on behavioral observations and analysis of stomach contents (Kingdon, 1974a,b, 1977, 1979, 1982a,b; Delaney & Happold, 1979; Happold, 1989; Estes, 1991; Skinner & Smithers, 1990).

Death assemblages. I included modern death assemblages in my analyses to see if biased samples taken from vegetative habitats in which the living community was known would accurately represent the environment in which they were collected. Thus, these death assemblage habitat reconstructions are compared directly with the living community to examine how accumulation factors influence habitat reconstructions.

Death assemblage data (Table 2) were taken from published accounts of mammals that produce bone assemblages (Kruuk, 1972; Schaller, 1976; Brain, 1981; Skinner *et al.*, 1986; Kitchener, 1991) and of a surface bone collection experiment (Behrensmeyer *et al.*, 1979).

Fossil localities. Specimen lists of fossil assemblages (Table 3) were taken from the literature (Coppens *et al.*, 1976; Harris, 1987; Brain, 1981; Leakey & Leakey, 1978; Leakey & Harris, 1987; Harris *et al.*, 1988; Harris & Leakey, 1993; Brain, 1993) and from personal identification and examination of faunas from Makapansgat, Swartkrans, Sterkfontein, Kromdraai A and B, Hadar, and some of the Omo and Usno collections from the Shungura Formation. Some of the localities do not contain hominids (e.g., Kromdraai A), or contain very few hominids (e.g., Tulu Bor, Koobi Fora). These were included for comparison with the hominid-bearing localities. Fossil species were assigned trophic and locomotor ecovariables in three different ways. First, for the fossil material I examined, morphological analyses were used to estimate trophic and locomotor preferences. These analyses (Reed, 1996) were based on methods from Van Valkenburgh (carnivores, 1987, 1989), Janis (ungulates, 1988), and Spencer (bovids, 1995; this volume). Second, other researchers have made morphological studies and assigned various trophic and locomotor behaviors to extinct taxa and these were used in many instances especially for material I did not examine (Geze, 1985; Benefit & McCrossin, 1990; Harris, 1987, 1991). Third, on occasion taxonomic uniformitarianism was used: a fossil taxon was assigned a trophic or locomotor category based on its relationship to an extant species, genus, tribe, or family. Assignments to trophic and locomotor ecovariables for all fossil taxa are listed in Reed (1996).

Analyses

Univariate analyses. After trophic and locomotor ecovariables were assigned to each species, the percentage of each ecovariable from each category was recorded for each modern habitat (for variable percentages used here, see Table 1). Thus all locomotor ecovariables for each community totaled 100%, as did all trophic ecovariables for each community. The percentages of each ecovariable across habitats were placed in bar graphs arranged by habitat type, i.e., forests were grouped together, closed woodlands, etc. This identified ecovariables that appeared to separate vegetative habitats and also showed how communities from different

Table 2 Death assemblages

Sites	Accumulator	Habitat	Species	Arboreality	Aquatic	Frugivory	Terrestrial	Meat/ bone	Fresh grass	Grass
Amboseli	Bone transect	Shrubland	34	2·9%	5·9%	8·8%	97·1%	5·9%	5·9%	17·7%
Andrieskraal	Porcupine	Open woodland	15	0·0%	6·7%	13·3%	100·0%	0·0%	6·7%	13·3%
Kafue Flats	Lion	Edaphic grasslands	18	0·0%	0·0%	5·6%	100·0%	0·0%	27·8%	27·8%
Kalahari-Gemsbok	Brown hyena	Shrubland	17	0·0%	0·0%	5·9%	100·0%	5·9%	0·0%	17·7%
Kalahari-Gemsbok	Leopard	Shrubland	12	0·0%	0·0%	8·3%	100·0%	0·0%	0·0%	16·7%
Kalahari-Gemsbok	Porcupine	Shrubland	11	0·0%	0·0%	9·1%	100·0%	9·1%	0·0%	36·4%
Kruger NP	Spotted hyena	Open woodland	27	0·0%	3·7%	3·7%	100·0%	3·7%	11·1%	25·9%
Kruger NP	Leopard	Woodland/riparian	28	0·0%	4·2%	17·9%	100·0%	3·6%	7·1%	25·0%
Tai Forest	Leopard	Rain forest	22	31·8%	4·6%	50·0%	68·2%	0·0%	4·6%	0·0%
Serengeti NP	Leopard	Bushland/woodland	18	0·0%	0·0%	5·6%	100·0%	0·0%	11·1%	33·0%
Serengeti Plains	Spotted hyena	Bush/woodland/plains	16	0·0%	0·0%	0·0%	100·0%	0·0%	6·3%	43·8%
Ngorangoro Crater	Spotted hyena	Edaphic grasslands/woodland	12	0·0%	0·0%	0·0%	100·0%	8·3%	8·3%	41·7%

Table 3 Plio–Pleistocene fossil localities

Sites	Date (m.y.a.)	Species	Arboreality	Aquatic	Frugivory	Terrestriality	Meat/bone	Fresh grass	Grass
Laetoli 1	3·6	25	12·00%	0·00%	24·00%	88·00%	8·00%	0·00%	24·00%
Laetoli 7	3·6	28	10·71%	0·00%	21·43%	89·29%	3·57%	0·00%	17·86%
Sidi Hakoma	3·34–3·2	44	5·00%	6·81%	13·00%	95·00%	6·08%	12·50%	15·00%
Tulu Bor	3·36–2·68	38	2·60%	7·89%	7·89%	97·40%	2·60%	15·78%	21·05%
Usno	3·36–3·0	32	6·25%	6·25%	15·63%	93·75%	6·25%	6·25%	15·63%
Makapansgat 3	3·2–3·0	55	5·45%	1·82%	14·55%	94·55%	3·64%	3·64%	16·36%
Makapansgat 4	3·0	31	6·45%	0·00%	19·35%	93·55%	6·45%	3·23%	12·90%
Denen Dora	3·2–3·18	43	4·65%	6·98%	6·98%	95·35%	6·98%	9·30%	16·28%
Shungura B	2·95	44	13·33%	4·44%	20·00%	86·67%	2·22%	11·11%	22·22%
Shungura C	2·85	54	5·56%	5·56%	14·81%	94·44%	3·70%	11·11%	16·67%
Burgi Member	2·68–1·88	53	3·77%	9·43%	11·32%	96·23%	5·66%	13·21%	22·64%
Sterkfontein	2·6–2·4	30	3·33%	0·00%	16·67%	96·67%	3·33%	3·33%	23·33%
Shungura D	2·52	31	6·45%	6·45%	16·13%	93·55%	0·00%	12·90%	16·13%
WT 17000	2·5	39	2·56%	5·12%	20·51%	97·44%	2·56%	23·08%	17·95%
Shungura E	2·4	33	6·06%	6·06%	21·21%	93·94%	0·00%	9·09%	12·12%
Shungura F	2·36	44	4·55%	6·82%	13·64%	95·45%	2·27%	6·82%	20·45%
Shungura G	2·3	52	5·77%	5·78%	9·62%	94·23%	1·92%	13·46%	25·00%
Kromdraai B	2·0–1·5	15	0·00%	0·00%	26·67%	100·00%	6·67%	0·00%	13·33%
KBS Member	1·88–1·6	67	1·49%	7·46%	7·46%	98·51%	1·49%	14·93%	37·31%
Swartkrans 1	1·8	36	0·00%	5·56%	13·89%	100·00%	5·56%	2·78%	25·00%
Swartkrans 2	1·6	34	0·00%	5·88%	8·82%	100·00%	8·82%	0·00%	32·35%
Swartkrans 3	1·4	48	0·00%	6·25%	6·25%	100·00%	3·13%	4·17%	25·00%
Natoo Member	1·51	30	0·00%	10·00%	3·33%	100·00%	0·00%	16·67%	46·67%
Kromdraai A	1·5–1·0	41	2·44%	0·00%	9·76%	97·56%	7·32%	2·44%	21·95%
Okote Member	1·6–1·39	38	0·00%	10·53%	7·89%	100·00%	2·63%	18·42%	39·47%
Sterkfontein 5	1·0	16	0·00%	0·00%	0·00%	100·00%	0·00%	0·00%	43·75%
Makapan 5	1·0	13	0·00%	15·38%	0·00%	100·00%	0·00%	15·38%	15·38%

Table 4 **Ranges of selected predictor ecovariables for each habitat type**

Habitat	Arboreality	Frugivory	Terrestriality	Grazing
Forests (n=7)				
X	30·77%	43·9%	69·22%	0%
S.D. (±)	3·8%	4·68%	3·81%	—
Range	23·52–37·5%	36·36–56·09%	62·5–76·5%	—
*Closed wood (n=2)				
X	13·47%	23·38%‡	84·63%	4·43%‡
S.D. (±)	1·61%	3·04%	3·5%	0·66%
Range	11·86–15·09%	20·3–26·46%	81·13–88·14%	3·77–5·08%
*Closed woodland bushland (n=2)				
X	7·1%	20·14%‡	92·75%	10·27%‡
S.D. (±)	0·41%	2·36%	0·59%	0·83%
Range	6·67–7·5%	17·78–22·5%	92·16–93·33%	9·43–11·11%
Bushland (n=4)				
X	5·7%†	19·15%‡	94·23%†	9·86%‡§
S.D. (±)	0·31%	2·28%	0·32%	1·51%
Range	5·33–6·25%	17·19–22·86%	93·75–94·67%	7·5–11·43%
Medium/open woodland (n=5)				
X	4·05%†	12·37%	96·96%†	13·04%§
S.D. (±)	0·97%	0·06%	0·98%	3·58%
Range	2·85–5·45%	11·43–13·2%	95·54–97·14%	7·84–17·14%
Shrubland (n=7)				
X	1·37%	7·58%	98·63%	14·79%
S.D. (±)	0·7%	0·66%	0·7%	3·77%
Range	0–2·17%	6·45–8·17%	97·82–100%	6·45–23·33%
Grasslands (n=3)				
X	0%	3·53%	100%	22·61%
S.D. (±)	—	0·34%	—	5·47%
Range	—	0–5·71%	—	17·14–26·31%
Kruskal–Wallis test statistic	30·76	31·35	30·76	22·90

Krustal–Wallis showed significant differences between groups for all pairs of habitat types at $\chi^2_{0.001[6]}=22.458$. *Combined for further analysis using Mann–Whitney U tests between each pair of communities. These tests showed significant differences at $P<0.05$, except for: †no significant difference between bushland/open woodland; ‡no significant difference between closed woodland/bushlands; §$P<0.10$ beween bushland/open woodland.

habitats changed in ecological composition (Figure 2). Ecovariables that appeared to visually separate vegetative habitats (predictor ecovariables) were analyzed statistically (Table 4) and examined graphically with box and whisker plots (Figure 4).

Bivariate analyses. The predictor ecovariables were used in bivariate plots to further analyze the communities (Figure 5). After modern habitats were analyzed, death assemblage data were plotted with and compared with their modern counterparts to see if they accurately reflected the vegetative habitat from which they were derived. Fossil locality data were then plotted with the modern community analogs to reconstruct the vegetative habitat for each fossil assemblage. Finally, the fossil localities were arranged in chronological order using grazing, total frugivorous, and arboreal adaptations to trace these ecovariables across time. These ecovariables were chosen to represent changing habitats across time.
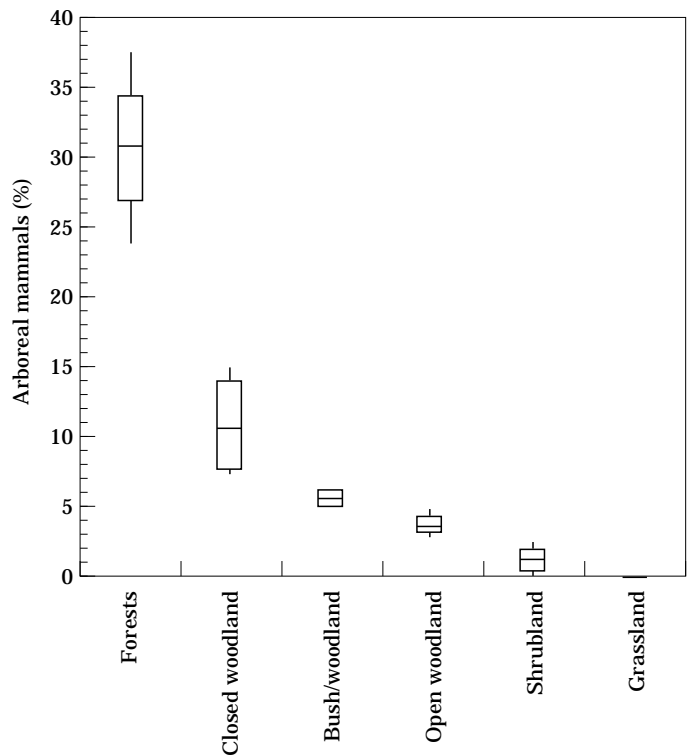
Figure 4. Box and whisker diagram of the percentages of arboreal mammals. Whiskers indicate range, boxes represent two standard deviations, and the horizontal lines are the means for each vegetative habitat grouping. Closed woodland includes closed woodland–bushland transition regions.

Results

Modern African communities

By examining the ecovariables separately, i.e., in univariate analyses across habitats, several predictor ecovariables emerged. These predictor ecovariables are proportions of adaptations that are similar in the same vegetative habitat types and change consistently across habitats. Locomotor adaptations whose relative abundances predict habitats are: (1) percentage of arboreal locomotion (Figure 2); or (2) its antithesis, the percentage of total terrestrial locomotion (including terrestrial, aquatic, fossorial, and terrestrial/arboreal adaptations); and (3) the percentage of aquatic locomotion (Table 1). The relative abundance of these mammalian ecovariables is dependent upon the vegetative regime such that as tree presence changes, the percentages of arboreal and terrestrial animals change. If more water is present in the habitat, then there is a greater relative abundance of aquatic mammals.

Relative abundances of trophic ecovariables also characterize habitats. The best trophic predictor ecovariable is percentage of total frugivory. The proportion of total frugivory changes from high in forest regions to low or nonexistent in shrubland and plains regions. When this variable is used in combination with arboreality or terrestriality, each habitat category is separated from one another. In addition, the bushland communities are successfully separated from the medium density woodland habitat (Figure 5). Other trophic ecovariables
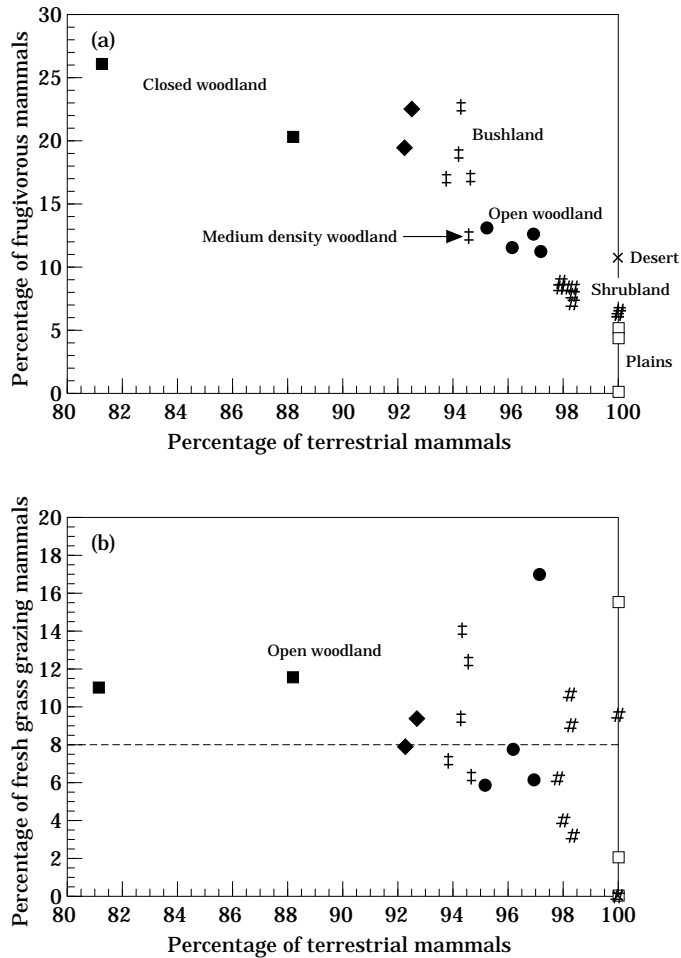
Figure 5. (a) Bivariate plot of the percentages of total terrestrial mammals *vs.* frugivorous mammals in vegetative habitats ranging from closed woodlands to desert (forests are not presented in this and subsequent diagrams so that other habitats are more easily compared). Both ecovariables separate habitats according to tree cover and rainfall. In addition, the medium density woodland of Kafue National Park has been separated from the more bushland communities (‡) because the percentages of frugivory are higher in bushland regimes. (b) Bivariate plot of the percentages of total terrestrial mammals *vs.* fresh grass grazers in vegetative habitats ranging from closed woodlands to desert. Habitats that contain large amounts of water and thus edaphic grasslands are positioned above the 8% dashed line. Key: (■) closed woodland, (◆) closed woodland–bushland transition, (‡) bushland, (●) open woodland, (#) shrubland/scrub woodland, (□) grassland/plains, (×) desert.

that can be used to analyze habitats are proportions of grazing, fresh grass grazing, and meat-bone eating.

Through an analysis of each community of mammalian adaptations, patterns between the vegetation types and the mammals that live within them became apparent. Arboreal mammals are evident in forest and closed woodland communities in high numbers. As trees grow shorter and further apart due to lessening rainfall, intense seasonality, and/or different soil content, the presence of arboreal animals decreases. As the total number of arboreal animals declines,

animals with other locomotor adaptations become more common. For example, under arid conditions in poor soils (shrublands), more fossorial animals exist. It is interesting that it is the adaptations that are measurable and consistent, rather than the taxonomic identity. There are ecological equivalents existing in similar types of habitats whether the mammals are closely or distantly related.

This analysis shows that ecological proportions of mammals in communities are correlated with vegetative structure. This relationship is predictable in two ways. First, if one knows the vegetative regime of a particular area, the proportions and types of ecovariables that will be exhibited by the mammals in the habitat can be estimated. Second, and this is important for reconstructing paleocommunities, if the adaptations, i.e., the proportions of each ecovariable in communities can be reconstructed, then habitats can be predicted.

Death assemblages

After the modern vegetative habitats were categorized by ecovariable proportions, I analyzed extant death assemblages in the same way. Table 2 shows the number of species and resultant ecovariable percentages for each of the death assemblages. The bar charts that I used to examine individual ecovariables are omitted here because of space limitations (but see Reed, 1996). The same results are obtained using bivariate plots, for example terrestriality *vs.* frugivory (Figure 6). The death assemblage based on leopard scats (Kitchener, 1991) from the Tai Forest predicted the vegetative habitat exactly. The Tai Forest assemblage exhibits high percentages of arboreal locomotion (31·82%) and total frugivory (50%), and no grazing nor meat–bone eating animals, all of which place the locality in a rain forest habitat.

The Amboseli Bone Transect (Behrensmeyer *et al.*, 1979) was positioned near the Amboseli National Park in the scrub woodlands area of the graph [Figure 6(b)]. The smaller sample size of the bone transect increases the percentage of arboreality, and thus, it appears closer to the open woodlands than the shrublands. However, percentages of frugivory (8·82%) and grazing (17·65%) are within shrubland habitat ranges (Table 4).

The other death assemblages were created by carnivores and rodents that exist in more open habitats, and thus, the assemblages are classified as open using the total terrestrial locomotion ecovariable (100%). First, this reflects that some of these accumulators hunt in microhabitats that possess greater percentages of terrestrial animals than appear in the entire national park community, for example. Second, the sample sizes are smaller than those found in living and fossil communities with a bias against smaller animals. In open woodlands and shrublands usually the only arboreal animal is a galago. Even if one of these creatures died and fell to the ground, a hyena would completely consume the remains, and a porcupine would not find the tiny skeletal elements of the galago appropriate for gnawing. Thus the death assemblages from the Kruger National Park and Andreiskraal are terrestrially aligned with more open and drier habitats than the living community. The modern Kalahari–Gemsbok communities contain small to no percentage of arboreal animals (1·29 and 0%), thus the three death assemblages from that region are positioned appropriately.

In the total fruit-eating ecovariable, however, all of the death assemblages are positioned with the habitats from which they were derived. The Kafue National Park lion kills contained 5·56% frugivorous species and the living community contains 5·71% frugivorous species; the spotted hyena dens and the leopard kills from Kruger National Park have 3·7 and 17·86% frugivorous species, respectively. The difference reflects the fact that hyenas are prone to hunt and scavenge in more open woodland, while the leopards in Kruger are apt to hunt in the riparian and more bushland areas. The entire park contains 12·7% frugivorous species, about
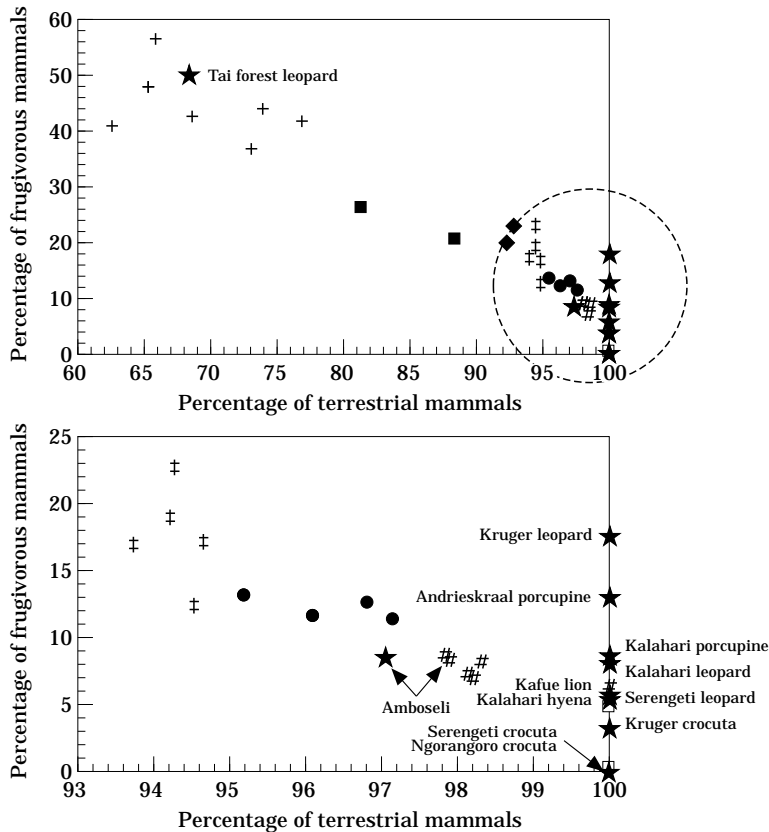
Figure 6. Bivariate plots of the percentages of terrestrial *vs.* frugivorous mammals in vegetative habitats from forests to desert including death assemblages. The top figure shows all habitats and the Tai Forest leopard death assemblage aligning with other forest habitats. Bottom figure is expansion for the circle in the top figure. Key: (+) forests, (■) closed woodland, (◆) closed woodland–bushland transition, (‡) bushland, (●) open woodland, (#) shrubland/scrub woodland, (□) grasslands/plains, (×) desert, (★) death assemblages.

midway between the two death assemblage abundances of fruit-eaters. Finally, the three assemblages from the Kalahari–Gemsbok National Park contained 5·88% (brown hyenas), 8·33% (leopard), and 9·09% (porcupine) frugivorous species, while the modern habitats contain 6·67% (Kalahari Thornveld) and 8·33% (South West Arid Region). Thus, total frugivory is useful for predicting habitats as the death assemblages reflect finer habitat separations than expected.

These death assemblage samples show that although predators and collectors can bias samples, relatively accurate habitat reconstructions can be made based on them. Fossil assemblages are usually formed over longer periods of time and contain more species from the living communities than these death assemblages. Fossil localities that were carnivore accumulated may be depauperate in arboreal and/or aquatic species, and this must be considered when reconstructing the paleohabitat. Nevertheless, high percentages of frugivores and fresh grass grazers may also indicate bushlands, woodlands and wetlands. In addition, the presence of particular animals that are known to occupy fairly narrow habitats, such as forest-dwelling duikers, can also be used to help make final habitat reconstructions. Thus,
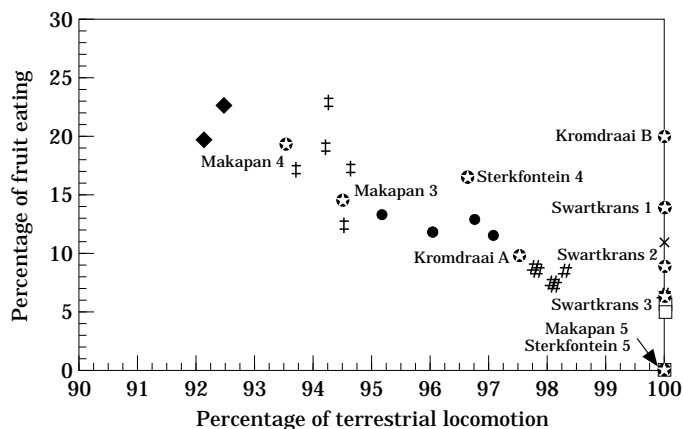
Figure 7. Bivariate plot of the percentages of terrestrial *vs.* frugivorous mammals in vegetative habitats ranging from closed woodlands to desert including southern African Plio-Pleistocene hominid localities. Key: (■) closed woodland, (◆) closed woodland–bushland transition, (‡) bushland, (●) open woodland, (#) shrubland/scrub woodland, (□) grasslands/plains, (×) desert, (☆) Plio-Pleistocene fossil localities.

death assemblages are biased in some ecovariables, but not others. However, the composite reconstructions of all of these death assemblages are fairly accurate predictions of the actual habitat.

Plio-Pleistocene fossil localities

Having shown that it is reasonable to expect that species found in death assemblages can predict the habitat in which they were found, I will now reconstruct the habitats for the Pliocene hominid sites based on fossil assemblages. Each individual assemblage, whether derived from a cave site, lacustrine environment, or surface landscape accumulation, is a sample of the living mammalian community, and as such, should provide fairly accurate habitat reconstructions. I will discuss southern African Plio-Pleistocene localities first, and then eastern African sites in chronological order. I will also compare these habitat reconstructions with previous environmental reconstructions that were based on geology, pollen, and faunal groups. Table 3 shows the number of species and resultant ecovariable percentages for each of the fossil localities.

Southern African hominid localities

Limeworks Cave, Makapan Valley. The Limeworks Cave is located in the northeastern part of the Transvaal in South Africa. The older deposits (Members 3 and 4) are suggested to be in the range of 3·2–2·7 Ma and are capped by a Pleistocene aged deposit (Partridge, 1979; MacFadden, 1980; Delson, 1984; Vrba, 1995).

Member 3. This deposit contains an extremely large number of mammalian specimens (greater than 30,000), of which 24 are *Australopithecus africanus*. The deposit was accumulated in the cave by fossil hyaenid and porcupine species (Maguire, 1985; Reed, 1996). There are relatively high percentages of frugivorous species (14·95%) and some arboreal animals (5·45%). Thus the habitat is positioned with bushland and medium density woodlands. Fresh grass grazers (3·44%) and aquatic mammals (1·84%) indicate the presence of a river and some edaphic grasslands (Figures 7 and 8). Previous reconstructions have ranged from woodland
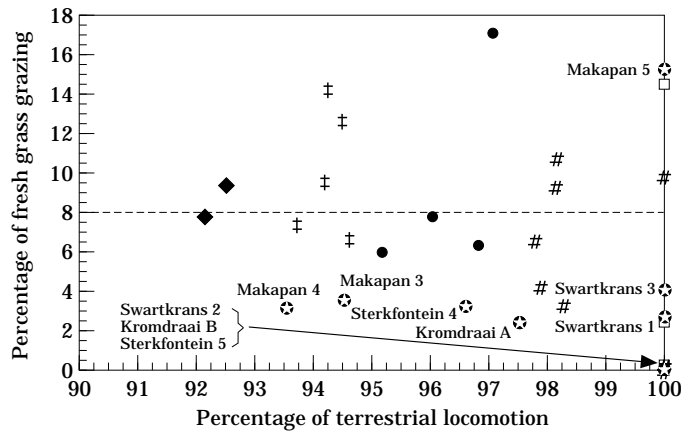
Figure 8. Bivariate plot of the percentages of terrestrial *vs.* fresh grass grazing mammals in vegetative habitats ranging from closed woodlands to desert including southern African Plio-Pleistocene hominid localities. Habitats that include rivers, wetlands, and edaphic grasslands are above the dashed line (8%). Key: (■) closed woodland, (◆) closed woodland–bushland transition; (‡) bushland, (●) open woodland, (#) shrubland/scrub woodland, (□) grasslands/plains, (×) desert, (☆) Plio-Pleistocene fossil localities.

(Vrba, 1980) to forest (Cadman & Rayner, 1989) to open savanna with nearby bushland (Dart, 1952; Wells & Cooke, 1956). However, the mammalian community suggests that this region was a habitat mosaic that contained riparian woodland, bushland, and edaphic grassland. Member 4. *A. africanus* is represented by only three specimens out of a total of 257 mammalian specimens. Cercopithecine monkeys make up 80% of the collection; and the likely accumulators were birds of prey and leopards (Reed, 1996).

Member 4 deposits contain even greater percentages of arboreal (7%) and frugivorous (20%) species than Member 3, which suggests a more wooded habitat. However, this is probably a function of sample size and predation bias rather than a change of habitat. Because this member may have been accumulated by birds of prey, there may be an exclusion of many bovid species. This would skew the results to the more wooded habitat than the ecovariables suggest. Thus, because Member 3 and Member 4 are roughly contemporaneous in time, both assemblages probably represent a woodland–bushland habitat.

Member 5. There have been no hominids or other primates recovered from this member. Member 5 is a Pleistocene deposit with very few species (13), and is included here for comparative purposes. The accumulating agent is not known, although as it is a cave deposit it is likely that either carnivores or hominids made the collection. There are aquatic animals (15·4%) and fresh grass grazers (15·4%) which indicate edaphic grasslands and a water source, but there are no frugivorous or arboreal mammals, indicating that the region might have been more open and xeric in the Pleistocene.

Sterkfontein, Sterkfontein Valley. The Sterkfontein cave has been continuously excavated for the last 27 years. Over 850 hominid remains have been recovered (L. Berger, pers. comm.). Extensive analyses of faunal remains of this locality were done by Brain (1981) and Vrba (1976) and the analysis here is based on these original studies.

Member 4. *A. africanus* has been recovered from this member, which has been faunally dated to between 2·4 and 2·6 m.y.a. (Delson, 1984), and the deposit may be the result of carnivore

activity (Brain, 1981). The mammalian community consists of few arboreal animals (3·33%), but a high percentage of frugivorous mammals (16·67%). There is also a fairly high percentage of terrestrial/arboreal animals (23·33%). There are no aquatic animals from this locality, and only 3·33% fresh grass grazers (Figures 7 and 8).

The fauna suggests a habitat reconstruction for Member 4 of an open woodland, with bushland and thicket areas. Other habitat reconstructions of this member at Sterkfontein have indicated a medium density woodland (Vrba, 1975), a moderately open savanna (Vrba, 1985), an open woodland to a forest (McKee, 1991), and an open savanna (Benefit & McCrossin, 1990). Thus, the mammalian community reconstruction is close to Vrba's 1975 interpretation. However, while there are few arboreal animals, the high percentage of frugivorous mammals falls within the range of bushland and medium density woodland, and this locality is likely similar to the more closed Makapansgat Member 3 deposit.

Member 5. Porcupines have gnawed a few of the specimens, as did carnivores, and likely they or the *Homo* sp. recovered from this member created the deposit (Brain, 1981). Other mammals recovered include 43·75% grazing animals with no arboreal or frugivorous species. These figures suggest an open or wooded grassland or plains region. Other habitat reconstructions (Vrba, 1975; McKee, 1991) suggest that the habitat at the time of this deposit was an open savanna, which agrees with the reconstruction presented here.

Kromdraai, Sterkfontein Valley. The Kromdraai cave sites consist of narrow solution cavities that are no more than 17 m apart (Brain, 1981). The two non-contemporaneous deposits are designated A and B.

Kromdraai A. Kromdraai A has produced no hominids, but is included here for comparative purposes (Figures 7 and 8). This deposit is the younger of the two and has been faunally dated to between 1·5 and 1·0 Ma old (Vrba, 1975; Delson, 1984). There are 2·44% arboreal and 9·76% frugivorous species. Kromdraai A has a relatively high percentage of grazers (21·95%) and no aquatic animals. These ecovariables reconstruct a vegetative habitat of scrub woodland with grasslands or perhaps wooded grasslands. Vrba (1975) suggested an open savanna for this site; my reconstruction agrees with that suggested by bovid tribe proportions.

Kromdraai B. *Paranthropus robustus* and three other primates were recovered from this site; there are very few other animals (11). This locality has been faunally dated to between 2·0 and 1·5 Ma (Vrba, 1983; Delson, 1984). Based only on the high percentages of terrestrially adapted animals (100%) it is likely that this was an open grassland. However, there is also a relatively high proportion (20%) of frugivorous species, indicating patches of riparian woodland. Vrba (1975), however, has also classified the habitat from Kromdraai B as an open savanna.

Swartkrans, Sterkfontein Valley. The Swartkrans Cave was thoroughly excavated between 1979 and 1986 and the complete faunal assemblage was studied by Brain (1981, 1993) and Watson (1993). Although there are three distinct members, Brain (1993) has suggested that there is no difference in the fauna, and thus, all members are roughly the same age. This places them in a range of time from 1·8–1·2 m.y.a. The deposits were likely accumulated by carnivores, probably leopards (Brain, 1981).

Member 1. *P. robustus* and *Homo* sp. are represented by this member. Although there are no arboreal species found in this Swartkrans deposit, there are 13·89% fruit and leaf eaters, as well as 5·56% aquatic animals (Figures 7 and 8). There is a small proportion of fresh grass grazers (2·78%). This gives the picture of an open habitat, with a river present as evidenced by aquatic animals. This river or stream probably supported a woodland or forest as suggested by

the percentage of frugivorous mammals that fall in the range of medium density woodland and bushland. In addition, there would have been patches of edaphic grasslands to support the fresh grass grazers. Previous reconstructions of this member include a moderately open savanna (Vrba, 1975); a mesic, closed woodland (Benefit & McCrossin, 1990); and a savanna woodland with riparian woodland and reed beds (Watson, 1993). The reconstructed habitat here agrees with that of Watson (1993).

Member 2. *P. robustus* and *Homo* sp. are recovered from this member. Despite the assertion that these deposits are roughly the same age (Brain, 1993), there appears to be a decline in fruit and leaf eaters from Member 1 (13·89%) to Member 2 (8·82%). There are no fresh grass grazers from this member, although there are still aquatic carnivores (5·88%). There is a very large percentage of meat–bone eaters (8·82%). There is also an increase to 32·35% grazing animals and 100% total terrestriality. Thus, this indicates a drier habitat than the previous member, perhaps a wooded grassland with wetlands. Vrba (1975) reconstructed the habitat of Member 2 as a moderately open savanna which agrees with the interpretation here.

Member 3. Only *P. robustus* has been found in these deposits (Watson, 1993). There is a further drop in fruit and leaf eaters in this member to 6·25%. However, there is also a decrease in grazing animals to 25%, which is accompanied by an increase in fresh grass grazing animals (4·17%). There are similar proportions of aquatic animals (6·25%) and fossorial animals (8·33%) to those in Member 2. Thus, the habitat of this member is reconstructed as an open grassland with a river or stream nearby supporting edaphic grasslands.

East African Deposits greater than 2·5 Ma

Laetoli, Tanzania (3·6 Ma). *Australopithecus afarensis* is found in the Laetolil Upper Beds. These are a conglomeration of localities that are separated by a variety of volcanic tuffs dating from 3·8–3·5 Ma. The vertebrate fauna does not appear until above Tuff 6 which is dated to about 3·6 Ma (Hay, 1987). Localities 1 and 7 are used here, rather than the complete fauna, in order to minimize time-averaging as both localities range from Tuff 6 to either the Yellow Marker Tuff or Tuff 8 (approximately 3·6–3·56 Ma). Specimens or foot prints of *A. afarensis* have been recovered from both localities.

There is a fairly high abundance of arboreal animals (12 and 10·71%) which are all primates. Even if some of these primates were terrestrial, Laetoli would still fall within the woodland–bushland range because of the high abundance of fruit eaters within the assemblage (24 and 25%). These localities are therefore reconstructed as closed woodlands (Figures 9 and 10).

The habitat of Laetoli has been previously reconstructed as a dry, open woodland because the deposits contain an abundance of dik-diks and other arid adapted grazing species (Harris, 1987). Andrews (1989), however, using the entire faunal list from the formation, also arrived at a more wooded habitat reconstruction. Walker (1987) suggests that there were trees in the vicinity because of the presence of galagos, and Gentry (1987) suggests that at least two of the bovid species were forest dwellers. Pollen analysis has indicated either wooded grassland with montane conifers in the vicinity or an evergreen bushland and *Acacia* savanna (Bonnefille & Riollet, 1987). Thus, my reconstructed habitat of a closed to medium density woodland is similar to those of Andrews (1989) and Walker (1987).

Hadar, Ethiopia (3·4–3·18 Ma). *A. afarensis* has been recovered from throughout the Hadar Formation in the Afar of Ethiopia. The data used here represent species lists from two geological members, as locality data are not yet analyzed. An overall habitat reconstruction
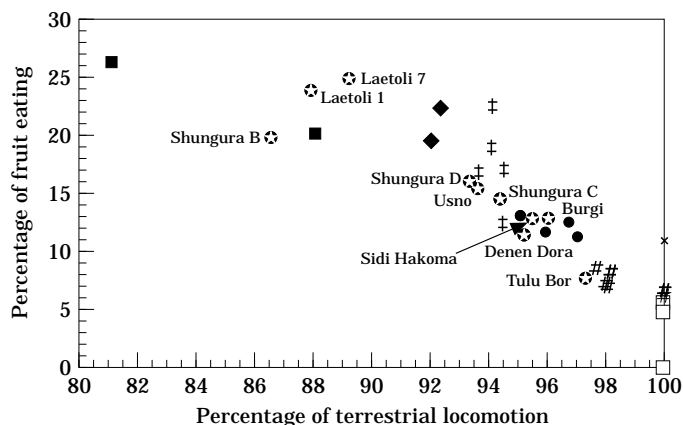
Figure 9. Bivariate plot of the percentages of terrestrial *vs.* frugivorous mammals in vegetative habitats ranging from closed woodlands to desert including East African Pliocene localities from before 2·5 m.y.a. Key: (■) closed woodland, (◆) closed woodland–bushland transition, (‡) bushland, (●) open woodland, (#) shrubland/scrub woodland, (□) grasslands/plains, (×) desert, (✿) Plio-Pleistocene fossil localities.
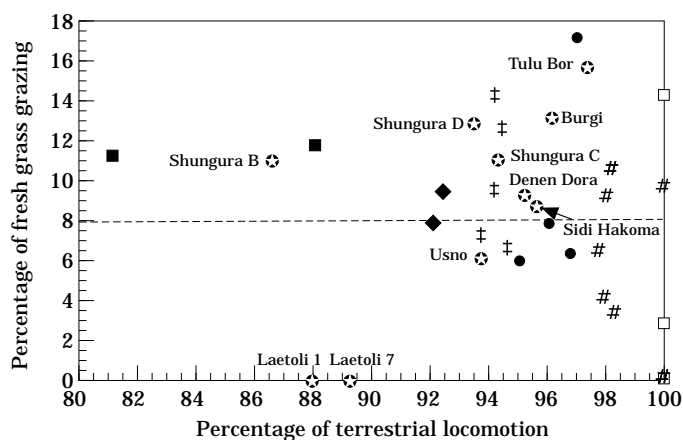

Figure 10. Bivariate plot of the percentages of terrestrial *vs.* fresh grass grazing mammals in vegetative habitats ranging from closed woodlands to desert including East African Pliocene localities from before 2·5 m.y.a. Habitats that include rivers, wetlands, and edaphic grasslands are above the dashed line (8%). Key: (■) closed woodland, (◆) closed woodland–bushland transition, (‡) bushland, (●) open woodland, (#) shrubland/scrub woodland, (□) grasslands/plains, (×) desert, (✿) Plio-Pleistocene fossil localities.

emerges for these members, but fluctuations in climate that occur over 200,000 years will not be reflected in this analysis. Aronson & Taieb (1981) note that the paleoenvironment at Hadar consisted of fluviatile flood plains and lacustrine sediments.

Sidi Hakoma. This member contains numerous fossils of extinct hippos, elephants, and crocodiles. Fresh grass grazing reduncines and hippos (8·7%) show that edaphic grasslands were present (Figures 9 and 10). The Sidi Hakoma falls within the ranges of extant medium to open density woodland communities rather than bushland, because of the lower percentage of fruit and leaf eaters (13·04%). There are 4·65% arboreal animals which is in the open woodland range, or could indicate the presence of a riparian woodland or forest. Because this

member covers about 200,000 years, there must have been habitat fluctuations within that time span. However, it is likely that at no time during this period was there an open, arid habitat.

Denen Dora. The Denen Dora spans from 3·2–3·18 m.y.a., and thus covers a relatively short amount of time. There is evidence of a lake with marshes in the early part of this member, but this changes to flood plains and deltas later in the section (Aronson & Taieb, 1981). This member contains many of the same species present in the Sidi Hakoma and the habitat of the Denen Dora was also a woodland with forest regions near water sources and edaphic grasslands.

Other reconstructions of habitats for Hadar suggest wooded to treeless savanna (Boaz, 1977) and an open grassland with humid conditions (Harris, 1991). Pollen analysis suggests an evergreen bushland close to forest (Bonnefille, 1983). Thus the reconstruction predicted from the mammalian community is closest to that suggested by the pollen recovered from the deposits.

Koobi Fora Formation (3·4–1·6 Ma). This formation is in the Turkana basin of Kenya. Similar deposits to the north in Ethiopia include those of the Omo River, the Shungura and Usno Formations. Many of the volcanic tuffs between these two regions have been correlated (Brown & Feibel, 1991). The Koobi Fora Formation includes members that range from the Tulu Bor at 3·36 Ma (which is the earliest containing hominid fossils) to the Chari at about 1 Ma old. The faunal lists for Koobi Fora were derived from localities within each member reported in Leakey & Leakey (1978). The members for which habitats are reconstructed here include the Tulu Bor (3·36–3·0 Ma), the Burgi (3·0–2·0 Ma), the KBS (1·88–1·5 Ma), and the Okote (1·6 Ma). The Tulu Bor and Burgi Members are discussed here with the other early East African Pliocene localities. The KBS and Okote Members are discussed later.

Tulu Bor. *A. afarensis* has been recovered from this member (Kimbel, 1988). Paleogeographic reconstructions of the Turkana Basin at 3·4 and 3·3 Ma indicate a river system with deposits laid down during axial flooding periods. These flood waters came from the Ethiopian Highlands, not from local rains (Brown & Feibel, 1991).

Fauna recovered from the Tulu Bor Member indicates fairly high percentages of aquatic animals (7·89%) and fresh grass grazing animals (15·78%) (Figures 9 and 10). However, the Tulu Bor deposits have very few arboreal animals (2·6%) and low percentages of fruit and leaf eaters (7·89%). Thus, this member appears to have been a scrub woodland region with a flooding river. Wetlands were probably extensive. Harris (1991) has noted that based on the fauna and pollen this member was probably a flood plain and gallery forest with edaphic grasslands to the south. The presence of a gallery forest is not reflected in the mammalian adaptations used to reconstruct this environment.

Burgi. There are two hominid species recovered from this member, *Homo* sp. and *Paranthropus boisei* (Harris, 1991). Brown & Feibel (1991) suggest this member was also an axially flooding river system.

The faunal community has high abundances of aquatic animals (9·43%), fresh grass grazers (13·21%), and fruit and leaf eaters (11·32%). There is also a fairly high percentage (15·09%) of terrestrial/arboreal animals (Figures 9 and 10). It appears as if there was slightly more flooding or rainfall contributing to the presence of more herbaceous vegetation during this time period as compared to the Tulu Bor Member. I reconstruct this member as an open woodland with edaphic grasslands and a riparian woodland. Harris (1991) reconstructed this member as being a more closed woodland in the north and more open to the south.

Usno Formation. The Usno Formation is part of the Omo River Deposits in Ethiopia. The U-10 deposits have been correlated with the Tulu Bor Member in the Koobi Fora Formation (Feibel & Brown, 1993). Hominids from the Usno Formation have been attributed to *Australopithecus* sp. The Usno contains a higher percentage of arboreal (6·25%) and terrestrial/arboreal (28·13%) animals than the Tulu Bor Member, and thus the Usno is positioned with the bushland–woodland regions (Figures 9 and 10). There is a high abundance of aquatic animals (9·38%), but not very many fresh grass grazers (6·25%). This suggests a wooded riverine habitat without extensive edaphic grasslands. The abundance of fruit and leaf eaters (15·63%) indicates that there were probably bushland and thicket areas, as well as riverine forest and woodland.

Shungura Formation. This sequence of deposits occurs in the lower Omo Valley, Ethiopia. The Members (A–L) are divided by a series of tuffs that are dated from 3·6 to about 1·0 Ma. Some of these tephras have been correlated with those in the Usno and Koobi Fora Formations (Feibel & Brown, 1993). While the Shungura Formation has produced an abundance of mammalian material with exceptional specimens of bovids and monkeys, hominids are represented by fairly scrappy remains (pers. obs.).

Member B. Hominids recovered have been assigned to *Australopithecus* sp. (Coppens *et al.*, 1976). Deposits from Member B range from 3·36–2·8 Ma, and thus, fauna from Member B includes almost 600,000 years of material from various depositional systems. However, most of this fauna derives from B-10 and is thus more constricted in time to around 2·95 m.y.a. (G. G. Eck, pers. comm.). Therefore, a habitat reconstruction is possible. Geologically, deposits were formed by a perennial river system with occasional riverine flooding which created flood plains (de Heinzelin *et al.*, 1976).

There is a high percentage of arboreal animals (13·33%) placing the locality within the closed woodland range (Figures 9 and 10). The percentage of frugivorous species is also quite high (20%), again within the range of closed woodland areas. Member B deposits also include some aquatic (4·54%) and some fresh grass grazing (11·11%) mammals. Member B fauna indicates a habitat of mostly closed woodland with riverine forest and edaphic grasslands. Other habitat reconstructions include a riverine forest based on pollen analysis (Bonnefille, 1984), and a wooded savanna and forest based on micromammals (Jaeger & Wesselman, 1976). The habitat reconstruction presented here agrees with both of these reconstructions.

Member C. There are *Australopithecus* sp. remains from this member and Suwa (1990) indicates that *Paranthropus aethiopicus* is represented in unit C7. This member was also deposited along a meandering river under flooding conditions (de Heinzelin *et al.*, 1976). The fossil assemblage includes 5·56% arboreal, 14% frugivorous, and 5·56% aquatic animals (Figures 9 and 10). These percentages are in the ranges of modern woodlands and bushlands that also encompass riverine forest. There are high proportions of fresh grass grazers (11·11%) that indicate a fairly extensive edaphic grassland, and terrestrial/arboreal animals (22·22%). Therefore, the entire deposit appears to contain animals that are derived from an overall bushland–woodland regime with a riverine forest and edaphic grasslands. Bonnefille (1984) has noted that the pollen recovered from this member indicates a grassland habitat, but the faunal community does not agree with that unless the pollen is reflecting the edaphic grasslands.

Member D. There are hominid remains from 10 localities in Member D which are attributed to *Australopithecus* sp. (Coppens *et al.*, 1976) and to *P. aethiopicus* (Suwa, 1990). Tuff D was deposited on flood plains in which plants quickly grew (de Heinzelin *et al.*, 1976). This was followed by extensive channeling of the river.
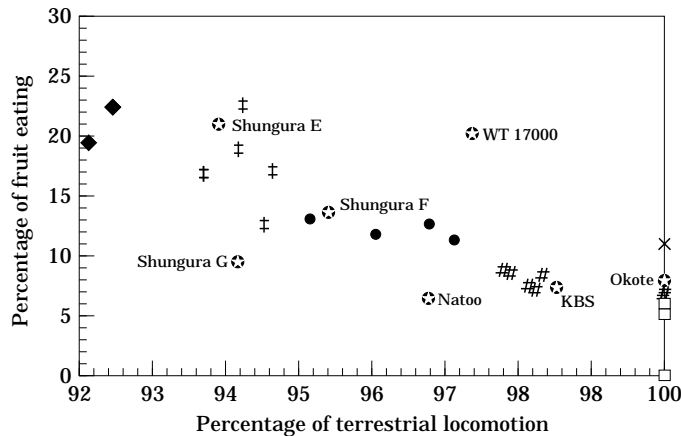
Figure 11. Bivariate plot of the percentages of terrestrial *vs.* frugivorous mammals in vegetative habitats ranging from closed woodlands to desert including East African Pliocene localities after 2·5 m.y.a. Key: (■) closed woodland, (◆) closed woodland–bushland transition, (‡) bushland, (●) open woodland, (#) shrubland/scrub woodland, (□) grasslands/plains, (×) desert, (☆) Plio-Pleistocene fossil localities.

There are slightly higher percentages of arboreal animals (6·45%) and frugivorous species (16·13%) than those found in Member C (Figures 9 and 10). There are also 6·45% aquatic mammals and 12·9% fresh grass grazers. Therefore, this habitat consisted of riverine forests within a woodland–bushland regime and included edaphic grasslands. Bonnefille (1984) notes that the pollen from this member indicates woodland, and this agrees with the habitat indicated by the mammalian fauna.

East African hominid fossil localities with dates <2·5 Ma
Koobi Fora Formation (1·88–1·6 Ma)

KBS Member. Hominids from this member include *Homo erectus* and *P. boisei*. Lacustrine sediments are evident from the KBS, however, the lake was probably shallow and throughout much of the deposit there are no vertebrate fossils except fish (Brown & Feibel, 1991).

The KBS mammalian fauna includes many aquatic and fresh grass grazing animals (7·46 and 14·93%, respectively), but very low percentages of arboreal (1·49%) and terrestrial/ arboreal (5·97%) adaptations (Figures 11 and 12). There are some adaptations to fruit and leaves (7·46%). The major change is in the percentage of grazing mammals (37%) which is greater than in any of the previous members at Koobi Fora. In addition, although KBS falls within the ranges of modern scrub woodland and arid shrubland for many of the ecovariables, it has many more grazing species. This implies that unlike the scrub woodland and shrubland habitats, there was an abundance of nonedaphic grasses present during the KBS depositional period.

Harris (1991) suggests dry open conditions for this member, based on percentages of various bovid tribes present. Two sets of pollen data indicate either a savanna or grassland/subdesertic steppe for the KBS Member (Bonnefille, 1984). Thus, all habitat reconstructions support a grassland or shrubland environment.

Okote Member. *P. boisei* has been recovered from this member. The Okote Member is again part of a river system, but the flooding was lateral rather than axial (Brown & Feibel, 1991). Fauna from this member includes no arboreal animals, and very few (5·26%) terrestrial/
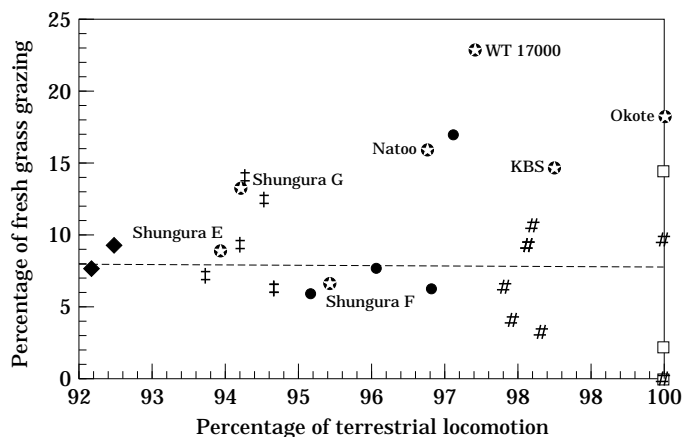
Figure 12. Bivariate plot of the percentages of terrestrial *vs*. fresh grass grazing mammals in vegetative habitats ranging from closed woodlands to desert including East African Pliocene localities after 2·5 m.y.a. Habitats that include rivers, wetlands, and edaphic grasslands are above the dashed line (8%). Key: (■) closed woodland, (◆) closed woodland–bushland transition, (‡) bushland, (●) open woodland, (#) shrubland/scrub woodland, (□) grasslands/plains, (×) desert, (☆) Plio-Pleistocene fossil localities.

arboreal ones (Figures 11 and 12). There are very high proportions of aquatic adapted (10·53%) and fresh grass grazing animals (18·42%), plus a high abundance (39·47%) of grazing animals. Thus it appears that at 1·39 m.y.a., this region was similar to the wetlands and edaphic grasslands of Kafue Flats (as described by Perera, 1982).

Nachukui Formation, West Turkana. The Nachukui Formation is on the west side of Lake Turkana. The formation is part of the extensive Turkana Basin and Omo Group defined by de Heinzelin (1983).

Lomekwi Member/WT-17000 Locality. The skull of *P. aethiopicus* was recovered 3·8 m below the Lokalalei Tuff in the Lomekwi Member. There is a great abundance of fresh grass grazing species (23·08%) from this locality. However, there are only 5·12% aquatic species (Figures 11 and 12). This suggests that the edaphic grasslands utilized by the fresh grass grazers were shallow wetlands or marshy swamps because there are few deep water aquatic species. There are 2·56% arboreal and 20·51% frugivorous species from this locality indicating the presence of trees and many fruiting plants, both trees and bushes. Walker *et al*. (1986) note that while alcelaphine and aepycerotine bovids dominate the horizons below this locality, this site is represented mostly by reduncine bovids, reflecting edaphic grasslands or marshes. I reconstruct the WT-17000 locality as an open woodland with bushland thickets, edaphic grasslands and wetlands, and a riparian woodland or forest.

Natoo Member. The *H. erectus* skeleton, WT 15000 was probably recovered within this member as it is above the equivalent J-4 Tuff (1·64 Ma), but below the Lower Nariokotome Tuff (1·33 Ma) (Feibel & Brown, 1993). The Natoo Member is correlated with the Okote Member of the Koobi Fora Formation. The paleogeographic reconstruction of this depositional member includes three alternative water sources flowing into the region. There is speculation as to whether a lake or river existed in the region (Brown & MacDougall, 1993).

The presence of a lake or river system is evident in the percentages of aquatic (6·45%) and fresh grass grazing animals (16·13%). Like those found in the Lomekwi Member, these

mammals could represent marshy wetlands. There are few arboreal animals (3·22%) and the percentage of frugivorous species is only 6·45% (Figures 11 and 12). The percentage of grazing animals is 46·67%. Thus the mammals of the Natoo deposits indicate wooded and edaphic grasslands, as well as swampy vegetation.

Shungura Formation, Omo, Ethiopia

Member E. *P. boisei* (Feibel *et al.*, 1989) and/or *P. aethiopicus* (Howell *et al.*, 1987; Leakey & Walker, 1988; Suwa, 1990) have been recovered from this member. According to de Heinzelin *et al.* (1976), there is an absence of "illuvation" in the soils above Tuff E, and they therefore suggest a drier climate. However, the fauna does not indicate a particularly dry habitat. There is about the same percentage of arboreal species (6·06%) and a slightly higher percentage of frugivorous animals (21·21%) than found in the Member D deposits (Figures 11 and 12). There are also fewer grazing animals in Member E (12·12%) than D (16·13%). However, the abundance of fresh grass grazers (9·09%) and aquatic animals (6·06%) has dropped slightly from the percentages of these ecovariables in Member D. Therefore, fauna from this deposit seems to indicate a fairly well-watered woodland–bushland with a riparian woodland or forest. Bonnefille (1984) suggests grassland pollen for this member, and while there probably was grass within the woodland and bushland, the total faunal assemblage does not indicate open grasslands for this member.

Member F. *P. aethiopicus* has been recovered from this member (Suwa, 1990), which was deposited when there were flood plains present, although the tephras were deposited on sandy soils, rather than on water indicating that the flood plains were not particularly widespread (de Heinzelin *et al.*, 1976). The terrestrial fauna from this member increases from previous members and thus, there appears to be less tree cover. There is also a decrease in fresh grass grazing animals to 6·82% and an increase in grazing animals to 20·45% (Figures 11 and 12). Therefore, there were few areas of edaphic grasslands, and more open woodland at the time of these deposits, and high abundance of frugivorous species indicates the presence of bushland. Bonnefille (1984) notes that the pollen indicates grasslands, and Jaeger & Wesselman (1976) note that the micromammals indicate open, arid conditions. While my data do not indicate particularly arid conditions, the region was probably more open and slightly drier than preceding habitats. In fact, the mammalian fauna agrees with the paleogeography in that the flood plains are reduced (de Heinzelin *et al.*, 1976).

Member G. A *P. boisei* mandible has been recovered from unit G3 and a fragmentary skull attributed to *Homo habilis* has been found in unit G28 (Kimbel, 1995). This member has a very similar community structure to that of Member F. There are arboreal animals (5·77%) and frugivorous species (9·62%), as well as aquatic (5·78%) and fresh grass grazing species (13·46%). And there is a slight increase in grazing animals from 20 to 25% in this member (Figures 11 and 12). This locality also reflects the presence of a river surrounded by open woodland, and the flood plain seems to have again expanded from Member F to include edaphic grasslands as indicated by the fresh grass grazing species.

Tracing ecovariables across time

It has been postulated that there were major turnovers in bovid and hominid lineages at around 2·7–2·5 m.y.a. (Vrba, 1988, 1995; Vrba *et al.*, 1989). These extinction and speciation events for bovids were proposed to be the result of a global cooling and drying event which

produced more open grassland-type habitats in Africa. Cerling (1992), however, suggests that the first evidence of significant C4 grasslands, and thus evidence of major environmental change, is at about 1·7 m.y.a. Vrba (1995) shows significant bovid species turnover, as represented by an FAD (first appearance date) pulse at 2·7–2·5 m.y.a. Were there major climatic changes at either 2·7–2·5 m.y.a. or 1·7 m.y.a.? I examine this issue ecologically, rather than taxonomically, by charting specific ecological characteristics across time to see if there are trophic and/or locomotor changes in communities that would support the hypothesized climate changes at these times.

By plotting grazing, arboreal, and total frugivory predictor ecovariables from each eastern and southern African fossil locality against time, changes in community structure can be observed (Figure 13). While percentages of these ecovariables cannot be inferred in temporal gaps, it is probable that the fossil localities included represent the trends discussed. The relative abundances of grazing mammalian species, of which bovids, at least, are indicatory of more open woodlands and grasslands (Vrba, 1974, 1975), fluctuate in East African localities from 15–25% until approximately 1·8 m.y.a. [Figure 13(a)]. At that time grazing animals increase to higher percentages (45%) than previously recorded. Although South African hominid localities give evidence of having been more dry and bushy than contemporaneous eastern African sites, percentages of grazing follow the same pattern.

The percentage of arboreality in East Africa at 3·6 m.y.a. is in closed woodland ranges (see Table 4). Percentages fluctuate between closed woodland and open woodland ranges until after 1·8 m.y.a. when they drop to shrubland and grassland ranges [Figure 13(b)]. The drops to open woodland ranges before 1·8 m.y.a. include the Tulu Bor Member of the Koobi Fora Formation and the WT-17000 locality from West Turkana which have already been recognized as slightly more open habitats. In southern Africa, arboreal percentages in mammalian communities begin in bushland–woodland ranges and fall into shrubland and grassland ranges. Because there is one site between 3·0 and 2·0 Ma, it is impossible to detect fluctuations in these variables. However, there is a definite change to open habitats from 3 to 2 m.y.a.

Percentages of frugivory in East African communities also fluctuate within woodland ranges until sometime between 2·45 and 1·88 m.y.a. when they drop to shrubland and grassland ranges. In South Africa, percentages of frugivory in communities remain relatively high from about 3·0 m.y.a. until about 1·8 m.y.a. when they drop into open woodland ranges and then to grassland levels at Sterkfontein 5 (Figure 13(c)].

Vrba (1988, 1995) reports a turnover in bovid species in Africa around 2·7–2·5 m.y.a. This taxonomic shift does not correspond to a dramatic increase in higher levels of grazing adaptations in bovids and other mammals. Although the percentages of grazing fluctuate until 1·8 m.y.a., a gradual decline in abundance of arboreal mammals within communities is apparent from around 3·4 Ma through 1 Ma, especially in South Africa. This could have been caused by either continuous, gradual climate aridification or an increase in seasonality. This gradual, but fluctuating, shift in ecological adaptations is supported by evidence for glacial cycles that began to fluctuate between 3·1 and 2·6 m.y.a. (deMenocal, 1995). Additionally, it has been reported (Kerr, 1996) that the Evolution of Terrestrial Ecosystems group at the Smithsonian Institution have not seen a taxonomic turnover pulse in any mammalian group from the Turkana Basin at 2·5 Ma, but did report a gradual taxonomic shift over about a million years. This study supports their detailed study of the Turkana Basin over a broader scaled examination of eastern and southern Africa. This pattern does not preclude various regions being more affected by local tectonism than by global climatic shifts. However, the
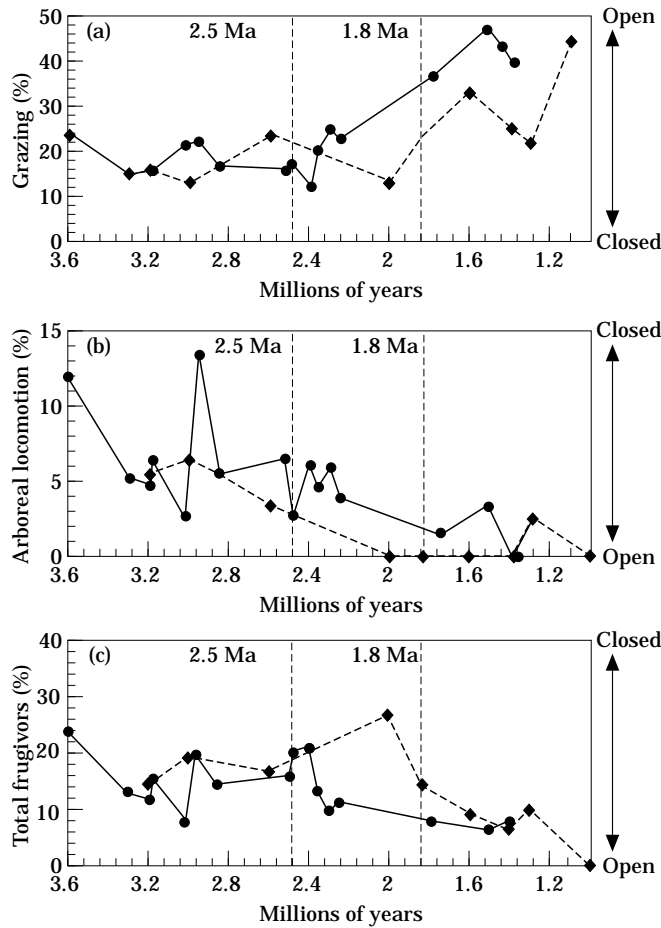
Figure 13. Bivariate plot of the percentages of (a) grazing mammals, (b) arboreal animals, and (c) frugivorous mammals found in each hominid fossil locality against time. Vertical dotted lines represent 2·5 and 1·8 Ma. An increase in grazing occurs between 2·3 and 1·8 Ma in eastern and southern Africa. Arboreal locomotion declines sharply at the same time in both southern and eastern Africa. Frugivory declines between 2·5 and 1·8 Ma in eastern Africa. Interestingly, although southern Africa is relatively drier, frugivory is somewhat higher in those hominid localities indicating a bushier habitat than those of eastern Africa. Note: if the hominid locality encompassed a dating range (e.g., 3·36–2·68), then the mean date was used on the plot. (●) East Africa; (◆) South Africa.

overall pattern shows gradual aridification or change to more pronounced dry seasons that possibly precipitated the movement or extinction of arboreal and frugivorous mammals so that they are no longer found in great abundance in hominid assemblages after 1·8 m.y.a. Grazing mammals do not show great expansion until about 1·8 m.y.a. when they exceed 30% in many eastern African hominid localities. This spike coincides with Cerling's (1992) suggestion of an expansion of modern type C4 (secondary) grasslands in Africa, and deMenocal's (1995) evidence of drier environments and seasonality at this time. Thus, it is likely that grazing adaptations did not increase substantially within communities until the development and expansion of secondary grasslands.

Habitats associated with hominids

The goal of reconstructing paleohabitats and tracing changing environments across time is to illuminate the conditions in which hominid species lived. In this section, I describe the overall and perhaps preferred habitats in which each hominid species existed with regard to their evolution.

Australopithecus *species*

The localities in this study that include *A. afarensis* or fossils that are only identified to the genus *Australopithecus* include Laetoli; Hadar Formation, Sidi Hakoma and Denen Dora Members; Shungura Formation, Members B, C (?), D (?), Usno (?); and Koobi Fora Formation, Tulu Bor Member. These localities have been reconstructed as closed to open woodland/bushland with edaphic grasslands. However, the fauna from the Tulu Bor Member is indicative of a shrubland with a deltaic flood plain, probably similar to the Okavango Delta. This reconstruction is interesting because this member contains just a few hominid specimens (Wood, 1994). It is possible that more hominids have not been recovered from the Tulu Bor because the paleohabitat was too open, i.e., the environment was not "preferred" by *A. afarensis*.

The Pliocene locality of Fejej from which *A. afarensis* has also been recovered has too few mammals to allow a thorough reconstruction of the community. However, the fauna from these Pliocene deposits includes crocodiles, cat fish, *Diceros bicornis*, *Nyanzachoerus* sp., *Tragelaphus* sp., and *Neotragini* sp. This preliminary faunal community reveals the presence of water and woodland–bushland animals, and as such it is similar to the constructions for the other early Pliocene localities.

A. afarensis is generally found in habitats containing water and trees. It is difficult to prove with habitat evidence alone that these early hominids had specific dietary, locomotor, or anti-predator adaptations that required trees or warm, mesic conditions. However, anatomical studies (e.g., Stern & Susman, 1983; Susman *et al.*, 1984) have indicated that the anatomy of hominids indicated morphological adaptations for some arboreal locomotion.

The sites of Makapansgat and Sterkfontein are the only localities in this study that include *A. africanus*. The habitat derived from the Member 3 and Member 4 fauna from Makapansgat is woodland and bushland with riverine forest. This river system also supported patches of edaphic grasslands. The habitat of Sterkfontein Member 4, later in time, is also reconstructed as woodland, but it is more open than that of Makapansgat. Thus, *A. africanus* also existed in woodland areas, similar to those in which *A. afarensis* existed, albeit slightly drier. However, as these are cave sites and probably animal accumulated, there could be a bias against arboreal and aquatic animals. Thus, it is possible that *A. africanus* existed in more mesic, closed woodlands or bushlands than are represented by these reconstructions.

These woodland/bushland habitats with plentiful water suggest that the environment in which these *Australopithecus* spp. existed was fairly static, that is, the habitats in which these hominids could exist are constrained by minimum and maximum amounts of rainfall and tree cover. This agrees with the hypothesis of Stanley (1992) that *A. africanus*, at least, existed in a fairly static environment. Over time, as the mammalian communities indicate that Pliocene habitats became more open, these hominids disappear from the fossil record. Perhaps a gradual change to drier, more open habitats and/or a more pronounced dry season forced these australopithecines across an environmental tolerance limit around 2·8–2·5 m.y.a., and resulted in their extinction.

Paranthropus *species*

P. aethiopicus has been recovered from the Shungura Formation, Members C–G (Suwa, 1990) and the West Turkana WT-17000 locality. Mammalian communities from these localities indicate that most were bushland to open woodland regions and all contain edaphic grasslands to greater or lesser extents. These habitats overlap with the more open end of those of *A. afarensis* and *A. africanus*. Because so few of these fossils have been recovered, it is not possible to make generalizations about the habitat preference of this species. However, these habitats appear to be more closed than those of later *Paranthropus* species.

P. boisei has been recovered from the KBS and Okote Members of the Koobi Fora Formation. These localities are fairly open (from woodland to scrub woodland), but all have edaphic grasslands and therefore plentiful water. Behrensmeyer (1978) has previously noted that *P. boisei* fossils were recovered from deltaic environments at Koobi Fora (KBS). In addition, Shipman & Harris (1988) indicate that Beds I and II at Olduvai sample lake margin regions, i.e., some edaphic grasslands. However, *contra* Shipman & Harris (1988) I found that this hominid does not necessarily prefer "closed" habitats (at least at non-Olduvai localities), but rather, habitats with abundant water and edaphic grasslands. This habitat differs from that of *P. aethiopicus* in being more open, but it cannot be considered dry.

P. robustus has been recovered from Swartkrans and Kromdraai. The habitats of Swartkrans have been reconstructed as an open or wooded/bushed grassland with edaphic grassland. Kromdraai B has been tentatively reconstructed as an open grassland, though it must be noted that this reconstruction is based on a small sample. Future excavations may recover fossils of aquatic or wetland mammals which could significantly affect this reconstruction. Nevertheless, the southern African *P. robustus* appear to be slightly more arid adapted than east African *P. boisei*.

Except for *Paranthropus* found at the Kromdraai B locality, the genus seems to have been recovered mostly from deltaic habitats that include edaphic grasslands. Wood *et al.* (1994) suggest that *P. boisei* exhibits evolutionary stasis throughout its existence in eastern Africa. It appears from this analysis that the habitats that are associated with *P. boisei* are extremely similar over its temporal range which supports the observations of Wood *et al.*

Grine (1981) has suggested that *Paranthropus* species had a diet that contained extreme amounts of grit, and perhaps the substances that they preferred in their diets were associated with river or lake margins and thus, edaphic grasslands. This study supports this suggestion as these species are always found in the vicinity of water courses with high percentages of mammals that eat the vegetation produced by this environment. *Paranthropus* is not found in early middle Pleistocene localities that were deposited in arid grassland environments. This suggests that as the environment became increasingly arid and open throughout the early Pleistocene, *Paranthropus* probably faced changing and diminishing resources. Further research into the time period between 1·2 million and 500,000 years ago may show that these flood plain habitats were also affected by seasonal changes. There was a drying event recorded in eolian dust after 1 m.y.a. (deMenocal, 1995). While other orders of mammals were able to withstand more arid or seasonal environments, perhaps these changes could have influenced the extinction of *Paranthropus* spp.

Homo *species*

Several localities from which *Homo* species are known were included in this research: Koobi Fora KBS and Okote Members, Nachikui Formation Natoo Member, Swartkrans Members 1 and 2, and Sterkfontein Member 5. Two localities in this study in which only *Homo* species

have been recovered are Sterkfontein 5 (an arid, plains habitat) and the WT 15000 locality of the Nachukui Formation (shrubland with possible riparian woodland). The differing reconstructions suggest that early *Homo* probably occupied a wider range of habitats than earlier hominids. However, it is worth emphasizing that there are several different species of *Homo* included in this analysis. Further study into hominid Pleistocene localities to examine habitats associated with various *Homo* species is necessary. Some of the earliest *Homo* species are found near edaphic grasslands, but are also found in habitats that have been reconstructed as open grasslands and dry shrublands. Many localities yield specimens of both *Homo* and *Paranthropus*. Perhaps *Homo* and *Paranthropus* were sympatric, but inhabiting different niches: *Paranthropus* foraging in edaphic grasslands and *Homo* utilizing other microhabitats. The appearance of later *Homo* in secondary grassland localities coincides with Stanley's (1992) suggestion that *H. erectus* was the first hominid adapted to life on the "open savanna".

Conclusions

In conclusion, these ecological diversity studies have shown that modern habitat types can be predicted by the ecovariables of the mammals found in them. Tests of modern death assemblages showed that taxonomic and taphonomic overprint were minimized using this methodology. Using the same methodology, Plio-Pleistocene habitats were reconstructed through analyses of mammalian fossil assemblages.

Australopithecus species have been recovered from fossil assemblages that indicate fairly wooded regions. It is possible that these woodland areas provided some protection against predation, an important consideration for these small bipedal apes. Their anatomy shows that they were adept at climbing (Stern & Susman, 1983; Susman *et al.*, 1984), and trees could have been used for not only predator avoidance, but also for sleeping and feeding. When *Australopithecus* disappeared from the fossil record, *Paranthropus* specimens become common and fossil assemblages associated with them indicate that they existed in slightly more open habitats that include wetlands. However, *P. aethiopicus* is not only associated with edaphic grasslands, but with woodland and bushland areas, i.e., in habitats that are similar to those utilized by *Australopithecus*. *Homo* species appear in the fossil record around 2 m.y.a. and are associated with habitats that also supported *Paranthropus* species. Later *Homo* species are also found in assemblages that indicate extremely arid and open landscapes. If these co-existing hominids partitioned the environment, it is possible that *Paranthropus* preferred edaphic grasslands and wetland regions, while *Homo* utilized the more open woodland and grassland habitats.

Acknowledgements

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