PALEOANTHROPOLOGICAL IMPLICATIONS OF VEGETATION AND WILD PLANT RESOURCES IN MODERN SAVANNA LANDSCAPES, WITH APPLICATIONS TO PLIO-PLEISTOCENE OLDUVAI GORGE, TANZANIA

by

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ABSTRACT OF THE DISSERTATION

Paleoanthropological Implications Of Vegetation And Wild Plant Resources In Modern Savanna Landscapes, With Applications To Plio-Pleistocene Olduvai Gorge, Tanzania

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The ways that early hominins used plants for food, shelter, and tools are important to our understanding of human evolution, but are elusive due to few plant fossils and few traces of plant use in the archaeological record. For this dissertation I developed and applied a methodology that uses modern vegetation to model the availability of ancient plant resources for hominins.

The case study is that of lowermost Bed II, Olduvai Gorge, Tanzania, a paleolandscape with traces of hominin land use about 1.75 million years old. I studied the vegetation in three modern analog settings in northern Tanzania: Lake Manyara, Serengeti, and Ngorongoro Crater. I examined the relationships between landscape units, physiognomy, species composition, plant foods, and refuge trees. The relationships are indirect and difficult to simplify, but some patterns were apparent, for example, bushland habitats tend to have edible fruit-bearing shrubs, forests have trees with edible fleshy fruits, and marsh habitats abound with edible underground parts from sedges and *Typha*. Physiognomic types, plant foods, and refuge tree distribution across semi-arid savannas reflect the uneven distribution of plant-available water and other environmental variables like soil salinity and alkalinity.

I applied the plant findings in the modern habitats to the Olduvai case study through landscape facets, which are similar in the modern habitats in terms of geomorphology, hydrology, and ecology to those reconstructed for lowermost Bed II. I created a series of maps depicting the possible distribution of plant resources (fruit, leaves, etc.) across the paleolandscape. At Olduvai, edible fruits, leaves/shoots, and refuge trees were concentrated in the alluvial fans, edible seeds/pods and underground parts were concentrated in the Eastern Lake Margin, and edible grass seeds and flowers characterized the western basin.

For paleoanthropology in general, this study suggests that hominin diets differed from those of modern apes, and edible sedges and grasses may have contributed to the C_4 isotopic signature that is characteristic of early hominins. This study demonstrates that modern analog vegetation studies can improve upon the simplistic vegetation reconstructions that exist for most early hominin sites, thereby contributing toward a better understanding of hominin paleoecology.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

CHAPTER 1. PLANTS AND EARLY HOMININS

Introduction

The role of plants and plant foods in the ecology of early hominins is little known because of poor preservation of plants in the fossil record, and few traces of plant use in the archaeological record. Nonetheless, early hominins, a term which includes all bipedal apes and bipedal ancestors of modern humans, must have depended in large part on plants for food and shelter. In this thesis, a study of modern vegetation as analogs for ancient settings was undertaken in northern Tanzania. Using field and analytical techniques from plant ecology and landscape ecology, I investigated the nature and abundance of plant resources for hominins in modern habitats.

The modern settings were chosen specifically as modern analogs to be applied to a case study of a Plio-Pleistocene paleolandscape, lowermost Bed II of Olduvai Gorge, Tanzania, where early hominins lived about 1.75 million years ago (mya). Plant findings in the modern habitats are applied to that Plio-Pleistocene setting through the common denominator of landscape units, specifically landscape facets, which are defined in terms of geomorphology, hydrology, and ecology. The rich vegetative details available in modern habitats with similar geomorphological, ecological, and hydrological characteristics are used to “flesh out” the fossil landscape, to help model hominin resource distribution at Olduvai, and to model hominin land use there. Since no modern analogs accurately replicate all aspects of ancient settings, I have begun in this thesis the development of a methodology that allows necessarily different modern vegetation analogs to be relevant to understanding ancient vegetation using relational analogies (e.g., Gifford-Gonzalez, 1991).

The results of the modern vegetation studies are relevant more broadly to paleoanthropology by improving our understanding of the nature and distribution of plant foods and refuge trees, and by beginning to clarify the relationships between vegetation structure or physiognomy on the one hand, and the nature and abundance of plant foods and arboreal refuge for hominins on the other. Theories concerning early hominin social behavior and the socioeconomic function of Plio-Pleistocene archaeological sites are often dependent on the distribution of trees (arboreal refuge) and/or plant foods, although those factors may be considered archaeologically invisible. In creating ways for us to better predict tree and plant food distribution across paleolandscapes, this thesis ultimately improves our ability to test competing ideas about the socioeconomic function of archaeological sites, among other aspects of early hominin lifeways.

Current Research at Olduvai Gorge (OLAPP)

In order to address issues concerning the relationships between plants and early hominins, I conducted a case study at Olduvai Gorge, Tanzania. The Olduvai Landscape Paleoanthropology Project (OLAPP), directed by Blumenschine, Masao, and Peters, is using a landscape paleoanthropology approach at that fossil locality (Blumenschine *et al.*, i.p.; Blumenschine and Masao, 1991; Peters and Blumenschine, 1995; Blumenschine and Peters, 1998). OLAPP’s long-term goal is to reconstruct the ecology and land use patterns of hominins living about 1.75 mya in the area of East Africa that is now Olduvai Gorge (Blumenschine and Masao, 1991). One of the goals of this thesis is to improve reconstructions of the vegetation at Olduvai, including plant foods and arboreal refuge, which will contribute to the broader goals of OLAPP.

The methodology being employed by OLAPP is discussed in more detail in a subsequent section of this chapter. Briefly, it includes modeling the geology and vegetation of the paleolandscapes, and modeling the distribution of resources and hazards for hominins in various landscape units. Based on clearly defined assumptions of hominin biology and likely patterns of behavior, models of hominin land use are created for the lowermost Bed II paleolandscape (Peters and Blumenschine, 1995; 1996). Subsequently, archaeological traces of that land use pattern are then predicted independently of any known archaeological evidence (Blumenschine and Peters, 1998). Finally, excavations are conducted in a semi-random way to sample landscape units across the paleolandscape and thereby test the archaeological predictions. As more evidence comes to light regarding aspects of the modeling process such as paleoenvironmental reconstructions, resource and hazard distributions, and hominin biology and behavior, various aspects of the models will be amended and reevaluated with respect to their test implications. This approach to landscape paleoanthropology thereby emphasizes predictive modeling, the generation of test implications, and use of the archaeological record to test those predictions. Cycles of predictions and testing will require multiple generations of research to improve our understanding of actual hominin behavior and ecology.

OLAPP's approach to landscape paleoanthropology emphasizes the importance of knowledge about the settings in which hominins foraged, survived, and reproduced, including aspects of their paleoenvironments like resource availability, competition, and predation. Reconstruction of the paleolandscape in terms of geomorphology, climate, vegetation, fauna, and ultimately resources and hazards is just as important to this method of landscape paleoanthropology as is the biology of the hominins themselves.

Hominin species present at Olduvai during our target interval of lowermost Bed II times included at least two species, the robust australopithecine *Australopithecus boisei* and some of the earliest members of our genus, *Homo habilis*. Blumenschine *et al*. (2003) suggest that species from Olduvai traditionally assigned to *Homo habilis* may in fact represent two species: the larger-brained proper *Homo habilis* with affinities to KNM-ER 1470 skull from Koobi Fora (includes OH 65 and OH 7), and hominins that might be classified as either a small and primitive early *Homo* or a gracile australopithecine (includes OH 13, OH 24, OH 62, and KNM-ER 1813). There is also a theoretical possibility of the presence of a fourth hominin species at Olduvai during lowermost Bed II times. The larger-bodied *Homo ergaster* (e.g., WT 15,000, also known as African *Homo erectus*) appears in northern Kenya by 1.78 mya (Feibel *et al*., 1989; Wood, 1992), within the time interval of focus that we are studying at Olduvai. To date though, its fossil remains have not yet been discovered at Olduvai.

Goals of this Thesis

The specific goals of this thesis involve reconstructing vegetation and plant resource availability at Olduvai Gorge. Fossil evidence from Olduvai such as pollen, macrobotanical remains, faunal remains, and stable isotope data provide a general picture of what the climate and vegetation were like. As described below, the more detailed levels of floristic and spatial information that we need for accurately modeling hominin resource distribution are not forthcoming from those techniques alone due to their inherent limitations. The fossil evidence at lowermost Bed II Olduvai, for example, indicates a mosaic of grassland to woodland habitats with a nearby Afromontane forest, and about 800 mm or less of rain per year (see Chapter Two). In order to model hominin resource distributions and activity across that paleolandscape, we need to know which portions of the basin were grassland, woodland, etc., and what types of hominin plant foods, animal foods, refuge trees, tool-making resources, and dangers were associated with each land unit of the basin.

One set of questions addressed in this thesis relates to how geomorphologically-, hydrologically-, and spatially-defined landscape units at several spatial scales relate to floristic composition, vegetation structure, plant food availability, and refuge trees. A second set of inquiries examines the relationship between structurally defined vegetation units such as woodland, forest, and grassland, to the vegetative details of floristic composition, plant food availability, and refuge tree availability. The issue of whether vegetation structure predicts resource nature and quality is especially important to paleoanthropology as a whole because so many paleoenvironmental reconstruction techniques result in purely structural descriptions of ancient vegetation.

The proximate goals of this thesis are summarized below.

1) Develop and implement a methodology for characterizing the relationships in modern habitats between vegetation structure, species composition, and plant resources for hominins in quantitative terms, at a landscape scale.

2) Determine quantitative and qualitative relationships between landscape units on the one hand, and vegetative details relevant to hominin ecology on the other, including floristic composition, physiognomy, plant foods, and refuge tree distribution.

3) Identify the relationships between vegetation structure or physiognomic units on the one hand, and vegetative details relevant to hominin ecology (plant foods, and refuge tree distribution) on the other.

4) Improve Peters and Blumenschine's (1995, 1996) models of vegetation and resource distribution for hominins across the lowermost Bed II paleolandscape at Olduvai, and address changes that might result in the modeling of hominin land use and in archaeological predictions (Blumenschine and Peters, 1998).

I have attempted to address those questions related to plant foods, refuge trees, and vegetation structure in this thesis by developing and implementing a methodology in which modern ecological settings can inform us about ancient ecological settings through relational analogies. As discussed by Gifford-Gonzalez (1991), all historical sciences including paleoanthropology use analogies to learn about the past. One key to the success of this approach is to apply relational analogies in "middle range research" (Binford, 1981). Relational analogies are those in which causal relationships that are apparent between present day traces and their source or context are assumed to also apply to the past. Inferences based upon relational analogies are preferable to those based upon formal analogies. In the latter, the relationship is based only on formal qualities and causality between process and product is not specified or demonstrated (Gifford-Gonzalez, 1991).

Actualistic methods that use modern vegetation to inform us about the very ancient past will always be complicated by the fact that no modern analog replicates the past situation. Furthermore, there are many factors controlling what type of vegetation exists in a certain area. Therefore, the ultimate goal of this sort of study is to develop relational analogies by studying modern analogs in order to understand causal relationships between fossilizable traces, like land features, and important features that are not directly fossilized, like plant food distribution.

Anthropological Relevance of Plant Foods and Arboreal Refuge

Historically, archaeologists have focused mainly on the potential importance of meat-eating in early hominin evolution, such as whether and how it was scavenged or hunted, because the early archaeological record *per se* consists almost entirely of stone tools and fossil bones in landscape context. Despite this, it is also recognized that plants must have played an important role in early hominin ecology. That plant foods were important to early hominin survival is evidenced in part by the general feeding behaviors of our closest relatives, the apes, all of whom are largely dependent on plant foods. It is parsimonious to assume that the common ancestors of chimpanzees and hominins were also mostly dependent upon plants for foods. Ethnographic studies of non-industrial societies today show that tropical populations tend to eat a high percentage of plant foods. For example, the ≠Kade San (Bushmen) hunter-gatherers of southern Africa depend on plant foods for 81% of their caloric intake, despite their desire for meat and their possession of sophisticated tools such as bows and arrows with which to hunt (Tanaka, 1976). While meat is generally preferred by hunter-gatherers, hunting success by an individual varies considerably between days, making it an unwise choice to rely upon for one’s daily nutritional needs (e.g., Hawkes, 1993; Hawkes *et al*., 2001). Plant foods, on the other hand, can provide predictable staple resources to feed the group every day, as they do for the Hadza of Tanzania (Hawkes, 1993) and the San of Southern Africa (Tanaka, 1976).

Plant Food Distribution

Wild plant foods are not distributed randomly across African savanna habitats, nor would they have been in the past. In many semi-arid habitats, riverine margins are lined with a woodland or gallery forest adjacent to grassy or bushland-covered floodplains. In such situations there is a steep gradient of vegetation structure between those habitats, which corresponds to strong contrasts in plant food density and distribution pattern (Sept, 1984; 1994). In the area of Tanzania near Lake Eyasi that is inhabited by modern Hadza foragers, important plant foods like baobabs occur in the woodlands of the basement hills, while patches of tubers are distributed across several kilometers of nearby deciduous bushland, berries occur along a river floodplain, and doum palms grow near the lake shore (Vincent, 1985a: Figures 1 and 2). There is little overlap in the distribution of these important resources, again depicting a non-random and patchy distribution of wild plant foods. Given the dearth of fossil information that can pinpoint the location of particular plants in the past, to be able to “predict” how plant foods were distributed across ancient landscapes requires first an ecological understanding of modern plant food distribution. Basic geomorphological and hydrological reconstructions of an ancient environment then form the basis for further detailed paleoenvironmental reconstructions that can be used to predict the most likely nature of ancient vegetation distribution, and ultimately ancient plant resource distribution.

Arboreal Refuge

Trees would have been important as refuge for early hominins, particularly for hominins that did not have controlled use of fire. It is possible that hominins controlled fire in Africa as early the Oldowan period, between 1.5 to 2.0 mya (Clark and Harris, 1985; Bellomo, 1994), but the evidence is mixed and inconclusive. Unequivocal evidence for hearths does not appear until the Middle Pleistocene, 250-400 thousand years ago (kya) (Clark and Harris, 1985; James, 1989). It is possible that early Pleistocene hominins only used ephemeral fires for cooking analogous to the way the modern Hadza cook some tubers (O'Connell *et al*., 1999). In order for fire to be used successfully as a predator defense strategy, it would need to be contained in longer-burning hearths that lasted overnight, for example.

Hominins' closest living relatives, the great apes, all make leaf-and-branch nests for sleeping at night or for day rests. All but the largest animals (male gorillas) typically nest high up in the trees (Fruth and Hohmann, 1996). Spending the night in a tree nest provides far more protection from night-prowling carnivores than being on the ground.

Further evidence of the importance of arboreal refuge for Plio-Pleistocene hominins comes from evidence of their post-cranial morphology. Hand, foot, and leg bones of *Homo habilis* from Olduvai Gorge (OH 7, OH 8, and OH 35) were shown by Susman and Stern (1982) to possess traits indicative of both a well-established bipedal gait and a significant component of climbing. Given the knowledge of how bones grow in response to use and environment, the thick-walled, robust, and heavily muscled character of the OH 7 hand suggests that that particular individual used its hands for significant arboreal climbing during its lifetime, rather than simply retaining vestiges of suspensory (hominoid) heritage (Susman and Stern, 1982). Since *Homo habilis* had a relatively small body size, it makes sense that this hominin would have had a selective advantage over fully terrestrial organisms due to its ability to sleep, escape, and perhaps feed in trees.

The Socio-economic Function of Early Archaeological Sites

Dense accumulations of Oldowan stone artifacts and faunal remains – early archaeological sites – dated from the early Pleistocene at Olduvai Gorge and Koobi Fora were initially interpreted as "living floors" (Leakey, 1971) or "home bases" (Isaac, 1971; 1978). Groups of hominins were thought to return to these temporarily occupied campsites after foraging, and there they prepared and ate food and had a family-based social structure that included sexual division of labor and food sharing, similar to the social structure of modern hunter-gatherers (Isaac, 1978; 1981). This lifestyle, it was suggested, ultimately provided important selective pressures for increasing brain size, language, and the development of cultural rules.

Since the 1970's much research has gone into scrutinizing the home base hypothesis, questioning the role of hominins in site formation processes, bone accumulation and manipulation, and whether such a human-like, family-based social system was realistic for early time periods. The results have led to alternative hypotheses of the nature or function of early archaeological sites, such as central-place foraging (Isaac,1983), feeding-as-you-go or "routed foraging" (Binford, 1981; 1984), stone-caching (Potts, 1984; 1988), riparian woodland scavenging (Blumenschine, 1986; 1987), nesting behavior (Sept, 1992; 1998), and a resource-defense model (Rose and Marshall, 1996).

In each of these models, the location of archaeological sites depends to some degree upon the distribution of vegetation. In the central-place foraging, stone caching, and resource defense models, a location to which scavenged or hunted carcass parts and possibly gathered plant foods are brought is chosen by hominins in part because it is a “safe place” (Isaac, 1983; Potts, 1984; 1988; Rose and Marshall, 1996). This is usually taken to mean the presence of trees for shade and protection. In a nesting model of site formation (Sept, 1992; 1998), again the presence of trees at the “site” is required, and furthermore they must be climbable nesting trees (as opposed to very thorny trees, for example). In riparian woodland scavenging, it is the presence of a riparian woodland itself that increases the chances for hominins to encounter scavenging opportunities, and it is in these woodlands where bones and stone artifacts would accumulate over time (Blumenschine, 1986; 1987). Binford’s (1984) routed foraging model implies that hominin activities were tethered to fixed resources such as water, lithic resources, or trees for shade or shelter. Hominins stopped repeatedly at those fixed resources, leading to the accumulation over time of tools and bone.

In sum, all of these theories regarding the socioeconomic function of early archaeological sites suggest that trees were likely to have been in the immediate vicinity of the bone and stone tool accumulation. In addition, in order to test the various models mentioned above, archaeologists would benefit from knowledge of the usually archaeologically invisible location of arboreal refuge and plant foods. In this thesis I examine how arboreal refuge and plant foods are distributed across modern landscapes with an eye toward reconstructing such distributions across paleolandscapes.

The many investigations that have been conducted to test various aspects of the home base hypothesis have re-affirmed the importance of an ecological approach to paleoanthropology, as suggested early on by Bartholomew and Birdsell (1953). The interactions of hominins with other organisms and their environment involved the traits on which selection pressures may have acted most directly. To understand early hominin ecology one must back up from a narrow or isolated view of the archaeological “site” itself and look at the landscape-wide distribution of resources and hazards for hominins, such as scavenging opportunities, raw materials, and plant foods. Only then can one have any hope of interpreting the social or economic function of a “site.” This attempt to understand the physical and ecological circumstances across a hominin population’s entire ranging area led Isaac and Harris (1980; Isaac, 1981) to the idea of the “scatter-between-the-patches,” and ultimately developed into the “landscape archaeology” approaches now being pursued in paleoanthropology. OLAPP’s landscape approach to reconstructing the paleoecology of the Olduvai basin is a continuation of this idea.

Fossil Evidence for Early Hominin Diets

Because much of this study deals with potential plant foods for hominins, here I review some of the fossil evidence for actual hominin diets. I do not directly test whether hominins consumed particular plant or animal foods in this study, but the evidence for actual hominin diets is used in the final chapter (Chapter Seven) to discuss the particular plant foods that might have been most likely to have been exploited, and what the nature of those plant foods might mean in terms of hominin ecology, foraging behavior, niche differentiation, and the function of early archaeological sites.

Morphological Evidence for Early Hominin Diets

Some of the fossil evidence for actual hominin diets comes from tooth size and shape, jaw biomechanics, and dental microwear. Among the early australopithecines, cheek teeth and the mandibular corpus became generally more massive over time, suggesting an increasing importance of hard, abrasive foods throughout the Pliocene from *Australopithecus anamensis* to *Australopithecus afarensis* to *Australopithecus africanus* to finally the most exaggerated megadonts like *Australopithecus robustus* (Teaford and Ungar, 2000). Dental microwear studies of *Australopithecus africanus* reveal similarities between the pitting and scratching of their molars and those of modern chimpanzees, which suggests a diet of fleshy fruits and leaves for *Australopithecus africanus* (Grine, 1986; Grine and Kay, 1988). However, the overall craniodental adaptations of the australopithecines are different than those of chimpanzees, which suggests that there were important differences in their diets as well (Robinson, 1954; Jolly, 1970; Hatley and Kappelman, 1980). This has recently been confirmed by stable isotopic evidence (see below).

Homo habilis appeared around 2.4 to 2.5 mya, and was characterized in general by a larger brain and smaller cheek teeth than the australopithecines (Klein, 1999). If the specimens grouped under the taxon *Homo habilis* actually are two different species, then the larger ones (e.g., KNM-ER 1470, OH 65, OH 7) probably had relatively large skulls combined with large *Australopithecus*-sized teeth, while the smaller ones (e.g., KNM-ER 1813, OH 13, OH 24, OH 62) had small skulls combined with small teeth (Klein, 1999).

The earliest stone tools also appeared around 2.5 mya (Semaw *et al*., 1997; 2003), but it is not clear whether this was an invention solely used by *Homo habilis* and later *Homo* species, or if other species like the robust australopithecines and *Australopithecus garhi* also used stone tools (Susman, 1988; 1991; de Heinzelin *et al*., 1999). Simple Oldowan stone tools could have helped hominins to obtain foods like meat, marrow, and brains from the carcasses of relatively large animals, and also might have been used to make wooden tools like digging sticks for extracting deep underground plant parts (Keeley and Toth, 1981; Vincent, 1985a,b; O'Connell *et al*., 1999).

Homo ergaster manifests a suite of important changes in hominin evolution that cause it to be considered a separate grade from the australopithecines and *Homo habilis* (Collard and Wood, 1999). *Homo ergaster* had reduced cheek teeth, and a new body form that was taller, leaner, and a fully obligatory biped (Walker and Leakey, 1993; Collard and Wood, 1999), without the arboreal adaptations of long arms and curving fingers seen in *Homo habilis* and the australopithecines (Susman and Stern, 1982). Gut size decreased with the new linear body build, and there was an increase in brain size. It has been proposed that a decrease in gut size and an increase in brain size were necessary correlates because of the high metabolic cost to the body of supporting a larger brain (Aiello and Wheeler, 1995). In order for the body to be able to maintain a larger, metabolically-expensive brain, it must have been able to allot less energy to digesting food by increasing the nutrient quality of the diet and decreasing gut size (Aiello and Wheeler, 1995).

The ranging size of *Homo ergaster* was also probably larger than that of other, earlier hominins, as the new taller, linear body form seems to have been better adapted to withstanding the heat stress involved in traversing large tracts of hot, open, arid savanna (Wheeler, 1991; 1992; Ruff, 1991). Stone artifacts are found further from their source with the emergence of *Homo ergaster*, as shown for example in the Karari at Koobi Fora, Kenya (Harris, 1978). Further confirmation for an increase in ranging size among *Homo ergaster* is the evidence that around this time *Homo* sp. spread out from the continent of Africa into the Middle East and East Asia (Brauer and Schultz, 1996; Huang *et al*., 1995; Gabunia and Vekua, 1995; Swisher *et al*., 1994).

Stable Isotopic Analyses of Early Hominin Diets

Isotopic analysis can be used to determine the ratio of C_3 to C_4 foods in a modern or prehistoric animal's diet by analyzing only a very small piece of its tooth enamel. In Africa, tropical grasses and some sedges use the C_4 photosynthetic pathway, while trees, shrubs, and forbs use the C_3 photosynthetic pathway. The result is that these plants have different ratios of $^{13}C/^{12}C$ in their tissues. Animals that eat C_3 vegetation will also be distinguishable from animals that eat C_4 vegetation since the $^{13}C/^{12}C$ ratios are passed down into the herbivores with predictable fractionation (Lee-Thorp *et al*., 1989; Cerling and Harris, 1999). Unfortunately, it is not possible to distinguish trophic level differences from $^{13}C/^{12}C$ ratios, so that it is impossible to tell the difference between a consumer of C_4 plants versus a consumer of animals that eat C_4 plants. Nonetheless, isotopic analysis is an increasingly important analytical tool for paleoanthropology.

As will be discussed in Chapter Two, the main nutrient-bearing plants of the arid or semiarid eutrophic savannas are grasses, most of which are C_4 plants. These are grazed by numerous herbivores and form the basis of a highly productive ecosystem. Since isotopic analysis reveals the proportion of C_3 versus C_4 foods in an animal's diet, it is in a sense a means of directly testing whether that animal was able to take advantage of the “grass-bound” nutrients that make certain savannas so productive, regardless of whether that advantage was taken from the plants directly or by eating animals that eat C_4 plants.

All of the published results from early hominins thus far analyzed for their isotopic content are from South Africa. Four approximately three million-year-old *Australopithecus africanus* individuals from Makapansgat derived an average of about 25% of their dietary carbon from C_4 foods (Sponheimer and Lee-Thorp, 1999). An additional ten *Australopithecus africanus* individuals from Sterkfontein Member 4 that date to approximately 2.0-2.5 mya averaged a 40% C_4 diet (van der Merwe *et al*., 2003). Eight individuals of the megadont *Australopithecus robustus* from Swartkrans about 1.7 to 1.4 mya had 20-25% C_4 diets (Lee-Thorp *et al*., 2000). Isotopic analysis of three *Homo ergaster* specimens, also from the 1.7 to 1.4 million year old sediments at Swartkrans, showed 20-25% C_4 diets, statistically indistinguishable from the robust australopithecines at the same site (Lee-Thorp *et al*., 2000).

Thus far then, all of the hominins tested appear to have incorporated a substantial proportion, from 20% to greater than 50%, of C_4 foods into their diets, while the majority of their diet was C_3 foods. This distinguishes hominins from modern apes, including chimpanzees, all of which eat nearly pure C_3 diets (Schoeninger *et al*., 1999; Tutin and Fernandez, 1992; Fleagle, 1999). Even though the habitat types of modern wild chimpanzees overlap somewhat with the types of early hominin habitats (e.g., Suzuki, 1969; Schoeninger *et al*., 1999; McGrew *et al*., 1981), chimpanzees that live in savannas do not eat grasses, or animals that eat grasses, even when they are locally abundant (McGrew *et al*., 1981).

Fossil Evidence for Vegetation

Plants tend to fossilize poorly in the contexts where early hominins have been found, and therefore plants are in many ways invisible in the fossil/archaeological record. One typically cannot reconstruct the location of patches of particular food plants or trees based on fossil and geological evidence alone. To realize the goal of modeling plant-hominin interactions across different portions of a landscape requires a high degree of spatial, physiognomic, floristic, and temporal resolution in vegetation reconstructions. Below I will briefly review the general kinds of fossil evidence (fossil fauna, pollen, phytoliths, macrobotanical remains, and stable carbon isotopes) available at early hominin sites and explain why they alone do not result in a vegetation reconstruction of adequate resolution for modeling hominin resource distribution and land use.

Faunal remains are typically used to reconstruct the different structural categories of vegetation in a paleoenvironment, such as the relative amounts of open, mixed, or closed vegetation. For example, faunal analyses of fossils from Bed I and Lower Bed II, Olduvai, indicate that habitat types there included patches of forest, woodland, bushland, and open grassland, so that in sum it was a mosaic environment (Andrews *et al*., 1979; Butler and Greenwood, 1976; Jaeger, 1976; Kappelman, 1984; Kappelman *et al*., 1997; Plummer and Bishop, 1994; Potts, 1988; Shipman and Harris, 1988). While this is useful in a general sense, it is not sufficient for OLAPP's goals of delineating the fine-scale spatial distribution of plant resources for hominins. An analysis of larger mammal fossils cannot resolve the question of where specifically on the landscape woodland versus grassland areas occurred because larger mammals do not strictly adhere to living within a particular vegetation type. In addition, a variety of taphonomic agents can transport their remains after death to other parts of a landscape. Thus with faunal-based vegetation reconstructions alone, the differential spatial distribution of archaeological remains cannot be interpreted in their proper vegetative contexts.

Plant microfossils come in a variety of forms and can complement other paleoenvironmental indicators such as the fauna just mentioned. The most well understood plant microfossils are pollen. The presence of fossil pollen at an early hominin site is welcome because it is often the only evidence for the actual plant taxa that grew in the vicinity of the site prehistorically. Unfortunately, pollen grains are typically identifiable only to the level of family, sometimes genus, and rarely species, due to their generalized morphology. Nonetheless they enable one to understand the general type of flora that existed regionally and in some cases a few taxa that were present locally.

Fossil pollen cannot be assumed to reflect the spatially discrete location of most taxa, nor the relative proportions of various taxa. Some pollen grains are transported by wind or water miles from their source, and plants vary tremendously in the amount of pollen they produce. Some pollen grains have been evolutionarily selected for their long-distance transport potential, which can maximize the reproductive success of the parent plant (Prentice, 1988). For example, the pollen grains of grass (Gramineae), sedges (Cyperaceae), and conifer trees can be transported for hundreds of kilometers by wind before finally being deposited at the site at which they became preserved (Moore *et al*., 1991). Other plants, such as *Trichilia* trees, *Ficus* (figs), and most members of the Caesalpinioideae subfamily are insect-pollinated and produce very small amounts of pollen, which therefore is not likely to get preserved in the fossil record (Bonnefille, 1984b), but if it does can be attributed to locally growing plants.

Pollen therefore is useful in that sometimes it provides the only evidence for actual plant taxa that existed in the past. By itself, however, pollen is not sufficient for the vegetation reconstruction purposes of OLAPP. This is because we want to know how different plant species were distributed across the landscape at fine enough spatial scales to model and predict archaeological traces of hominin land use, so that the archaeological record can be used to test ideas about hominin behavior. Due to long-term transport, pollen is more useful as a general indicator of regional flora, with the exception of several taxa that are likely to have been present locally near the preservation site.

Phytoliths are another microscopic component of plants that may be preserved as microfossils, though the study of them is not as developed as that of pollen. Phytoliths are natural silica mineral deposits that are formed in the body of some plants where water is used or lost through transpiration (Piperno, 1988). When the plant decays, the non-organic, mineral phytoliths remain behind. Usually phytoliths occur in the geological record as decay-in-place plant residues, which remain quite stable following deposition if they are not in a highly acidic or alkaline environment.

Phytoliths are limited as paleoenvironmental indicators in that their shapes are not taxonomically unique. Thus, wholly unrelated plants can produce identical looking phytoliths. However, certain grasses, other monocots like sedges (Cyperaceae) and palms, and even a wide variety of dicots produce phytoliths diagnostic to subfamilies, or even species or sub-species, such as the case of domesticated corn versus its wild predecessor teosinte (Piperno, 1984). Unlike pollen, phytoliths reflect local conditions, unless sediment already containing phytoliths gets mixed up with the archaeological sediment of interest. Many plants are not silica accumulators and do not produce phytoliths. Phytoliths provide selective information, especially on monocots, in places where plants have decayed and the non-decaying parts can be preserved, such as wetlands. Rosa Albert is currently undertaking an analysis of the phytoliths from lowermost Bed II, Olduvai.

Macrobotanical remains, such as fossilized wood, seeds, leaves, or other large plant parts, can provide a welcome complement to microbotanical evidence for ancient vegetation, and thus the techniques are best when used together. When fossil pollen and fossil wood have been compared from East African Plio-Pleistocene sites, the resulting botanical lists are not identical, and have only a few overlapping species. For instance, in Pliocene and Pleistocene localities at Omo, Ethiopia, fossil wood remains identified 74 woody taxa in 54 different genera, but only 10 of those genera were found in the pollen list (Bonnefille, 1984b). Fossil wood remains do not speak to the herbaceous record, while palynological remains tend to under-represent the trees of a riverine forest (Bonnefille and Dechamps, 1983). Marion Bamford is currently studying plant macrofossils from Olduvai, which include fossil wood and fossil sedges.

Ideally one would retrieve macrofossils from each of the various paleolandscape units being investigated, but unfortunately macrobotanical fossils are usually much too rare at early hominin sites for this to work. Therefore they cannot be relied upon to give information about how vegetation varied across a paleolandscape.

Paleosol carbon isotopes indicate the original proportion of vegetation with the C_4 photosynthetic pathway (mainly tropical grasses) to those that use the C_3 photosynthetic pathway (most trees, shrubs, and forbs) with a high degree of spatial resolution in modern habitats (Cerling and Hay, 1986; Sikes, 1994). That is, stable carbon isotopes appear to be able to roughly determine the physiognomic structure of the past vegetation at a local spatial scale for the time in which those paleosol carbonates formed. The temporal resolution of paleosol carbon isotopes is still a matter of debate. It may be difficult to know whether the signal from a particular carbonate nodule or layer of nodules corresponds to the vegetation that grew when the ancient land surface was one meter above them, or two meters above them, or perhaps the signal is an average over long periods during which the vegetation changed. If these temporal issues are resolved, it may be possible to apply this methodology toward reconstructing within-landscape-scale details of vegetation. Since this technique basically reconstructs vegetation structure (the proportion of herbaceous versus woody plants), a translation of the results into terms of hominin plant resource availability then depends on the extent to which particular plant resources correlate to vegetation structure. Therefore, defining the nature of such correlations is one of the goals in this thesis.

In sum, the fossil indicators of vegetation discussed here are useful in providing general and often complementary information on what the vegetation and climate were like in the past. In order to model and test hominin behavior and ecology within and across a particular paleolandscape, however, more detail and finer spatial resolution is needed. That detail can only be found in modern, living environments, so it is there that we must look for informative analogs.

Previous Modern Analog Studies of Vegetation

Several previous studies have measured modern vegetation with the goal of reconstructing early hominin plant resource availability. The temporal and spatial scales for which the studies are relevant depend on their methodology. In Table 1-1, I summarize these previous studies and their characteristics, which are described in detail below.

The ultimate determinants for how modern analogs can be linked to paleoenvironments are the units into which the modern vegetation is divided, and the characteristics of vegetation that are recorded. Similar units must be recognizable, either directly or indirectly, in both modern settings and fossil/geological settings (see the first column in Table 1-1). As detailed above, fossil plants, bones, and other paleo-indicators alone do not serve as adequate links because they cannot usually reconstruct hominin plant resources at landscape spatial scales.

In an attempt to remedy the situation in which virtually nothing was known of the potential plant food resources of early hominins, Peters and O'Brien (1981; O'Brien and Peters 1991) compiled a list of modern edible plants in sub-Saharan Africa. Based on an extensive review of the literature and herbarium records, they named all of the wild plant food species recorded to have been eaten in natural settings by humans, chimpanzees, or baboons in eastern and southern Africa. They have continued to expand the list, and published much of the results as a book (Peters *et al*. 1992).

This list is useful for a variety of purposes. For example, it was used in this thesis to identify which of the plants encountered in the modern study sites were edible (Chapter Three). Peters and O'Brien (1981; O'Brien and Peters, 1991) used their list to

Table 1-1. A summary of modern analog studies of vegetation for paleoanthropology.

Modern unit of study (serves as the "link" between modern habitats and the fossil record)	**Information that is "predicted" for the past**	**Spatial scale**	**References**
All edible plants in sub-Saharan Africa (edible to baboons, chimps, humans)	Fundamental plant food niche for hominins	Sub-continental	Peters and O'Brien, 1981; O'Brien and Peters, 1991
Climate	Edible plant diversity and nature of plant foods	Regional to sub-continental	O'Brien, 1988; O'Brien and Peters, 1991; Peters and O'Brien, 1994
Keystone species	Actual species that were important foods for hominins, including their nutrition, ecology, technology required for processing "Predict" where they grew in past; centers of endemism	Sub-continental	O'Brien and Peters, 1991 Peters, 1987
Ecological groupings of plants (e.g., deciduous shrubs)	Types of food, seasonality, and diversity typical of each ecological grouping	Local to regional	Peters, O'Brien, and Box, 1984
Physiognomic categories (e.g., grassland, bushland)	Nature and abundance of plant foods	Local to regional	Sept, 1990; **This study**
Depositional environments (e.g., channel, floodplain)	Nature and abundance of plant foods	"site" (local)	Sept, 1984; 1986
Landscape units (facets)	Nature and relative abundance of plant foods	"landscape" (local)	**This study**

predict a fundamental plant food niche for hominins. Assuming that the list represented a sample of all plant foods that were available to, though not necessarily used by, early hominins, they extrapolated a fundamental plant food niche for hominins including the relative diversity of plants with particular edible parts, and the potential competition between primates for certain food types. For example, based on the numbers of genera with edible parts, they concluded that leaves and/or fruits would be the most common food-item types exploited by the early hominins (Peters and O'Brien, 1981).

The notion of a fundamental plant food niche for hominins that could be identified by modern plant composition in Africa is mainly relevant at broad temporal and spatial scales: millions of years across the entirety of sub-Saharan Africa. Thus, while this approach helps to define in general the types of plant foods that hominins might have had available to them, it will not help to discern local, within-landscape differences in plant resources. In that sense, the fundamental plant food niche cannot address the ecology of a particular hominin population across a particular paleolandscape.

O'Brien and Peters have also explored the role of climate as a potential predictor of edible plant foods for hominins. O'Brien (1988) found correlations at a sub-continental scale between climate and edible woody plant species richness. Across southern Africa, 83% of the variation in the geographic pattern of edible woody plant species richness could be explained by a combination of geographic variability in the amounts of minimum monthly potential evapotranspiration (energy) and maximum monthly precipitation (moisture). In general, O'Brien and Peters (1991) surmise that for southern Africa, as climates become less mesic, the number of edible taxa present decreases, the diversity of edible plant parts drops, and fruits and seeds/pods are the plant food parts that become increasingly available.

Using climate as a predictor of potential plant foods for hominins is currently limited to regional and sub-continental spatial scales. Assuming that plant resources can be predicted by climate, the application of this approach to the past requires one to be able to reconstruct climatic parameters of ancient settings in relative detail, which is difficult even at regional scales. Even given future advances in the techniques of paleo-climate reconstruction, the climatic parameters in question are themselves mainly regional phenomena, and thus would never be able to differentiate the desired detail of within-landscape-scale variations.

In another approach, modern plant species from across southern Africa were grouped according to "ecophysiognomic" types, that is, plants with similar form (size, shape, seasonal habits, leaf structure, etc.) and ecological requirements, for example, evergreen trees and annual forbs (Peters *et al*., 1984). In this approach, these ecophysiognomic units are the potential link between the present and the past. The hominin edible resources characteristic of each ecophysiognomic type were measured as the diversity of edible parts and their seasonal availability (Peters *et al*., 1984). Ecophysiognomic types relate to environment and effective precipitation and temperature, including the timing, duration, and cycle of rains throughout the year, among other physical factors such as soils and topography. Thus, in order to place such units in paleoenvironments, it would be necessary to reconstruct those rather detailed climatic parameters at fossil settings. At present we are not able to reconstruct paleoenvironments with that much detail at fine landscape scales. It would also be necessary to show a functional/causal relationship, or relational analogy, between such ecophysiognomic types and particular physical and/or climatic parameters, in order to support the notion that the relationships in the present would also hold in the past when actual plant species composition might have been different (Gifford-Gonzalez, 1991). This is a promising approach in that it potentially avoids the problem of species change over time.

Another approach focuses on individual plant species that exist today and are likely to have been important in early hominin diets, perhaps even as “keystone species” in paleoecosystems (O’Brien and Peters, 1991). Peters (1987), for example, focused on several important modern species that produce edible nut-like oil seeds. By examining the species’ distributions across Africa, and their ecology, seasonality, and nutritional composition, he concluded that some may have provided the highest-ranking items in the diets of the robust australopithecines who lived in Africa between about 2.5 and 1 mya. Since the edible fruits and nut-like oil seeds are available only seasonally, other resources would have been required during the rest of the year.

The keystone species approach provides useful information when considering what regions of the continent might have supported more hominins overall. Data on the ecology of keystone species could theoretically be used in landscape-scale reconstructions as well, if it were possible to predict the most likely microhabitats in which those species would have occurred. This will require climatological, soil, hydrological, and other environmental parameters to be reconstructed with more detail and at finer spatial scales.

Sept's concept of using modern analogs to infer distribution of plant foods in early hominin habitats has focused mainly on site-scales, in that the goal is to be able to reconstruct the vegetation at a particular archaeological site (Sept, 1984; 1986; 1990; 1994). Recently, she incorporated GIS techniques to apply those data to landscape scales as well (Sept, 2001). The site-scaled approach focuses on first defining a fossil site in terms of its landscape terrain, and then developing "sedimentary-unit-specific hypotheses about the patterns of plant food availability and quality" using modern analogs (Sept, 1994:302-3).

Working at semi-arid settings in Kenya, Sept (1984, 1986) sampled the vegetation at modern riparian habitats, including ephemeral streams and perennial rivers. The terrain crossed by her vegetation transects was divided into different sedimentary zones, such as channel margins, alluvial plains, and unflooded zones. Abundance of plant foods (defined as those edible to humans, great apes, or ground-dwelling omnivorous monkeys that live in African savanna habitats) was then compared between sedimentary zones and between rivers.

Sept (1986) found that the majority of trees and shrubs bearing edible fruits occurred along the channel margins at the drier Il Sej Naibor River, but the pattern was more complicated along the wetter Voi River. There, shrubs with edible fruits occurred at highest densities in the unflooded zone and the channel margin, and woody plants with large edible fruits occurred in the alluvial plains and unflooded zones during the rainy season. Overall there was a great deal of variation in the relative magnitude of energy available from the flesh of edible fruits in these habitats.

Since the paleoenvironmental reconstructions of most early hominin sites are defined broadly, Sept (1986) found it difficult to choose the most appropriate modern analog for a particular “site”. She found that the range of modern riverine settings which “fit” the paleoenvironmental information from FxJj 50 at Koobi Fora included both the Voi River with ca. 546 mm rain per year, which was rich in edible fruits year-round, and the Il Sej Naibor River, ca. 200 mm rain per year, which produced very few edible fruits except during the dry season. The degree of variability between modern analogs for the site of interest was too great given the broad nature of the paleoenvironmental evidence from FxJj 50. Therefore it was not possible to model hominin fruit resources there with the degree of accuracy useful for then testing against the archaeological record.

An important lesson from Sept’s work has been the realization that reconstructing the vegetation from a localized site will necessarily be vague, because one has to allow for a wide range of possible vegetation types given the variation that exists among modern analogs. By increasing the spatial and temporal scope of both the paleoenvironment of interest (from a site to a paleolandscape) and the modern analog study areas (from the sedimentary zones near river channels to broader landscape units), it is possible to overcome some of those difficulties. In part they can be overcome by focusing on *relative* differences in resource abundance between more broadly-defined landscape units.

For example, rather than focusing on a single archaeological site, one might seek to determine plant resource availability across a paleolandscape by focusing on the differences between the river margin versus a nearby lacustrine plain. A variety of modern analog settings could be studied in which rivers are near lacustrine plains.

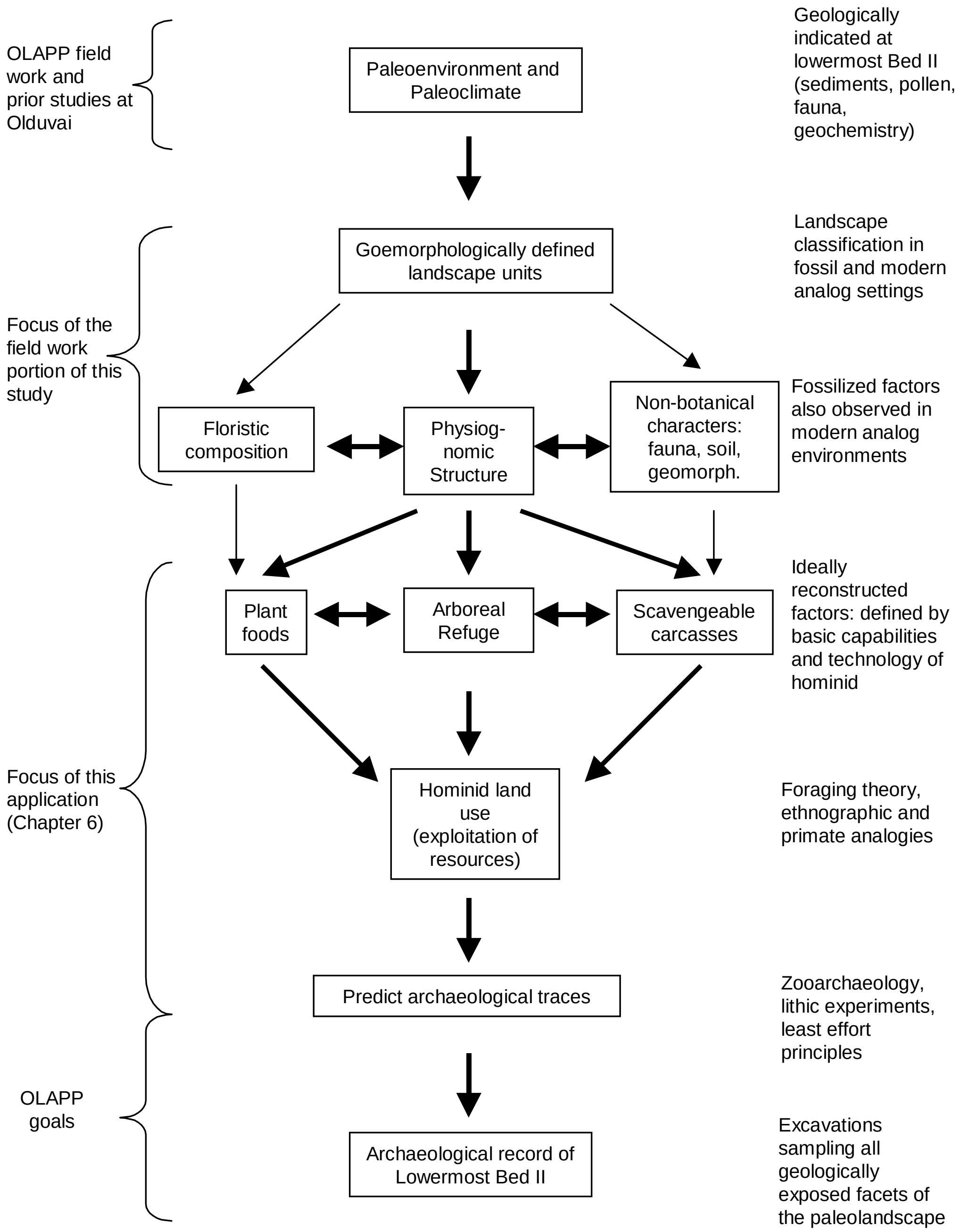
Although the absolute density of plant resources may vary greatly between the various river margins studied, if the modern analogs show a pattern in which the river margin is consistently more dense in plant resources compared to its nearby lacustrine plain, then one could predict a similar juxtaposition for the past. The archaeological remains in an ancient river margin versus its lacustrine plain could then be compared and contrasted with that in mind. This is the general idea behind the approach to modern analog studies of vegetation that were implemented in this thesis.

A New Conceptual Framework for Modern Vegetation Analog Studies

The previously used methods reviewed above are either too broad-scaled to be relevant for application to a landscape-scale analysis, or are too specific to particular modern situations to apply the results with confidence to any past situation for which detailed parameters are not established. A broader-than-site but smaller-than-regional scale of vegetation modeling is needed, one comparable to that of hominin home range sizes (ca. 100-1000 km^2).

The conceptual framework developed and employed for the lowermost Bed II Olduvai paleolandscapes by OLAPP, and expanded upon in this thesis, is depicted graphically in Figure 1-1, and described in more detail below. It involves 1) defining physical, climatological, and ecological parameters and landscape units (especially landscape facets) for the focal fossil setting, 2) documenting the relative nature of vegetation resources in sets of analogous modern settings at a landscape spatial scale, 3) creating models of resource and hazard distributions across the paleolandscape based on

Figure 1-1. The conceptual framework used in this thesis for integrating data from the fossil/geological record with information about modern vegetation structure, composition, and distribution. The steps of the investigation proceed down the central portion of the figure, cumulatively incorporating lines of evidence as indicated in the column on the right.



the modern analog study, 4) modeling hominin land use, 5) predicting archaeological traces, and 6) testing those predictions against a landscape archaeological record.

The main methodological steps are depicted in the central column of Figure 1-1. To move from each step to the next requires cumulatively incorporating paleoenvironmental and modern analog information, biological, ecological, and uniformitarian theory, and increasingly higher levels of inference. The column on the far right indicates lines of evidence that are necessary components of the model, some of which are not being directly investigated by this project or OLAPP. The column on the far left shows which steps are encompassed by this thesis project in particular, and how they fit into the larger research goals of the lowermost Bed II case study. The overall conceptual framework could be applied to other fossil hominin localities that are also investigated at a landscape scale.

Starting at the top of Figure 1-1, the foundation for the research is the geological and fossil record which exists at Olduvai Gorge, from which general reconstructions of the paleoenvironment and paleoclimate have been made. These are described in detail in Chapter Two. From that, the paleolandscape is theoretically divided into a series of hierarchically ordered landscape units, the system for which is described in the next section. Peters and Blumenschine (1995; 1996) undertook the initial attempt to define the paleolandscape units at Olduvai, and their work forms a foundation for this thesis.

Having described the paleolandscape units in terms of geographic and climatic parameters, the next step in this conceptual framework is to choose modern settings that fall within similar parameters, and therefore serve as sets of landscape units analogous to those of the lowermost Bed II paleoenvironment. Given the need to model a variety of particular landscape units, a variety of different modern settings must be used, with each providing a model for specified portions of the paleo-Olduvai basin.

A successful methodology for using modern analogs to understand biological and physical processes that are relevant to paleolandscapes requires that there be a way to link information learned in modern environments to the past, incorporating relational analogies (Gifford-Gonzalez, 1991). Here, landscape units are the links; they can be reconstructed from fossil/geological evidence and observed in modern settings. The features that define landscape units, e.g. geomorphology, soil properties, hydrology, etc., also relate to vegetation composition, structure, and resource characteristics. The goal is to understand the relationships among all of those factors well enough that useful vegetation properties can be "predicted" for the past, given an adequate landscape unit reconstruction from the fossil record.

In Blumenschine and Peters' (1998) approach, there are three main categories of resources that would ideally be reconstructed across a paleolandscape given the biology and technology of the hominins of lowermost Bed II age. First is the availability of plant foods, on which hominins probably depended for the majority of their calories and nutrients. Second is the availability of refuge, specifically trees on which hominins were likely dependent for protection and sleeping sites. Third is the availability of scavengeable carcasses, which in Blumenschine and Peters' (1998) model was the primary determinant of the predicted nature and landscape distribution of artifacts and bones in the fossil record. The availability of scavengeable carcasses depends upon competition among larger carnivores (Blumenschine, 1986), but the types of carnivores present, and the ratio of carnivores to carcasses, may be a function of the physiognomic structure of the vegetation (Blumenschine, 1986; 1989; Blumenschine and Peters, 1998).

The proposed relationship between scavengeable carcasses and physiognomic structure is central to Blumenschine and Peters' model because most archaeological traces are predicted to result from the scavenging activities of hominins. This thesis did not monitor scavengeable carcass availability (that has been done by Blumenschine, 1986; Tappen, 1995; Dominguez-Rodrigo, 2001), but does focus on physiognomic categories and their relationship to plant resource availability and landscape features. Currently, physiognomic structure is the most commonly reconstructed aspect of vegetation since it relates to all of the paleo-indicators: faunal remains, botanical remains, and especially paleosol carbon isotopes. These are the reasons for the central positioning of physiognomic structure in Figure 1-1.

Analysis of field data from modern analog settings leads to new insights regarding the relationships between vegetation and environmental factors, as well as quantitative measures of cover and plant resource abundance. Relative abundances of plant resources between landscape facets in the modern habitats will be shown by transforming the measures of cover and density into categories, and then depicting general contrasts with a series of maps (Chapter Six). Thus, an idea of contrasts between landscape units is developed and presented. As mentioned at the end of the previous section, the notion of contrasts is extremely important in this methodology, because ultimately the archaeological "tests" of models of hominin land use are dependent upon archaeological evidence (fossils and stone tools) showing significant contrasts between adjacent landscape units. If the difference is not significant, then it is impossible to test (archaeologically) whether hominins were engaged in different types of activities in those different landscape units.

Since order of magnitude degrees of contrast between adjacent landscape facets is the level at which the fossil and archaeological evidence is predicted to show patterning, modern study areas with analogous adjacent landscape facets have been chosen in which to study such contrasts (for example, the adjacent riverine, interfluve, and lacustrine areas at Manyara). The modern study areas and details of their vegetation are described in Chapters Three, Four, Five, and Six.

The next step in the methodology is to create or refine models of hominin resource availability for the paleolandscape(s) in question using the information collected in the modern analog settings. In this thesis I build upon Peters and Blumenschine's (1995, 1996) initial attempts to model hominin affordances at Olduvai based on their general actualistic experiences in modern habitats. The concept of affordances is broader than "resources" because it includes the notion of both the resources and hazards in an environment for a particular animal, or what an environment "affords" an individual (Gibson, 1977). In this study, a more quantitative analysis of the vegetation of modern analog environments is used to test and refine Peters and Blumenschine's initial models (Peters and Blumenschine, 1995, 1996; Blumenschine and Peters, 1998).

Based on the hypothetical distribution of resources, models of hominin land use can be improved. Of the four hominin species that potentially visited the Olduvai basin during lowermost Bed II times, each has particular physiological and technological attributes which can be contrasted to show how, for example, a mostly vegetarian hominin would exploit the basin versus a scavenging and plant-eating hominin. These issues are addressed in Chapter Six.

As one of OLAPP's broader goals, predictions of archaeological traces across the landscape are based on the hominin land use models. The predictions of bone and stone tool assemblages draw upon the literature regarding lithic technology and taphonomic studies of bone and a number of ecological principles (Blumenschine and Peters, 1998). Archaeological predictions are then tested through excavations of the paleolandscape, excavations which randomly sample as wide a variety of paleolandscape facets as is possible given the nature of the outcrops.

The lowermost Bed II Olduvai paleolandscape is now accessible only as the outcrops along the length of the gorge and at a few other localities such as the Fifth Fault (Hay, 1976). Excavations were begun by OLAPP in 1989, and are being conducted across an area of ca. 400 square kilometers. The entire paleo-Olduvai basin is estimated to have been about 2000 square kilometers in size (Blumenschine *et al.*, 2000). Blumenschine and Peters (1998) have made archaeological predictions for some of the paleo-Olduvai land units. In Chapter Six, I suggest how my refined models of resource distribution and hominin land use at Olduvai might affect their previously described archaeological predictions.

This thesis does not attempt to determine which specific vegetation resources Olduvai hominins actually used, or the nutritional value and processing costs of wild plant foods. Those are higher-level goals dependent on the more fundamental information toward which this project is geared at collecting. The vegetation models created here are dependent upon the *relative* nature of vegetation and affordances between the component landscape units of the entire landscape, and are not dependent upon the detailed and absolute reconstruction of the ecological details of each site-scaled portion of the landscape. The size of the landscape units examined here can be small or large, with different questions being addressed at different levels such as landscape facets, landscape associations, or regions. The hierarchical landscape unit system used for Olduvai is described below.

In sum, I have developed a methodology for reconstructing vegetation resources at a particular fossil locality in which the fossil/geological record and modern analogs are mutually informative. The fossil/geological record serves to define the parameters within which modern analog settings are appropriate in terms of climate, topography, ecology, etc., in which the ecologically relevant aspects of hominin-plant interactions can be modeled at landscape scales. The modern analogs, in turn, are used to determine the relative relationships between vegetation resources and landscape units, and potentially "fossilizable" features of the landscapes are identified, thus further enhancing the interpretations that can be made based upon the fossil/geological record.

Landscape Classification

For consistency and ease of comparisons, I follow the same landscape classification approach for the modern study areas as that outlined by Peters and Blumenschine (1995) for the paleo-Olduvai basin. It is a hierarchical design based on geomorphic and ecological principles, following Mabbutt and Stewart (1963), Christian (1958), Webster and Beckett (1970), and Gerresheim (1974).

The landscape units of interest are regions, landscape associations, landscape facets, and landscape elements. A region is the broadest unit of classification and is defined by a common geologic and geomorphic history, and a local climate pattern (Peters and Blumenschine, 1995). In this study there are three modern study regions: Serengeti, Manyara, and Ngorongoro Crater. These are described in detail in Chapter Three.

A landscape association (Gerresheim's "land system asssociation") is "a group of closely related adjacent land systems… [that] are similar in morphology and genesis but show subtle differences in lithology, soil, water regime, catenary sequence, terrain proportions, ecological position, vegetation and/or microclimate" (Peters and Blumenschine 1995:333). For example, within the Manyara region there are four landscape associations that were sampled: the Lacustrine Plain, the lacustrine terrace, the fluvial terrace, and the alluvial fans. In the Serengeti region there are three landscape associations that were sampled: the eastern Serengeti Plain, the western Serengeti Plain, and the Serengeti Woodland. The area of Ngorongoro Crater that I studied is a single landscape association, a lacustrine plain. Within and between these landscape associations one can expect variation in the vegetation, some of which may be predictable according to factors such as geomorphology, water distribution, and soil chemistry.

Each landscape association contains landscape facets. A landscape facet can usually be portrayed at map scales of 1:50,000, and comprises "an ecologically homogeneous part of the landscape with a distinct morphology on a common parent material. Environmental factors such as hydrology, soils, vegetation and microclimate are either uniform over the whole landscape facet or vary in a simple, consistent and predictable way" (Gerresheim, 1974:3). Landscape facets are the most refined landscape unit which can at once 1) take into account the complex interactions of many environmental and ecological factors, and 2) potentially be preserved as a distinct unit in the fossil record at broad enough spatial scales, and narrow enough temporal scales, to enable archaeological comparisons between different landscape facets of a paleolandscape.

Spatial and Temporal Scales

In a landscape-scale study, the goal is to document the synchronic evidence of hominin activity across paleolandscapes, rather than the diachronic evidence of hominin activity within a constrained area or "site". Paleolandscapes cannot be examined and studied the way that modern landscapes are. A Plio-Pleistocene landscape is typically exposed to the Earth's surface only as a narrow strip of sediments along an outcrop (Isaac, 1981). Such is the case for lowermost Bed II Olduvai, where modern Olduvai Gorge creates a natural transect through what remains of a multitude of paleolandscapes that existed there from 2 mya through the present. The sediments comprising the paleolandscapes of lowermost Bed II are defined as those lying above volcanic Tuff IF, aged about 1.75 mya (e.g., Walter *et al.*, 1991), and below the Lemuta Member or Tuff IIA. Although there are no current, reliable dates for the top of the target horizon, the best estimate for the age of Tuff IIA is approximately 1.70 mya (Hay, 1996). The duration of the deposition of lowermost Bed II is estimated to be about fifty thousand years (Blumenschine *et al.*, i.p.).

There are likely to have been climatic fluctuations during the fifty thousand year interval encompassed by lowermost Bed II. From 2.52 mya to 0.95 mya, the global benthic oxygen isotope (O^{18}) record indicates that climate fluctuated at a dominant 41,000 year period, which corresponds to some of the earth's orbital properties (Denton, 2000). This is also confirmed by marine eolian dust records (deMenocal, 1995). The amplitude of climatic fluctuations were considerably less than those of the late Pleistocene and Holocene Ice Ages, when a 100,000 year periodicity dominates. Nonetheless, climatic changes would have occurred, and these are in evidence as the interfingering of lake deposits with lake margin deposits within the lowermost Bed II outcrops at Olduvai. Lake levels changed not only seasonally, but also cycled through periods of wetter and drier conditions, each perhaps lasting several thousand years.

Landscape reconstructions and hominin land use modeling for lowermost Bed II must account for these environmental dynamics in order to be realistic. The key to OLAPP's landscape approach is that strict contemporaneity between lateral subsections of the landscape is not required. This holds for time periods constrained by two conditions: 1) that hominin biology and technology are not changing during that time period, and 2) that the boundaries between relevant ecological and geomorphological attributes of interest do not change in spatial distribution during that time period (Blumenschine *et al*., 2000).

The first condition will almost certainly be met when considering paleolandscapes of Middle Pleistocene age or older that span only a few tens of thousands of years. Actual hominin fossils are too rare to show biological changes over such a time period. Stone tools are more abundant than hominin fossils, but more important is the fact that the archaeological remains of early hominin technology – stone tools and cut-marked bones – show extreme conservatism over time during the earlier stages of hominin evolution. The Oldowan Industrial Complex persisted for roughly a million years from about 2.6 to 1.7-1.6 mya (Semaw *et al*., 1997), while the Acheulean Industrial Complex lasted almost one and a half million years, from 1.6 mya to 250 or 200 kya (Clark, 1994; McBrearty *et al*., 1996).

The second condition, that the time span of a fossil paleolandscape not exceed the duration in which unique landscape units remain spatially coherent, ecologically homogeneous, and distinct from other nearby landscape units, can only be met for portions of the landscape in most cases. Some landscape units will persist over many millennia (for example, a geomorphologically-induced, persistent wetland or a gallery forest along a spatially constrained stretch of river). On the other hand, a growing body of evidence suggests that other landscape units change with climate and other factors as it fluctuates over time spans such as centuries and millennia (e.g., Sinclair, 1979a), in addition to the orbital cycles mentioned previously (deMenocal, 1995). Studies suggest that cycling is an important and natural aspect of East African savannas, and some areas seem to fluctuate from grassland to woodland even within a century (Dublin, 1995; Belsky, 1989; Sinclair, 1979a). In Chapter Four I discuss which of Olduvai's paleolandscape units would likely have been subject to short-term change, and which would have more likely persisted for many millennia.

Conclusion

Through a field investigation of the vegetation and landscape ecostructure in several modern habitats in northern Tanzania, I obtain information in this study that is relevant to understanding potential interactions between plants and early hominins. The specific goals outlined in the beginning of this chapter include developing a methodology for characterizing the relationships between vegetation structure, species composition, and plant resources in modern habitats. I apply that methodology to several modern habitats, and use the information to model plant resource distribution for hominins across the lowermost Bed II paleolandscape at Olduvai.

This thesis also addresses some of the broader issues in paleoanthropology today. The role of plant foods in early hominin lifestyles has been speculated upon for decades. Based upon this study of wild plant food distribution in some modern habitats, I aim to identify the general types of plant foods that were available to hominins living in semiarid savannas.

Recent evidence from isotopic studies of hominin teeth suggests that hominins have a significant C_4 component to their diets. Could it be plant food consumption that accounts for a C_4 component, or does it necessarily imply animal food consumption?

Several recent theories suggest that it was new ways of using plant foods that caused the significant changes from *Homo habilis* to *Homo ergaster*, such as an increase in body size, changes in digestive anatomy, and success in colonizing new habitats. This differs from propositions that it was an increase in meat consumption that caused such changes. Does the actual availability of wild plant foods support these new theories?

Finally, what do the results of these modern analog vegetation studies imply regarding various interpretations of the socio-economic function of early archaeological sites in Africa? Do the characteristics and distributions of wild plant foods lend themselves towards being collectable items that would be consistent with central place foraging? I address these broader paleoanthropological issues in Chapter Seven.

CHAPTER 2. AFRICAN VEGETATION AND OLDUVAI'S LOWERMOST BED II PALEOENVIRONMENT

Introduction

In this chapter I set the stage for the reconstruction of Olduvai's past vegetation by first reviewing the general distribution of vegetation across the African continent, including its important physiognomic, floristic, and ecological characteristics, and then reviewing the paleoenvironmental evidence for lowermost Bed II, Olduvai. The information presented in this chapter helps to justify the modern analog methodology, including choice of analog study sites, that I use to reconstruct the nearly two-million-year-old vegetative details that would have been ecologically important to early hominins.

Throughout the chapter, I discuss vegetation according to two major classifications: by its physiognomy, which includes the physical shape and structure of plant communities, and in terms of floristics, or the taxonomic composition of the communities. When seen at a continental scale, the vegetation of Africa is clearly divided into several zones that evidence suggests have been distinct for the past few million years. Thus, while modern African vegetation is not identical to that in the Plio-Pleistocene, it is at least similar physiognomically and floristically. The broad array of previously conducted paleoenvironmental studies of Olduvai Gorge serve to suggest the nature of the general climatic, geographical, and floristic patterns during the past, and therefore the particular modern settings in Africa that would be most appropriate as analogs.

In Africa, an important ecological distinction exists between moist savannas, including miombo woodlands, and arid savannas, such as those of the Serengeti ecosystem. This aspect of African savanna ecology has not been well explored in the literature regarding its potential relevance to early hominin evolution. An examination of the issue in this chapter, including a review of how other large primates (chimpanzees and baboons) exploit African savannas can help to shed some light on the ecological preferences or tolerances of early hominins. This issue is explored further in Chapters Six and Seven.

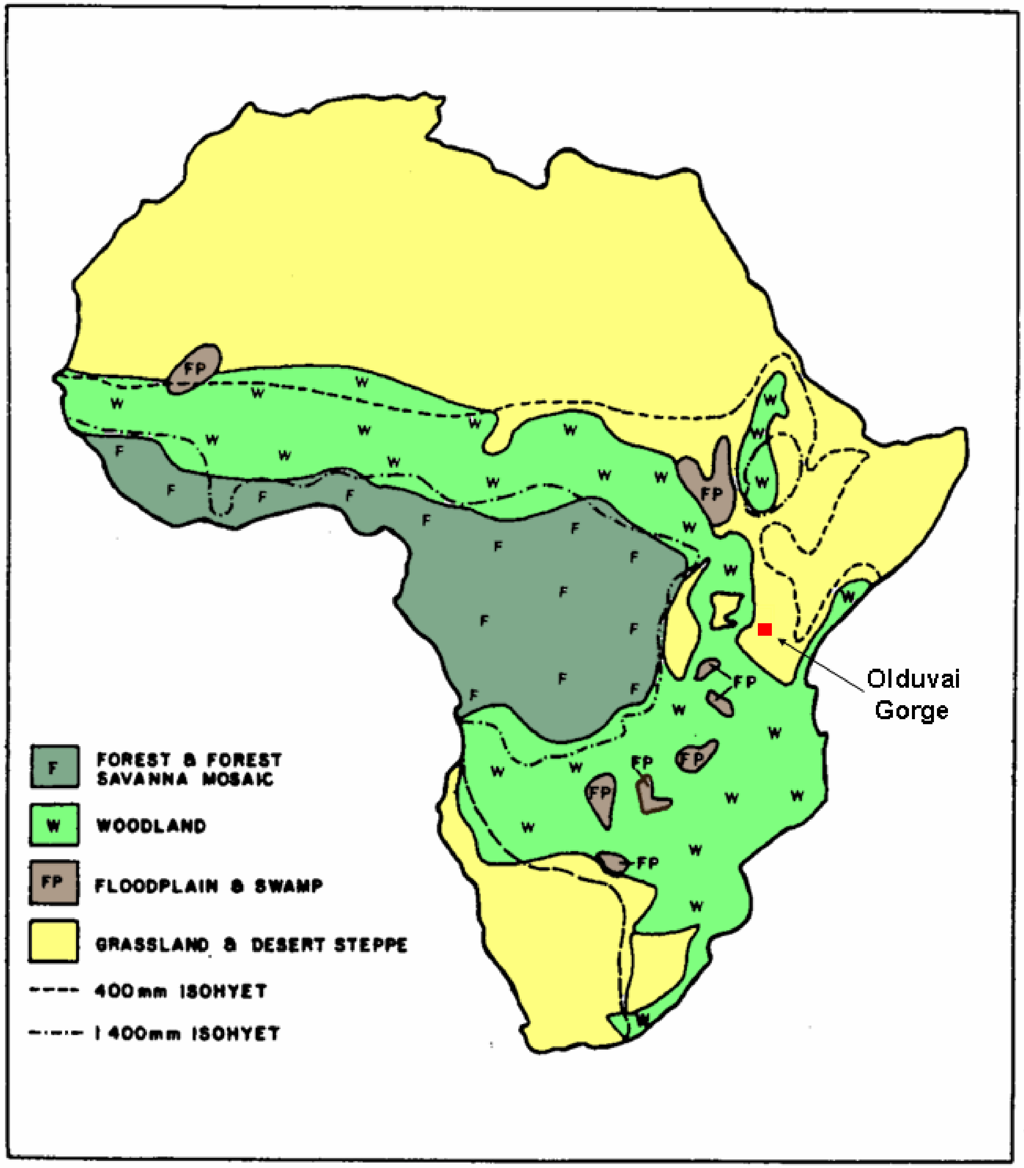
In this chapter I also discuss the nature of long-term vegetation change, which is well understood for temperate environments of the late Pleistocene and Holocene, but has not been so well studied in tropical latitudes and earlier time periods.

In the second half of the chapter I describe the modern setting of Olduvai Gorge, its paleogeography, and previous studies of its paleoenvironments and climate during lowermost Bed II times. This includes evidence from floral and faunal remains, isotopic evidence, and other geological indicators. Ultimately, I describe the time of duration of lowermost Bed II, and the hypothesized landscape units of the paleo-Olduvai basin that form the foundation for applying the modern vegetation to the Olduvai case study in Chapter Six.

Physiognomic Vegetation Patterns of Africa

The general vegetation pattern of Africa consists of concentric zones of progressively drier vegetation that radiate out around the wettest zone occupying the Congo Basin (Figure 2-1). The Congo Basin supports a vast tropical rain forest that

Figure 2-1. Basic physiognomic vegetation types of Africa today. Based on Bell (1982), simplified from Clark (1967).



extends west along the coastal strip bordering the Gulf of Guinea. Rain forest is but one of many tropical forest types, the characters of which are determined by factors such as temperature, altitude, and precipitation regimes. Rain forests in general are characterized by a tall canopy with multiple canopy strata, and a terrestrial herbaceous stratum which lacks narrow-leafed grasses (Livingstone, 1975; Hamilton, 1982; White, 1983). Tropical rain forests are associated with warm, moist, tropical lowlands, and are the most complex type of tropical forest in terms of the mosaic of niches, which support a great diversity of smaller plants and animals (Archibold, 1995). The Congo Basin supports a tropical rain forest fed by moisture from the Atlantic Ocean that is drawn inland and produces abundant rain (about 2000 mm per year) that falls evenly throughout the year (Livingstone, 1975; Kano, 1984).

Surrounding the Congo rainforest to the north, east, and west is a great arc of savanna vegetation. The term "savanna" has a variety of colloquial and scientific meanings. I use “savanna” in a very general sense in this thesis. It refers to tropical areas marked by strong seasonality in which the majority of rain falls in the summer. Grasses that use the C_4 photosynthetic pathway dominate the herbaceous stratum, and the woody plants, which may or may not be present, tend to be fire tolerant (Huntley, 1982). Areas in Africa that I refer to as savannas range from treeless grasslands, to areas with sparse tree and/or shrub cover, to woodlands with a grassy ground layer. Therefore, areas that are categorized as woodland to bushland to grassland all fall under the general heading “savanna”. Annual rainfall in the savanna zones of Africa ranges from 1800 mm in moist savannas to as low as 50 mm in drought years of the most arid savannas (Huntley, 1982).

Beyond the savanna zones, in the northern and southwestern areas of the continent, lie the most arid and sparsely vegetated environments: the deserts. To the north is the Sahara Desert, and in the southwest is the Namib Desert (Figure 2-1).

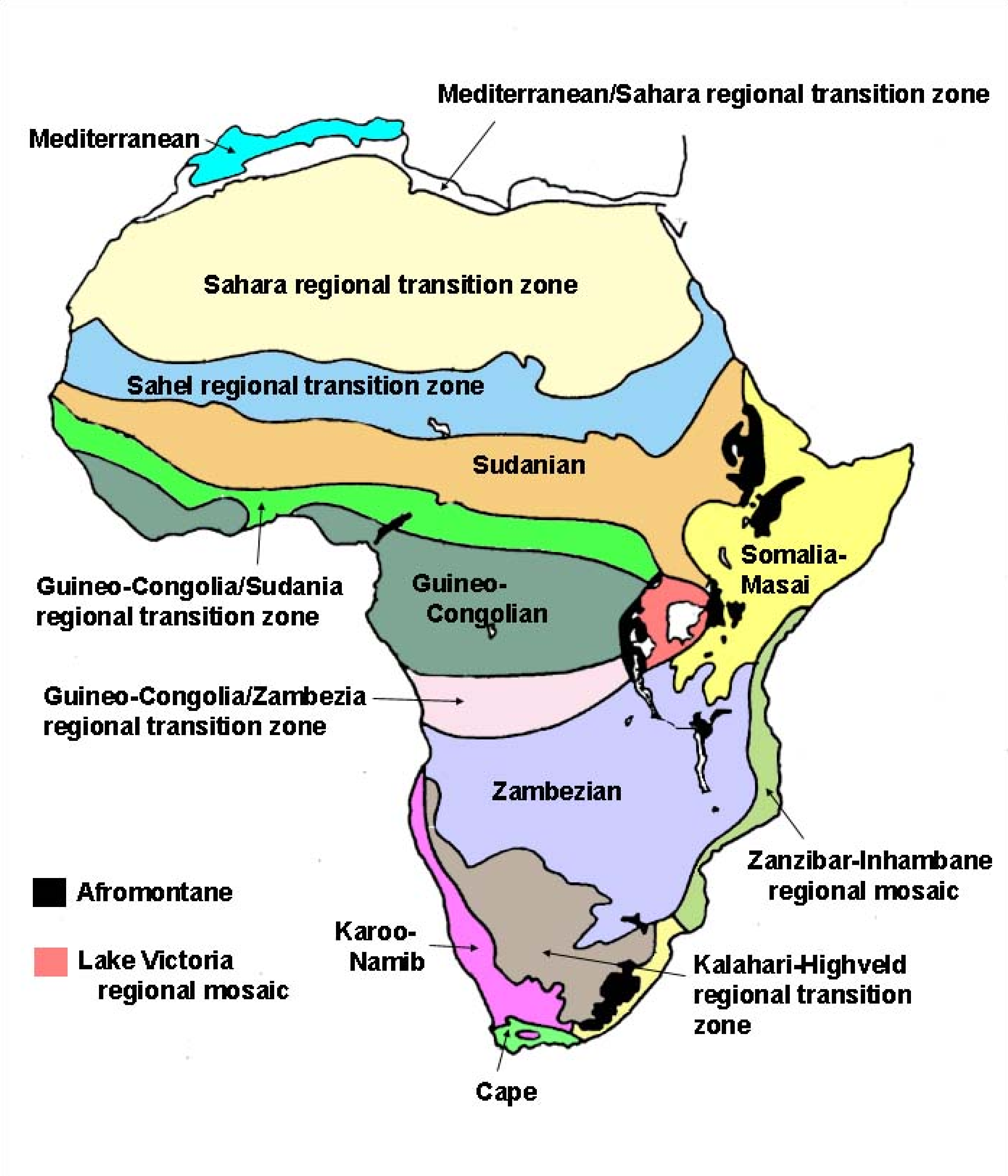
Floristic Zones of Africa

The African continent can be divided into biogeographical zones based on the distribution of plant taxa. Zones based on the most general taxonomic affinities of plants tend to mirror the physiognomic vegetation patterns I described above, centered around the Congo Basin.

The floristically defined zones described by White (1983) are in common usage by ecologists, and are shown in Figure 2-2. White's major zones are called phytochoria, or regional centers of endemism. Each is defined by having 50 % of its entire plant species confined within the given area, and a total of more than 1000 endemic species. There are seven phytochoria in Africa. Between these are nine regions referred to as "transition zones", many of which are as large as the phytochoria themselves (Figure 2-2). The placement and composition of the phytochoria today reflect the present climate, geography, and soil types, as well as the evolutionary history of plant taxa, plant migrations, climatic changes, continental movements, and other environmental factors. Note, however, that White's phytochoria are defined by common and endemic plant *species*, regardless of higher levels of relatedness between plants (e.g., genera, families). Therefore, possible affinities between certain phytochoria at the genus and family level are not depicted in White's map. Some phytochoria do share more genera or families in common, such as those in the savanna regions, as discussed below. Since plant species may have migrated or evolved over the 1.75 million year time period since the deposition of lowermost Bed II, Olduvai, then it is important to also consider plant associations at the level of genus and broader categories when trying to understand the floristic history of Africa.

The Congo Basin is occupied by the Guineo-Congolian phytochoria, which also extends along the Gulf of Guinea (Figure 2-2). The desert areas in the northern and southwestern portions of the continent accommodate the Sahara regional transition zone

Figure 2-2. Phytochoria of modern Africa, modified from White (1983: Figure 4).



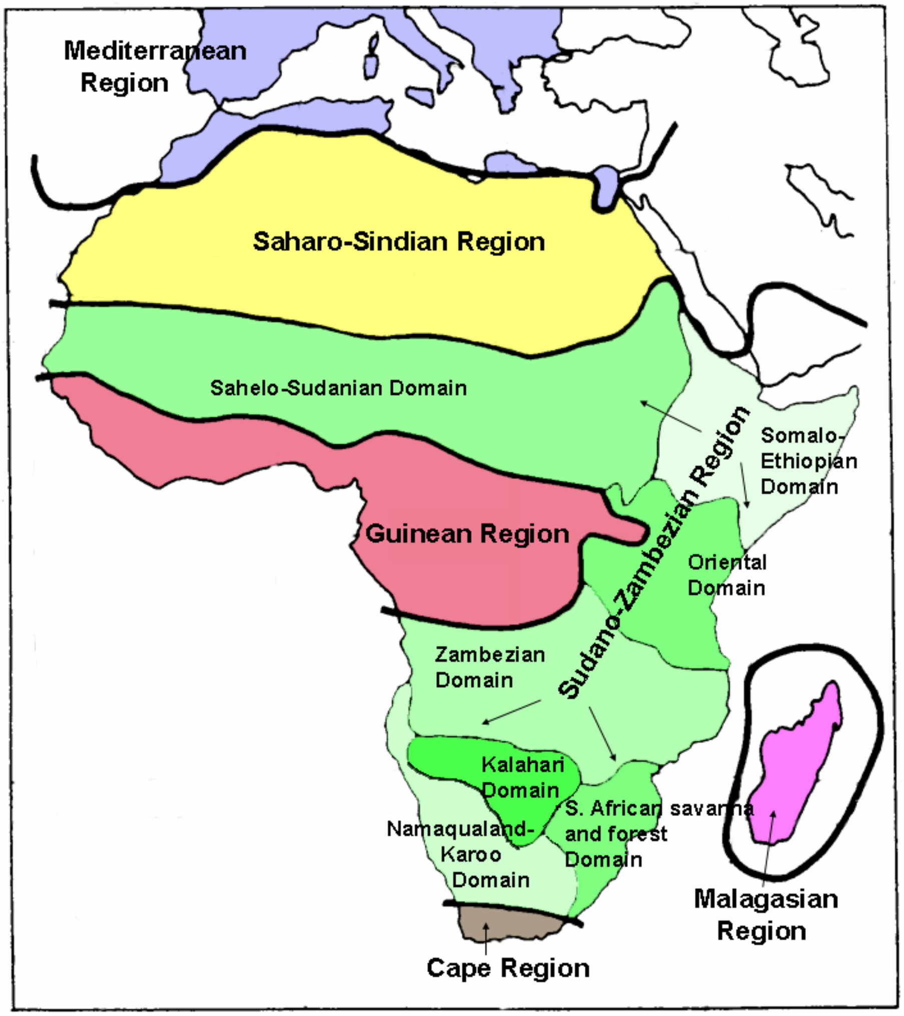
flora and the Karoo-Namib phytochoria, respectively, with other distinct flora along some of the coastlines.

Between the rain forest and the deserts is the aforementioned great arc of savanna vegetation, occupying the largest portion of the African continent. According to White's classification, the savanna arc consists of three distinct phytochoria and several floristically-defined transition zones (Figure 2-2). The strip of savanna south of the Sahara, but north of the rain forests, contains the Sudanian regional center of endemism, which is buffered by northern and southern transition zones. East African savanna, including Olduvai Gorge and the Manyara, Serengeti, and Ngorongoro modern study areas, belongs to the Somali-Masai regional center of endemism. Southern African savanna is dominated by the Zambezian center of endemism and the Kalahari-Highveld regional transition zone.

The Afromontane archipelago-like regional center of endemism exists in several disjunct highland areas along the Great Rift Valley, and in a few isolated areas of West Africa (see the black areas in Figure 2-2). These mountainous areas tend to trap moisture and therefore have a local climate distinct from that of surrounding lowlands. The Afromontane areas support forest vegetation as well as sparsely vegetated zones at very high altitudes. All pockets of Afromontane flora are adjacent to lowlands supporting vegetation of other phytochoria, including Zambezian, Sudanian, and Somalia-Masai.

White's (1983) phytochoria are the most widely used floristic references for Africa today, but sometimes reference is made to earlier phytogeographical schemes. Most notable is the system developed by Lebrun (1947) and later modified by Monod (1957). Their system consisted of hierarchically organized chorological units, particularly Regions that are sub-divided into Domains, as shown in Lebrun's map in Figure 2-3 (Werger 1978: 152-153). Regions and Domains are defined based upon the distributions of all species of flora collectively (White, 1965). This differs from White's phytochorial approach, which takes advantage of subsequently collected herbarium records and field studies, and is focused on areas in which a minimum number of plants (50%) have their

Figure 2-3. Phytogeographical map of modern Africa according to Lebrun (1947), based on the map published in Werger (1978: Figure 8).



centers of endemism. White's approach is preferable because when the distributions of *all species* are used to categorize or sub-divide a Region, "the distinctive patterns of any particular ecological element will be masked by those of other ecological elements or swamped in the mass of statistics produced by such a crude approach" (White, 1965:652).

Lebrun's map (Figure 2-3) depicts six main Regions of African flora, the largest of which is the Sudano-Zambezian Region that forms a wide arc around the Guinean Region of central-west African rainforest. The Sudano-Zambezian Region is composed of several Domains such as the Oriental Domain of East Africa (including Olduvai Gorge) and the Zambezian Domain of south-central Africa. One advantage of Lebrun's system is that the relationship between Domains is apparent due to the hierarchical nature of the system. In White's centers of endemism classification (Figure 2-2), the fact that certain phytochoria have more species in common than others is not immediately apparent. White does refer to the higher-level taxonomic relationships between his phytochoria in written descriptions, however (see below).

Floristic Relationships and Historical Distributions

Several interesting disjunctions of flora exist on the African continent. There appear to be greater floristic affinities between the Zambezian and Sudanian phytochoria than between either of those and the Somalia-Masai flora, despite the fact that the Somalia-Masai and Guineo-Congolian phytochoria geographically separate the Zambezian and Sudanian phytochoria (Figure 2-2). About 24% of Zambezian tree species also occur in the Sudanian zone, and the relationship between herbaceous and small woody species are thought to be similar in the two zones (White, 1983).

The Somalia-Masai zone has about 50 endemic genera, as opposed to the Zambezian and Sudanian zones, which each have less than 10. The Sudanian zone is particularly poor in species. The Somalia-Masai zone has important concentrations of endemic species within several genera. For example, there are 30 endemic species of *Acacia* within this zone, 60 of *Commiphora*, and 10 of *Maerua*. These are all woody species and these genera were encountered often in the modern analog studies as described in Chapters Four and Five. Most of the non-endemic species are also widespread in other dry parts of Africa, while some are found only within the Somalia-Masai zone and the drier parts of South Africa (see below). A few arid-adapted tree species which occur in all three savanna zones (Somalia-Masai, Zambezian, and Sudanian) are *Balanites aegyptiaca*, *Boscia angustifolia*, *Boscia salicifolia*, *Commiphora africana*, and *Maerua angolensis*.

The historical explanation for this juxtaposition of floristic zones is not well understood, in large part due to the poor record of plant fossils in Africa. Using the relatively sparse fossil evidence from lowland areas of Africa in combination with some evidence for paleoclimates, Axelrod and Raven (1978:88) suggested that between 30-25 mya, large areas of savanna woodland existed across the northern and southern parts of the continent, separated by a full band of rainforest that extended east to the Indian Ocean. By the Late Miocene/Early Pliocene, the savanna zones connected in East Africa, forming an arc of savanna vegetation.

The floristic composition of plants across the early arc is unknown. If the arc originally supported a single type of flora (as suggested by the similarities between Zambezian and Sudanian phytochoria), then at some point it was split into northern and southern portions. Given the numerous endemic species within the Somalia-Masai phytochoria, and the relatively slow rate of evolution in plants relative to that in animals (Hamilton, 1974:202; Bonnefille and Dechamps, 1983:193), that flora might have taken more than a million years to become established in East Africa. It may have been influenced by plants migrating from the Middle East and Western Asia via the Horn of Africa.

There are a number of common plant species, and even some genera, which occur in the arid parts of northern East Africa (such as Somalia) and in arid South-west Africa, but not in-between those two arid zones. Several modern animals, such as Kirk's dik-dik (*Madoqua kirkii*) and the oryx (*Oryx gazella*) have similar disjunct distributions in these arid zones (Alden *et al*., 1998). These areas may have been connected by corridors of arid or semi-arid country, particularly during periods of glacial maxima when the climate of the African continent as a whole was colder and drier (van Zinderen Bakker, 1978). It is possible that the most recent corridor may have been present around 12,000 years ago (Hamilton, 1974). Detailed floral comparisons between these areas that would test this hypothesis have not yet been done, and the claim remains unsubstantiated.

Isolated lowland forests along the coasts of Kenya and Tanzania have many taxa in common with the Guinea-Congolian rainforest, although they are separated from it by a minimum of 650-1100 km, and those taxa do not occur in the savanna vegetation in-between (Hamilton, 1974). Furthermore, there are at least two plant species represented by different subspecies in the East Coast and Western forests (Hamilton, 1974). The interpretation is that there have been at least two periods of connection between these forests: a relatively recent one, and a more ancient one that would explain similarities at a generic level (more specific dates were not suggested) (Hamilton 1974). The connection may have formed as a loop of forest around Tanzania passing south along the east side of Lake Tanganyika, across northern Malawi, and back north along the coast of Tanzania (Verdcourt, pers. com., cited in Hamilton, 1974:206). The climate would necessarily have been significantly wetter than at present, which suggests a time period for connection perhaps as far back as the Pliocene or late Miocene.

The major zones of Afromontane flora have important phytogeographic and zoogeographic similarities that suggest recent biotic interchange between the East and West Afromontane zones in Africa (Moreau, 1966; Morton, 1972; White, 1981). Isolated small patches of plants with Afromontane elements exist in an area extending west from Lake Malawi to close to where the Congo River empties into the Atlantic. Recent pollen studies from Lake Malawi extending back 37,500 years suggest that during the last glacial maximum, montane forest expanded in the vicinity of Lake Malawi, indicating cool and moist conditions in southern equatorial Africa, as opposed to the cool and dry conditions indicated for equatorial Africa at this time (DeBusk, 1998). Under cooler and moister conditions, Afromontane vegetation may have formed a continuous belt across the continent along the highlands on the divide between the Congo and Zambezi Basins.

Ecological Differences among Savannas

African savannas fall into at least two ecologically distinct types: arid/eutrophic savannas and moist/dystrophic savannas (Bell, 1982; Huntley, 1982; East, 1984). The arid/eutrophic savannas have high soil nutrient availability, low rainfall (less than 650 mm per year), and a low biomass of high-quality vegetation supporting a high biomass of large herbivores. Arid savannas typify the Somalia-Masai phytochoria of East Africa (Figure 2-2), including Olduvai Gorge and the modern study areas of this thesis, but also occur patchily within the Zambezian phytochoria and southern Africa. They are characterized by short- or medium-length grasslands and open woodlands whose trees have fine, multiple leaves and thorns, typically *Acacia* and *Commiphora*. Other characteristic plant genera are *Colophospermum* (mopane tree), and *Panicum, Enneapogon*, and *Aristida* (grasses) (Huntley, 1982).

The second ecologically distinct type of African savanna is the moist/dystrophic savanna with low soil nutrient availability, high rainfall, and a high biomass of vegetation supporting a low biomass of large herbivores (Bell, 1982; Huntley, 1982; East, 1984). In central Africa, these "miombo" savannas have closed-canopy woodlands characterized by broad-leaved tree species without thorns, and an understory of patchy open areas with medium to tall grasses. Characteristic woody genera are *Brachystegia, Julbernardia, Burkea,* and *Ochna.* Typical grasses are *Andropogon* and *Diheteropogon* (Huntley, 1982). The Sudanian savanna, which runs along the southern border of the Sahara Desert, can also be categorized as an area of moist/dystrophic savanna (East, 1984). The vegetation of the Sudanian zone is physiognomically and floristically similar to those in the Zambezian zone, as mentioned above.

The combination of soil nutrient status and moisture availability determine whether an area will support arid/eutrophic savanna, moist/dystrophic savanna, or something in-between. Soil nutrient status is mainly a result of the parent material from which the soil was derived, which in turn is a factor of the geomorphological evolution of an area. Soils of volcanic origin are high in nutrients, and occur across East Africa where the volcanoes associated with the Great Rift Valley have spread their ashes for the past several million years (Bell, 1982). Thus arid/eutrophic savannas encompass the greater Serengeti region, northern Tanzania, Kenya, and Ethiopia, and have probably existed since at least the late Pliocene (e.g., Hay, 1976). These soils tend to be calcareous, or non-calcareous and eutrophic. A soil is defined as eutrophic when a relatively large number of nutrients are available for plant uptake, and the sum of exchangeable Ca, Mg, K, and Na, expressed in me/100 g clay (milliequivalents of cations absorbed per 100 grams of clay), is greater than 15 (Huntley, 1982). The arid savannas of southern Africa are not necessarily on high nutrient soils, but usually receive less than 650 mm rainfall per year, and the physiognomic structure (open woodlands of thorny, fine-leaved trees) and floristic composition (e.g., *Acacia*- and *Commiphora*-dominated) are similar to the arid savannas of East Africa (Huntley, 1982; East, 1984).

Soils forming from ancient granitic continental shields tend to be relatively low in nutrients. The Great African Plateau, which stretches across Central Africa from central and southern Tanzania through Zimbabwe, is a Pre-Cambrian continental shield from which the soils of the miombo woodlands have been derived. These soils are usually dystrophic, meaning that the sum of exchangeable Ca, Mg, K, and Na, expressed in me/100 g clay, is less than five, and the soils are therefore nutrient poor (Huntley, 1982). Occasionally moist savanna occurs on mesotrophic non-calcareous soils. The soils of the Great African Plateau are more likely to contain laterites than calcretes (Huntley, 1982). The rainfall in areas of miombo woodlands is often greater then 650 mm, but falls in distinct seasons, as in all savanna areas of Africa.

Since all parts of an ecosystem are to certain degrees interdependent, the effects of these edaphic and climatic factors also extend to floral and faunal physiognomy and dynamics. Eutrophic soils produce more nutrient-rich vegetation, which in turn supports a larger biomass of herbivores (Bell, 1982; East, 1982). The palatability of plants to herbivores is basically a function of the ratio of metabolic to structural components in the plant (Bell, 1982). Structural components such as cellulose, hemicellulose, and lignin reduce the availability of the nutritious metabolic constituents such as proteins and soluble carbohydrates. The production of plant metabolic constituents is related to cation exchange capacity, which is higher with increased soil nutrient availability. Structural carbohydrate production is much less dependent on soil nutrient availability. Therefore, plants that grow on the eutrophic soils of arid savannas are in general richer in metabolic constituents, and lower in structural components, thereby being nutrient-rich, palatable foods for herbivores (Bell, 1982; East, 1984). Hence, arid savannas growing on eutrophic soils can support a large biomass of herbivores, such as that seen in many national parks in East Africa (Coe *et al*., 1976). The miombo woodlands of moist savannas, on the other hand, produce a greater plant biomass, but most of the vegetation is high in structural materials (e.g., wood) and very low in nutrients. This helps to explain why the herbivore biomass in these systems is dominated by buffalo and elephant – large animals that can digest extremely low-quality herbage (Owen-Smith, 1982).

Many plants in nutrient-rich savannas have developed thorns as a defense mechanism against the threat of predation by the large biomass of herbivores (Huntley, 1982). Plants in areas of poor soil nutrients, in addition to being higher in structural components, may also invest more in secondary compounds (e.g., tannins, hydrocyanins) which make them less palatable to herbivores (Janzen, 1974).

While there are areas of distinct and clear-cut transitions between arid and moist savannas, there are also areas in which one type occurs in patches surrounded by the other (Huntley, 1982). Arid savanna plant species extend into moist savannas on base-rich termitaria, while moist savannas extend into arid ones on acidic sands overlying crystalline rocks or sandstones (Huntley, 1982). In Serengeti, for example, some areas of basement exposure occur in the Western corridor and Northern extension, and they are covered by broad-leaved woodland and medium to long grasses, which are typical of moist savannas (Bell, 1982).

In sum, savanna areas that receive higher rainfall, that is “moist savannas” or miombo woodlands, have different overall landscape vegetation patterns than arid and semi-arid savannas (Belsky, 1989). Semi-arid savannas are typified by green/brown contrasts on the landscape between water-supplied landscape facets and adjacent, dry landscape facets. In moist savannas, riverine vegetation often grades imperceptibly into similar communities in non-riverine landscape facets, whereas in semi-arid savannas that only happens in areas with a ubiquitous high groundwater table like the Manyara alluvial fans (see Chapter Four). Saline and sodic soils are less common in moist savannas, and disturbances from fire or large herbivores, for example, recover more quickly since heavy rainfall promotes more rapid weathering of the soil and faster plant growth (Belsky, 1989).

Most of the literature regarding ecological differences among arid versus moist savannas, such as Bell (1982), Huntley (1982), East (1984), and Belsky (1989), were written with the goal of understanding the distribution and ecology of the large mammals in Africa, such as the grazing ungulates. However, this information, coupled with information on African flora, may be helpful in understanding early hominin ecology. Modern apes inhabit forests and montane vegetation, and some chimpanzees live in moist savannas. Modern humans are the only living hominoids that inhabit arid or semi-arid savannas. Interestingly, many fossil hominins have been found in areas that are now arid or semi-arid savannas, such as northern Tanzania, Kenya, and parts of Ethiopia. As I will discuss in the first part of Chapter Six, some of these places, including Olduvai, may have also supported semi-arid savannas during the time of hominin occupation. What do the distinctive types of savannas and other vegetation zones in Africa offer for large primates' subsistence? This thesis begins to address these questions for one particular area of Africa around the Serengeti ecosystem.

Floristic Zones Inhabited by Chimpanzees, Baboons, and Early Hominins

Chimpanzees are the closest living relatives of modern humans and extinct hominins. Chimpanzees retain some primitive traits that are also present in early hominins, such as relatively long arms, a funnel-shaped torso, a flat cranial base, forward projection of the face and jaws, a U-shaped dental arch, and a brain size that is similar to that of australopithecines. Chimpanzees live in the wild in Africa in several types of environments: evergreen tropical forests (e.g., Boesch and Boesh-Achermann, 1991), miombo or moist savanna woodlands with riverine forests (Suzuki, 1969; Goodall, 1986; Schoeninger *et al*., 1999), and even in more open grassland and savanna with thick riverine forests along perennial rivers (McGrew *et al*., 1981; 1988). Despite their relatively broad range of habitats, chimpanzees nonetheless seem to be tied to forests or heavily wooded areas for survival. In the open Mt. Assirik habitat of Senegal, chimpanzees stay almost exclusively in the three percent of the area that is forested and obtain nearly all of their food there, rather than in the adjacent grasslands (McGrew *et al*., 1981). In wooded savannas, chimpanzees do eat seeds and pods from the leguminous savanna trees, but supplement them with "juicy fruits" from the riverine forests (Suzuki, 1969). Overall, chimpanzees are characterized as “fruit specialists” in that they eat high quality fruits as the mainstay of their diets (Wrangham *et al*., 1998).

Modern baboons are not as closely related to hominins as chimpanzees, because baboons are monkeys and not apes. However, baboons are the only large-bodied primates that live in the relatively arid tropical African habitats thought to be similar to those occupied by hominins such as *Homo habilis*, *Homo ergaster*, and *Australopithecus boisei* (Reed, 1997). Thus baboons can serve in some ways as models for early hominins, particularly in terms of diet. In the past, they have also served as models for hominin social behavior (e.g., Jolly, 1970; DeVore and Washburn, 1963).

Across Africa, baboons inhabit a wide variety of environments, from the cold and barren Drakensberg mountains (Byrne *et al*., 1993) to the arid savannas of Amboseli (Altmann and Altmann, 1970). Baboons eat fleshy tree fruits when available, but they are different from chimpanzees in that they are not tied to forests, and are able to subsist solely on foods from open, semiarid or arid savannas in the Somalia-Masai phytochoria (McGrew *et al*., 1982; White, 1983). At Amboseli in Kenya, for example, the baboons’ main foods are grasses and *Acacia* seeds, pods, flowers, and gum (Altmann and Altmann, 1970). Baboons will also catch and eat small animals like grasshoppers, rabbits, or even baby antelopes when the opportunity arises.

Many early hominins appear to have been able to survive in more arid types of savannas than those occupied by chimpanzees, especially after about 2 mya (Vrba, 1985; 1988; Bonnefille, 1995; Reed, 1997). Even hominins that seem to have preferred wooded or bushy habitats at earlier times, such as *Australopithecus afarensis* and *Australopithecus africanus*, did not necessarily live in the vicinity of riverine forests

(Reed, 1997). Therefore it seems that early hominins managed to find ways to survive and prosper in types of habitats that extant apes do not occupy – semiarid or arid savannas – but which modern baboons do inhabit, and it is likely that novel dietary adaptations were a key part of this success. This idea is revisited in Chapter Seven, where I discuss how early hominins might have been able to subsist in arid savannas, how this is reflected in the isotopic analyses regarding C_3 and C_4 components of their diets, and what that means in terms of their diet and foraging behaviors.

Long-term Vegetation Change

Since this study deals with the issue of reconstructing very ancient vegetation, on the order of 1.7 to 1.8 million-year-old plant communities, some discussion is warranted on the nature of long-term vegetation change.

The nature of modern plant community composition has important implications for long term vegetation change. It was the subject of a famous debate early in the twentieth century between plant ecologists F. E. Clements and H. A. Gleason. Clements likened modern plant communities to an organism, in which the interactions of plant species maintained stable plant communities (Clements, 1916; 1920, cited in Noy-Meir and van der Maarel, 1987). If modern associations between plant species are tightly knit and interdependent because they evolved that way, one would expect current mixes of plants, or communities, also to have existed in the past.

Gleason (1926, cited in Barbour *et al.*, 1980:131) on the other hand, argued for the individualistic concept of plant associations in which species combinations were the result of individual responses to the environment, and by chance events of dispersal following environmental changes (Noy-Meir and van der Maarel, 1987). Thus, current species associations may not have appeared in the past. The implications of Gleason's ideas for the dynamics of plant communities over thousands and millions of years are that plant species should migrate or evolve independently with changes in the earth's environmental conditions, and furthermore, that plant associations may have existed in the past for which there are no modern examples.

Ultimately, Clements' organismic view did not withstand the scrutiny of the constitution of modern plant communities, because plant species tend to be distributed independently of others over environmental gradients in space. Gleason's individualistic view has been supported by paleobotanical evidence, which shows that plant taxa have migrated independently in the past, rather than as discrete plant communities. For example, fossil pollen studies from late Pleistocene/Holocene temperate North America and Europe show that certain plant species quickly colonized freshly deglaciated regions, while others migrated slowly (e.g., Delcourt and Delcourt, 1987; Webb, 1987; 1988). At least in temperate regions, then, plant associations as we see them today have not remained in their current geographic positions in "equilibrium" for thousands of years.

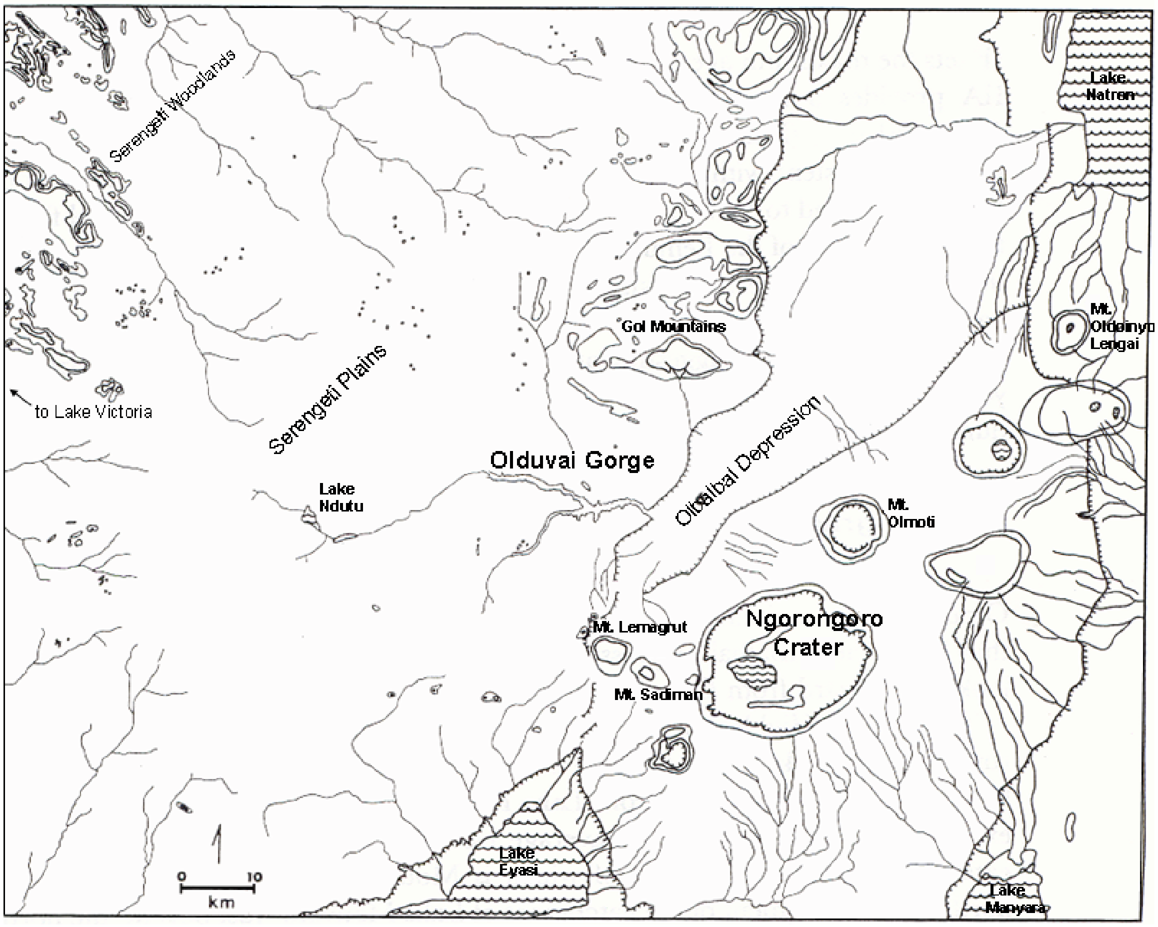
The long-term history of tropical vegetation, including African vegetation, is not nearly as well-documented as that of the temperate zones, in part because in temperate zones the lakes formed by retreating glaciers have provided many opportunities to take pollen cores. In Africa, most of the pollen cores come from mountain lakes, and only a few provide evidence for up to 30,000 years ago. One of the few pollen cores from lowland areas (less than 2000 meters elevation) in East Africa is from Lake Victoria (Kendall, 1969), but it spans only the past 15,000 years.

Unlike the case in North America and Europe, where the independent migrations of particular tree species and unique types of mixed forests can be documented over the past glacial cycle, we do not know how the ranges of East African savanna trees and shrubs might have changed over the past thousands or even millions of years. For the purposes of this study, however, we can gain some confidence in using modern East African vegetation as analogs for ancient East African vegetation because the important ecological distinctions between arid and moist savannas described above are likely to have existed since at least the late Pliocene, and therefore the arid versus moist distinctions would have been in place during the time of lowermost Bed II, Olduvai. The distinction is thought to persist that far back in time because volcanic activity in the Crater Highlands has been ongoing for the past several million years, thereby creating the nutrient-rich volcanic soils that are the hallmark of the arid savannas (Bell, 1982). Similarly, the granitic shield from which the nutrient-poor soils of the moist savannas of southern Africa derive has been present for millions of years, so there is nothing to indicate that soils would have been different during early hominin times. Floristic evidence from Olduvai pollen also can indicate whether the flora during lowermost Bed II times was more akin to arid or moist savannas. I deal with that topic later in this chapter and in Chapter Six.

Modern Setting of Olduvai Gorge

Olduvai Gorge is incised through the grasslands of the Serengeti Plain of northern Tanzania, where it stands out as a scrubby, tree-lined linear formation that runs about 22 km from west to east (Figure 2-4). The plains in the vicinity of the gorge have an

Figure 2-4. The regional setting around modern Olduvai Gorge, based on Peters and Blumenschine (1995: Figure 1).



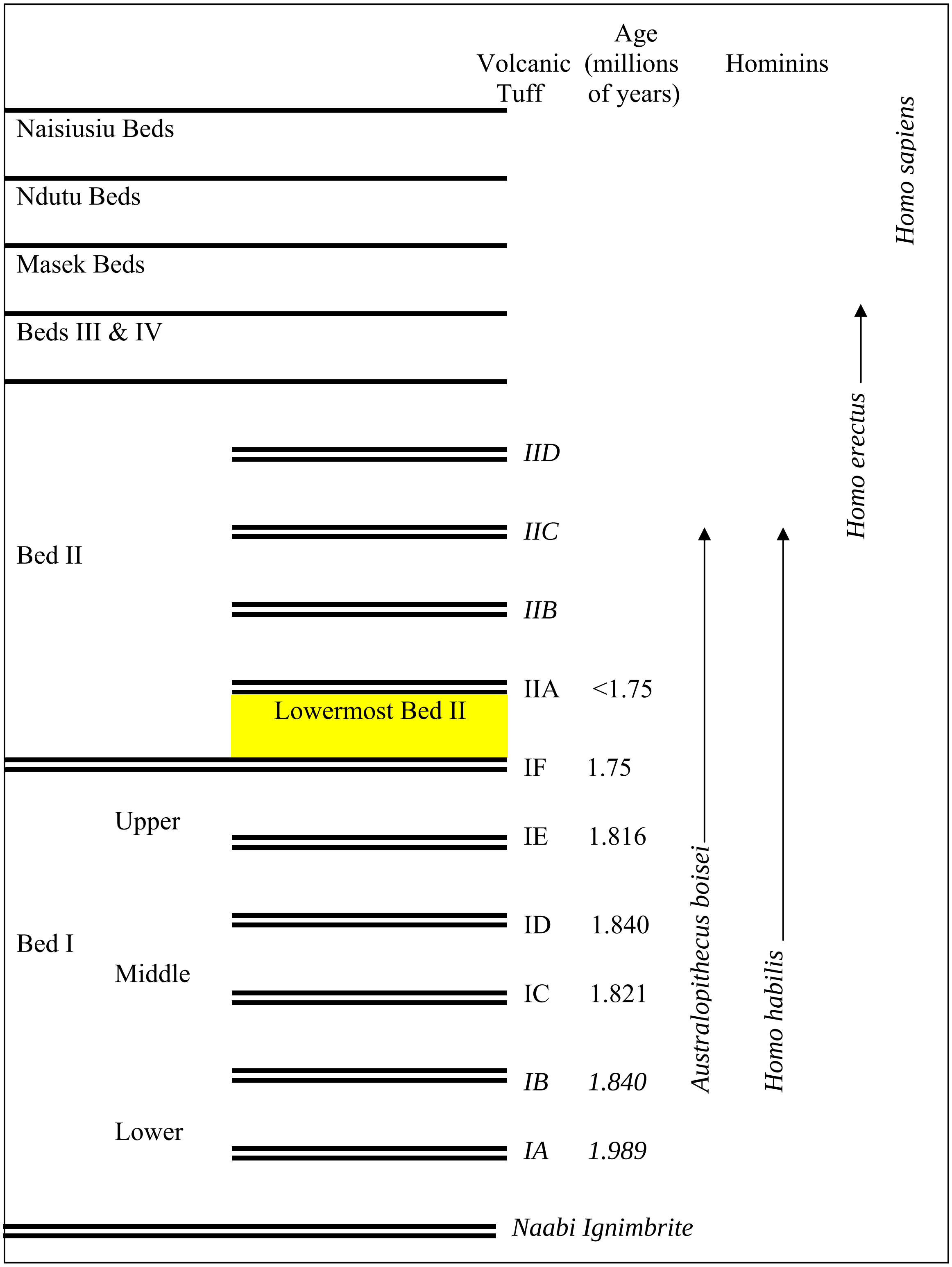
elevation of 1350 to 1520 meters. In its steeper, eastern portions the gorge is 46 to 90 m deep and 0.5 to 1.5 km wide (Hay, 1976). Water sometimes flows through the gorge during the wet season, ending at the marshy drainage sump known as the Olbalbal Depression east of Olduvai Gorge. To the east and south of Olduvai Gorge are the Crater Highlands, a volcanic range with elevations ranging from 2100 to 2400 meters at the rim of Ngorongoro Crater (Hay, 1976:13).

The climate at Olduvai today is semi-arid. As in most of northern Tanzania, there are two rainy seasons and two dry seasons each year. The “short rains” occur from about November to January, although these are very unpredictable and may fail altogether. The somewhat more reliable “long rains” that are caused by large monsoonal systems occur between February and May. At Olduvai, the amount of rain received each year can vary greatly, but averages around 400-600 mm per year (Norton-Griffiths *et al*., 1975; Cerling and Hay, 1986). The nearby Crater Highlands trap moisture from air masses moving north and northwest and consequently are sub-humid, receiving about 1400 mm of rain per year (Prins and Loth, 1988:45). The highlands create a rain shadow on Olduvai and the Serengeti Plain to the northwest, which is why rainfall there is much lower.

The vegetation at Olduvai today is semi-arid (eutrophic) savanna, characterized by scrubland and wooded grassland with *Acacia* and *Commiphora* trees and a variety of shrubs and succulents, surrounded by the grasslands of the Serengeti Plain. The nearby Crater Highlands support Afromontane forest, which is different structurally and floristically from surrounding lowland savanna vegetation (White, 1983).

The layers of sediment exposed in the walls of the gorge range in age from around two million years old at the base, to Holocene age (ca. 10,000 years BP) near the top (Hay, 1976). Hay (1976) mapped the stratigraphy of the gorge, which is divided into Beds I, II, III, and IV, and the Masek, Ndutu, and Naisiusiu Beds, listed in order from oldest to youngest (Figure 2-5). OLAPP’s work focuses on Beds I and II, and particularly on lowermost Bed II, which is constrained by volcanic Tuff IF at the bottom, and Tuff IIA or the Lemuta Member at the top. Tuff IF is a distinctive marker tuff visible throughout most of the gorge, and dates to approximately 1.75 mya (e.g., Walter *et al*., 1991). Tuff IIA is visible in the eastern basin, though it has not yet been identified in the far western portions of the gorge. Tuff IIA has a range of age estimates from 1.72 mya to

Figure 2-5. Basic stratigraphy of Olduvai Gorge showing the ages of some of the volcanic tuffs and the hominins that have been found in different levels. Vertical axis not to scale. Based on Klein (1999:167).



1.66 mya (Manega, 1993), with a best, conservative estimate of approximately 1.70 mya (Hay, 1996).

The exposed strata of the gorge contain fossils and stone artifacts even in the oldest layers, and this has made Olduvai one of the most important paleoanthropological sites in the world. Louis Leakey pioneered the paleoanthropological studies at Olduvai in the 1930s, and Mary Leakey continued to work there until the early 1980s, where she documented the cultural sequence of the Oldowan, Developed Oldowan, Acheulean, Middle Stone Age, and Late Stone Age tool assemblages (Leakey, 1971). In the mid-1980s, Institute of Human Origins (IHO) worked at Olduvai Gorge and found a partial skeleton of *Homo habilis*, OH 62 (Johanson *et al*., 1987). Since 1989, Blumenschine and Masao (1991; Blumenschine *et al*., i.p.) have headed OLAPP, a project at Olduvai that focuses on landscape-scale paleoanthropology and paleoecology.

A variety of previous research has been conducted regarding the paleogeography and paleoenvironments of Olduvai during Bed I and Lower Bed II times. Peters and Blumenschine (1995; 1996; Blumenschine and Peters 1998) summarize many of the findings; here I also present a summary, but concentrate on studies relating to vegetation reconstruction.

Paleogeography at Olduvai

Regional Paleogeography Today

In regional view, the modern landscape to the east and southeast of Olduvai Gorge is dominated by features related to the formation of the Great Rift Valley: a string of volcanoes that make up the Crater Highlands, the down-faulted Olbalbal Depression, and Rift Valley lakes including Lake Manyara, Lake Eyasi, and Lake Natron (Figure 2-4).

The Crater Highlands began to form at least 4 mya, with some volcanoes now extinct that were active during the Plio-Pleistocene (including lowermost Bed II times), while newer volcanoes, such as Oldonyo Lengai, are active now that were not present 1.75 mya (Hay, 1976).

The drainage sump in the vicinity of modern Olduvai Gorge is in the Olbalbal Depression at the eastern edge of the gorge. The Olbalbal Depression began to appear around 400,000 years ago as a result of faulting associated with the Great Rift Valley (Hay, 1976:154). It is not a lake, but rather a seasonally-inundated wetland that can stay dry all year during a drought, or may remain partially flooded even in the dry season after an extremely wet rainy season.

Surrounding the modern Olduvai Gorge are the grassy, low, rolling hills of the Serengeti Plain. The soil is highly volcanic, derived from volcanoes in the Crater Highlands that periodically spew ash into the air. The airborne ash is transported by the westward-prevailing winds toward Olduvai and the Serengeti, where it settles (Hay, 1976). In the eastern Serengeti Plain, a calcrete hardpan has developed about a meter below the surface due to the leaching of the carbonatite-rich volcanic soil (Anderson and Talbot, 1965). Below the volcanic soils of the Plains lie Precambrian Basement rocks composed of granitic gneisses, quartzites, and shists (Anderson and Talbot, 1965:36). West of the Plains, the topography of the Serengeti Woodland is more undulating, characterized by tree or shrub covered hills and valleys. The underlying rock here is the granitoid shield or basement rock known as the Precambrian Tanganyika Shield (Hay, 1976).

Most of the Serengeti rivers drain towards the west to Lake Victoria, about 130 kilometers west of Olduvai Gorge (Figure 2-4). The divide between the Olbalbal watershed, of which Olduvai is a part, and the Lake Victoria watershed runs north-south just west of Lake Ndutu (Hay, 1976).

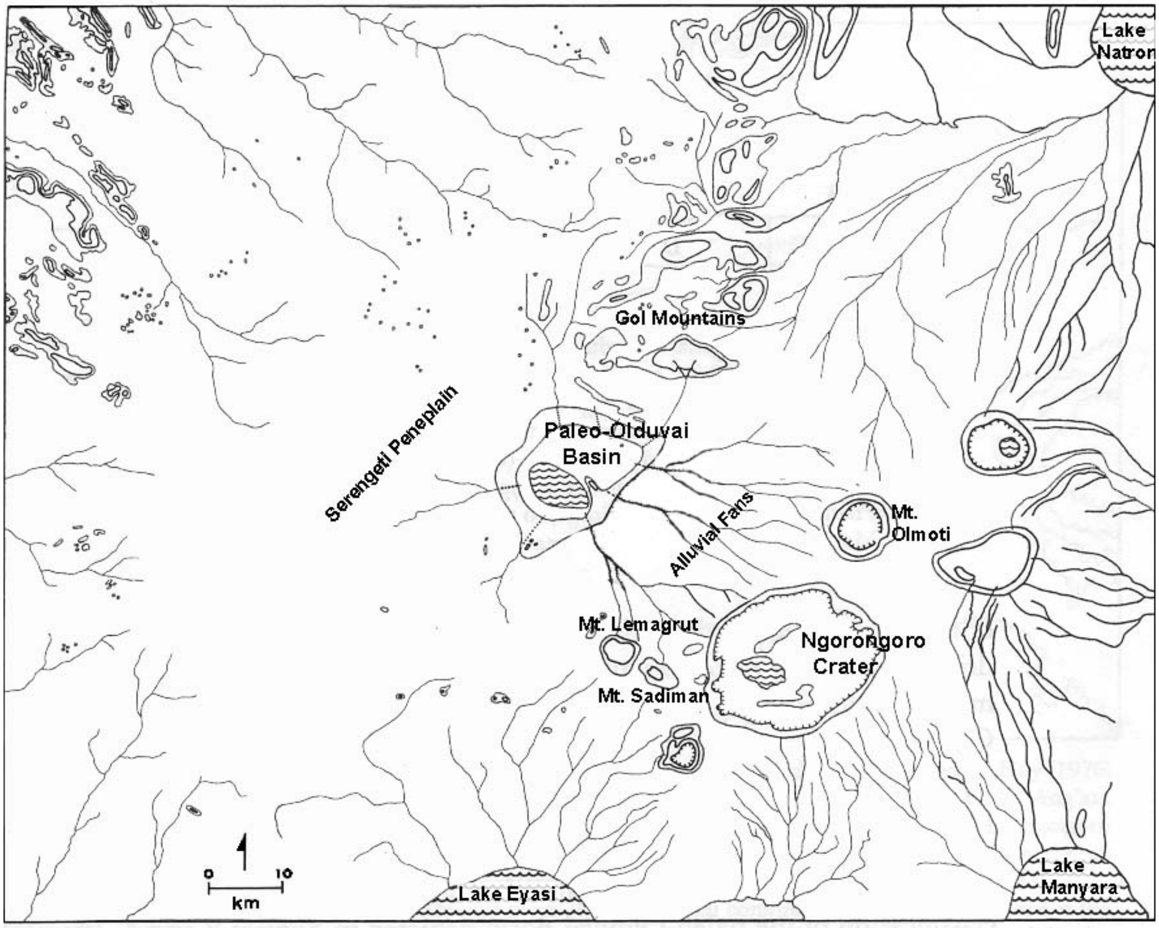
Regional Paleogeography in Lowermost Bed II Times

At the time that lowermost Bed II was deposited, approximately 1.75 mya, the regional topography was somewhat different than at present (Figure 2-6). The most important difference was the lack of the rift-associated down-faulting that now creates the Olbalbal Depression drainage sump between the Crater Highlands and Olduvai Gorge. The northwestern sides of the mountains Ngorongoro, Olmoti, Sadiman, and Lemagrut drained directly into the paleo-Olduvai lake basin via an extensive area of alluvial fans, and an alluvial plain on the east and southeast sides of the lake (Hay, 1976). The drainage sump of the region was in the area that is now the central portion of Olduvai Gorge. From about 2 mya until about 400,000 years ago, sediments, organic remains, and occasionally hominin artifacts accumulated in an Olduvai lake basin (Hay, 1976).

Basin-Wide Paleogeography in Lowermost Bed II Times

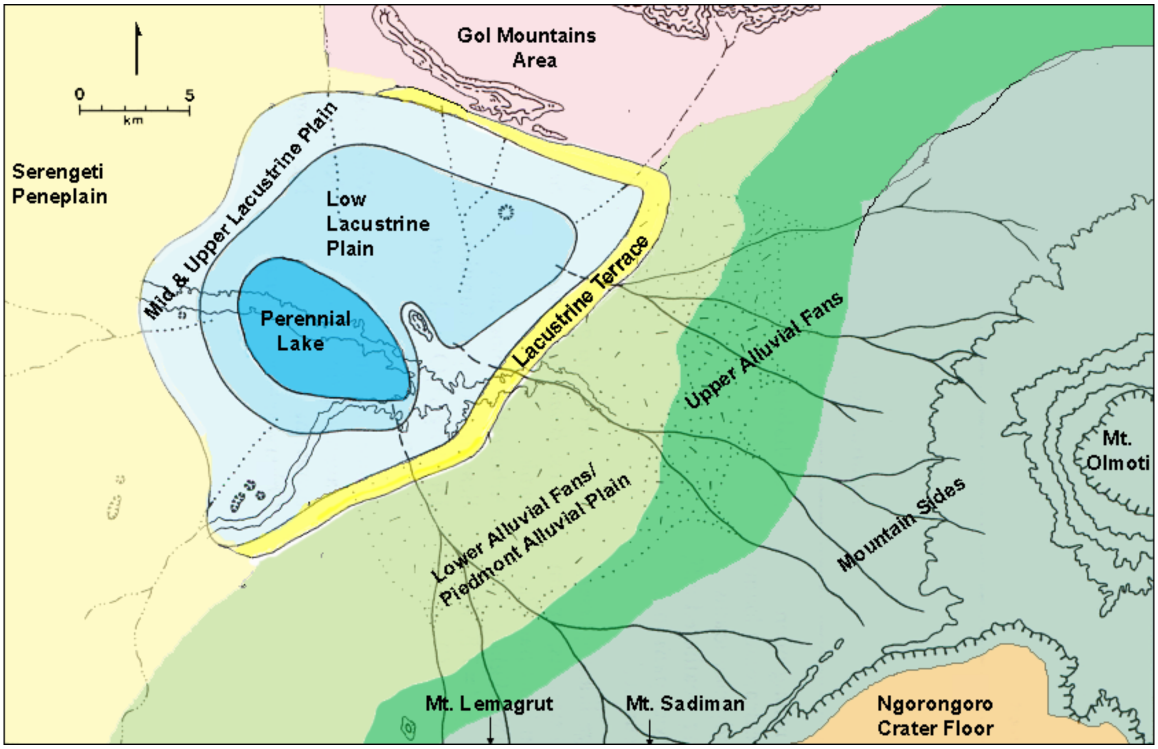
Focusing on the paleogeography of the Olduvai Basin itself, the lake was shallow, saline-alkaline, and fluctuated in size seasonally and with drought years, but generally was about 10-15 km long and 5-20 km wide (Hay, 1976) (Figure 2-7). The concentric

Figure 2-6. The regional setting at Olduvai during lowermost Bed II times, about 1.75 mya. Based on Peters and Blumenschine (1995: Figure 2).



zones around the lake shown in Figure 2-7 follow Hay's (1976:109) original descriptions and Peters and Blumeschine's (1995; 1996) landscape unit divisions. The innermost zone is the perennial saline lake, the first concentric zone is the intermittently dry portion of the lake, and the outer concentric zone is the intermittently flooded lake-margin. I have also indicated a lacustrine terrace zone around much of the lake, which marks the zone of extreme high lake levels during the wettest of climates, but which most often existed as a perennially dry zone. The lacustrine terrace was not depicted by Hay (1976) or in the map by Peters and Blumenschine (1995: Figure 4), but some modern analogs, such as Lake Manyara, suggest that it might have been present (see Chapters Three and Six).

Figure 2-7. Hypothetical paleolandscape of lowermost Bed II, Olduvai, showing landscape associations. Follows Peters and Blumenschine (1995; 1996) and Hay (1976).



The geomorphology of the southern and eastern portions of the basin was dominated by the processes of mountain erosion due to surface run-off, and eruptions of the nearby active volcanoes, particularly Olmoti. Below the steep, high mountain sides of Olmoti, Ngorongoro, Sadiman, and Lemagrut lies the upper alluvial fan zone. The lower alluvial fans had a lower gradient, and were referred to as a piedmont alluvial plain by Peters and Blumenschine (1995). Recent geological work at Olduvai by Stanistreet does not define a piedmont alluvial plain, but rather considers that the evolving alluvial fan system extended all the way to the Lacustrine Plain with subdivisions such as midfan, lower fan, marginal fan, and subaqueous fan (Blumenschine *et al*., 2000). In this thesis I use the unit Lower Alluvial Fan as synonymous with Peters and Blumenschine's (1995;

1996) Piedmont Alluvial Plain in order to allow for direct comparisons between my results and theirs.

The Lacustrine Plain adjacent to the lake itself was a very low gradient surface, probably with seasonally inundated mudflats and marshlands. The exact location of the lake margin/lacustrine plain zones shifted depending on the current climatic regime, wetter at some times and therefore closer to the mountains, drier at others and further toward the center of the lake basin. Streams crossed all of these landforms, starting in the steep montane areas where, like today, rainfall was probably much higher than at Olduvai. Those streams then crossed the upper and lower alluvial fan zones, and some, at least, eventually emptied into paleo-lake Olduvai. Groundwater flow would have occurred as well, perhaps emerging as freshwater springs around the lake margin (Hay, 1996; Ashley and Feibel, 1995). The streams and any springs would have had important ecological significance to animals of the region including hominins.

On the western side of the basin, the topographic relief was more gradual than in the east. Evidence for the paleogeography of this region is sparse compared to the well-studied eastern basin. The major topographical changes since the Plio-Pleistocene are those related to the Rift formation, which caused down-faulting in the eastern Olduvai catchment area, but there is no evidence for major changes in the west. Rivers that drained the easternmost Serengeti Plain would have emptied into the western side of paleo-lake Olduvai. From Bed I times there is evidence for ephemeral rivers with fluvial flooding conditions in the western basin (Blumenschine *et al.*, 2003). It is unclear whether the divide between the Lake Victoria and Olduvai watersheds was in the same place then as it is now. In any case, for the paleo-Olduvai basin the water catchment from the west, like today, was much smaller than that from the highland-dominated east. This is reflected by the fact that the western lake waters were more saline-alkaline, while the eastern lake waters were fresher due to greater fresh water input (Hay, 1976). These hydrological differences of the eastern versus the western sides of the paleo-Olduvai basin were important to the ecology of the basin and hominin land use (see Chapter Six).

The northern side of the paleo-Olduvai basin is even more poorly understood than the west, since the gorge does not expose sediments there. There are some outcrops of lowermost Bed II age along the Fifth Fault, and these indicate that the lake extended to the north as depicted in Figure 2-6 (Hay, 1976). The Gol Mountains begin about 15 km north of the modern Olduvai Gorge, and exist as a series of roughly east-west running ridges of metamorphic Early Paleozoic basement rocks, dominantly quartzite and gneiss/shist (Hay, 1976). The soils in this vicinity are heavily influenced by the eroding Gol Mountains, and consequently contain a relatively high proportion of the quartzite and gneiss/shist material. As described in the first part of this chapter, soils derived from basement rocks tend to be less nutrient rich than those of recent volcanic origin, and produce different vegetation than volcanic-dominated soils (Bell, 1982; Huntley, 1982).

Paleoenvironments of the Olduvai Basin

The paleoenvironmental studies from Olduvai and their results are summarized in Table 2-1, and described below. Most of the studies give a very general reconstruction of vegetation; they serve to indicate the basic structure and floristic associations of the past plant communities. The studies complement one another well, but still lack the ability to describe how the mosaic of physiognomic types and flora were distributed across the basin.

The hydrology of the paleo-Olduvai basin plays a key role in understanding its paleoecology. There is abundant evidence for the existence of marshes on the eastern side of the lake in those areas where incoming rivers became low in sinuosity or where freshwater springs emerged. The Eastern Lake Margin was the focus of Leakey's (1971) excavations, and it is these sites from which most paleoenvironmental results based on fauna are derived.

Multiple lines of evidence suggest that the climate at Olduvai changed throughout the deposition of Beds I and II. Lower Bed I was relatively moist and cool, followed by a hotter, drier episode just after the deposition of Tuff ID. There was a shift back to moister, cooler conditions during the deposition of Tuff IF and throughout lowermost Bed II, and then another very hot and dry spell subsequent to lowermost Bed II times during the deposition of the Lemuta Member (Bonnefille, 1984a; Jaeger, 1976; Kappleman, 1984). Evidence that the climate was cooler and possibly moister than at present during lowermost Bed II times comes in part from carbon and oxygen stable isotopic studies of soil carbonates (Cerling and Hay, 1986:74). These suggest that the climate was similar to today in terms of having distinctive wet and dry seasons, but that the mean annual temperature was 15-17°C, compared to a mean of 22°C at Olduvai today. Soil carbonates and calcretes are relatively scarce in Beds I and Lower Bed II, which is consistent with (but not necessarily diagnostic of) an annual rainfall exceeding 750 to 850 mm, as opposed to 400-600 mm in the region today (Cerling and Hay, 1986:74).

The fossil pollen record corroborates the evidence of distinctive wet and dry seasons and a semi-arid climate during the Plio-Pleistocene. Bonnefille (1984a) collected pollen samples from Olduvai in the 1970s yielding 11 successful pollen samples from Beds I and II, five of which derive from lowermost Bed II. All five are from the Junction Area of the Main Gorge and Side Gorge, which translates in terms of paleogeography to the Eastern Lake Margin zone.

For analysis and interpretation, Bonnefille divided the fossil pollen into several categories (Bonnefille and Riollet, 1980; Bonnefille, 1984a). The arboreal pollen was divided into two floristic groups, Afromontane and Sudano-Zambezian. Other pollen groupings were grasses (Gramineae), sedges (Cyperaceae), *Typha* (Typhaceae, or cattails), "others" (other herbaceous plants), and spores. In phytogeographical terms, according to LeBruns' (1947, published in Werger 1978:153) vegetation map of Africa (Figure 2-3), the Sudano-Zambezian region is equivalent to the great arc of savanna and woodland vegetation that reaches from South Africa to Somalia to Senegal. Much of the Sudano-Zambezian arboreal pollen derived from plants that grew near the paleo-lake basin itself. Components such as Capparidaceae shrubs are insect-pollinated, and therefore do not create pollen grains that are easily transported by wind (Bonnefille, 1984a). Their presence in the lake margin indicates that they were present locally in the basin. One sample included a relatively large proportion of *Acacia* pollen (Bonnefille, 1984a), which suggests that it might be characterized as semi-arid savanna. This subject is explored further in Chapter Six, where the results of the modern vegetation study are compared to the list of fossil pollen taxa from Olduvai.

Table 2-1. Summary of the results of previous studies in terms of vegetation and climatic reconstructions for Olduvai Gorge, Bed I and Lower Bed II times (about 1.9-1.67 million years ago). AAC is the alcelaphine plus antilopine criterion developed by Vrba (1980) as a means of using the proportion of different tribes of bovids to indicate wet versus dry and closed versus open habitats.

FOSSIL EVIDENCE	VEGETATION RECONSTRUCTION	CLIMATE RECONSTRUCTION	REFERENCES
Fossil Bovids Habitat preferences for particular tribes of bovids.	Ranges from open/arid habitats to closed/wet habitats, but no evidence for closed/arid habitats.		Shipman & Harris (1988)
(AAC + others)	Mixture of open and closed habiats: some closed canopy, but also isolated patches of grassland and marsh.		Kappelman (1984)
(AAC)	Open, dry areas followed a period of moist, closed vegetation in eastern basin (Lower & Mid Bed I), followed by open habitats (Upper Bed I).	Increasingly more arid throughout Bed I, resulting in arid environment by Upper Bed I.	Potts (1988:181)
Habitat/dietary preferences of bovids plus catenary sequence of modern African lakes (Lake Nakuru).	Lake margins were edaphic grasslands w/ high protein grasses, surrounded by belt of woodland or evergreen forest (cut by streams lined w/ riparian woodland), which in turn is surrounded by wooded grassland to open grassland.		Marean & Ehrhardt (1995)
Bovid metapodial morphology.	Mixture of closed, intermediate, and open habitats all present around the lake basin, but more closed than modern Serengeti.		Plummer & Bishop (1994)
Fossil Fauna, all vertebrates Community structure analysis in terms of 4 categories: taxonomy, body size, locomotion, feeding.	Woodland-bushland to grassland (Upper Bed I, eastern lake margin).		Andrews *et al*. (1979)

FOSSIL EVIDENCE	**VEGETATION RECONSTRUCTION**	**CLIMATE RECONSTRUCTION**	**REFERENCES**
Fossil microfauna			
Murid rodents (particularly *Oenomys* and *Grammomys*)	Lakeshore had marshes surrounded by woody savanna, including areas of Acacia woodland, riverine forest, or dense bushland (Mid Bed I).	More humid than present (Middle Bed I), with increasing aridity during Upper Bed I.	Jaeger (1976)
Rodents (mostly Murinae and Gerbillinae)	Rodent assemblages have species with bushland, grassland, and woodland savanna affinities. Mid Bed I: Thickly wooded habitats, richer than any present-day savannas, dominated by a single tree canopy with abundant ground vegetation consisting of grasses and herbs. By Upper Bed I times, open canopy of low bush and ground ephemeral and seasonal vegetation.		Fernandez-Jalvo *et al*. (1998)
Elephant shrews (insectivores)	Upper Bed I, lake margin: moist savanna woodland.	Slightly moister than present.	Butler & Greenwood (1976:48).
Urocyclid slugs	Areas of evergreen forest at eastern lake margijn (Lower and Mid Bed I).	Damp conditions, rainfall exceeds 35 inches (889 mm/yr), semiarid climate, but wetter than today.	Hay (1976:47,53)
Fossil Pollen	Sudano-Zambezian wooded grassland in basin, including *Acacia*, *Commiphora*, *Ximenia*, Capparidaceae, Cyperaceae, Graminae. Afromontane forest in nearby highlands was 2-3 times the extent of modern (in LMBII), and included Ericaceae, *Podocarpus*, and *Juniperus*.	Arid to semiarid with seasonal variations in climate.	Bonnefille (1984a), Bonnefille & Riollet (1980), Bonnefille *et al*. (1982).

FOSSIL EVIDENCE	VEGETATION RECONSTRUCTION	CLIMATE RECONSTRUCTION	REFERENCES
Root markings, “Rootcasts,” silicified plant stems	Lowermost Bed II: Marsh at eastern, southern, and western lake margins, grass and brush at western lake margin and alluvial fan.	Semiarid climate.	Hay (1976:71-73).
	Lower-Mid Bed I: At eastern lake margin, marsh w/ *Typha*, shore grasses and reeds, *Cyperus papyrus*, plant c.f. *Potamageton*.	Fluctuating lake level, frequent occurrence of standing water.	Hay (1976:46-48).
Carbon & Oxygen Isotopes From paleosol carbonates	40-60% C_4 vegetation (grasses), and flora dominantly (>50%) shrubs and trees.	Wetter and cooler than now, mean annual temp 13-16º C, rainfall greater than 800mm/year.	Cerling & Hay (1986)
	Riparian forest to grassy woodland at Eastern lake margin.		Sikes (1994, 1995)
Sedimentology Trona molds, chert nodules, rare K-feldspar.	Lake salinities highest in the western portion of the perennial lake, with other localized areas of brine.	Semiarid climate.	Hay (1976:97)
Earthy and waxy claystones with substantial proportions of biogenic opal.	Lake margin zone flooded by fresh to brackish water with large areas of marshland (Lowermost Bed II).		Hay (1976:71)
Dust Record, sediment cores in Indian ocean: aeolian dust from Africa.		For East Africa in general, increase in quantity of dust from 1.8 to 1.6 mya indicates either decrease in rainfall or increase in climatic aridity due to the effects of prolonged dry seasons.	deMenocal (1995)

Afromontane is the phytogeographical designation depicted by White (1983) that describes the unique flora occurring on the mountains of Eastern, Central, and Southern Africa (Figure 2-2). The presence of Afromontane pollen in the lowermost Bed II lake margin sediments does not necessarily indicate that such flora grew at that very spot. Rather, the pollen was probably transported by wind into the paleo-lake basin from the nearby Crater Highlands, as modern pollen collections have confirmed that it does today (Bonnefille and Riollet, 1980; Bonnefille, 1984a). Some pollen may also have been transported by rivers from the mountains into the lake.

Fossil pollen suggests that during lower Bed I and lowermost Bed II times, the Afromontane forest of the nearby Crater Highlands was two to three times the size that it is presently (Bonnefille, 1984a). The relative size of the modern Afromontane forest as a climate indicator, however, should be taken with caution since, as pointed out by Bonnefille (1984a), such direct comparisons do not take into account recent deforestation that has occurred due to the modern human activities of intentionally burning, collecting firewood, agriculture, and settlements.

Paleosol carbon isotope research has been conducted by Sikes (1994; 1995) toward the goal of reconstructing ancient vegetation structure at fine spatial scales for different portions of the lowermost Bed II paleolandscape. Stable carbon isotopes from paleosol organic matter and co-existing pedogenic carbonates reflect the original proportion of plants using the C_4 photosynthetic pathway (tropical grasses) to plants using the C_3 photosynthetic pathway (trees, shrubs, and forbs) that were growing there when the paleosol or carbonate was formed. Since this is basically a way of examining the ratio of woody to herbaceous plants, stable carbon isotopes should reflect basic physiognomic structure of the past vegetation at a fine spatial scale.

Sikes’ (1994, 1995) results suggest that within a 1 km^2 area at the Eastern Lake Margin, the vegetation was grassy woodland (or bushland or shrubland) to riparian forest during lowermost Bed II times. These results must be viewed with caution given the uncertainty as to when the carbonates formed. Lake margin and other areas can change from woodland to grassland over a period of decades, such as the *Acacia xanthophloea* die-off at Amboseli (Western and Van Praet, 1973) or the fluctuations from woodlands to grasslands in the Serengeti (Sinclair, 1979a). If and how such changes are reflected in paleosol carbonates is not well understood.

Fossil macrobotanical remains from Olduvai are currently under analysis by Bamford, and include fossilized pieces of wood and sedges from the Eastern Lake Margin area (Blumenschine *et al*., 2000). Rootmarkings or rhizoliths (Klappa, 1979) and concretions are common throughout lowermost Bed II. Hay (1976:72) noted that the waxy claystones of the Eastern Lake Margin, thought to represent lacustrine environments, commonly contain “coarse, vertical rootmarkings”, suggestive of marsh vegetation. In western lake margin deposits, Hay (1976:72) found rootmarkings suggesting that “marshland was greatly subordinate to grass and brush”.

The task of reconstructing vegetation physiognomy or composition based on rhizoliths is probably premature at this point until a more detailed analysis of the structures is undertaken. Whether certain structures are indeed related to roots as opposed to animal burrows or pedogenic processes is not clear in most cases (e.g., Klappa, 1979).

Groundwater in semi-arid habitats can be even more important than rainfall in determining local vegetation (Coughner and Ellis, 1993). While today the groundwater and surface run-off from the northeastern sides of the Crater Highlands drain into the Olbalbal Depression, in the past they drained into the paleo-lake Olduvai basin. If the groundwater table under the lower alluvial fans/piedmont alluvial plain was high, it could have supported a dense woodland or forest, even during times of low rainfall. A modern example of this is Manyara's groundwater forest, a multi-layered, closed canopy forest with trees exceeding 30 meters in height in an area with an average annual rainfall of around 650 mm (Loth and Prins, 1986).

Although a relatively high groundwater table is suggested by localized fresh, non-zeolitized glasses in Tuff IF (Hay, 1996, Blumenschine *et al.*, 2000), the only fossils that support the existence of evergreen forest near paleo-lake Olduvai are those of urocyclid slugs (Hay 1976:47, 53), found in Lower and Middle Bed I (Table 2-1). The slugs indicate damp conditions in evergreen forests "where the rainfall exceeds 35 inches per year or where damp conditions are maintained by regular mists" (Verdcourt, 1963, cited in Hay 1976:47). If evergreen forests existed during lowermost Bed II times, they may have been ephemeral, or were concentrated along riverine corridors in the alluvial fans.

Faunal analyses of fossil vertebrates from Bed I and Lower Bed II indicate that a mosaic of physiognomic vegetation types existed within the region of paleo-lake Olduvai including open grassland, bushland, and woodland (see references in Table 2-1). Several studies of the fossil bovids (Bovidae) have been undertaken, including those that use direct analogy of the habitat preferences of modern tribes of bovids to assume similar preferences for extinct members of that tribe. For example, the alcelaphine plus antilopine criterion, or “AAC” (Vrba, 1980) was applied by several researchers (Shipman and Harris, 1988; Kappelman, 1984; Potts, 1988:181). All of these studies found that the vegetation of Beds I and/or Lower bed II contained a mosaic of habitat types ranging from open grassland to woodlands.

Other bovid studies have applied a “taxon-free” approach that uses observable modern relationships between bone shape and habitat structure of bovids, and then applies these criteria to infer degrees of “closed” versus “open” vegetation in Plio-Pleistocene settings based on fossil bovids, without having to assume bovid dietary preference based on tribal affiliation (Kappelman *et al*., 1997; Plummer and Bishop, 1994; Spencer, 1997).

A reconstruction of the Olduvai paleo-basin was offered by Marean and Ehrhardt (1995) based in part on the known habitat and dietary preferences of bovid tribes present at Olduvai and also on their general knowledge of the catenary sequence of modern African lakes, particularly Lake Nakuru in Kenya. They suggest that the paleo-Olduvai lake margins were edaphic grassland with high protein grasses, surrounded by a belt of woodland or evergreen forest cut by streams lined with riparian woodland, which in turn is surrounded by wooded grassland to open grassland further away from the lake. Although their conclusions are based on casual observations as opposed to quantitative data, the Lake Nakuru analog in Kenya is an interesting comparison for my Tanzanian analog sites, and deserves more detailed study as a potential modern analog for the paleo-Olduvai basin.

The Bed I Olduvai fossils of mammalian microfauna, such as murid rodents (Murinae), gerbils (Gerbillinae), and elephant shrews (insectivores), have been studied, but not those from lowermost Bed II (Jaeger, 1976; Fernandez-Jalvo *et al*., 1998; Butler and Greenwood, 1976). Andrews is currently undertaking a new study of mammalian microfauna from lowermost Bed II in conjunction with OLAPP (Blumenschine *et al*., 2000). The Bed I microfauna results concur with other studies that Lower to Middle Bed I had a slightly more humid climate than present, which became more arid by the time of Upper Bed I. Fernandez-Jalvo *et al*. (1998) interpret the Middle Bed I environment based on rodent fossils as is a thickly wooded habitat, richer (in terms of numbers of species) than any present-day savannas, and dominated by a single tree canopy with abundant ground vegetation consisting of grasses and other herbs (Table 2-1).

While most fossil fauna studies are derived from the eastern side of paleo-lake Olduvai, OLAPP uncovered a middle-upper Bed I-aged hominin maxilla/lower face belonging to *Homo habilis* in the western basin (Blumenschine *et al*., 2003). The hominin was situated in a freshwater ephemeral channel setting, in association with Oldowan stone tools and butchered bones of large mammals. Grazing animals were abundant among the fauna, suggesting that much of the interfluvial areas in the west were grassland during Bed I times (Blumenschine *et al*., 2003). Although the find is not lowermost Bed II in age, it suggests more hominin activity in the western part of the basin than was previously suspected, and provides some more details about the paleoenvironments west of the lake.

In sum, these paleoenvironmental studies tend to focus on the changes in proportion of more closed versus more open habitats over time, such as throughout the deposition of Bed I and Lower Bed II. From the perspective of this thesis, in which an understanding of the distribution of physiognomic types *across* the basin during a single, short time interval is most important, these results serve as a broad guideline as to the possible range and proportions of wooded versus open landscape facets present. Other lines of evidence must be brought in to predict the locations of that mosaic of habitat types.

Time encompassed by Lowermost Bed II

The lowermost Bed II paleolandscape sampled by OLAPP is thought to have existed for approximately 50,000 years duration, and better dates for Tuff IIA in the future should provide a more exact estimate (Hay, 1976; Manega, 1993). The target horizon therefore encompasses climatic changes ranging from those that are seasonal, to those that fluctuate within 10's to 100's of years, up to one entire climatic cycle resulting from changes in the earth's orbit.

During the Plio-Pleistocene, the time frame that includes lowermost Bed II, the most important climatic cycle was a 41,000 year period as opposed to the 100,000 year "ice age" cycle that dominates current climate (deMenocal, 1995). Climatic changes that related to the earth's orbit were also of a much lower amplitude prior to the late Pleistocene. In other words, the climate did not change as dramatically over the period of orbital precessions as it has done in late Pleistocene and Holocene times. Presumably vegetation did not change as dramatically either. Still, some climatic shifts would have occurred over the 50,000 years when lowermost Bed II was deposited, and models of the paleolandscape need to account for that variation.

In terms of more local, basin-wide changes at Olduvai, the geology suggests that the lake expanded and contracted with wetter/cooler and hotter/drier periods, respectfully.

During wetter periods, high lake stands would have shifted lake margin wetlands higher up on the Lacustrine Plain, affecting marshes and possibly woodlands associated with those springs or rivers. Some ephemeral streams around the basin may have become perennial, and the vegetation of the alluvial plains might have changed with the raising or lowering of the groundwater table. Specific predictions of how vegetation of the different paleolandscape facets at Olduvai would have changed over time are discussed in Chapters Four, Five, and Six.

Landscape Units Hypothesized for Lowermost Bed II

In the methodology for paleoenvironmental reconstruction followed in this thesis, the ideal landscape unit for connecting past and present settings is the landscape facet. Landscape facets are fundamentally defined in terms of geographic relief, soil type, water regime, and climate (Gerresheim, 1974; Webster and Beckett, 1970; see Chapter One). Not only are these factors potentially recognizable in the fossil record, but they are also the factors that to a large degree control the nature of the vegetation and the ecology of each landscape facet.

The hypothetical landscape associations and their landscape facets that existed during lowermost Bed II times in the paleo-Olduvai basin are summarized in Table 2-2. The major landscape associations are shown in the map in Figure 2-7. These are based in large part on Peters and Blumenschine (1995; 1996), who in turn followed Hay (1976). The aforementioned geological and paleoenvironmental studies are the evidence for the existence of these paleo-landscape units.

Table 2-2. Hypothetical landscape units of the lowermost Bed II, Olduvai paleolandscape. Based on Peters & Blumenschine (1995; 1996), Blumenschine & Peters (1998), and this thesis.

Landscape Association	**Landscape Facet**	**Description**
Serengeti Woodlands	Riverine	A hilly area with basement rock-derived soil not modeled by Peters & Blumenschine. I modeled only the ephemeral rivers.
Serengeti Peneplain	Non-Riverine Riverine (crossing the plains)	Gently rolling open plains; calcareous loams and sandy clay loams overlying weathered tuff. Ephemeral streams cross the plains.
Western Lacustrine Plain	Riverine Non-Riverine	Low gradient intermittently flooded to intermittently dry zone on the west side of the lake. Possible ephemeral streams entering the lake in places.
Eastern Lacustrine Plain -Lower, Mid, and Upper	Stream-fed wetlands	Intermittently flooded zone of the lake. Low gradient, clay-dominated landform with some sand and pebbles. Lower portions flooded for extended periods of time with saline alkaline lake water; upper portions flooded rarely. Fresh water input from low-sinuosity streams create stream-fed wetlands. In places small or large springs emerge supporting marsh and possible localized shrubland or woodland adjacent to the springs.
	Dry lands adjacent to stream-fed wetlands	
-Upper with springs	Small spring wetlands	
	Dry lands adjacent to small springs	
	Large spring wetlands	
	Dry lands adjacent to large springs	
-Upper	Non-Riverine	
	Riverine	
Lacustrine Terrace	Non-Riverine Riverine	Narrow transition zone corresponding to an old high lacustrine plain, not modeled by Peters & Blumenschine; soils somewhat alkaline and non-saline and coarser than the lacustrine plain (include more silt and sand). Woody vegetation character depends on availability of groundwater.
Major Rock Outcrops		Isolated inselbergs, some of which have unique vegetation from the surrounding areas. Not modeled specifically in this thesis.
Lower alluvial fans (Piedmont alluvial plain)	Non-Riverine Riverine	More sandy, deeper, better drained soils than the lacustrine plain and terrace, but soils still somewhat alkaline. Ephemeral and possibly perennial streams.
Upper alluvial fans	Non-Riverine Riverine	Not modeled specifically in this thesis. Upper fan zone with deep, sandy soils and gravelly apices, regularly flooded and partially water-logged during wet season, groundwater within tree rooting depth throughout the year. No analogs studied for this thesis.
Mountain sides	Slopes Riverine	Not modeled specifically in this thesis. Coarse, shallow volcanic soils with gravel and sand (elevation 1370->2600m); steep slopes and freshwater streams.

In this thesis, I use modern analog sites in northern Tanzania to better understand the likely vegetation and plant resources for hominins in those Olduvai paleo-landscape facets. I did not study modern analogs relevant to reconstruction of the major rock outcrops, upper alluvial fans, or mountainside landscape associations. Those landscape associations are poorly represented in the geological exposures at Olduvai, but will need modeling in more detail in the future for a fuller understanding of hominin land use of the basin and adjacent regions.

Conclusion

In this chapter, I reviewed the physical setting of Olduvai in terms of the modern distribution of vegetation and the paleoenvironmental evidence. The continent-wide distribution of floristic zones in Africa appears to have been established for several million years, with the existence of an arc of savanna vegetation surrounding the Central/ West African rainforest since perhaps the late Miocene or early Pliocene (Axelrod and Raven, 1978). The ecological distinction between arid/eutrophic and moist/dystrophic savannas could be of importance to understanding early hominin evolution, since hominins seem to be the only hominoids capable of surviving in arid savannas. The distinction between arid/eutrophic and moist/dystrophic savannas probably dates back to at least the late Pliocene (e.g., Bell, 1982; Hay, 1976).

The setting of the paleo-Olduvai basin during lowermost Bed II times, around 1.75 mya, was in what is now the Somalia-Masai floristic zone. Paleoenvironmental evidence suggests that it was a semi-arid savanna with a mixture of grassland, bushland, and woodland. The paleogeography consisted of an expanding and contracting shallow, saline and alkaline lake surrounded by a lacustrine plain, alluvial fans, and the Crater highlands to the east. The paleolandscape has been divided into a series of hierarchical landscape units by Peters and Blumenschine (1995; 1996), which will be used in Chapter Six to apply the modern analog results to the Olduvai paleolandscape.

Paleoenvironmental evidence from Olduvai was used to understand the general climatic, geographical, and floristic parameters within which the modern analog study areas should be chosen for the Olduvai case study. The details of those modern study areas and the field methods used in them are the subject of the next chapter.

CHAPTER 3. MODERN STUDY AREAS AND FIELD METHODS

Introduction

In the methodology developed for this study, modern vegetation is used to model the types of vegetation and plant foods that early hominins might have encountered in the past, but that are not directly visible in the fossil record. Previously conducted research on lowermost Bed II, Olduvai, reveals its general paleoenvironmental setting in terms of geology, climate, physiognomy, and flora, as reviewed in Chapter Two. In this chapter, I use those geological, climatic, physiognomic, and floristic parameters to choose modern analog study localities within which to conduct quantitative analyses of modern vegetation. After the plant descriptions of the modern study areas are complete (Chapters Four and Five), the relationships between plant foods, refuge tree distribution, vegetation structure, and land units are used to reconstruct those aspects of vegetation for the Olduvai paleolandscape (Chapter Six).

I chose modern analog study localities in northern Tanzania within Serengeti National Park, Manyara National Park, and Ngorongoro Conservation Area that represent landscape associations with landscape facets broadly similar to particular portions of the reconstructed lowermost Bed II Olduvai paleolandscape. It was necessary to choose a subset of all potential modern analog settings due to limitations of time and resources. Therefore, within each of the three modern regions I tried to choose study areas that were representative of the variety of land features and vegetation types within that modern region. In this chapter I describe those modern study areas in detail.

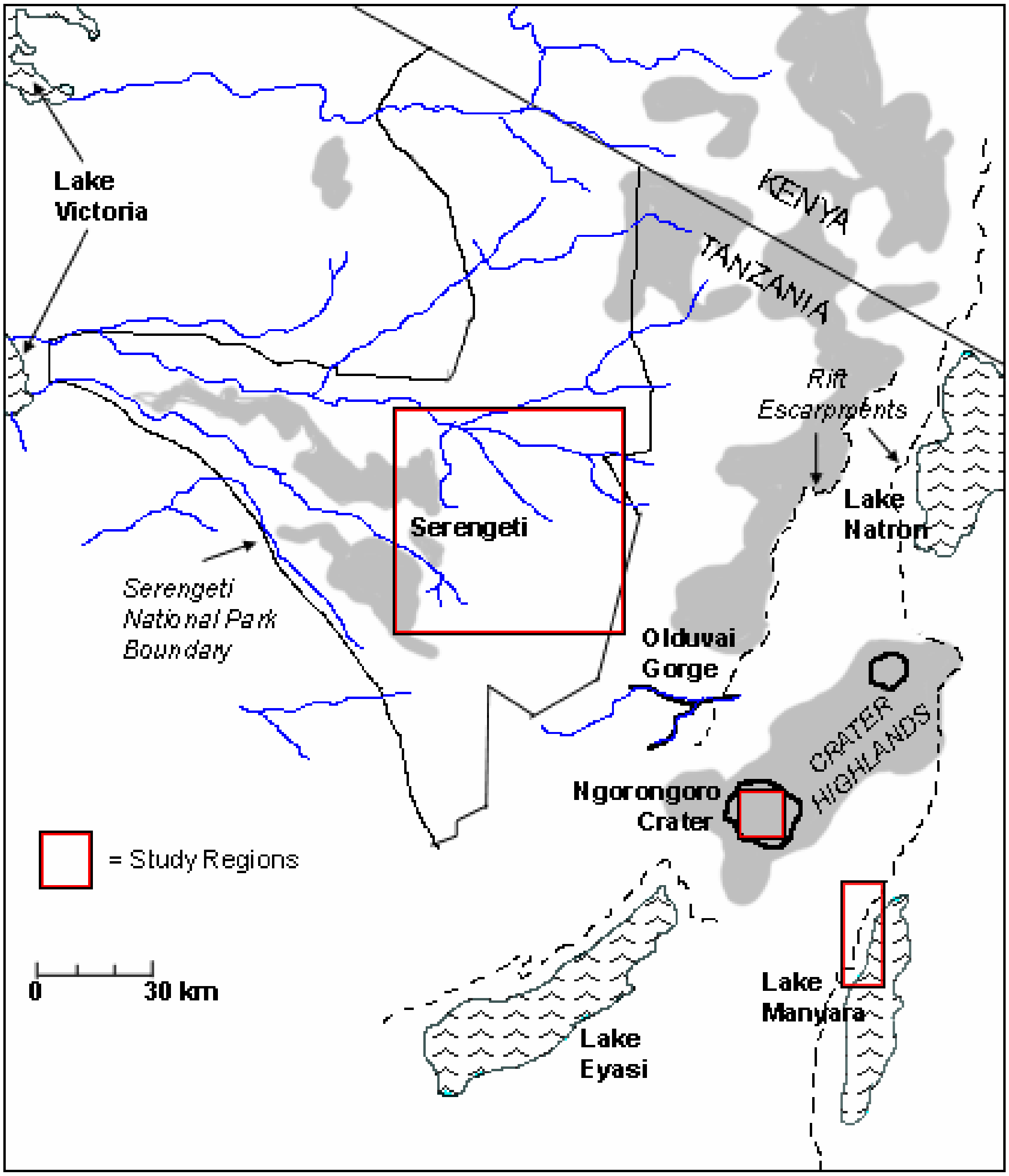
The national park and conservation area status of the modern study areas means that their flora and fauna may be less impacted by recent human activities such as farming, clear-cutting, and burning, when compared to areas of modern East Africa outside of parks. Since we are only beginning to understand the long-term, natural dynamics of ecosystems and the effects of recent human activities on those ecosystems (e.g., Sinclair, 1979a), I discuss the historical circumstances of each modern land region in addition to a description of is physical character.

Also in this chapter, I describe the sampling techniques that I used to record, measure, and analyze the modern vegetation. This includes definitions of measurements and analytical techniques used in later chapters such as calculated cover, importance values, and detrended correspondence analysis (DCA).

Descriptions of the Modern Study Areas

The modern study localities all fall within what can be described as the greater Serengeti ecosystem in northern Tanzania (Figure 3-1). They are near Olduvai Gorge, which records the paleo-lake basin that the modern study areas are meant to model. This area in northern Tanzania is dominated by features associated with the Great Rift Valley, including escarpments, the volcanoes of the Crater Highlands, and rift valley lakes such as Natron, Eyasi, and Manyara. The climate is semi-arid and soils are largely volcanic. The mountains of the Crater Highlands are forested, but the surrounding lowlands are typical semi-arid savannas, alternating between areas of grassland, woodland, and bushland. Paleoenvironmental and geological evidence suggest that the general situation was similar in the past, although the rift valley was in earlier stages of development (Hay,

Figure 3-1. Map of northern Tanzania showing the locations of the land regions that were sampled in this study: Serengeti, Ngorongoro Crater, and Lake Manyara. Shaded areas are higher in elevation. Based on Sinclair (1979a: Figure 1.1).



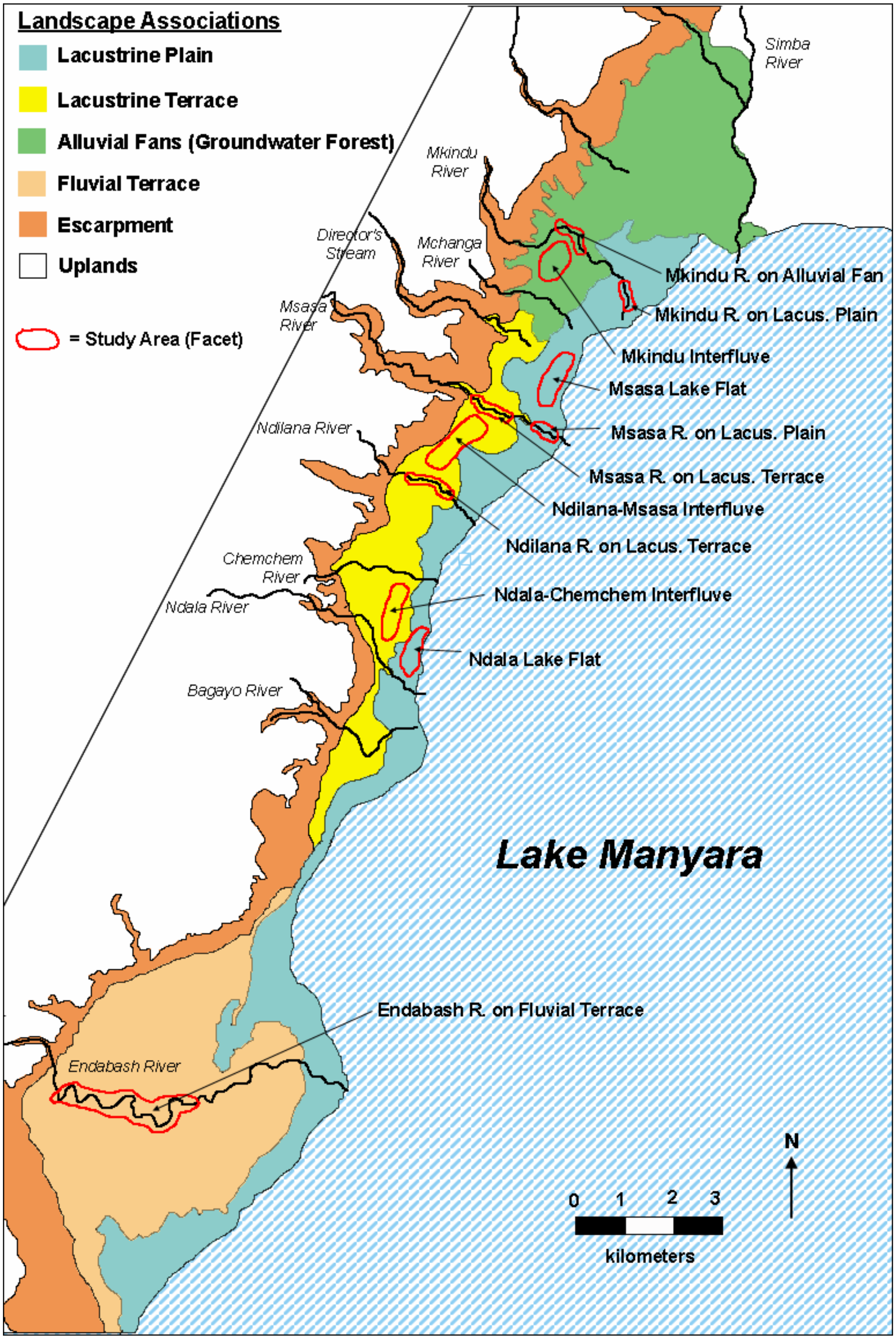
1976). The Crater Highlands began forming during the early and middle Pliocene (Hay, 1976).

Lake Manyara National Park

Lake Manyara is a rift valley lake on the southeastern side of the Crater Highlands (Figure 3-1). The lake is situated in a down-dropped portion of a half-graben, with the rift escarpment rising steeply near the western edge of the lake, and a very gently sloping surface east of the lake. Lake Manyara National Park includes the narrow strip of land between the northwestern edge of the lake and the escarpment, shown boxed in on the map in Figure 3-1. The average elevation of the lake level is about 960 meters, while the adjacent rift escarpment rises to approximately 1200-1300 meters (Loth and Prins, 1986). The perennial Simba River forms the northeastern border of the park. My modern analog study localities in Manyara are located within this strip of land, shown in detail in Figure 3-2. Rivers that drain the highland plateau run down the rift wall and empty into the lake. Other rivers emerge from springs at the base of the escarpment, particularly near the northernmost portions of the lake. The lake itself is shallow, alkaline, brackish, and fluctuates in size with the seasons.

The climate of Manyara follows the typical wet and dry seasons, and annual rainfall is about 650 mm per year based on an average over 25 years (Loth and Prins, 1986). The northwestern-most side of the lake is dominated by well-drained alluvial fans that support a lush, evergreen “groundwater forest” despite the relatively low rainfall in the land region (Greenway and Vesey-Fitzgerald, 1969). In the majority of the park, however, the vegetation is more typical of East African savannas: *Acacia* bushland and

Figure 3-2. Map of the Lake Manyara land region showing the landscape associations and facets that were sampled in this study. Based on the map by Loth and Prins (1986).



woodland with patches of open grassland, particularly near the lake edge. The Endabash river, which is the southernmost study area for this project, creates a large delta or “fluvial terrace” that extends into the lake (Loth and Prins, 1986). The fluvial terrace is occupied by a mixture of broad-leaved trees, *Acacia* trees, and many shrubs and grasses.

Fire has been absent from Lake Manyara national park since at least 1958 (Wardens’ Reports, cited in Prins and Van der Jeugd, 1993:306), and probably since 1934 (based on Prins and Van der Jeugd, 1993, who cite personal communication from A. Seif, a professional hunters’ guide in Manyara between 1934 and 1958). One factor that likely accounts for some of the vegetation differences between Manyara and the frequently burned Serengeti, such as differences in herbaceous species composition, is probably fire.

The vegetation history of Manyara is more obscure for times earlier than the past century. Ancient stromatolites about 20 m above the modern lake level of Lake Manyara show high lake stands at periods of tens of thousands of years apart: at around 10,000 – 12,000 B.P., at 25,000 B.P., and around 90,000 B.P (Casanova and Hillaire-Marcel, 1992). At those same times, what are now the Lake Natron basin of northern Tanzania and the Lake Magadi basin of southern Kenya merged to form a single lake with a stand 60 m higher than present (Casanova and Hillaire-Marcel, 1992). The vegetation of my study areas at Lake Manyara were submerged under the lake during those times, and the affect of these humid periods on species composition and physiognomy for non-submerged areas is unknown. Nonetheless, the situation of lake levels fluctuating between maximum lake levels and minimal lake levels over several thousand years mimics the conditions of paleo-lake Olduvai, which fluctuated during the period that lowermost Bed II sediments accumulated (Hay, 1976).

The year that I conducted my field work at Manyara, from 1997-1998, happened to be a strong El Niño year, which in East Africa manifested itself with abnormally heavy rains. By April of 1998 the lake level at Manyara had risen to well above its typical elevation for the late wet season, and some of the *Acacia xanthophloea*-lined streams were inundated and the trees died. Such lake level fluctuations are expected to occur every few decades, as exemplified by Polhill's (1989) account of the El Niño rains in East Africa in 1961. This is analogous to the high lake levels described by Hay (1976) for paleo-lake Olduvai, though the El Niño events are of a shorter duration than the geologically more conspicuous high lake levels that occurred during the Plio-Pleistocene. As a result of the El Niño conditions, I was never able to study Manyara's lower and middle lacustrine plain because they were flooded by the lake.

Serengeti National Park

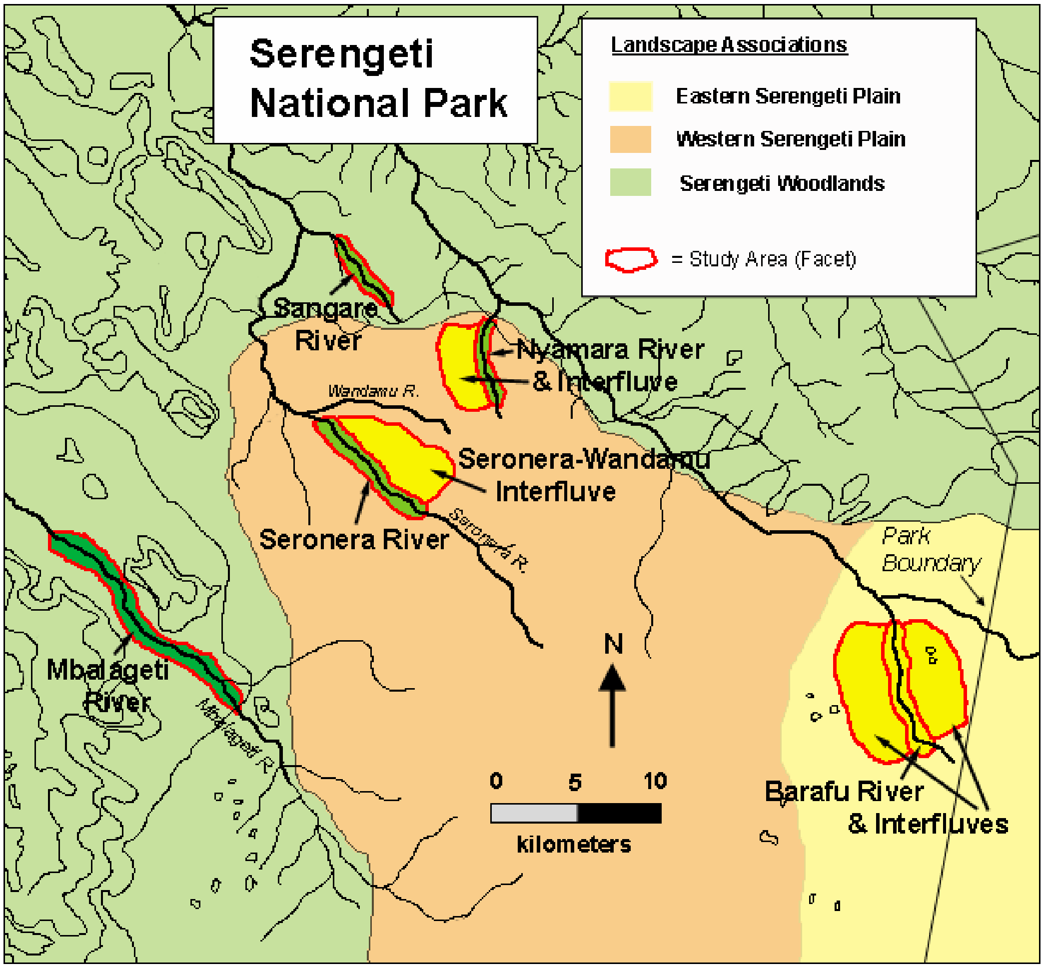
Serengeti National Park is immediately west of Olduvai Gorge and the Crater Highlands. The park is on the high interior plateau of East Africa at an altitude that ranges from 1850 meters in the eastern plains to a low of 920 meters where the Western Corridor ends at Lake Victoria (Sinclair, 1995). The southeastern portion of the park, the Serengeti Plain, are gently rolling hills comprised of very old (2.5 billion year old) rocks of the Tanganyika Shield overlain by layers of volcanic ash (Sinclair, 1995). The plains are dotted with kopjes, protrusions of granitic gneisses and quartzite that jut out from the volcanic soil forming rocky islands. The northern and western portions of Serengeti National Park are formed by Late Precambrian sedimentary rocks that unconformably overlie the Tanganyika shield (Hay, 1976). These areas are characterized by hills and valleys with soils that have higher proportions of basement rock-derived particles mixed in with volcanic ash.

Prevailing winds blow in a northwesterly direction, which largely accounts for the rainfall and soil patterns in the land region. The Crater Highlands directly to the southeast of the Serengeti (Figure 3-1) draw moisture out of the air which creates a rain shadow downwind of the highlands, in the vicinity of Olduvai Gorge and the Serengeti Plain. The strong rainfall gradient ranges from approximately 500 mm annual rainfall in the semi-arid southeastern plains near Olduvai Gorge to 1200 mm rainfall per year in the sub-humid north (Norton-Griffiths *et al*., 1975). Volcanoes in the Crater Highlands have been spewing volcanic dust into the atmosphere periodically for the past 4 million years (Hay, 1976), and the winds consistently transport this volcanic dust to the northwest, dumping most of the volcanic ash in the southeastern portion of the Serengeti, while the finest-grained particles sometimes gets carried further west. Since most of the rivers in the Serengeti drain west toward Lake Victoria, there is also fluvial transport of volcanic materials westward.

The vegetation of Serengeti is categorized most simply by gross physiognomic types, where the southeastern portion of the park is open grassland, and the central and northern hills and valleys are woodland, including areas of bushland, shrubland, and grassland (Figure 3-3) (physiognomic terms following Pratt and Gwynn, 1977).

The Serengeti Plain can be sub-divided based on the height and species composition of the grasses. The short grasslands, typically containing *Cynodon* and *Sporobolus* (Anderson and Talbot, 1965), are furthest to the east and are referred to as the Eastern Serengeti Plain in this study (Figure 3-3). The medium and long height

Figure 3-3. Map of the Serengeti land region showing the landscape associations and facets that were sampled in this study. Based on a map by the Frankfurt Zoological Society (1971).



grasslands with *Themeda* and *Pennisetum* (Anderson and Talbot, 1965) are further west and border the woodland, and are referred to as the Western Serengeti Plain in this study. Forbs and sedges such as *Indigofera* and *Kyllinga* comprise a large component of the grassland vegetation in the Plains. There are some portions of Serengeti's Western Corridor that are also grassland, but those are not dealt with in this thesis.

The wooded portion of the Serengeti is comprised of a patchwork of landscape facets, each of which has a unique dominant tree species composition (Herlocker, 1975).

Most of the Serengeti Woodland is semi-arid and support trees with microphyll leaves such as *Acacias* and *Albizias*. There are patches of *Terminalia-Combretum* woodland in northern Serengeti (Sinclair, 1979b), which are broad-leaved trees reminiscent of portions of the miombo woodlands that dominate southern Tanzania in the Zambezian phytochoria (White, 1983; Figures 2-2 and 2-3). These landscape facets of broad-leaved woodlands in the Serengeti may be relics from the past when they were more widespread, or their existence may be due to unique soil and climate conditions. The largest, perennial rivers in the Serengeti, such as the Grumeti of the Western Corridor, support tall, lush, evergreen forest along their banks. On the isolated, rocky kopjes, one can also find a unique suite of plant species including succulents and trees such as *Euphorbia candelabria*.

Portions of the Serengeti were established as a game reserve in 1929, as a Protected Area in 1940, and as a National Park in 1951 (Sinclair, 1995). Pastoralist tribes such the Masai historically occupied the area. They practiced little agriculture but tended cows and goats. Pastoralists often burn large swaths of land, as they still do in places surrounding the park today. Places inside Serengeti National park are also still burned today in the form of controlled fires set by park authorities. Pellew (1983) estimated that 10% of the grassland areas of the park are burned each year. Natural fires are a feature of the Serengeti land region as well, given that lightning strikes are frequent during the wet seasons.

It is not known how long humans have set fires in the Serengeti, but it may have been practiced since before the invention of agriculture or the domestication of animals. The most important, but unanswered question is whether the Serengeti of the Plio-

Pleistocene burned less frequently due to a lack of human-created fires, and what affect that had on the structure and composition of the vegetation.

Studies of the Serengeti ecosystem's history over the past century suggest that it has experienced changes in physiognomic structure during this short time (e.g., Sinclair, 1979a). In the late 1800's, the Serengeti was described by explorers, traders, and hunters as an open grassland with lightly wooded patches, but by the time of colonial administrators in the 1930's and early 1940's, the area had become densely wooded. In the 1950's, the woodlands and thickets began a rapid decline and reverted to grasslands.

The alternation of Serengeti vegetation between open grassland and dense woodland shows that the ecosystem is dynamic and may be subject to long-term vegetation cycles or transitions between stable states following ecological perturbations (Dublin, 1995:71). The term climax community does not pertain to the savanna woodland ecosystems because of fire, herbivore dynamics, and other dynamic factors (Dublin, 1995:71). This idea is discussed in more detail in Chapter Four.

The reason for the existence of grasslands in the southeastern Serengeti, and explanations for tree/grass ratios in general in savanna habitats, continues to be a controversial topic. Understanding is important for reconstructing paleoenvironments, especially since tree to grass ratios, or general woody cover, is the character of ancient vegetation most feasibly reconstructed by fossil and geological indicators. Low rainfall is probably not the primary factor maintaining the Serengeti Plain because areas in East Africa with about 400-700 mm of annual rainfall, the same as the Serengeti Plain, support shrubland, bushland, or woodland. Herbivory has been implicated as the most important factor (Bell, 1982; McNaughton, 1983), but trees did not grow in plots protected from grazing animals and fire (Belsky, 1986a; 1986b; 1990).

Perhaps the most important factor in the Serengeti Plain is that the soil has developed a calcareous hard pan about one meter below the surface due to the influx of sodic, carbonitic volcanic ash (Sinclair, 1979b; Belsky, 1990). This hard pan prevents tree roots from penetrating into moisture-rich deeper soils, and therefore trees will not grow on the plains. The trees that do exist in the Serengeti Plain grow along natural disruptions of the calcrete where they also have access to water sources, such as along Olduvai Gorge. In areas of high soil salinity, many trees cannot grow because the water in their root cells moves out by osmosis and the plant eventually becomes dessicated (Ricklefs, 1990). In sum, it is not herbivores nor rainfall that deter tree growth in the Serengeti Plain, but rather high salinity and shallow soils (Belsky, 1990:485). The Serengeti Plain can therefore be described as an edaphic grassland.

Ngorongoro Crater

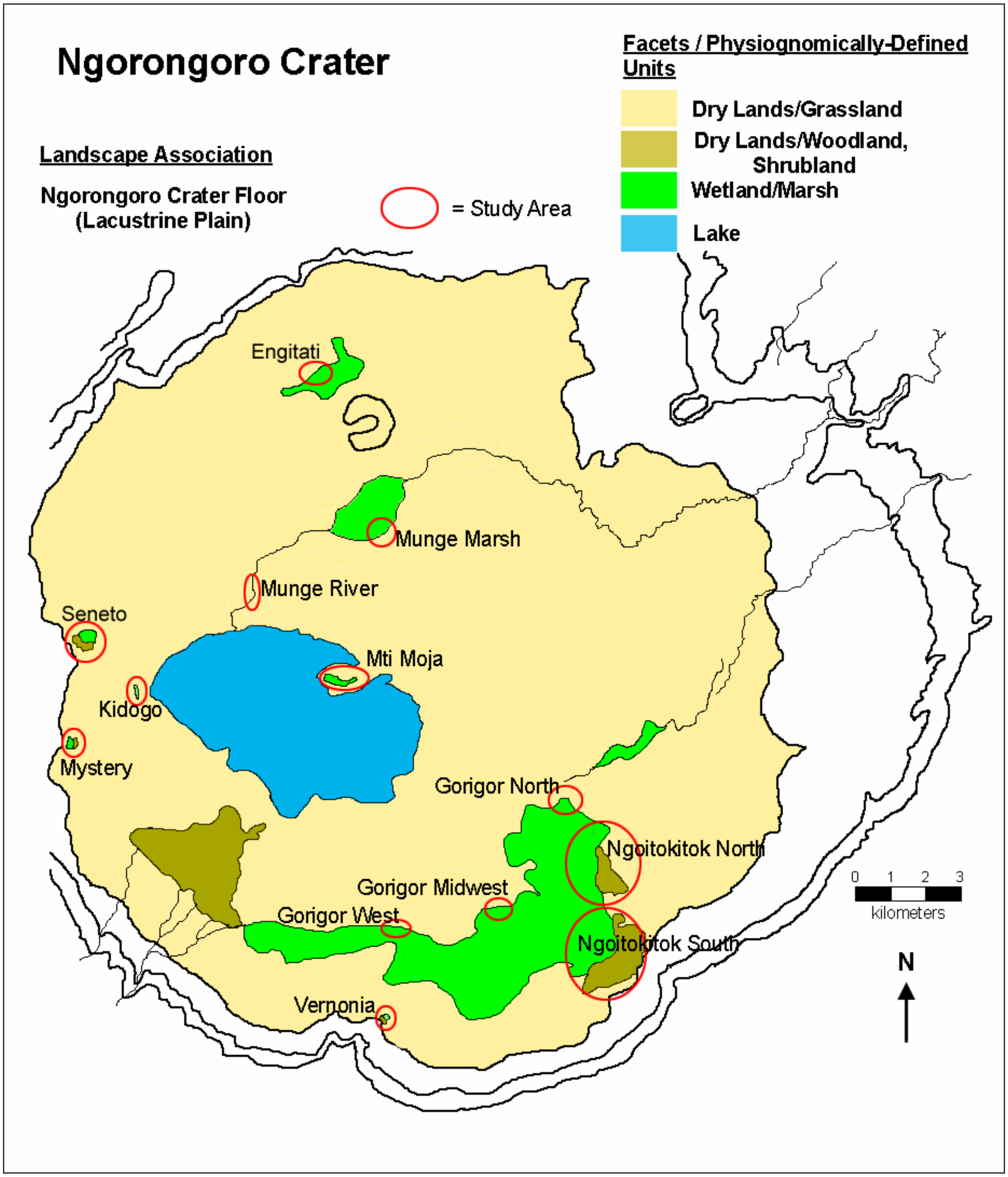
Ngorongoro Crater is a caldera within the Crater Highlands, immediately southeast of Serengeti and Olduvai, and northwest of Lake Manyara. The Crater is an oval bowl 21 by 18 km across (Estes and Small, 1981), and covers about 310 square kilometers in area, 250 of which compose the Crater floor and another 60 square kilometers are the slopes (with slopes of greater than 13 degrees) (Herlocker and Dirschl, 1972). The Crater Floor is at an elevation of about 1737 meters, while the Crater rim is around 2100-2400 meters (Hay, 1976).

The Ngorongoro volcano grew to its present size between a period of about 2.45 to 2.0 mya (Hay, 1976). The caldera formed almost 2 mya in association with rift faulting (Hay, 1976). Colluvial deposits of basalts, tuffs, and scoria cover most of the southern, eastern, and northern parts of the caldera, and lacustrine deposits dominate around the area of Lake Makat. The caldera forms a closed basin which is fed by springs and both perennial and ephemeral streams.

The Crater floor receives an annual rainfall of 762-797 mm according to Anderson and Herlocker (1973; NCAA data from rainfall gauges, 1987-1994) although the figure varies greatly from year to year. According to Estes and Small (1981:177), the Crater floor "probably receives no more than 510-560 mm precipitation annually and as little as 300-380 mm in the driest western sector, compared to 875 mm on the southern rim (19-year average at Crater Lodge)."

The vegetation of the Crater floor is dominated by open grassland, interrupted most conspicuously by the Lerai woodland in the southwest, the Ngoitokitok/Gorigor marsh in the southeast with the Ngoitokitok pool and woodland fringing its eastern edge, the Munge River lined by a sparse woodland, and the seasonally fluctuating, shallow lake near the center of the Crater (Figure 3-4). The wetlands within the Crater range from the vast Gorigor Marsh that is about 50 to 100 square kilometers in area, to small, spring-fed seeps on the order of 300 square meters in area. The Lerai Woodland (often referred to as "Lerai Forest") is fed by a spring that is estimated to produce on million gallons per day in the dry season from Mt. Oldeani (Estes and Small, 1981). The largest spring in the Crater is Ngoitokitok, but the source of its water remains unknown (Estes and Small, 1981).

Figure 3-4. Map of the Ngorongoro Crater land region showing the single landscape association and multiple facets that were sampled in this study.



The Crater sustains its own year-round population of mammals such as zebra and wildebeest, which elsewhere migrate for long distances throughout the year. Elephants, hippos, buffalo, the highest density of lions in Africa, and numerous other savanna animals inhabit the Crater. Although it is tempting to consider it as such, the Crater is not an isolated ecological "island," but rather many of its wildlife depend on land use, resources, and water outside of the Crater (Estes and Small, 1981).

Ngorongoro Crater has had a protected status since 1921. Since 1975 the Ngorongoro Conservation Area Authority has administered it as part of a larger, 8292 square kilometer multiple land use area that allows for protection from hunting for the wildlife, but also allows for use of lands by the Masai for grazing their goats and cattle (Runyoro *et al.*, 1995:147). According to Anderson and Herlocker (1973), although climate, grazing, burning, and soils all influence the vegetation of the Crater, soil factors are "of the greastest importance in determining the distribution and nature of the vegetation types and their utilization by wild animals" (p.627). While the edaphic grasslands of Ngorongoro Crater are associated with poorly drained soils and anaerobic conditions, the edaphic grasslands in the Serengeti Plain are due to the shallow, alkaline soils derived from sodic, carbonitic ash, underlain by shallow calcrete layers (Belsky, 1990).

There were periods during the late Pleistocene when the majority of the Crater Floor was submerged by a lake, as evidenced by high lake-level marks in the eastern portion of the Crater (Hay, 1976). Ngorongoro's high lake levels may well have corresponded to the high lake levels at Manyara, assuming that northern Tanzania experienced similar, broad-scale changes to a wetter climate during those periods. As was the case at Manyara, the expanding and contracting lake at Ngorongoro therefore may duplicate the scenario at Olduvai of episodically high and low lake levels over thousands of years.

Landscape Classification of the Modern Study Areas

I used the same landscape classification approach for the modern study areas as that outlined by Peters and Blumenschine (1995) for the paleo-Olduvai basin. The main landscape units of interest are land regions, landscape associations, and landscape facets. In this study there are three land regions: Serengeti, Manyara, and Ngorongoro Crater (Figure 3-1). Each land region is sub-divided by landscape associations, defined in Chapter One as areas with common geomorphology and sediment composition, but which encompass a variety of hydrological, soil, microclimate, and ecological differences. Landscape facets are the smaller units within landscape associations, equivalent to what is often referred to as a "habitat." Landscape facets are localities in which the hydrology, soil, microclimate, and ecology are relatively uniform or predictable. Landscape elements exist within landscape facets, such as a shade tree or termite mound, but I did not sample landscape elements separately in these modern analog studies.

The three regions in which I worked were chosen because of their similarity in physical and climatological aspects with the paleo-Olduvai basin, their relatively protected status as national parks or conservation areas, and their relative proximity to one another, which was a logistical concern of conducting the field work. These areas were also amenable to my field study because I had been able to participate in several reconnaissance trips to those areas in the company of other, experienced researchers prior to the field work conducted for this thesis.

Within the Manyara Land Region, I chose to sample all of the previously designated landscape associations in the northern portion of the park (following Loth and Prins, 1986) except for the rift escarpment, for which there clearly is no analog in the paleo-Olduvai basin. The four landscape associations I did sample were the upper Lacustrine Plain (the lower portions were flooded), lacustrine terrace, fluvial terrace, and alluvial fan (Figure 3-2). Within each of those landscape associations, I chose several rivers and interfluves to sample that seemed to be representative of the diversity of vegetation types present. Paired riverine and non-riverine sites were between 0.5 and 2.0 km apart. Description and sizes of the landscape facets are given in Table 3-1.

In the Serengeti Land Region I sampled each of the three landscape associations that were present, the Eastern Serengeti Plain, Western Serengeti Plain, and the Serengeti Woodland (Table 3-1; Figure 3-3). Because the Serengeti is not centered around a lake like the paleo-Olduvai basin, I focused on its rivers and interfluves as potential analogs for the various rivers and interfluves at Olduvai away from the lake. The particular rivers that I sampled within each landscape association were chosen randomly except for the Seronera River, for which I was interested in potentially comparing my results to those of previous vegetation studies (Lamprey *et al*., 1967) and larger mammal scavenging opportunity studies (Blumenschine, 1986). The size and description of the rivers and non-riverine sites are given in Table 3-1. Non-riverine sites were located between 0.5 and 2.0 kilometers from the riverine sites.

All samples from the Ngorongoro Land Region were from a single landscape association: the Crater Floor, which is a lacustrine plain (Table 3-1; Figure 3-4). In general, the wetlands and freshwater springs of Ngorongoro Crater are considered to be

Table 3-1. Sample characteristics and area sampled of the modern analog study areas.

Region	Landscape Association	Facet	Study Area	Description	# of plots	Total area sampled, m^2	Estimated size of facet	Date samp-led	Propor-tion of facet sampled.
Manyara	Alluvial Fan	Non-Riverine	Mkindu interfluve (M-MKII)	Interfluve of the lower alluvial fan, in groundwater forest.	10	17,500	1km x 1km	Sept. 1997, Feb. 1998	2%
		Riverine	Mkindu River on Alluvial Fan (M-MKIR)	Perennial, spring-fed stream, 3-5m wide, in an inter fan depression of the lower alluvial fan, in groundwater forest.	2	2,500	50m x 1.5km	Sept. 1997, Feb. 1998	3%
	Fluvial Terrace	Riverine	Endabash River on Fluvial Terrace (M-END)	Fluvial terraces of 100m wide ephemeral stream..	4	3750	300m x 5km	Sept. 1997	0.3%
	Lacustrine Plain	Non-Riverine	Msasa Lake Flat (M-MLF)	Low and middle lacustrine flats, north of the Msasa River outlet into the lake.	10	25,000	200m x 1.5km	Mar. 1998	8%
		Non-Riverine	Ndala Lake Flat (M-NLF)	Middle lacustrine flats north of the Ndala River outlet into the lake.	10	25,000	200m x 2km	Mar. 1998	6%
		Riverine	Mkindu River on Lacustrine Plain (M-MKILF)	Perennial, spring-fed stream, 1-3m wide, crossing upper lacustrine plain.	3	1500	200m x 2km	Mar. 1998	0.4%
		Riverine	Msasa River on Lacustrine Plain (M-MSALF)	Ephemeral river, 25m wide, fluvial terraces and deltas crossing minor deltas of the lacustrine plain.	2	5000	200m x 800m	Mar. 1998	3%

Region	Landscape Association	Facet	Study Area	Description	# of plots	Total area sampled, m^2	Estimated size of facet	Date sampled	Proportion of facet sampled.
Manyara (cont.)	Lacustrine Terrace	Non-Riverine	Ndala-Chemchem Interfluve (M-NCI)	Low lacustrine terrace between the Ndala and Chemchem Rivers.	10	25,000	800m x 2km	Mar. 1998	2%
		Non-Riverine	Ndilana-Msasa interfluve (M-NMS)	Low lacustrine terrace between the Ndilana and Msasa rivers.	19	47,500	1km x 3km	Sept. 1997, Feb. 1998	2%
		Riverine	Msasa River on Lacustrine Terrace (M-MSA)	Ephemeral river, 20m wide, fluvial terraces and deltas crossing low lacustrine terraces.	10	20,000	150m x 2km	Sept. 1997, Feb. 1998	7%
		Riverine	Ndilana River on Lacustrine Terrace (M-NDI)	Ephemeral river, 17m wide, fluvial terraces and deltas crossing low lacustrine terraces.	20	25,000	150m x 3km	Sept. 1997, Jan. 1998	6%
Serengeti	E. Serengeti Plain	Non-Riverine	Barafu Plain (S-BPL)	Gently rolling plains underlain by hardpan, fluvially-reworked volcanic ash soil over basement rocks.	20	50,000	1km x 3km on each side of the valley	Apr. 1998	1%
		Riverine	Barafu River (S-BAR)	Shallow valley in gently rolling plains, some basement rock outcrop.	20	50,000	200m x 3km	Mar., Apr. 1998	8%
	Serengeti Woodland	Riverine	Mbalageti River (S-MBA)	Meandering channel in valley between 2 ridges of basement rock outcrop.	20	50,000	100m x 10km	Oct. 1997	5%
		Riverine	Sangare River (S-SAN)	Meandering channel in area of small hills of basement rock, near edge of plains.	6	15,000	100m x 5km	Apr. 1998	3%
	W. Serengeti Plain	Non-Riverine	Seronera-Wandamu interfluve (S-SWI)	Gently sloping plain, fluvially-reworked volcanic ash soil over basement rocks.	10	25,000	1km x 5km	May 1998	1%

Region	**Landscape Association**	**Facet**	**Study Area**	**Description**	**# of plots**	**Total area sampled, m^2**	**Estimated size of facet**	**Date samp-led**	**Propor-tion of facet sampled.**
Serengeti (cont.)	W. Serengeti Plain (cont.)	Non-Riverine	Nyamara interfluve (S-NIN)	Gently rolling plains, fluvially-reworked volcanic ash soil over basement rocks.	10	25,000	2km x 5km	Nov. 1997	0.3%
		Riverine	Seronera River (S-SER)	Channel and floodplains crossing gently rolling plains of fluvially-reworked volcanic ash soil over basement rocks.	10	25,000	150m x 5km	Oct. 1997, May 1998	3%
		Riverine	Nyamara River (S-NYA)	Channel and floodplains crossing gently rolling plains of fluvially-reworked volcanic ash soil over basement rocks.	10	25,000	150m x 5km	Nov. 1997	3%
Ngoro-ngoro	Crater Floor	Large spring dry land (grassland)	Ngoitokitok North (N-NGG)	A large spring source site that feeds the Gorigor marsh. There is a pool of open water, marsh, and adjacent dry land including grassland and woodland.	2	10x10m	500x800m grassland surrounding marsh	July, Aug. 1995	0.03%
		Large spring dry land (woodland)	Ngoitokitok North (N-NGW)		1	50x50m	200x800m woodland	July, Aug. 1995	2%
		Large spring wetland	Ngoitokitok North (N-NGP)		1	10x50m	10x200m marsh along edge of pool	July, Aug. 1995	25%
		Large spring dry land	Ngoitokitok South (N-NGS)	A series of spring sources near the Crater wall that feed the Gorigor system, with woodland between marsh and Crater wall, and seasonally dry marsh *C. immensus*-dominated.	3	25x25m	300x1500m woodland	July, Aug. 1995	0.1%
		Large spring wetland	Ngoitokitok South (N-NSM)		1	10x10m	50x50m of *Cyperus immensus* dominated marsh	July, Aug. 1995	4%
		Small spring wetland	Engitati (N-ENG)	Small, isolated marsh area north of Engitati hill.	3	10x10m	1km x 2km	July, Aug. 1995	0.01%

Region	Landscape Association	Facet	Study Area	Description	# of plots	Total area sampled, m^2	Estimated size of facet	Date samp-led	Propor-tion of facet sampled.
Ngoro-ngoro (cont.)	Crater Floor (cont.)	Small spring dry land	Kidogo Spring (N-KSG)	A series of spring seepages adjacent to western edge of lake, each with marsh vegetation (*C. laevigatus*), surrounded by short grassland.	1	10x2m	10x100m, whole area of spring seepages	July, Aug. 1995	2%
		Small spring wetland	Kidogo Spring (N-KSM)		1	10x5m			5%
		Small spring dry land	Mti Moja (N-MTG)	A small sping that emerges from a slightly elevated peninsula on the Crater's lake margin; marsh wetland surrounded by open grassland and mud flats.	2	5x50m transects	1 square kilometer (peninsula)	July, Aug. 1995	0.03%
		Small spring wetland	Mti Moja (N-MTM)		4	10x40m	600x100m wetland		1%
		Small spring dry land	Mystery Spring (N-MSS)	A small spring adjacent to Crater wall on west side of crater, with marsh wetland surrounded by 3 patches of shrubs and a few *A. xanthophloea* trees.	2	10x20m	35x10m shrub zone 1, 10x5m shrub zone 2	July, Aug. 1995	50%
		Small spring wetland	Mystery Spring (N-MSM)		1	10x20m	30x15m marsh		44%
		Small spring dry land (grassland)	Seneto (N-SEG)	A medium sized spring, immediately adjacent to the western Crater wall, supports an area of marsh, small woodland, and is surrounded by the open grassland of the Crater floor.	1	10x10m	25x200m grassland adjacent to marsh	July, Aug. 1995	2%
		Small spring dry land (woodland)	Seneto (N-SEW)		1	10x25m	50x20m		25%
		Small spring wetland	Seneto (N-SEM)		1	10x25m	100x150m marsh		2%
		Small spring dry land	Vernonia (N-VSW)	A small spring immediately adjacent to southern Crater	1	5x15m	5x15m woodland	July, Aug.	100%

Region	**Landscape Association**	**Facet**	**Study Area**	**Description**	**# of plots**	**Total area sampled, m^2**	**Estimated size of facet**	**Date samp-led**	**Propor-tion of facet sampled.**
Ngoro-ngoro (cont.)	Crater Floor (cont.)	Small spring wetland	Vernonia (N-VSM)	wall, small marsh and overhanging the 3m spring head wall is a zone of trees and shrubs on the Crater wall.	1	10x20m	25x50m marsh	1995	16%
		Stream-fed dry land	Gorigor Midwest (N-GMG)	N. side of Gorigor, border of wetland/dry land	2	10x10m	100x100m (10km x 7km whole Gorigor Swamp)	July, Aug. 1995	1%
		Stream-fed wetland	Gorigor Midwest (N-GMM)		1	10x10m	100x100m		1%
		Stream-fed dry land	Gorigor North (N-GNG)	N. side of Gorigor, includes a patch of open water, marsh veg, and short grassland near the road.	1	30x10m	100x100m	July, Aug. 1995	3%
		Stream-fed wetland	Gorigor North (N-GNM)		1	30x30m	100x100m		9%
		Stream-fed wetland	Gorigor West (N-GWE)	N. side of Gorigor, there is a stream here.	1	50x10m transect	100x100m	July, Aug. 1995	5%
		Stream-fed dry land	Munge Marsh (N-HPG)	Marsh near distal end of the Munge R., a hippo pool, has open water and *Cyperus immensus*-dominated marsh.	1	1x5m	100x300m, whole marsh area	July, Aug. 1995	<1%
		Stream-fed wetland	Munge Marsh (N-HPM)		1	20x20m			1%
		Stream-fed dry land	Munge River (N-MRG)	A stream that originates from eastern Crater rim, meanders with occasional trees, then trickles between Munge marsh and lake with sparse marsh vegetation.	2	2x5m	River is about 1km x 1m between Munge marsh and lake.	July, Aug. 1995	1%
		Stream-fed wetland	Munge River (N-MRM)		3	2x10m	1 km x 1m		1%

analogs for potentially similar wetlands and/or springs near the paleo-Olduvai lake shore. A sample of the broad range of wetlands around the Crater Floor should indicate the potential variability in wetlands at paleo-Olduvai. In 1995, I conducted a study in Ngorongoro Crater with Daniel Deocampo (then a geology graduate student) in which we located many of the freshwater springs in the Crater, and they became sampling localities for vegetation data. I also sampled various points along the edges of the larger wetland systems, including both wooded and non-wooded habitats.

The next sections provide general descriptions of the specific landscape facets sampled in the modern study areas.

Lake Manyara National Park

Manyara's lacustrine plain landscape association is the area around Lake Manyara immediately adjacent to the lake (Figure 3-2). The lower lacustrine plain is flooded with saline/alkaline lake water during wet seasons, while the upper lacustrine plain is flooded only during extremely wet rainy seasons. During "El Nino" years such as 1961 (Polhill, 1989) and 1997-98, when I conducted my study there, the lowermost portions of the upper lacustrine plain were inundated with water during the wet season.

The lacustrine plain consists of grassland, mudflats, non-riverine areas with sparse shrubs and palm trees on the uppermost portions, tree-lined rivers, and some areas of marsh at the lake shore. Due to El Niño conditions, my study areas were all in the uppermost lacustrine plain, along two riverine landscape facets and at two non-riverine landscape facets. The riverine landscape facets were the small, spring-fed, perennial stream Mkindu in the north, and the wider but ephemeral Msasa River slightly further south. I sampled non-riverine landscape facets of the lacustrine plain at the Msasa lake flat just north of the Msasa River, and at the Ndala lake flat, just north of the Ndala river (Figure 3-2).

Manyara's lacustrine terrace landscape association is the gently sloping ground at a slightly higher elevation (five to ten meters) than the lacustrine plain. It was formed during late-Pleistocene high lake levels and is now exposed maximally as a 2-3 km wide strip between the rift escarpment and the lacustrine plain, north of the Endabash river and south of the groundwater forest (Loth and Prins, 1986). The vegetation of the lacustrine terrace is mainly bushland, with scattered large trees, many shrubs, and an annual flush of grasses and forbs at ground level following the rains. I sampled two riverine landscape facets on the lacustrine terrace, along the Msasa River and along the Ndilana River. I sampled two non-riverine, interfluvial landscape facets of the lacustrine terrace, the interfluve between the Msasa and Ndilana Rivers, and the interfluve between the Ndala and Chemchem Rivers.

The alluvial fans of Manyara are at the northern end of the park, where they formed as a result of sediment washing down from the rift escarpment and areas of higher elevation to the north. The vegetation on the alluvial fans is strikingly different from the rest of the park, as a groundwater forest covers it with trees up to 35 meters tall that form a mostly continuous canopy. I sampled the alluvial fans at one riverine landscape facet, the Mkindu River, which is the small, perennial, spring-fed stream that runs through an inter-fan depression and eventually drains out to the lacustrine plain. I sampled one non-riverine landscape facet of the alluvial fan near the Mkindu River, in the lowermost portions of the fans, close to where they level out onto the lacustrine plain.

Manyara's Endabash River has created a landscape association, a fluvial terrace, from the deltaic-like deposition of large volumes of sediment that the river carries down from the uplands. I sampled a riverine fluvial terrace landscape facet along the Endabash River. The ephemeral Endabash River has a width of 100 meters in some places, and so is about 10 times wider than the ephemeral Msasa and Ndilana rivers that cross the lacustrine terrace. The sediment within the fluvial terrace is also coarser and contains more basement rock- derived elements as opposed to reworked volcanic ash than the Manyara sites further north (Prins and Van der Jeugd, 1992). The vegetation along the fluvial terrace is a bushland, with scattered trees and shrubs with varying degrees of cover, but the trees are much taller than those of the lacustrine terrace.

Serengeti National Park

The Eastern Serengeti Plain landscape association is a rolling plain of Paleozoic basement rock overlain by a thick layer of airfall-derived volcanic soil, created from millions of years of volcanic activity in the Crater Highlands (Anderson and Talbot, 1965). The plain's grasslands are grazed annually by more than two million migrating wildebeests and zebra, as well as other resident herbivores. Few trees and shrubs grow there except along rivers or other geological features that break up the thick, impenetrable layer of calcrete that lies about a meter below the surface. I sampled the Eastern Serengeti Plain's vegetation at one riverine landscape facet and one interfluvial, non-riverine landscape facet, both in the vicinity of the Barafu Valley. The Barafu River is ephemeral, and usually dry, but after rains creates a small flow. It may also be fed by a slow-seeping spring that creates a permanent marsh at the head of the river. My non-riverine samples were taken about one kilometer from the lowest point in the Barafu Valley in order to assure that they sampled the high, open plains of short grasslands and not the edge of the valley itself.

The Western Serengeti Plain landscape association refers to the western side of the Serengeti Plain (and not the grassy plains of Serengeti's Western Corridor) (Figure 3-3). Here the soil is deeper than in the Eastern Serengeti Plain, and the calcrete hardpan below the surface is a bit broken up and therefore more penetrable by tree and shrub roots (Anderson and Talbot, 1965). The soil in the Western Serengeti Plain has more basement rock-derived elements than further east, though it is still mainly volcanic. The vegetation is characterized by intermediate and long grasslands (Anderson and Talbot, 1965), crossed by small rivers fringed with narrow strips of sparse trees and shrubs. I sampled the Western Serengeti Plain at two riverine landscape facets, along a portion of the ephemeral Seronera River and along a portion of the ephemeral Nyamara River. I sampled two interfluvial, non-riverine landscape facets, one area of open grassland between the Seronera and Wandamu Rivers, and one grassy area with sparse shrubs and trees just west of the Nyamara River (Figure 3-3).

The Serengeti Woodland landscape association as defined for this thesis refers to the northern and western areas of Serengeti National Park. These areas have much greater topographic relief than the Plains, with soils deriving from the parent rock of granite and quartzite. They lack a calcrete hardpan, and have low salinity and alkalinity soils. Those factors combined with more consistent and higher amounts of annual rainfall than the Eastern Serengeti Plain means that the Serengeti Woodland is predominantly woodland and bushland. Throughout the Serengeti Woodland landscape association, different tree and shrub species dominate in different areas, forming a patchwork of landscape facets (Herlocker, 1975).

I randomly chose to sample two of the riverine landscape facets in the Serengeti Woodland. The Mbalageti River in the south is ephemeral, but with a large catchment area and an apparently good supply of year-round underground water to support its riverine woodland of *Acacia xanthophloea* trees. The Sangare River is to the north of the Seronera area, and is also an ephemeral stream, slightly smaller in width than the Mbalageti. Since the Serengeti Woodland landscape association is so large and diverse in terms of tree species (Herlocker, 1975), these two landscape facets cannot be assumed to be representative of that entire landscape association. Nonetheless, I felt that it was important to include them in order to expand the range of modern analogs beyond those preliminarily surveyed by Peters and Blumenschine (1995; 1996), who focused mainly on the Western Serengeti Plain as analogs for the paleo-Olduvai basin.

Ngorongoro Crater

I considered the Ngorongoro Crater Floor to be a single landscape association, a lacustrine plain, within which I sampled several types of landscape facets. Unlike at Serengeti and Manyara where landscape facets are either riverine or non-riverine, in Ngorongoro there are three hydrologically-defined landscape units, each of which has a wetland landscape facet and a dry-land landscape facet thereby totaling six different types of landscape facets that I sampled on the Crater Floor. Small streams and stream-fed wetlands are areas with low-velocity fresh water input and contain two defined landscape facets: the wetland area itself and the dry land adjacent to, and within about 25 meters of the wetland. Small springs within the Crater are those that result in an area of permanent wetland that is less than one square kilometer. Small springs are divided into the permanent wetland landscape facet and the adjacent (within 25 meters) dry land landscape facet. Large springs on the Crater Floor produce a permanent wetland area that is greater than one square kilometer in area. They are also constituted by two landscape facets, the wetland itself, and the dry land adjacent to and within 100 meters from the wetland.

Some of the dry land landscape facets are composed of two distinct physiognomic portions, woodland or shrubland, and grassland. For the purpose of certain analyses in this thesis I sub-divide the dry land landscape facets associated with small springs and large springs according to these physiognomically-defined categories. The full list of Ngorongoro sites and their landscape classifications, as well as all study areas from Manyara and Serengeti, are shown in Table 3-1.

Sampling Strategies for the Modern Vegetation Study

The goal in sampling the modern vegetation was to obtain quantitative and qualitative descriptions of the vegetation structure, species composition, and plant resources for hominins. As described above, the landscape facets that I chose to sample fell within the physical, hydrological, and environmental parameters thought to have existed in various parts of the lowermost Bed II Olduvai basin.

Defining Landscape facets or Study Areas

Each landscape facet that I sampled is referred to as a study area, and was given a representative abbreviation such as M-MSA. The first portion of the abbreviation stands for the land region, either Manyara (M-), Serengeti (S-), or Ngorongoro (N-). The second portion designates the study area, and derives from a place name or other terms. For example, -MSA stands for the Msasa River and -NLF stands for Ndala lake flat. In Table 3-1 I show a name (e.g., Msasa Lake Flat) and an abbreviation for each study area. The study areas on the maps of each land region and are outlined in red in Figures 3-2, 3-3, and 3-4.

The spatial extent of each individual modern landscape facet, or study area, was defined based on published landscape classification systems and maps, and/or reconnaissance trips to the area. The published reference material for Manyara was Loth and Prins' (1986) *Landscape Ecological Vegetation Map of Lake Manyara National Park*. The smallest units depicted on their map can also be considered the equivalent of landscape facets as they are defined in a similar manner: "…the units are delineated and described on the basis of landscape-forming factors such as climate, geology, geomorphology and soil characteristics – in addition to vegetation." (Loth and Prins, 1986:115).

A Serengeti landscape classification system that refers to landscape facets was set up by Gerresheim (1974). This is complemented by the classification of Serengeti's woody vegetation and accompanying map by Herlocker (1975), for which the mapping units are homogeneous in terms of dominant trees, and are "essentially the land facet of

Gerresheim (1971)" (Herlocker, 1975:15). My own reconnaissance field trips were also important in locating and defining landscape facets in the Serengeti based upon geological factors such as changes in slope, and obvious vegetative changes that coincided with landscape facet boundaries.

The published vegetation descriptions of the Ngorongoro Conservation Area by Herlocker and Dirchl (1972) were based on physiognomic categories, and were an important guide for my reconnaissance trips around Ngorongoro Crater. Initial field trips were aimed particularly at finding and sampling fresh water spring landscape facets. This led to the "wetland" versus "dry land" landscape facet comparisons at Ngorongoro for large springs, small springs, and stream-fed wetlands. These wet and dry landscape facets are easily distinguished in the field.

Sampling the Landscape facets in Serengeti and Manyara

Once the spatial extent of each landscape facet was defined in the field, I set up a sampling strategy of multiple square or rectangular plots which were distributed semi-randomly throughout the sample landscape facets within Serengeti and Manyara. The distribution of the plots was determined based upon the size and shape of the landscape facet. For example, to sample the vegetation along rivers in the Serengeti I used a stratified random distribution technique (Greig-Smith, 1983:22) by placing one plot at a random point within each 500 meter stretch of the river. In some of the smaller rivers and landscape facets at Manyara, the plots were closer together, located randomly within 200 meter stretches of the river. Riverine plots had one side immediately adjacent to the channel bed itself. In larger, interfluvial landscape facets I modified the sampling strategy to incorporate a broader area by placing plots in a similar stratified random manner, but along a series of parallel transects throughout the landscape facet.

The basic unit of measurement within the Serengeti and Manyara study areas was a 50 x 50 meter square plot. I used nested plots to sample the different growth forms: trees, shrubs, and herbaceous plants. The 50 x 50 meter area was used to record trees. Nested within the tree plot was a 50 x 10 meter sub-plot to record shrubs, and a 5 x 2 meter sub-plot for grasses and forbs. In cases where the herbaceous cover was very sparse, the forb and grass sub-plot was expanded to 10 x 4 m. Each plot was situated by laying a 50 meter tape out in a straight line through the area to be sampled. Trees rooted within 25 m of each side of the tape were recorded as being inside the tree plot. The tape also served as the center line for the shrub sub-plot, but in this case only shrubs rooted within 5 m of each side of the 50 meter long tape were recorded in order to total a 50 x 10 meter sampling area for shrubs. The forb sub-plot was placed with the tape being the center line for 5 m in length, and then forbs and grasses were recorded within one meter of each side. The location of the 5 meter length was chosen randomly along the 50 meter interval.

The proportions of actual vegetation that were sampled in Serengeti and Manyara ranged from about one to eight percent, based upon the sum of the plot sizes divided by the estimated size of the landscape facet as shown in Table 3-1. My general sense during field work in these areas was that the plots did capture the diversity of vegetation patterns and variability, especially for trees and shrubs. The variety of herbaceous vegetation was more difficult to capture in some places using this sampling technique, and that is discussed further in Chapters Four, Five, and Seven.

Sampling the Landscape facets in Ngorongoro Crater

The sampling strategy at Ngorongoro Crater was necessarily different from that of Serengeti and Manyara because many of the landscape facets were much smaller, as can be seen in Table 3-1. Also, many of the Ngorongoro landscape facets are wetlands, which are not amenable to transect sampling due to the presence of water and hippos, for example.

The Ngorongoro field work was conducted two years prior to that in Serengeti and Manyara, and initially I was only collecting percent cover area data (see below for explanation of percent cover). Ultimately, many of the analyses were based on cover, so this difference in sampling strategies was only a minor hindrance (see Chapters Four and Five). At the Ngorongoro wetlands, rather than defining actual plot boundaries, I visually estimated the percent cover area of each marsh plant species. For small, localized wetlands, I could visually scan most of or the entire wetland area. For larger wetlands like Gorigor, I estimated percent cover for the area in close proximity, which was generally about 100 x 100 meters (see estimates for each landscape facet sampled in Table 3-1). After some practice in plant species identification, this proved to be an effective and relatively easy sampling strategy.

In the open grassland areas that were sampled at Ngorongoro, I was able to use one by five meter plots in order to estimate the cover of each “dry land” herbaceous species. The shrubland areas near some of the small springs were also small enough that I could visually estimate the cover of shrub or tree species within the entire landscape facet. When that was not possible, such as in the woodlands associated with the large springs, Ngoitokitok North and Ngoitokitok South, I used the same 50 by 50 meter plots for tree sampling as those used in Serengeti and Manyara.

As shown in Table 3-1, a similar proportion of the vegetation was sampled in many of the Ngorongoro landscape facets as that of Serengeti and Manyara, between about one and eight percent. Others, such as the Vernonia spring wetland and adjacent shrubland, and the small woodland adjacent to Seneto spring, were sampled by 25-100% of their total area because they were very small landscape facets. I am confident that this sampling strategy was adequate for capturing the vegetation patterns and variability of the wetlands in Ngorongoro Crater. Some of the wooded “dry land” portions were not sampled as thoroughly as those of Serengeti and Manyara since the abundance of species was only measured by visual cover, but the data was still adequate for comparing those Ngorongoro landscape facets with others in that region and in Serengeti and Manyara.

Seasons of Data Collection

The modern analog vegetation studies were conducted in Ngorongoro Crater during July-August 1995, which is the dry season. In Lake Manyara National Park and Serengeti National Park I conducted field work from September 1997 through July 1998. The specific month(s) of sampling for each study area are listed in Table 3-1. Since I did not sample each of the study areas in both wet and dry seasons, seasonal comparisons were limited to general observations as opposed to quantitative contrasts.

Plant Data Recorded

The types of vegetation data that I collected in the modern study areas included species composition, physiognomic structure, size, growth forms, and abundance. Abundance measures included density for trees and shrubs, and percent cover for all growth forms (see below). A separate data recording form was used for each growth form of plants: trees, shrubs, forbs, and grasses.

Plant Identification

I attempted to identify all plant species of the growth form of interest for each plot or sub-plot. Plants were considered to be inside a plot or sub-plot if rooted within the boundaries. Presence/absence data for species of all growth forms is available for all plots in Appendix 1.

Upon the first encounter with each new plant species in the field, a sample was collected, pressed, and assigned a sample number. Sample numbers were the three letters of the study area followed by a number in chronological order (e.g., BAR-3 for a plant specimen collected at Barafu in Serengeti). During field work at Lake Manyara, I employed botanical assistants from the National Herbarium in Arusha to help collect and identify plants. My assistants were Daniel Sitoni, Emanuel Mboya, and Vetes Kalema. We first attempted to identify plant specimens at the field herbarium at Ndala Research Camp, where we stayed while working at Manyara. In Serengeti, I made a first attempt at plant identification at the herbarium at the Serengeti Research Institute in Seronera. If field identification was not possible, then specimens were taken for identification to the

National Herbarium of Tanzania in Arusha. All Ngorongoro samples were taken to Arusha for identification.

Plants were identified to species when possible, which was usually the case. The plant specimens are stored in the Human Origins Laboratory at the National Museum of Natural History in Arusha, Tanzania. Plant names and spellings were checked for accuracy using the references in Table 3-2. Appendix 1 provides a comprehensive list of all plant species that were encountered in this study (n = 476) and the locations from which they were recorded. I did not have a chance to make herbarium vouchures during the field seasons, but plan to on a future trip to Tanzania. The specimens are currently stored at the Arusha Museum of Natural History.

Growth Forms

The categories of plant growth forms used in this thesis are as follows. Forbs are herbaceous, non-woody, plants, including sedges, that do not belong to the family Gramineae (Allaby, 1992). Grasses are plant species belonging to the family Gramineae. Shrubs and trees are woody plants differentiated by height and number of stems, following Pratt and Gwynne (1977). Shrubs include all woody plants that are six m or less in height, and woody plants that are up to 10 m in height and have multiple stems (at least three or more) and a generally bushy character. Trees are defined as all woody plants greater than 10 m height, and any woody plants greater than six m height that have one to three stems. A single species may occur in more than one growth form. For example, *Acacia tortilis* and *Acacia xanthophloea* commonly occur in both shrub and tree forms, often within the same plot.

Table 3-2. References used to check plant names and spellings.

References for Plant Names
Beentji, H.J. 1994. *Kenya Trees, Shrubs, and Lianas*. National Museums of Kenya, Nairobi.
Blundell, M. 1987. *Collins Photo Guide to the Wild Flowers of East Africa*. Harper Collins Publishers, Hong Kong.
Coates Palgrave, K. 1993. *Trees of Southern Africa*. Struik Publishers, Cape Town.
Haines, R.W. and Lye, K.A. 1983. *The sedges and rushes of East Africa – A flora of the families Juncaceae and Cyperaceae in East Africa with a particular reference to Uganda.*. East African Natural History Society, Nairobi.
Ibrahim, K.M. and Kabuye, C.H.S. 1987. *An illustrated manual of Kenya Grasses*. FAO, Rome.
Peters, C.R., O'Brien,E.M., and Drummond, R.B. 1992. *Edible Wild Plants of Sub-Saharan Africa*. Royal Botanical Gardens, Kew.
The Plant Names Project (1999). *International Plant Names Index*. Published and periodically updated on the Internet; http://www.ipni.org [accessed May 15, 2001].

Height

I recorded tree height to the nearest meter in each plot. A clinometer was used to measure the heights of trees greater than 10 m, while heights of smaller trees were estimated visually. Shrub height was estimated visually to the nearest 0.1 m. The average height of forbs and grasses was also estimated for each plot as part of the plot's general physiognomic description.

Crown diameter

I measured the maximum crown diameter of each tree to the nearest 0.5 m by laying a 50 m tape out on the ground underneath the crown of that tree. The entire length of the maximum crown diameter was recorded even if the crown area extended beyond the borders of the tree plot. I recorded shrub maximum crown diameter to the nearest 0.5 m also using a measuring tape.

Cover

Cover is defined as the proportion of ground occupied by vertical projection to the ground of the aerial parts of the individual(s) or growth form(s) under consideration, and is generally expressed as a percentage (Greig-Smith, 1983:5). At Manyara and Serengeti I recorded two different measures of cover: visually estimated cover and calculated cover. All measurements at Ngorongoro are visually estimated cover.

I recorded visually estimated vegetation cover for each plot as a whole, after quantitative measures had been taken on the individual plants. Visual cover estimates were only made by myself, and were compared to calculated cover values (see below) in order to check for accuracy. From a vantage point in which the entire plot was visible, I estimated top cover of the entire plot area separately for trees, shrubs, forbs, and grasses. Top cover describes the proportion of ground for which each growth form provides the uppermost cover (Greig-Smith, 1983:5), and therefore is never greater than 100% for each growth form. Top cover is the measure generally referred to in definitions of physiognomic structure.

Calculated cover was derived from the measures of maximum crown diameter for trees and shrubs. First, crown area is calculated by assuming that each crown is a solid circle with crown diameter measured as described above. The calculated crown areas for all individuals of interest are added and transformed to a percentage based on the total area of the plot in which the data was collected. The total amount for a given growth form may exceed 100% if plant crowns overlap in the three-dimensional space above the ground. Unlike the visual cover estimates which refer to the entire plot area, calculated cover can be calculated as a cover abundance measure that refers to individual plants, all the plants of one species, all edible plants, etc.

Several features of the calculated values may cause them to overestimate actual top cover of trees and shrubs within a plot, although this is not necessarily a problem if the measures are treated as a means by which to compare relative abundance of species or other designated groupings of plants. The area calculation assumes that the crown of each individual is a solid circle, and therefore it does not take into account the spaces between leaves and branches, which should not in theory be included in the computation of cover area. Calculated cover estimates also include all individuals that are rooted inside the plot boundaries, even though the crown may extend beyond the plot borders. The calculated crown area estimations assume that the shape of the tree or shrub crown is circular. Since it was the maximum crown diameter of the tree or shrub that was measured, the crown area calculation is actually the maximum possible crown area for that individual. Finally, since calculated cover estimates for a given growth form are the sum of individuals, they do not take into account the possibility of overlap in the space above the ground. While visual estimates are estimates of top cover, calculated estimates are actually the sum of the top cover of each individual, which may be more (but will never be less) than the actual top cover of the growth form in question.

In actuality, woody plants in many of the study areas are widely spaced with roughly circular crowns, and therefore the visual and calculated cover estimates are quite similar. Only in forested areas with high tree densities do calculated covers greatly exceed visual cover estimates.

Relative cover, a measure that is used to calculate importance values (see below), is the calculated cover of a given species in a given study area divided by the sum of the calculated cover of all species in that study area.

Density

Density is a measure of the number of individuals per unit area. The tree and shrub density measures reported for each study area are the average of the densities in the plots or subplots within that study area, having taken into account any differences in actual plot sizes before averaging. These means are expressed as numbers of individuals per hectare.

Relative density, a measure that is used to calculate importance values (see below), is the density per hectare of a given species in a study area divided by the sum of the density per hectare of all species in that study area.

Frequency

The frequency of a species is the chance of finding that species within the study area in any one trial (Greig-Smith, 1983:9). In a given a number of plots, a species' frequency is expressed as the percentage of plots within a given study area in which a species occurred. Since frequency is simply an extension of presence/absence data for each species, it can be calculated for all growth forms in this study including forbs and grasses. Cover and density measures are not available for forbs and grasses in this study.

Relative frequency, a measure that is used to calculate importance values and diversity indices (see below), is the frequency of a given species in a given study area divided by the sum of the frequencies of all species in that study area.

Importance Values

It can be difficult to choose a particular measure to express the abundance of a plant species because measures like cover, density, and frequency each reflect a different aspect of the vegetation. An importance value is a way to combine these elements into a single number (Greig-Smith, 1983:152; Causton, 1988:58). I calculated importance values in this study as the average of relative cover, relative density, and relative frequency. The importance value is expressed as a percentage between zero and 100.

For a species A *within a single study area*:

$$\text{Importance Value} = \frac{\left(\dfrac{\text{freq. sp. A}}{\text{freq. all spp.}}\right) + \left(\dfrac{\text{calc. cover sp. A}}{\text{calc. cover all spp.}} \times 100\right) + \left(\dfrac{\text{dens. sp. A}}{\text{dens. all spp.}} \times 100\right)}{3}$$

Species Richness

Species richness is the number of species present in a given area. For this project, species richness of a study area is the number of species that occurred at least once in any of the plots or subplots within that study area.

Species Diversity

Species diversity indices provide a way to express the number of species present in a given area while also taking into account differences in their abundance. I used the Shannon-Weaver index, in which $H = -\Sigma\, p_i \log_e p_i$, where p is the proportional abundance of the ith species (i) in the total sample of all species (Greig-Smith, 1983:163). Proportional abundance here was estimated by relative frequency as defined above, since that measure is available for all trees, shrubs, forbs, and grasses. The results are expressed as e^H, which is proportional to the number of species and therefore more easily interpreted than H, which is proportional to the logarithm of the number of species (Ricklefs, 1990:721). For example, if five species occur in a study area, then the maximum possible value of $e^H = 5$, and that occurs only when all species are present in equal abundance.

Physiognomy

Physiognomic categories are often the only description of vegetation that results from paleoenvironmental reconstructions, so this measure plays a central role in modern analog research (Figure 1-1). Physiognomy is essentially a subjective measure that refers to the appearance of the vegetation as a whole. It considers proportions of individuals of different growth forms, but also relates to size, phenology, and the arrangement of individual plants (Greig-Smith, 1983:155).

I used the physiognomic categories defined by Pratt and Gwynne (1977) that are commonly used for East Africa, and these are described in Table 3-3. In theory, the data from this project could be reorganized according to any physiognomic classification system based on the cover, height, and floristic data for each plot.

Table 3-3. Physiognomic categories used in this thesis, as defined by Pratt and Gwynne (1977:44-50).

Physiognomic Category	**Definition**
Forest	Closed stand of trees of one or more stories, with an interlaced canopy, 7 to 40 m height. Ground cover is dominated by herbs and shrubs.
Woodland	Tree up to 20 m in height have an open or continuous, but not thickly interlaced canopy, and canopy cover > 20%. Shrubs, if present, constitute less than 1/10th of the canopy cover. Grasses and other herbs dominate the ground cover.
Shrubland	Shrubs, usually not more than 6 m in height, with a canopy cover > 20%. Trees, if present, constitute less than 1/10th of the canopy cover.
Bushland	Trees and shrubs are both present. May be dominated by shrubs, but trees are always conspicuous. Tree + shrub cover > 20%.
Wooded Grassland	Grassland with scattered or grouped trees, the trees always conspicuous, with cover area from 2 to 20%.
Shrub Grassland	Grassland with scattered or grouped shrubs, the shrubs always conspicuous, with cover area from 2 to 20%.
Bush Grassland	Grassland with scattered or grouped trees and shrubs, both always conspicuous, but tree + shrub cover from 2 to 20%.
Grassland	Dominated by grasses and other herbs. Tree + shrub cover < 2%.
Marsh	Herbaceous swamp with permanent or ephemeral wetland.

Ordination – Detrended Correspondence Analysis (DCA)

Detrended correspondence analysis (DCA) was developed by Hill and Gauch (1980), and is an ordination technique that I use to analyze the data on modern plant species composition in this thesis. Ordinations are multivariate techniques, frequently used in ecology, that allow one to create a two-dimensional graph in which sample sites (plots or study areas) are arranged along axes based on species composition. Sites that are similar in species composition are in close spatial proximity on the graph, while sites that are dissimilar in species composition are far apart on the graph. In a DCA analysis and graph, the theoretical variable that maximizes dispersion is the first ordination axis. A second and further DCA axes are constructed by the same procedure as the first, but with the constraint of being uncorrelated with the previous DCA axis. Thus new information is expressed on each subsequent axis. In practice, the variation in most of the species data is represented in two or three axes. The eigenvalue is the measure of dispersion of the species scores on the ordination axis, and it becomes progressively smaller with each subsequent axis.

The graph axes represent unknown, latent, or theoretical environmental variables that determine the occurrence of all species under consideration (Jongman *et al.*, 1995:93). The DCA is an indirect gradient analysis because it creates theoretical environmental variables based solely on species composition. In contrast, direct gradient analyses compare the occurrence of a species to a measured environmental variable. There are advantages to the indirect gradient approach, particularly in an exploratory study such as this thesis, where it is not the behavior of a particular plant species or particular environmental variable that is in question, but rather features of whole plant communities. In such a case, one often does not know which environmental gradients are important, and therefore which to measure. Furthermore, general patterns of coincidence of several species with the environment may prove a more “robust” way of getting at how environmental variables actually shape vegetation (Jongman *et al.*, 1995). The task after doing such an ordination is to figure out which actual environmental variables are being represented by the axes.

Another commonly used technique, principal components analysis (PCA), assumes a linear model, that is, that the abundance of any species either increases or decreases with the latent environmental variable. In contrast, DCA assumes that any species occurs in a limited range of values of each of the latent variables, and thus is "unimodal" (Jongman *et al*. 1995:93-94). In nature, plant species often do show bell-shaped curves (which are unimodal) with respect to environmental gradients, so DCA is used in this thesis to analyze species data from a variety of sites.

Conclusion

In this chapter I described the environmental setting of the modern study areas at Manyara, Serengeti, and Ngorongoro Crater. These modern study areas were chosen because they are similar in geological, climatic, physiognomic, and floristic parameters to reconstructions of the paleolandscape of lowermost Bed II, Olduvai. In this chapter I outlined the landscape classification system and defined the specific land units that were sampled in those modern study areas. Each of the modern land units corresponds to one or more paleo-land units at Olduvai. For example, the rivers and interfluves of Manyara's alluvial fans ultimately will be used to model vegetation resources for hominins along the rivers and interfluves of Olduvai's paleolandscape. In this chapter I also described the sampling techniques and field methods that I use to describe and measure the modern vegetation.

The results of these modern vegetation studies are presented in Chapters Four and Five following the methods and definitions that were outlined in this chapter. In Chapter Six, those modern vegetation descriptions and measurements are applied to the fossil case study of Olduvai, where I attempt to reconstruct how plant resources for hominins were distributed across a paleolandscape.

CHAPTER 4. VEGETATION IN THE MODERN ANALOG ENVIRONMENTS

Introduction

In this chapter I look in detail at the vegetation of the modern analog environments in order to begin to develop the relational analogies that are needed to predict important aspects of vegetation in the past. The central question that is being addressed is: what is the nature of the relationships between physiognomy, plant species composition, and landscape units in the modern analog settings at Serengeti, Manyara, and Ngorongoro Crater?

As outlined in Chapter One, an understanding of the relationships between these factors in modern habitats is essential if we are going to be able to use the paleoenvironmental information that exists in order to reconstruct elements that were important to the ecology of early hominins. Landscape units, for example, can be partially reconstructed from geological and other fossil evidence, so can we predict the most likely plant species and cover abundance of trees and shrubs that existed on those landscape units? On the other hand, if stable isotopes of pedogenic carbonates can indicate the likely nature of past vegetation structure (e.g., woodland) for a particular fossil locality, does that mean that we can reconstruct the plant resources for hominins that also existed in that locality?

Physiognomy, or specifically woody cover, is of central importance to predictions of archaeological traces at Olduvai (Blumenschine and Peters, 1998). That is because models of hominin resource availability, land-use, and ultimately archaeological traces for OLAPP are dependent on the proposed relationship between woody cover and scavengeable carcass availability (Blumenschine and Peters, 1998). Ultimately, we need to know something about the physiognomy of different landscape units in the paleo-Olduvai basin in order to predict those key variables that will allow us to measure hominin behavior.

In order to address these questions, I first focus on quantitative descriptions of the physiognomy or vegetation structure of the modern analog study areas at the various landscape scales: land regions, landscape associations, and landscape facets. I use the measures of cover and density for trees and shrubs, and cover for forbs and grasses, in order to quantitatively characterize vegetation structure.

Next I describe the community composition of the various landscape units by identifying the actual plant species present and discussing species diversity and richness at various landscape scales. I bring in ecological information about the modern plant species when possible in order to better understand the degree of ecological differences or contrasts between particular landscape facets, landscape associations, and regions. The relationships between environmental variables, physiognomy, and community composition are explored with DCA ordinations. I do not yet discuss the potential plant resources for hominins of the modern analog localities in this chapter; that is the subject of Chapter Five.

The results of this chapter show that the relationships between vegetation structure, community composition, and landscape units are indeed complicated, but some patterns begin to emerge that are useful from a paleoanthropological perspective. After summarizing my findings, I discuss the results of previous research regarding the plant ecology and vegetation structure of East African savannas.

At the end of this chapter I address the issue of the relatively long time duration of the paleolandscape in question, Olduvai's lowermost Bed II, by creating a predictive model of the likely time duration of vegetation in the modern landscape facets. During the 50,000 years or so encompassed by lowermost Bed II, landscape facets and vegetation probably changed across the landscape. The predictive model I developed helps to address the frequency of those changes so that they ultimately can be incorporated into models of hominin resource distribution and land use.

Methods

Details of site selection, landscape classification system, data collection, and definitions of terms are described in Chapter Three. The site names, abbreviations, classification, and size were summarized in Table 3-1, and the localities of the study sites were shown in Figures 3-1 through 3-4.

The vegetation of study areas was compared in terms of visually-estimated cover and density for trees and shrubs, tree height, and species richness (number of species) and species diversity (Shannon-Weaver Index, presented as e^H) for all growth forms (see Chapter Three). For richness and diversity, the mean of all riverine sites was compared to the mean of all non-riverine sites with a t-test for independent samples. For tree and shrub cover and density, the mean of all riverine sites was compared to the mean of all non-riverine sites with a t-test for independent samples. Groupings of sites by landscape associations and by landscape facets were too small for valid statistical comparisons, as the number of sites of any landform is between 2 and 4, and the number of sites per landscape facet is 1 or 2 (Table 3-1).

Species commonness was measured relative to the number of plots of occurrence for each growth form across Serengeti and Manyara, and for all species within each landscape association at Serengeti and Manyara.

Species composition of sites was analyzed with the ordination technique of detrended correspondence analysis (DCA) (Hill and Gauch, 1980) using importance values for trees and shrubs, and presence/absence for forbs and grasses. Rare species (that occurred at only one site) were removed before analysis, and for the remaining species, rarer ones were down weighted. DCA ordinations were performed in Canoco 4.02 (ter Braak, 1999). An explanation of this technique is given in Chapter Three.

Vegetation Structure

At the modern analog sites examined for this thesis, vegetation structure, which is roughly synonymous with physiognomy, is quantified through measures of cover, density, and the heights of trees and shrubs. As described in Chapter Three, different proportions of tree, shrub, and ground cover are used to define physiognomic types such as woodland or bushland (Table 3-3). Table 4-1 summarizes the cover, density, tree height, and physiognomic category (Pratt and Gwynne, 1977) for all of the modern landscape facets that I studied, grouped by regions and landscape associations. These measures are compared in graphic form later in this chapter. However, I begin with a description of the general physiognomic characteristics of each land region, landscape association, and landscape facet that is included in this study.

In the Lake Manyara region, my study areas are a mosaic of bush grassland, bushland, and forest habitats. The southeastern portion of Serengeti National Park, where

Table 4-1. Structural features of the vegetation in the modern analog study areas (Manyara, Serengeti, and Ngorongoro Crater).

Region	**Landscape Association**	**Facet**	**Study Area**	**Physiognomy** (Pratt & Gwynne, 1977)	**Visually-Estimated Cover** (%)				**Density** (indiv. / hectare)		**Height** (m)
					Trees	**Shrubs**	**Forbs**	**Grass**	**Trees**	**Shrubs**	**Trees**
Manyara	Alluvial Fan	Non-Riverine	Mkindu interfluve (M-MKII)	Forest	83	13	19	0	92	1590	19.2
		Riverine	Mkindu River on Alluvial Fan (M-MKIR)	Forest	88	23	8	0	110	3520	17.2
	Fluvial Terr	Riverine	Endabash River on Fluvial Terrace (M-END)	Bushland	46	34	1	46	40	2246	11.2
	Lacustrine Plain	Non-Riverine	Ndala Lake Flat (M-NLF)	Bush Grassland	7	8	31	35	16	122	7.4
		Non-Riverine	Msasa Lake Flat (M-MLF)	Bush Grassland	3	3	4	79	8	50	9.5
		Riverine	Mkindu River on Lacustrine Plain (M-MKILF)	Forest	70	33	15	28	367	2747	16.2
		Riverine	Msasa River on Lacustrine Plain (M-MSALF)	Bushland	52	48	1	3	18	1724	22.7
	Lacustrine Terrace	Non-Riverine	Ndala-Chemchem Interfluve (M-NCI)	Bushland	38	10	34	32	58	488	8.9
		Non-Riverine	Ndilana-Msasa interfluve (M-NMS)	Bushland	24	24	9	37	31	555	8.2
		Riverine	Msasa River on Lacustrine Terrace (M-MSA)	Bushland	20	44	7	22	21	1105	8.9

Region	**Landscape Association**	**Facet**	**Study Area**	**Physiognomy** (Pratt & Gwynne, 1977)	**Visually-Estimated Cover** (%)				**Density** (indiv. / hectare)		**Height** (m)
					Trees	**Shrubs**	**Forbs**	**Grass**	**Trees**	**Shrubs**	**Trees**
Manyara (cont.)	Lacustrine Terrace (cont.)	Riverine	Ndilana River on Lacustrine Terrace (M-NDI)	Bushland	46	46	11	29	56	926	8.5
Serengeti	Eastern Serengeti Plain	Non-Riverine	Barafu Plain (S-BPL)	Grassland	0	0	18	81	0	0	
		Riverine	Barafu River (S-BAR)	Bush Grassland	8	6	33	61	7	251	7.8
	Serengeti Woodlands	Riverine	Mbalageti River (S-MBA)	Bushland	26	10	1	49	52	1103	11.1
		Riverine	Sangare River (S-SAN)	Bushland	30	13	13	90	32	732	9.6
	Western Serengeti Plain	Non-Riverine	Nyamara interfluve (S-NIN)	Grassland	0	2	1	48	0	122	7.5
		Non-Riverine	Seronera-Wandamu interfluve (S-SWI)	Grassland	0	0	6	96	0	0	
		Riverine	Nyamara River (S-NYA)	Bushland	21	8	1	63	22	703	11.7
		Riverine	Seronera River (S-SER)	Bushland	16	10	2	78	5	285	12.7
Ngoro-ngoro	Crater Floor	Large spring dry land	Ngoitokitok North (N-NGG)	woodland	80	25	5	90	103		18.0
		Large spring dry land	Ngoitokitok North (N-NGW)	grassland	0	1	10	80	0		
		Large spring wetland	Ngoitokitok North (N-NGP)	marsh	0	0	98	5	0		
		Large spring dry land	Ngoitokitok South (N-NGS)	woodland	75	80	30	30	53		17.0

Region	**Landscape Association**	**Facet**	**Study Area**	**Physiognomy** (Pratt & Gwynne, 1977)	**Visually-Estimated Cover** (%)				**Density** (indiv. / hectare)		**Height** (m)
					Trees	**Shrubs**	**Forbs**	**Grass**	**Trees**	**Shrubs**	**Trees**
Ngoro-ngoro (cont.)	Crater Floor (cont.)	Large spring wetland	Ngoitokitok South (N-NSM)	marsh	0	0	98	5	0		
		Small spring wetland	Engitati (N-ENG)	marsh	0	0	80	5	0		
		Small spring dry land	Kidogo Spring (N-KSG)	grassland	0	0	5	50	0		
		Small spring wetland	Kidogo Spring (N-KSM)	marsh	0	0	5	80	0		
		Small spring dry land	Mti Moja (N-MTG)	grassland	0	0	5	60	0		
		Small spring wetland	Mti Moja (N-MTM)	marsh	0	0	73	2	0		
		Small spring dry land	Mystery Spring (N-MSS)	shrubland	5	50	10	10	2		10.0
		Small spring wetland	Mystery Spring (N-MSM)	marsh	0	0	70	0	0		
		Small spring dry land	Seneto (N-SEG)	grassland	0	0	10	80	0		
		Small spring dry land	Seneto (N-SEW)	woodland	65	15	30	20	20		10.0
		Small spring wetland	Seneto (N-SEM)	marsh	0	0	80	5	0		
		Small spring dry land	Vernonia (N-VSW)	shrubland	0	70	10	15	0		
		Small spring wetland	Vernonia (N-VSM)	marsh	0	0	50	2	0		
		Stream-fed dry land	Gorigor Midwest (N-GMG)	grassland	0	0	5	60	0		
		Stream-fed wetland	Gorigor Midwest (N-GMM)	marsh	0	0	90	5	0		
		Stream-fed dry land	Gorigor North (N-GNG)	grassland	0	0	0	70	0		

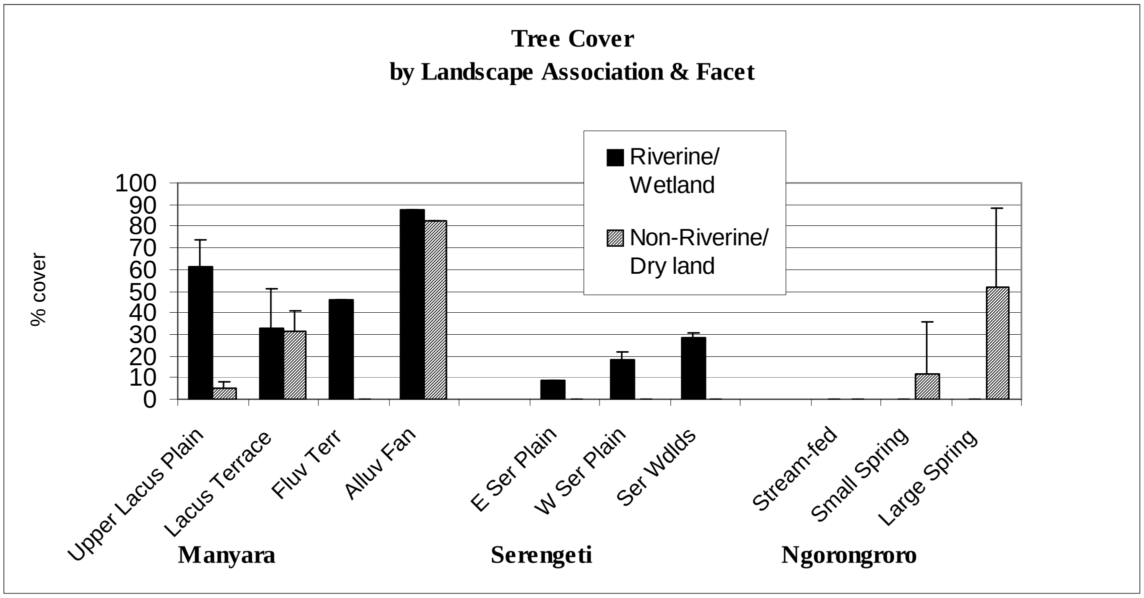
Region	**Landscape Association**	**Facet**	**Study Area**	**Physiognomy** (Pratt & Gwynne, 1977)	**Visually-Estimated Cover** (%)				**Density** (indiv. / hectare)		**Height** (m)
					Trees	**Shrubs**	**Forbs**	**Grass**	**Trees**	**Shrubs**	**Trees**
Ngoro-ngoro (cont.)	Crater Floor (cont.)	Stream-fed wetland	Gorigor North (N-GNM)	marsh	0	0	90	0	0		
		Stream-fed wetland	Gorigor West (N-GWE)	marsh	0	0	20	10	0		
		Stream-fed dry land	Munge Marsh (N-HPG)	grassland	0	0	10	80	0		
		Stream-fed wetland	Munge Marsh (N-HPM)	marsh	0	0	90	5	0		
		Stream-fed dry land	Munge River (N-MRG)	grassland	0	0	0	90	0		
		Stream-fed wetland	Munge River (N-MRM)	marsh	0	0	50	5	0		

I conducted investigations, contains a mosaic of grassland, bush grassland, and bushland habitats. In the Ngorongoro region, the Crater Floor supported grassland, woodland, shrubland, and marsh habitats. Within each of my landscape units defined as regions, then, the physiognomy varies widely. Not surprisingly, there is also much overlap between the physiognomies of regions. To categorize a region by a single physiognomic type in modern East Africa would blur significant physiognomic differences that are often vital to animals living within that region.

At Manyara, there is a catena of landscape associations based upon riverine and lacustrine environments: a shallow and fluctuating lake with mud-flats, a grassland and bush grassland-dominated lacustrine plain, a bushland-dominated lacustrine terrace, and a forest-covered alluvial fan (see Figure 3-2). The order in which the landscape associations radiate from the lake is not consistent around the lake's perimeter. In the far north the lake gives way to a lacustrine plain, abutted by the alluvial fans and finally the rift escarpment to the west. Slightly to the south the catena goes from lake to lacustrine plain to lacustrine terrace to rift escarpment. In the area of the Endabash River the catena is lake to lacustrine plain to fluvial terrace to rift escarpment.

At a finer scale, there can be sharp contrasts between the physiognomic types of landscape facets within the same landscape association at Manyara (e.g., Figure 4-1). In the upper lacustrine plain, the riverine landscape facet along the Mkindu River is lined by a dense but narrow strip of tall *Acacia xanthophloea* trees rooted within about five meters of each side of the small, perennial stream, but the adjacent interfluvial lacustrine plain landscape facet is open grassland. Despite the very dense trees along the Mkindu of the upper lacustrine plain (Figure 4-1), the highest tree cover at Manyara is in the riverine

Figure 4-1. Visually estimated tree cover of the modern analog study areas. Bars show the mean of study areas within each facet with one standard error. Note that no samples were taken for the non-riverine fluvial terrace nor for the non-riverine Serengeti woodlands.



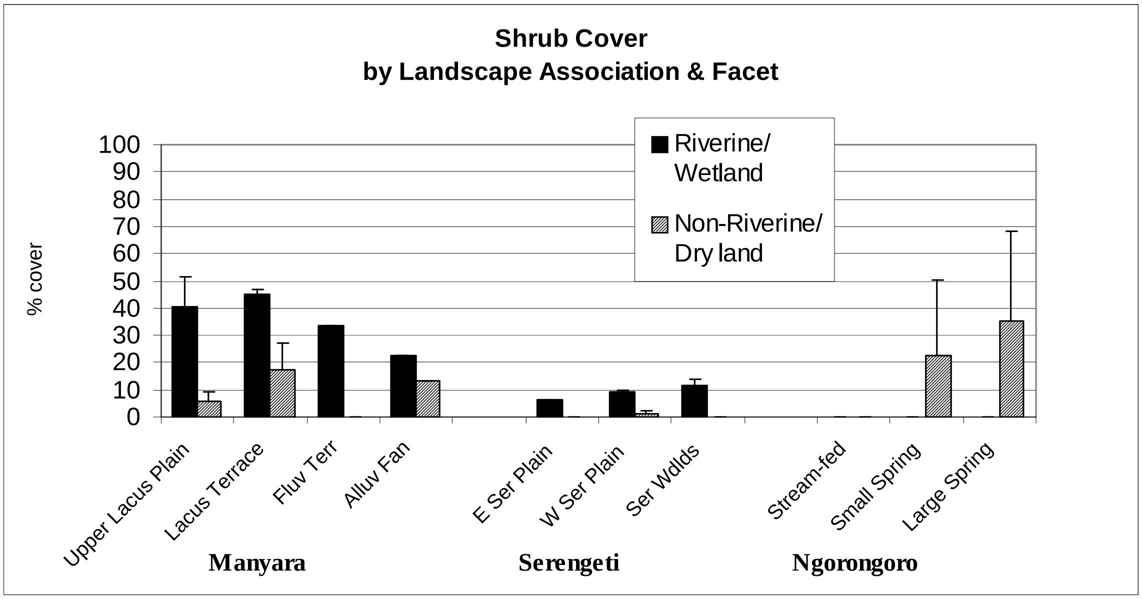
and interfluvial landscape facets of the alluvial fan in the north. The lower alluvial fan supports a tall groundwater forest and unlike the lacustrine plain, there is virtually no contrast between the vegetation structure of adjacent riverine and non-riverine landscape facets within the alluvial fan's groundwater forest (Figure 4-1).

In the Serengeti, the three landscape associations that I studied are adjacent to each other along a roughly southeast to northwest direction (Figure 3-3). Although it is not a lake catena, there are several environmental gradients in the southeast-northwest direction. For example, rainfall increases from the semi-arid rain shadow in the southeast around Olduvai toward the sub-humid northwestern Serengeti Woodland (Norton-Griffiths *et al.*, 1975). The soil is affected by a gradient in terms of amount and grain size of air-blown volcanic dust (Hay, 1976). The source of the dust, the Crater Highland volcanoes, are in the southeast and the prevailing winds blow toward the northwest. Thus in the southeast are large amounts of volcanic ash with many large particles, while there are increasingly finer particles in the northwest toward western and northern Serengeti (Anderson and Talbot, 1965).

The Eastern Serengeti Plain and Western Serengeti Plain are dominated by grasslands. The Serengeti Woodland is a vast area that I sampled in two study areas near its eastern edge; those areas contained a mixture of bushland and woodland. Each of the Serengeti landscape associations is comprised of riverine and interfluvial landscape facets. In the Eastern Serengeti plain, the interfluves are short-height grasslands. The riverine landscape facet that I studied in the Eastern Serengeti Plain, the Barafu Valley, stood out distinctively compared to its interfluvial, grassland surroundings due to its trees and shrubs, but those were relatively sparse and only qualified it as a bush grassland. The interfluvial landscape facets of the Western Serengeti Plain are grassland, with medium- and long-height grasses (Anderson and Talbot, 1965). The Western Serengeti Plain has a higher density and cover of trees and shrubs in its riverine landscape facets than those of the Eastern Serengeti Plain, so its rivers were bushland (Figures 4-1 and 4-2).

In the Serengeti Woodland landscape association, the trees along the riverine landscape facets form a bushland or woodland. Although I did not systematically sample non-riverine areas of the Serengeti Woodland, casual observation suggests that the non-riverine areas would be categorized as shrubland, bushland, or bush grassland, but definitely not as grassland because trees and shrubs were present. The trees along the riverine landscape facets were taller than the trees and shrubs of the surrounding interfluvial landscape facets.

Figure 4-2. Visually estimated shrub cover of the modern analog study areas. Bars show the mean of study areas within each facet with one standard error. Note that no samples were taken for the non-riverine fluvial terrace nor for the non-riverine Serengeti woodlands.



The Ngorongoro Crater Floor is classified as a single landscape association in this investigation, but within it I studied a greater variety of landscape facet types and physiognomic types than in the other landscape associations. Stream-fed wetlands, large spring wetlands, and small spring wetland landscape facets all consistently support marsh vegetation (Table 4-1). Some of the marshes are far more extensive than others, and the large marshes tend to support taller marsh plants. The dry lands adjacent to the stream-fed wetlands that I studied were all grassland. The dry lands adjacent to small springs that I studied were grassland in some cases, and very localized shrubland or woodland in others. The dry land landscape facets adjacent to large springs that I studied, Ngoitokitok North and Ngoitokitok South, contain both woodland and grassland sub-landscape facet areas. These large spring woodlands are much more extensive than the woodlands near the small springs.

Components of Vegetation Structure in the Landscape Units

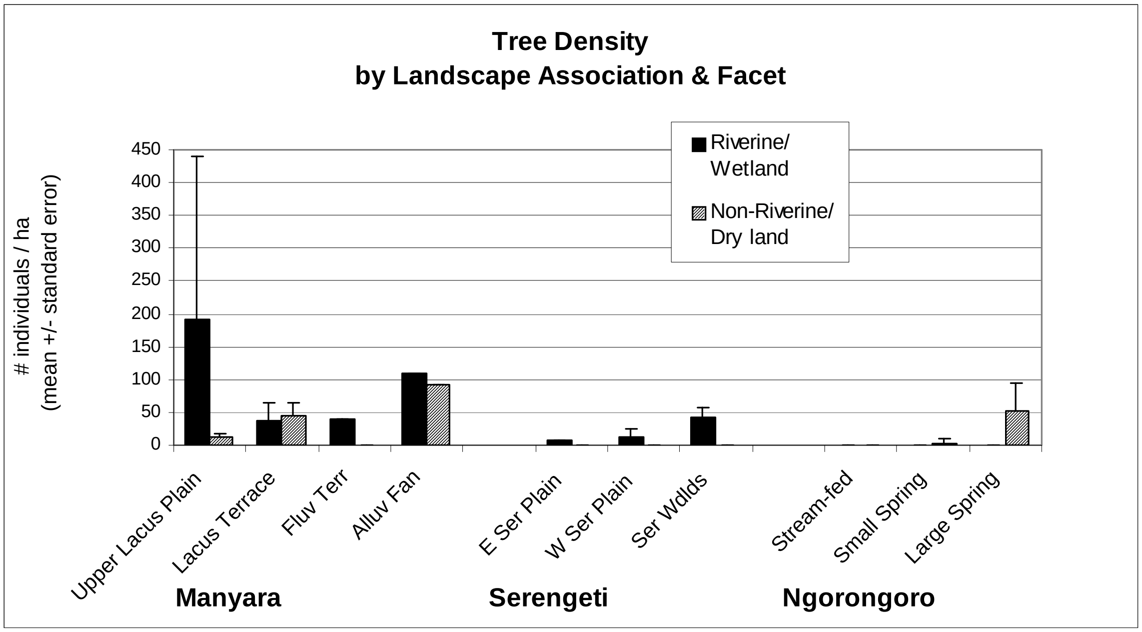
The measures of vegetation structure are depicted graphically in Figures 4-1 through 4-5 to enable easy comparisons across landscape units. Shrub density is not shown for Ngorongoro because data on shrub density were not collected there.

At a regional level, Manyara supports the highest tree and shrub cover and density. At the level of landscape associations, tree cover, shrub cover, tree density, and shrub density all vary considerably, even within each single region. Ngorongoro's stream-fed wetlands and dry lands had no woody cover at all (Figures 4-1 and 4-2). The dry lands of Ngorongoro's large springs have higher tree and shrub cover than the dry lands of the small springs, but there is also a great deal of variability between landscape facets (see error bars, Figures 4-1 and 4-2). This is because some of those dry lands had no woody vegetation. According to the classifications of Pratt and Gwynne (Table 3-3), the wetland landscape facets at Ngorongoro were all marshes, while the dry lands were either grassland, shrubland, or woodland (Table 4-1).

In Serengeti's landscape associations, tree and shrub cover and density increase from the Eastern Serengeti Plain to the Western Serengeti Plain to the Serengeti Woodland (Figures 4-1, 4-2, 4-3, and 4-4). Overall, there are fewer trees and shrubs in Serengeti than in Manyara.

The relationship between tree and shrub proportions, shapes, and heights is an important way in which the physiognomy differs between landscape associations. For example, in the riverine part of Manyara's lacustrine terrace, the shrub layer is thick with leafy, multi-branched shrubs that present physical obstacles, as well as potential food or shelter, for large mammals including hominins (>40% shrub cover, Figure 4-2).

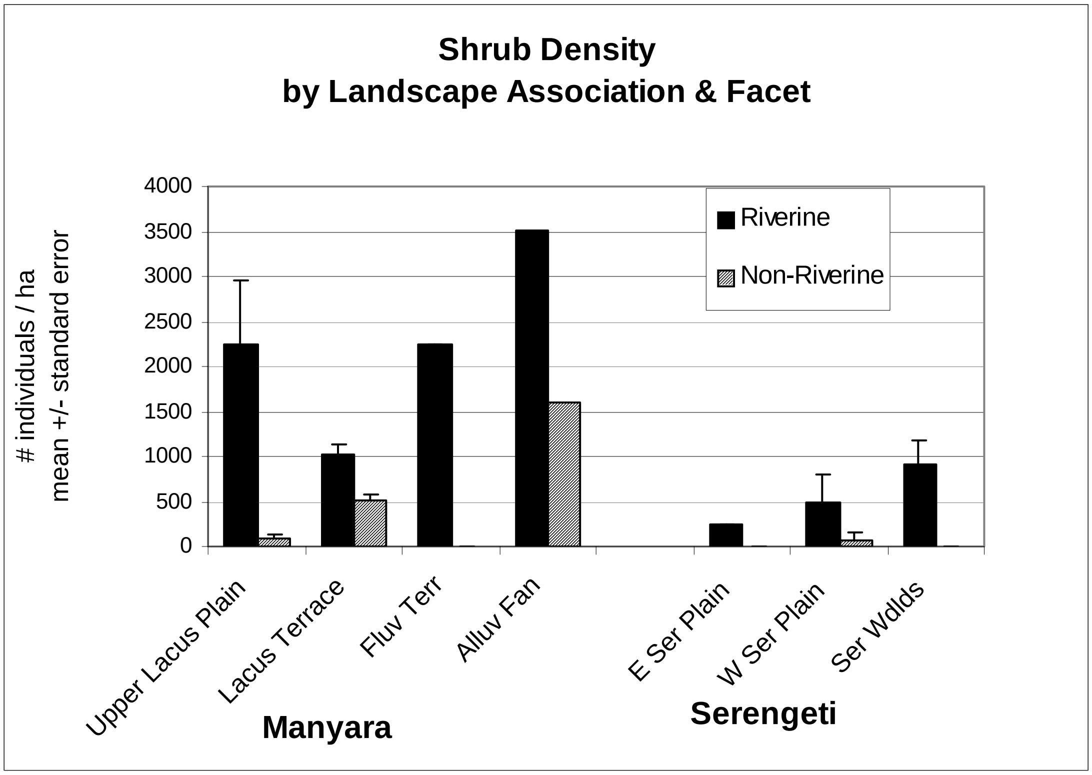
Figure 4-3. Tree density in the modern analog study areas. Bars show the mean of study areas within each facet with one standard error. Note that no samples were taken for the non-riverine fluvial terrace nor for the non-riverine Serengeti woodlands.



Manyara's alluvial fan, on the other hand, consists of a thinner shrub cover (about 20%, Figure 4-2), that is shaded by a dense, tall tree canopy. Manyara's alluvial fan "shrub" layer has an overall more spacious and open appearance because it consists of tree saplings with a single stem and few leaves, which are less than six meters tall and hence are classified as shrubs. Thus, even though the shrub density at the riverine alluvial fan is higher (3500/hectare, Figure 4-4) than that of the riverine lacustrine terrace (1000/hectare, Figure 4-4), the cover produced by the thin, tall saplings in the alluvial fan is lower (Figure 4-2). The ecological ramifications for hominins of these more subtle differences in physiognomy between landscape units are explored in Chapter Five.

In the current theoretical orientation of the OLAPP landscape paleoanthropology project it is the potential contrast in the vegetation structure at the level of landscape facets

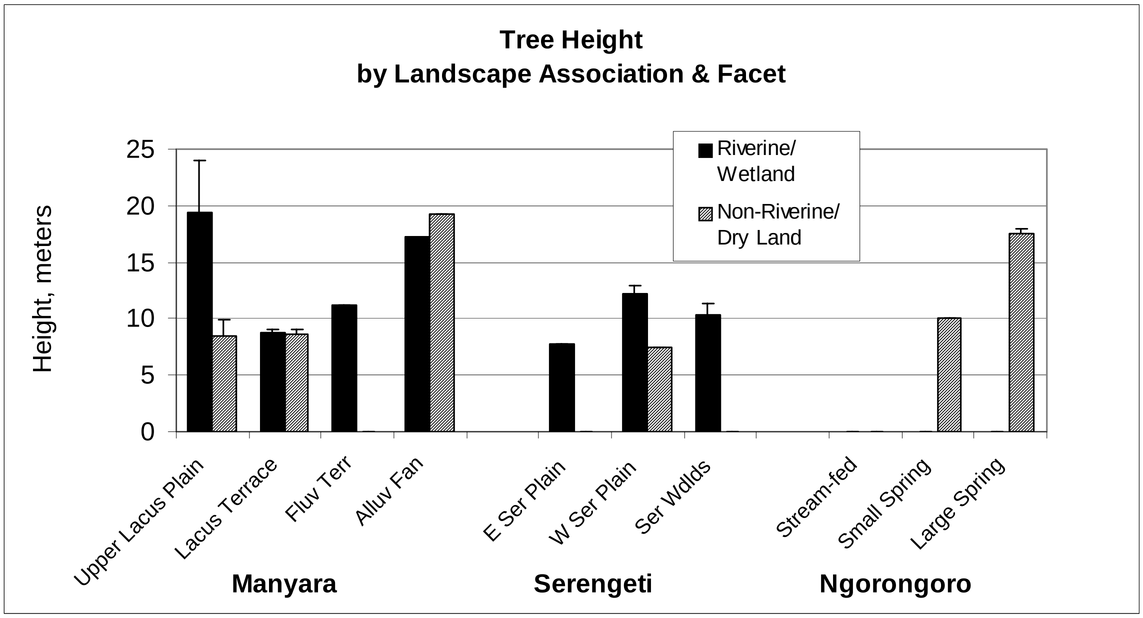
Figure 4-4. Shrub density in the modern analog study areas at Serengeti and Manyara. Bars show the mean of study areas within each facet with one standard error. Note that no samples were taken for the non-riverine fluvial terrace nor for the non-riverine Serengeti woodlands. Ngorongoro study areas are not included because no data on shrub density was collected there.



that is most pertinent to reconstructions and testing of the archaeological record for paleolandscapes. Since all of the landscape facets at Manyara and Serengeti can be classified as riverine or non-riverine, regardless of their particular landscape association, then another way to compare landscape facets is to compare all riverine versus all non-riverine landscape facets.

Shrub cover and density are consistently higher in the riverine versus non-riverine landscape facets within any given landscape association (Figures 4-2 and 4-4). Even at the lacustrine terrace and alluvial fan, where tree structure did not vary between adjacent landscape facets (Figure 4-1), shrubs are more abundant at the riverine landscape facets.

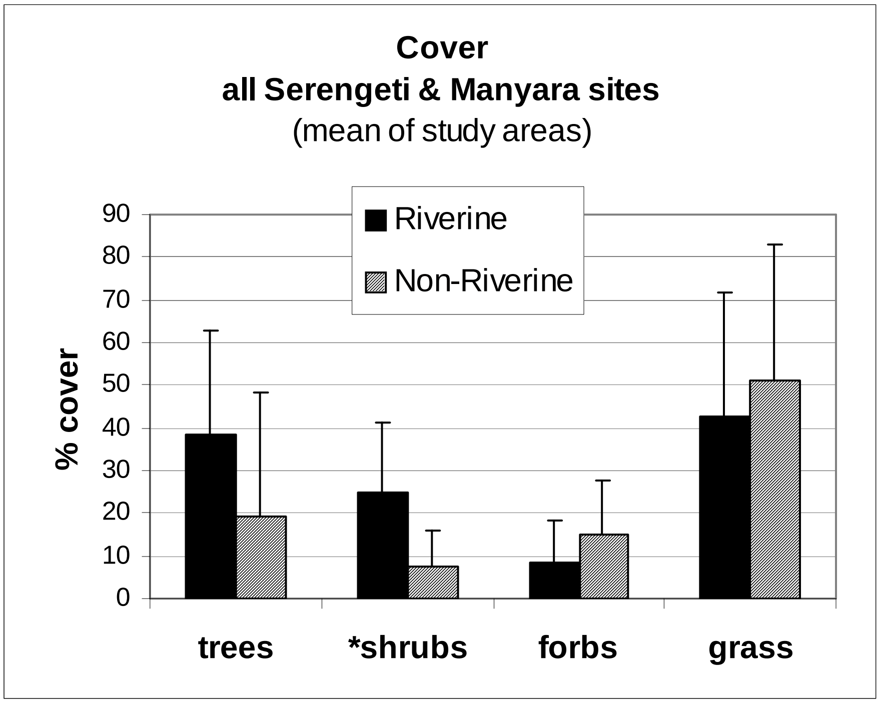
Figure 4-5. Tree heights of the modern analog study areas. Bars show the mean of study areas within each facet with one standard error. Note that no samples were taken for the non-riverine fluvial terrace nor for the non-riverine Serengeti woodlands.



When the percent cover of all riverine landscape facets is compared to that of all non-riverine landscape facets for each plant growth form, only shrubs show a significant difference of higher cover along rivers (t-test, d.f.=16, p=0.010; Figure 4-6).

Trees are tallest in Manyara's alluvial fan, the riverine landscape facet of the lacustrine plain, and the large spring dry land landscape facet at Ngorongoro (Figure 4-5). Most landscape associations show great contrast in tree height between adjacent landscape facets, with the exception of Manyara's lacustrine terrace and alluvial fan. For pairs of adjacent landscape facets at the small and large springs in Ngorongoro and the eastern Serengeti Plain, it is a comparison between one landscape facet that has trees and another that has no trees. For Manyara's lacustrine plain and the Western Serengeti Plain, where both riverine and interfluvial landscape facets have trees, the riverine trees are taller than the non-riverine ones.

Figure 4-6. Visual percent cover area for each growth form of all riverine versus all non-riverine study areas. Bars show the mean of study areas within each facet with one standard error. The difference between riverine versus non-riverine mean cover was only significant (*) for shrubs (t-test, d.f.=16, p=0.010).



To summarize, contrasts in vegetation structure among adjacent landscape facets are high between the riverine and non-riverine landscape facets of Manyara's lacustrine plain and the Eastern and Western Serengeti Plain, between the woodland and grassland sub-landscape facets of Ngorongoro's large springs, and between the Ngorongoro wetlands themselves with marsh vegetation and surrounding dry lands, whether grassy or wooded. Shrubs are distributed across landscape units somewhat differently than trees, with shrubs having higher densities and percent cover along riverine versus interfluvial landscape facets. Also, the shrub layer of the alluvial fan groundwater forest consists of single-stemmed tree saplings with few leaves versus the more bushy shrub growth forms in other habitats.

The possible explanations for differences in vegetation structure between landscape units are numerous, and before trying to explain those differences, it is necessary to take into account differences and similarities in species composition between landscape units. The next section explores the vegetation community composition of the modern study areas.

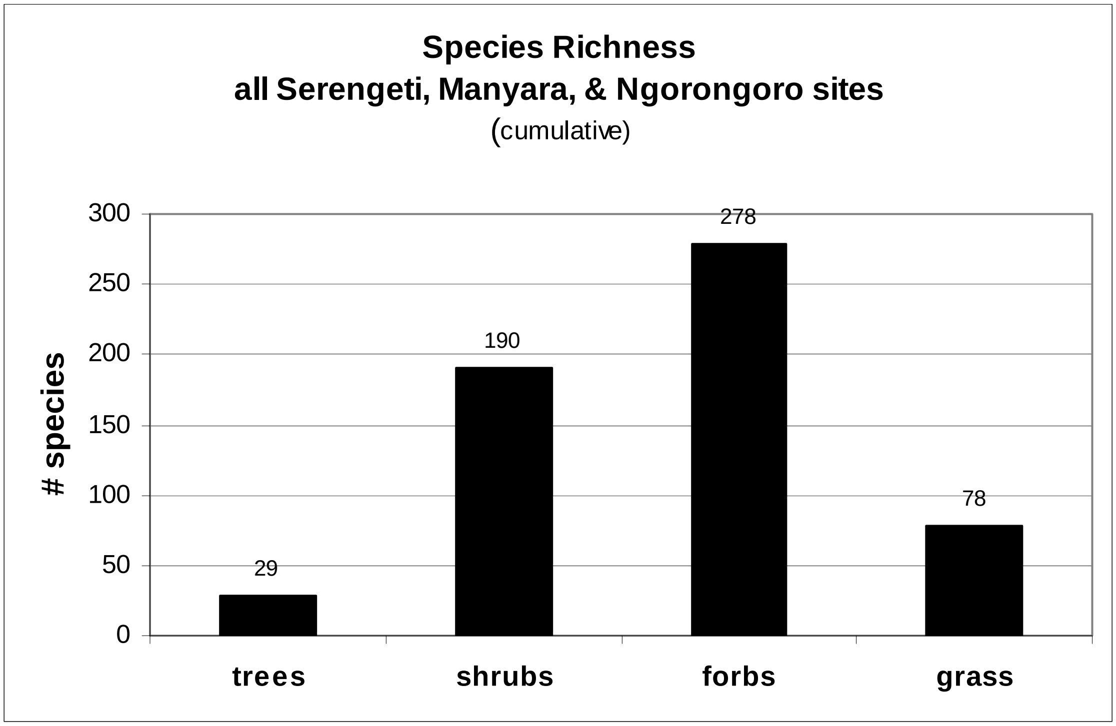
Community Composition

In all of my vegetation plots in Serengeti, Manyara, and Ngorongoro I encountered 476 plant species. When divided according to growth forms, 58% of species are forbs, 40% occur as shrubs, 16% are grasses, and 6% occur as trees (Figure 4-7). Some species were found in more than one growth form, for example, *Acacia tortilis* occurs as both a tree and a shrub. Consequently, the sum of the numbers of species by growth form is larger than the actual total of 476 unique species. Below I describe quantitative comparisons between landscape units by growth forms, followed by a description of the main species that occurred at the modern analog study sites and their known ecologies.

Quantitative Analyses of Community Composition

Quantitative analyses of community composition often compare species diversity, an index related to the number and abundance of species in an area. Species diversity is created and maintained by a range of different processes that relate to each habitat's ecology.

Figure 4-7. Cumulative species richness of all trees, shrubs, forbs, and grasses encountered in the Serengeti, Manyara, and Ngorongoro study areas.



For this study, I use species richness as an approximation of species diversity, as the landscape distribution pattern of those two measures was similar, and species diversity values could not be calculated for the Ngorongoro samples. The comparison of species richness and species diversity index values for the Serengeti and Manyara landscape facets are shown in Figure 4-8.

Trees

In this study I encountered twenty-nine species at least once in the tree growth form, one of which (*Ficus* sp.) was identified only to genus (Figure 4-7, Appendix 1). The mean number of tree species found within each single landscape facet ranges from 0

Figure 4-8. Comparison of species richness values with species diversity values for trees, shrubs, forbs, and grasses in Serengeti and Manyara. Paired data points represents the mean species richness values for the plots in one landscape facet, and the Shannon-Weaver index, e^H, calculated for the plots in that facet.

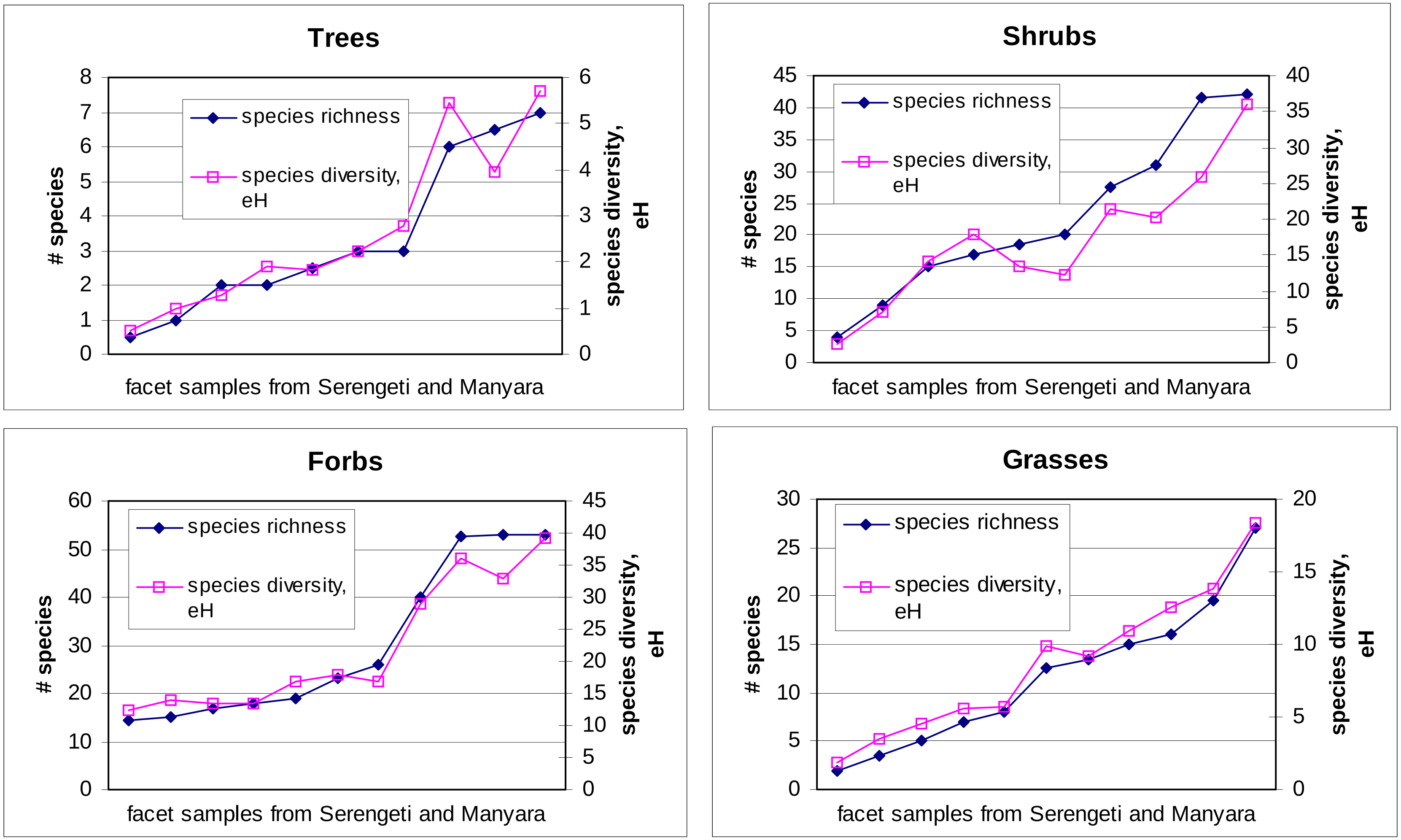
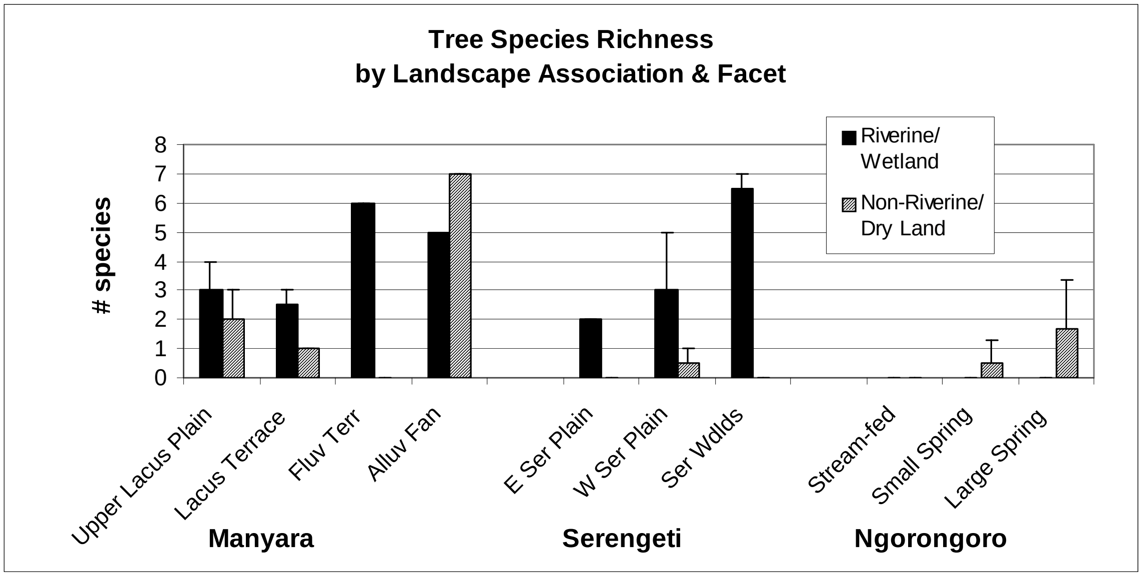


Figure 4-9. Tree species richness in the modern analog study areas. Bars show the mean of study areas within each facet with one standard error. Note that no samples were taken for the non-riverine fluvial terrace at Manyara nor for the non-riverine Serengeti woodlands.



to 7 (Figure 4-9). Most tree species were relatively rare overall, with only six species appearing in greater than five plots of all 206 plots within the 19 study areas at Manyara and Serengeti (Figure 4-10a). In terms of cumulative percentages, 36% of tree species occurred in only one plot, 57% occurred in one or two plots, and 93% of tree species occurred in less than 7% of the area sampled, that is, in 15 plots or less. This pattern persists for overall species richness within each landscape association at Manyara and Serengeti, that is, most species are rare, and very few occur in all of the plots within a single landscape association. Figures 4-11a and 4-11b depict this graphically, where the y-axis shows the number of species that occurred in the percentage of plots as depicted on the x-axis (0-9%, 10-19%, etc.). In the case of the fluvial terrace there were only four plots total, so the percentage designations in 25% intervals refer to whether species occurred in one, two, three, or four plots.

Figure 4-10. Frequency of occurrence for a.) trees, b.) shrubs, and c.) forbs and grasses in plots in the modern study areas at Manyara and Serengeti. Note different scales on the y-axes.

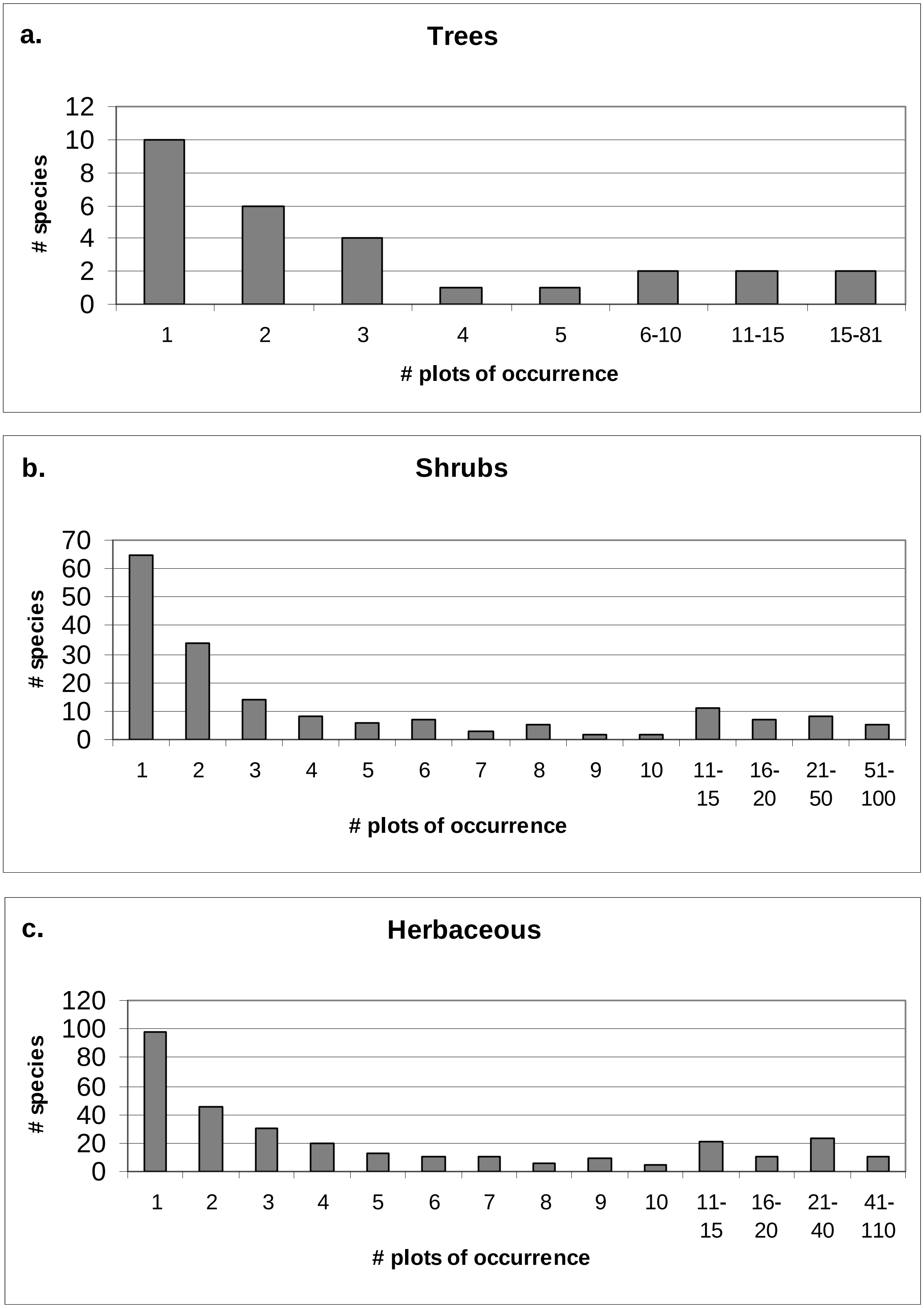


Figure 4-11a. Frequency of occurrence of plant species at the **Manyara** landscape associations.

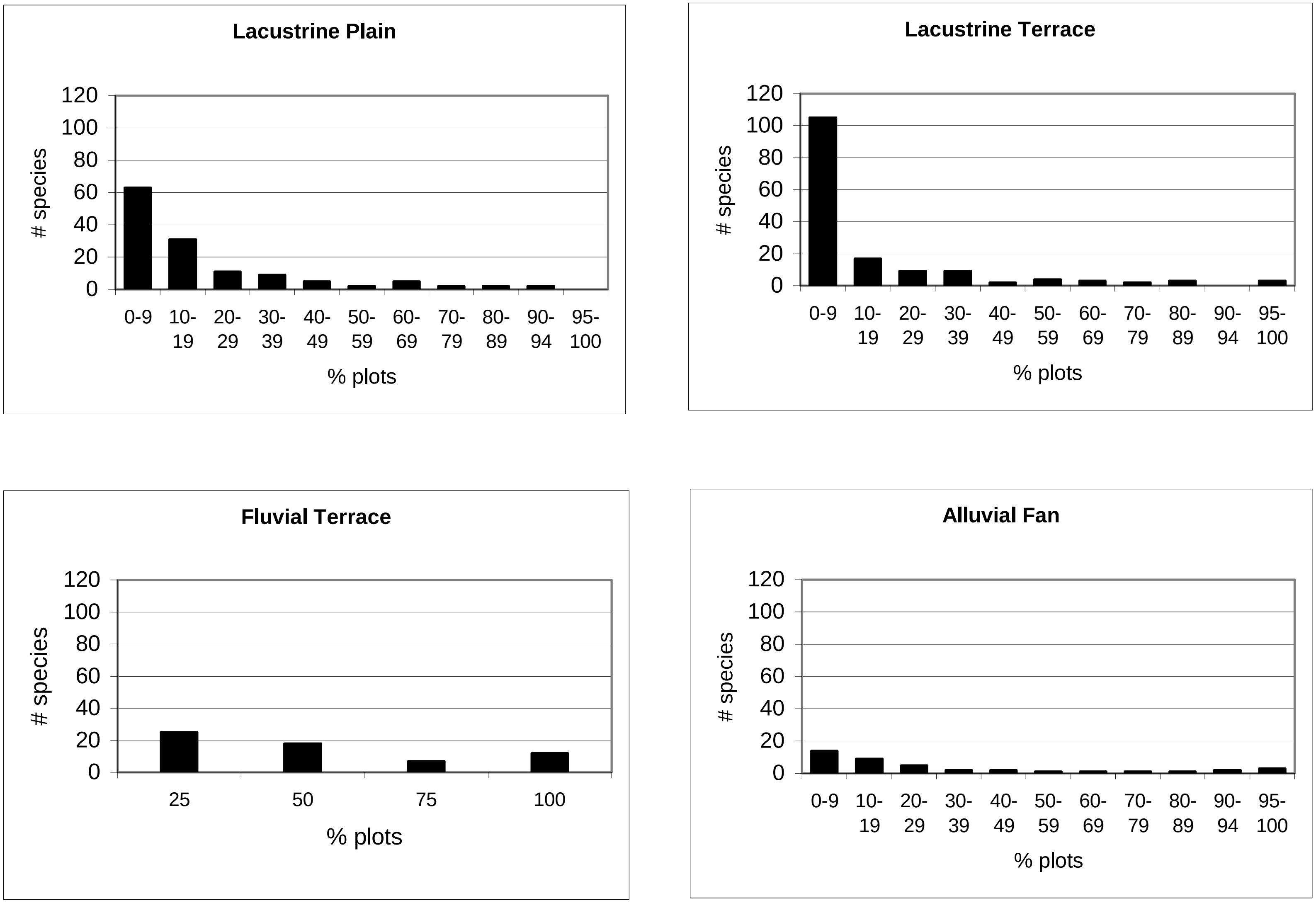
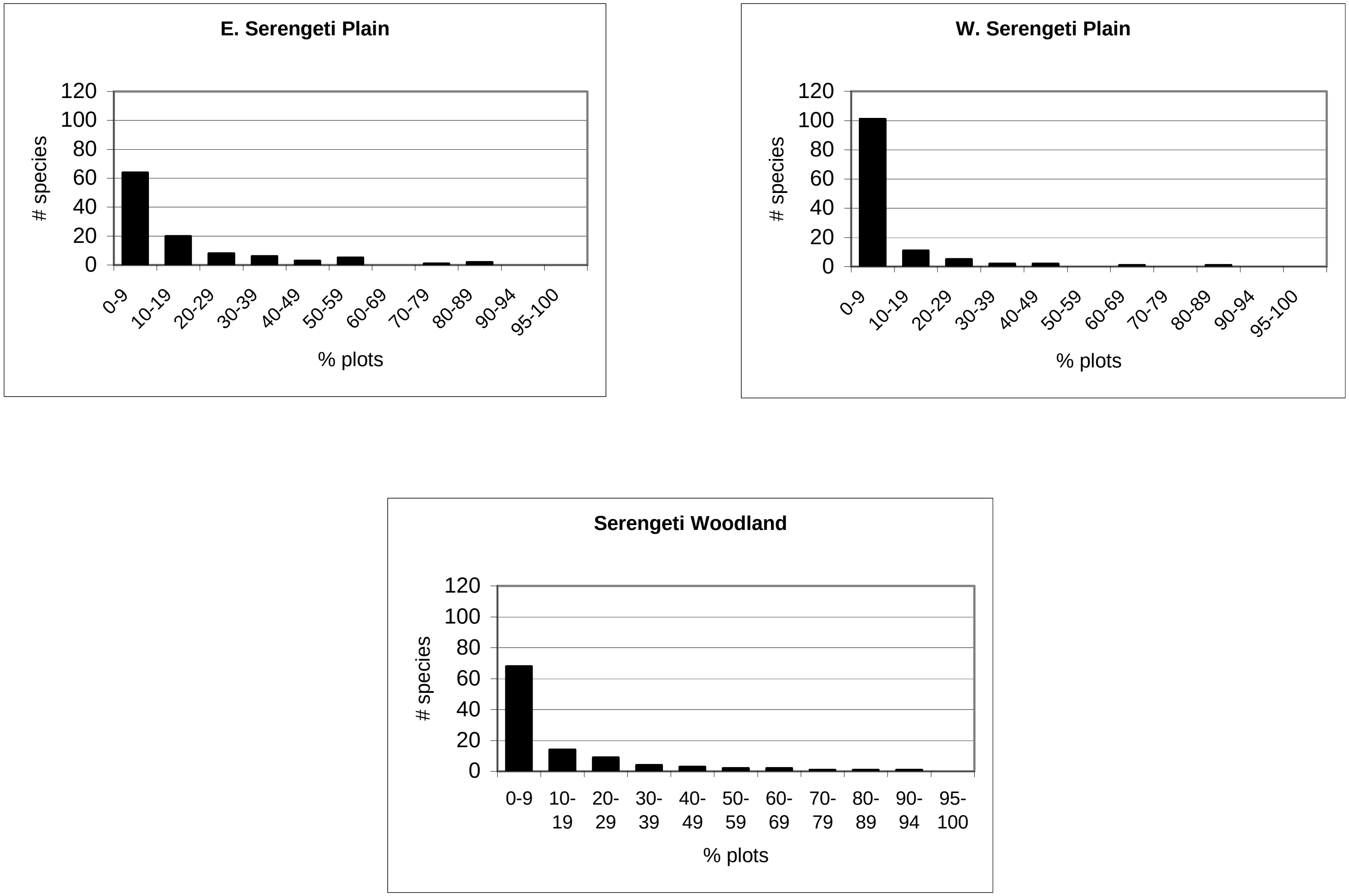


Figure 4-11b. Frequency of occurrence of plant species at the **Serengeti** landscape associations.

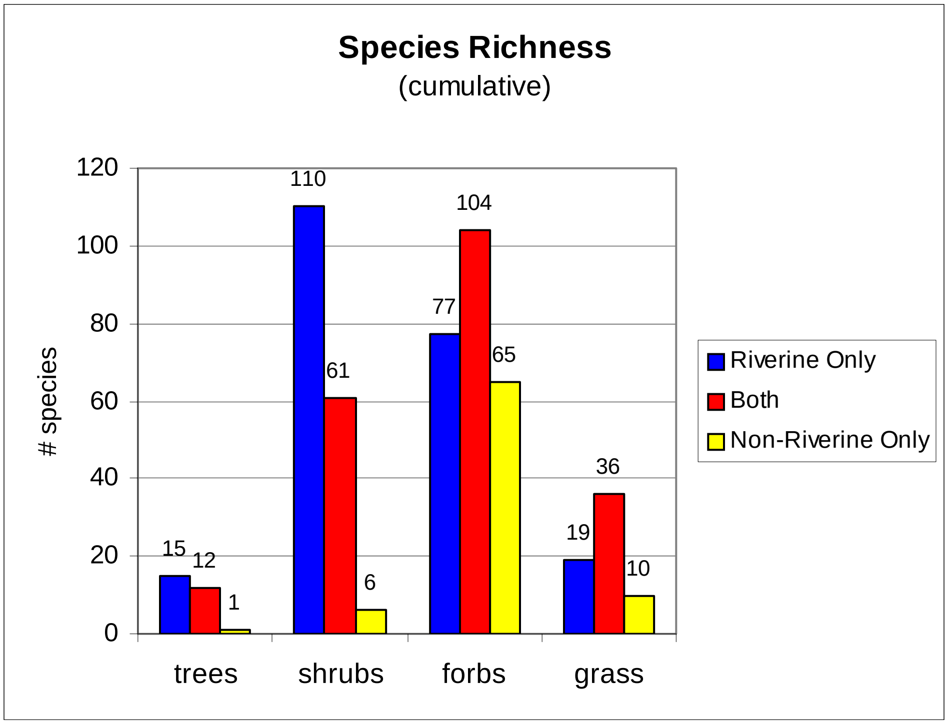


Landscape associations with the highest tree species richness values tend to be those that are forested or more heavily wooded, such as the alluvial fan/groundwater forest, the fluvial terrace, and the Serengeti Woodland (Figure 4-9). The variation within regions among tree species richness is similar in Serengeti and Manyara, and lower in Ngorongoro (Figure 4-9). This probably relates to the differences in types of landscape facets tested at Ngorongoro, many being wetlands without tree growth.

Tree species richness at the level of landscape associations varies widely, somewhat in conjunction with variations in tree cover values. Similarly, landscape facets vary according to their ability to support trees at all. Variations among and within landscape facets may also reflect the environmental variation, age, or successional stage of that particular landscape facet at any given time (e.g., Dublin, 1995; Belsky, 1989). Evidence from the recent history of the Serengeti suggests that the turnover period for physiognomic types in some landscape facets may be on the order of centuries or less, going from grassland to woodland, and back to grassland again within the past century (Sinclair, 1979a; Dublin, 1995). On the other hand, riverine landscape facets might be predicted to remain somewhat more stable throughout those fluctuations due to their relatively constant water availability.

Comparing pairs of riverine versus non-riverine landscape facets at Serengeti and Manyara, tree species richness is always higher along rivers except at the alluvial fan (Figure 4-9). In general, higher tree species richness is expected along rivers in semi-arid habitats because during the dry season, sufficient water may only be found deep below the surface, following the dry river channels. Water is one of the most important limiting factors for vegetation in savanna habitats (Cole, 1986). Therefore productivity should be higher where water is more readily available along the rivers, and tree species diversity in general may be expected to be higher in riparian zones (Naiman and Décamps, 1997). The lack of contrast in tree species richness among riverine and non-riverine landscape facets of Manyara's alluvial fan probably relates to the ubiquitous high groundwater table in that landscape association, which may be relatively independent of the small rivers on the surface. Despite the large variation in tree species richness of riverine landscape facets overall, only one tree species occurred exclusively at non-riverine sites (within the study areas), while 15 species occurred exclusively at riverine sites and 12 were found in both (Figure 4-12).

Figure 4-12. Cumulative species richness for the Manyara and Serengeti study areas, by growth form and according to whether the species occurred in riverine facets only, non-riverine facets only, or both riverine and non-riverine facets.

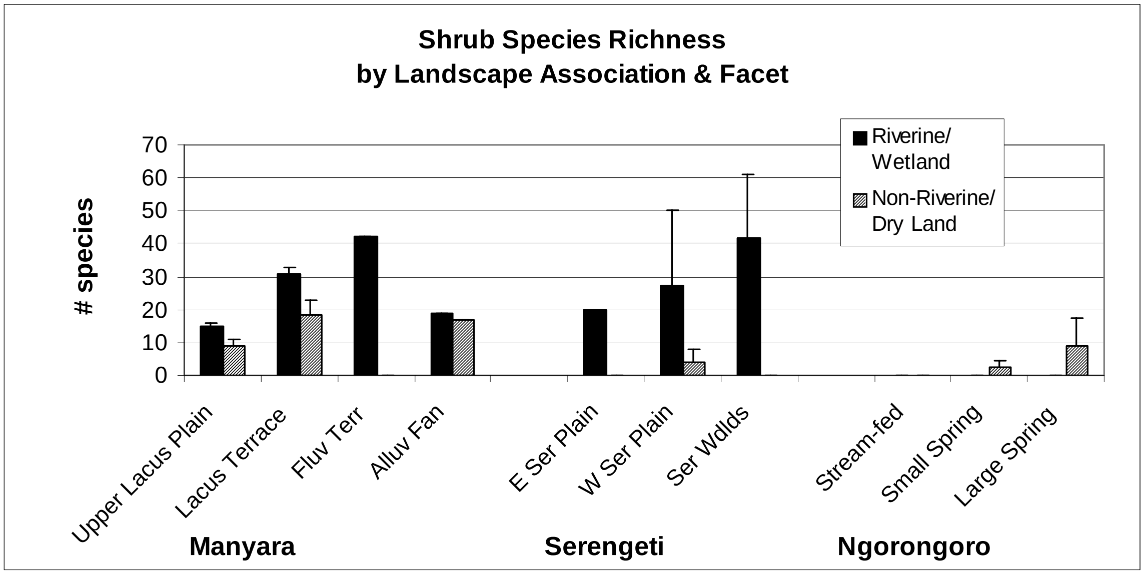


Shrubs

Within the Serengeti, Manyara, and Ngorognoro sites, 190 species were recorded as shrubs, 22 of which were identified only to genus (Figure 4-7, Appendix 1). Shrub species richness was higher in the Manyara and Serengeti regions compared to Ngorongoro Crater (Figure 4-13). Many of the landscape units sampled at the Crater did not have shrubs because they were marshes or open grassland.

Among landscape associations, shrub species richness was highest in Manyara's fluvial terrace with 42 shrub species, and in the Serengeti Woodland, averaging 42 species and ranging from 22 at the Sangare River to 61 at the Mbalageti River (Figure 4-13). Of the landscape associations in which both riverine and non-riverine landscape facets were sampled, the riverine sites were always higher in shrub species richness (Figure 4-13).

Figure 4-13. Shrub species richness in the modern analog study areas. Bars show the mean of study areas within each facet with one standard error. Note that no samples were taken from the non-riverine fluvial terrace nor from the non-riverine Serengeti woodlands.



When all riverine landscape facets are compared to all non-riverine landscape facets, regardless of landscape association, the shrub species richness along rivers is significantly higher than away from rivers (t-test, d.f.=16, p=0.01). Shrub structure - cover and density - were also significantly higher along all riverine versus non-riverine sites (see Figure 4-6 for the cover comparisons). For trees, none of these measures showed significant differences between all riverine and all non-riverine landscape facets, mostly because of the lack of contrast in tree values at the alluvial fan and lacustrine terrace landscape associations.

Shrub species richness contrasted strongly in adjacent riverine versus non-riverine landscape facets within the Western Serengeti plain and in the Eastern Serengeti Plain. In Ngorongoro Crater, only the dry land landscape facets adjacent to springs had shrubs (Figure 4-13). Shrub diversity contrasted moderately in Manyara's lacustrine plain and lacustrine terrace. At Manyara's alluvial fan, there was virtually no contrast between adjacent riverine and non-riverine landscape facets.

Cumulative species richness values confirm shrubs' overall preference for riverine landscape facets: of all shrub species 110 were exclusively riverine, 61 were found at both riverine and non-riverine sites, and six species were found in non-riverine sites only (Figure 4-12).

Like trees, most shrub species were relatively rare, with 37% occurring in only one plot, 56% in two plots or less, and 88% in 15 plots or less (Figure 4-10b). The five most common shrubs each occurred in 60 or more of the 206 plots total. Within each landscape association, very few shrub species occur in many or all of the plots (Figures 4-11a and 4-11b).

Herbs (Forbs and Grasses)

In the ground layer of the Serengeti, Manyara, and Ngorongoro sites, I encountered 278 forb species, 27 of which were identified only to genus, and 78 grass species, seven of which were identified only to genus (Figure 4-7, Appendix 1). The Serengeti and Manyara regions contain similar ranges of values for forb and grass species richness, while the Ngorongoro study sites have fewer species (Figures 4-14, 4-15).

Unlike shrubs, there is no marked difference in species richness of forbs and grasses at riverine versus non-riverine sites (Figure 4-12). The greatest number of forb species (104) occurred in both riverine and non-riverine habitats. The difference between those that were exclusively riverine (31% of forbs, and 29% of grasses) and those that were exclusively non-riverine (26% of forbs and 15% of grasses) was smaller than the differences between trees and shrubs that were exclusively riverine (54% of trees and 62% of shrubs) versus those that were exclusively non-riverine (4% of trees and 3% of shrubs). Like trees and shrubs, most forb and grass species were relatively rare: 31% occurred in only one plot, 46% in two plots or less, and 86% in 15 plots or less of the 206 plots total (Figure 4-10c).

Forbs and grasses have notably high species richness values in four landscape facets: the riverine and non-riverine landscape facets of Manyara’s lacustrine terrace, the non-riverine landscape facet of Manyara’s lacustrine plain, and the riverine landscape facet of the Eastern Serengeti Plain (Figures 4-14). Grasses are also fairly diverse in the other Serengeti facets (Figure 4-15). One possible explanation is that in areas with fewer trees and shrubs, herbaceous species diversity is higher due to lack of competition for resources with the woody plants (see Discussion). The landscape facets rich in

Figure 4-14. Forb species richness in the modern analog study areas. Bars show the mean of study areas within each facet with one standard error. Note that no samples were taken from the non-riverine fluvial terrace nor from the non-riverine Serengeti woodlands.

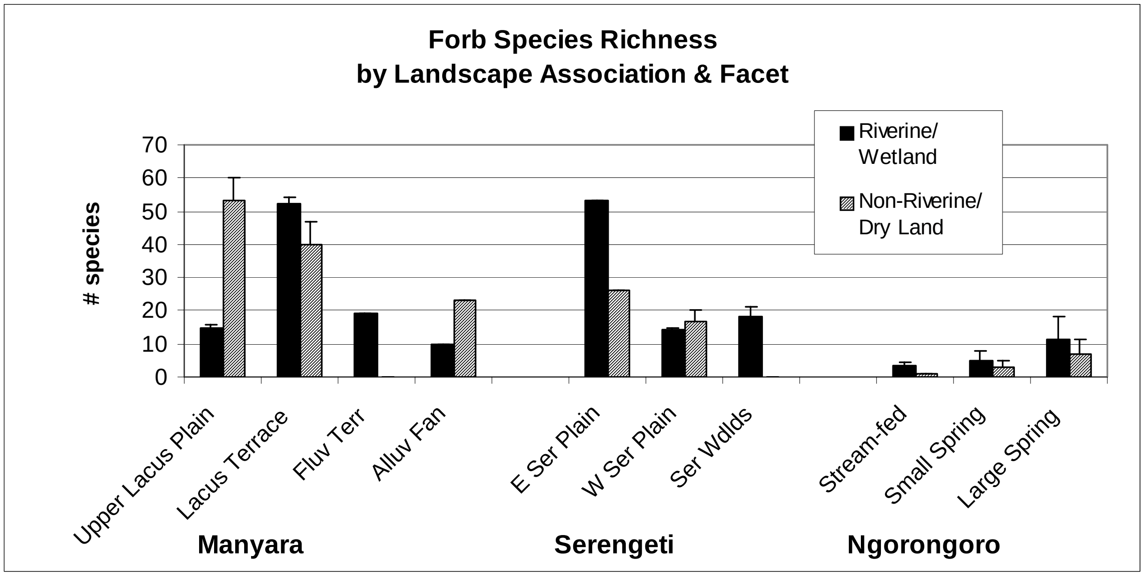
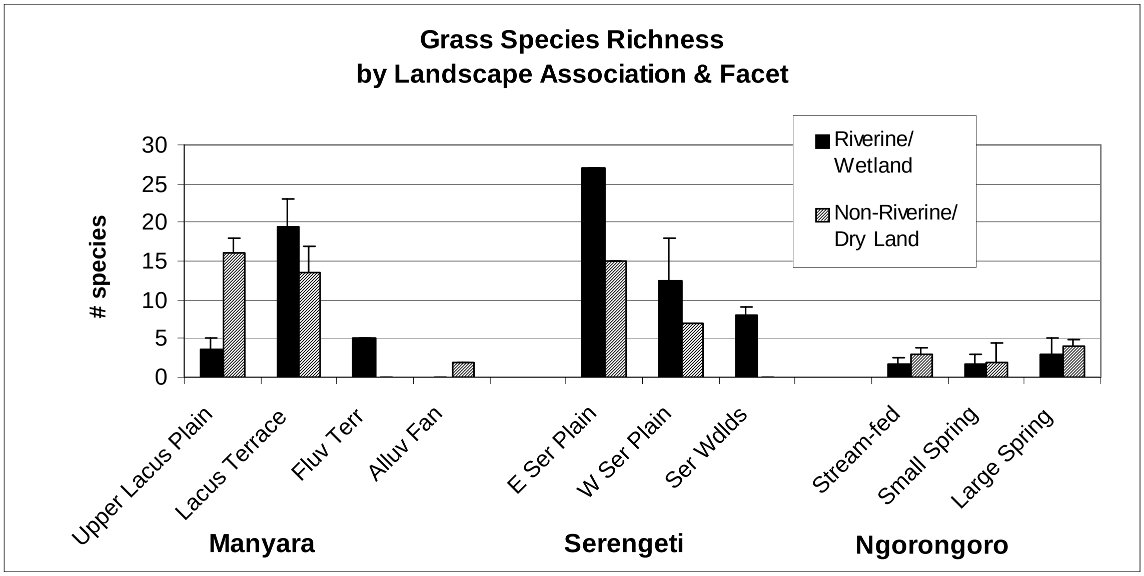


Figure 4-15. Grass species richness in the modern analog study areas. Bars show the mean of study areas within each facet with one standard error. Note that no samples were taken from the non-riverine fluvial terrace nor from the non-riverine Serengeti woodlands.



herbaceous species are not unique in terms of vegetation structure, however: three are bushland and one is bush grassland. Forb species richness does increase with decreasing tree cover across all Serengeti and Manyara sites, but it is not a significant relationship (regression, R-square = 0.11, p=0.161). There was also no discernable pattern between forb species richness and shrub cover across all sites (regression, R-square = 0.01, p=0.65). The two grassland landscape facets which had the fewest trees and shrubs, the interfluves of the Eastern and Western Serengeti Plain, had relatively low forb and grass species richness (Figures 4-14 and 4-15).

Species Composition

Tree Species Composition

The tree species composition of sites is depicted in Figure 4-16 in a layout that enables easy comparisons between landscape facets, landscape associations, and regions. The importance value for each species at a single landscape facet or study area is based on a combination of measures of relative cover, relative frequency, and relative density (see Chapter Three). Each of those relative measures is based upon, for example, the frequency of a species in all of the plots within a given study area, or the average cover or average density of a species in all of the plots within a given study area (also described in Chapter Three). Importance values are shown as a relative percentage in Figure 4-16. Species that did not have an importance value of 12% or more in at least one study area were lumped into a category called “other”, which is shown as the white area at the right hand side of some of the bars.

Figure 4-16. Tree species composition of the modern analog study areas based on importance values for a) Manyara and Serengeti and b) Ngorongoro.

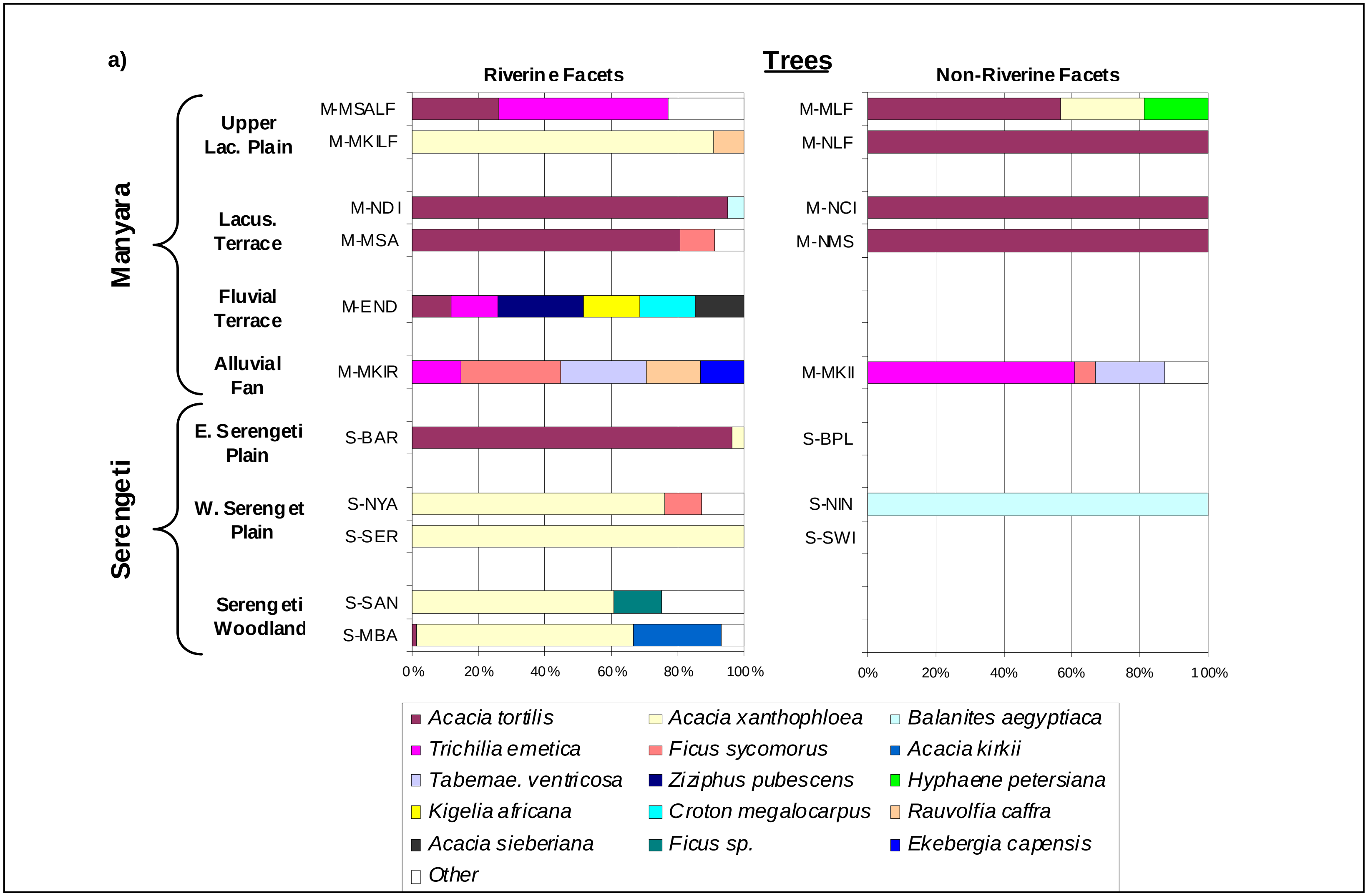
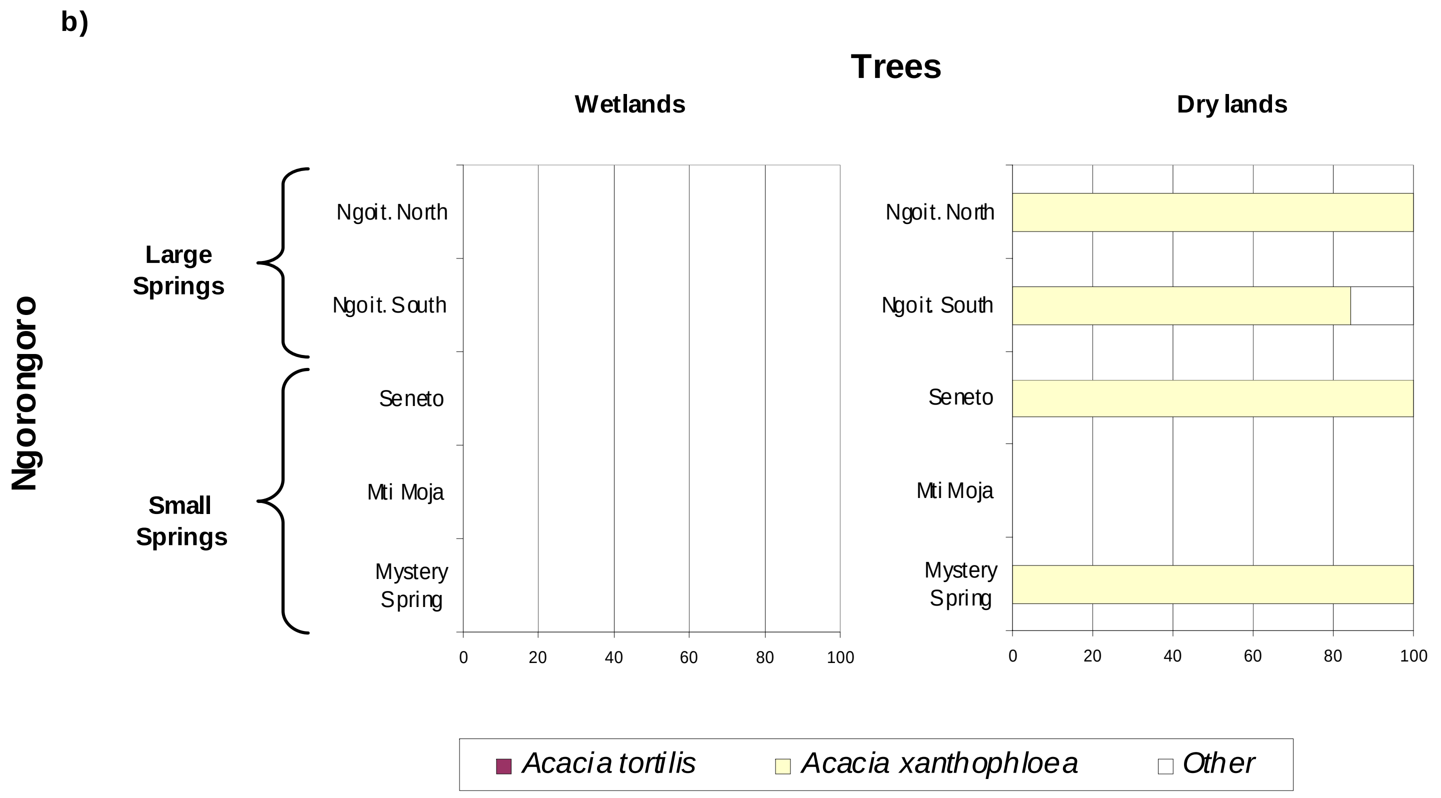


Figure 4-16 (cont.)



The two most common tree species across all three regions are *Acacia tortilis* and *Acacia xanthophloea*. *Acacia tortilis*, commonly known as the umbrella tree, or as one of many East African "thorn trees," prefers relatively well-drained soils and in general is common along ephemeral or dry river channels (Beentje, 1994; Mbuya *et al*., 1994). *Acacia xanthophloea* is a tall, thorny tree with very distinctive yellow bark. It typically grows in groups where its roots have access to a high ground water table, such as along rivers, lakes, or in low-lying, swampy areas (Coates Palgrave, 1993; Lind and Morrison, 1974:87). *Acacia xanthophloea* derived its common name, the fever tree, from its association with these swampy habitats which tend to harbor malaria-carrying mosquitoes.

At Manyara, *Acacia tortilis* is by far the most common tree in the bushland-covered lacustrine terrace, and also grows on the upper lacustrine plain (Figure 4-16). In Serengeti *Acacia tortilis* is the dominant tree in the Barafu Valley of the Eastern Serengeti Plain. It did not grow in the Ngorongoro Crater sites.

Acacia xanthophloea grows in each of the three regions: it is the dominant tree along the riverine landscape facets of the Serengeti Woodland and the Western Serengeti Plain, it occurs in dense numbers on the lowest reaches of Manyara's Mkindu River on the lacustrine plain, and it is the dominant tree in all of the Small and Large Springs at Ngorongoro Crater that support tree growth.

Trees are sparse or absent altogether in the interfluvial landscape facets of the Eastern and Western Serengeti Plain. An exception is a single tree that was within plot borders at the Nyamara Interfluve, a specimen of *Balanites aegyptiaca*, which is technically assigned a 100% importance value for that site (Figure 4-16). *Balanites* species are common in the arid habitats of Africa, and *Balanites aegyptiaca* tends to grow in relatively well-drained localities where its roots still have access to a source of water. This species occurred in small numbers in Manyara's lacustrine terrace as well.

The tree species that occurred in the dry land landscape facets near several Ngorongoro Small Springs were relatively short *Acacia xanthophloea* trees (Figure 4-16). Ngorongoro's Large Spring dry land landscape facets were dominated by *Acacia xanthophloea* trees, and other tree species were present in the more elevated regions of Ngoitokitok South on the footslopes of the Crater wall. Ngorongoro wetland sites have marsh vegetation and do not support trees.

The groundwater forest in Manyara's alluvial fan landscape association is quite different from many other landscape associations in Manyara, Serengeti, and Ngorongoro in terms of tree species composition (Figure 4-16). The alluvial fan's broad-leaved, tall groundwater forest trees are those typically found in riverine forests in other parts of Africa. *Trichilia emetica*, common in the groundwater forest/alluvial fan, reaches heights of 30-40 meters and is also found in the evergreen forests of large riverine floodplains along the Tana River in Kenya (Hughes, 1988). It prefers well-drained, rich soil and a perennially high ground water table, such as is found in the northern end of Lake Manyara National Park (Mbuya *et al*., 1994; Greenway and Vesey-Fitzgerald, 1969; Loth and Prins, 1986). *Ficus sycomorus*, a potentially huge fig tree, is also a common feature of the groundwater forest/alluvial fan. *Trichillia* sp. and *Ficus* sp. have broad leaves unlike the common arid-adapted tree species at Serengeti and Manyara, such as *Acacia tortilis* and *Acacia xanthophloea*, which have tiny microphyll leaves and abundant thorns.

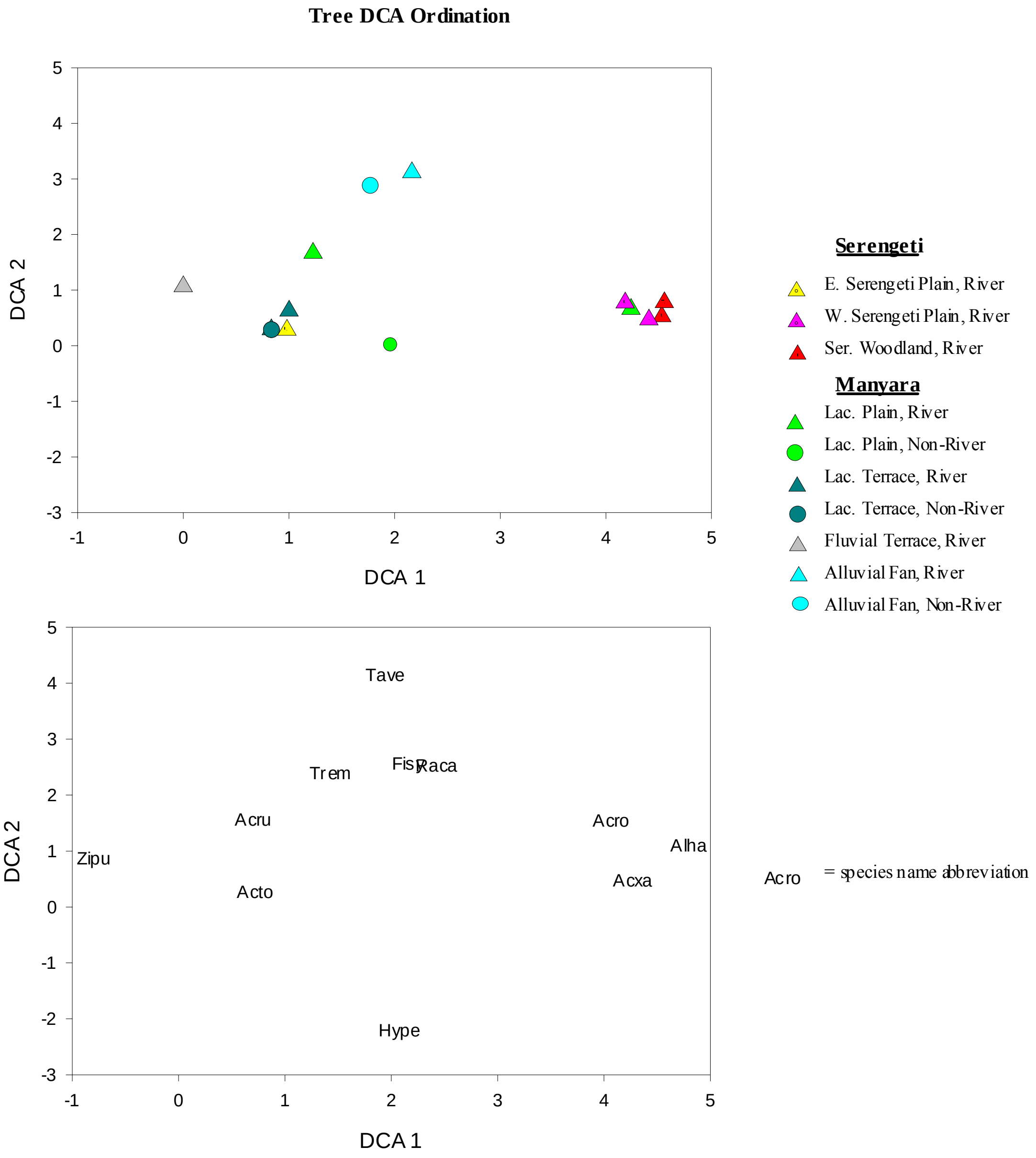
Manyara’s fluvial terrace shares a few tree species in common with the groundwater forest, such as *Trichilia emetica*, and is like the groundwater forest in being more species rich in trees than other landscape associations (Figures 4-9, 4-16). Also growing in the fluvial terrace are tree species common in drier landscape associations, such as *Acacia tortilis*. The large Endabash River delta (fluvial terrace) was created by fluvially transported sediment and provides soil that is well-drained, but is derived from a larger proportion of granite basement rock in addition to volcanic ash (Prins and Van der Jeugd, 1992). Manyara’s alluvial fan sits on top of a relatively high water table, and may have slightly less well-drained soils due to their higher content of volcanic origin (Prins and Van der Jeugd, 1992).

Tree DCA Results

A detrended correspondence analysis (DCA) ordination was performed on tree species importance values from Manyara and Serengeti (Figure 4-17). Sites with no trees in Manyara and Serengeti were excluded, and the Ngorongoro sites were excluded due to a lack of comparable data. Since most of the tree species variation occurred in Manyara and Serengeti, the results are still informative.

Much of the tree species variation is captured in axis one, which has a high eigenvalue (λ=0.902). This suggests that a strong environmental gradient accounts for that variation (Jongman *et al*., 1995). The seasonally water-logged, *Acacia xanthophloea*-dominated riverine landscape facets of the Western Serengeti Plain and the Serengeti Woodland fall at the right-hand extreme of axis one, while just left of center are the well-drained *Acacia tortilis*-dominated sites of Manyara’s lacustrine terrace and upper

Figure 4-17. DCA Ordination of trees in the Serengeti and Manyara modern study areas. The top figure shows the study areas and the bottom shows species. Full species names can be found in Appendix 1. In the top figure, symbols that are not visible because they are behind one lacustrine terrace non-river site at DCA 1= 0.85, DCA 2=0.28 are: an

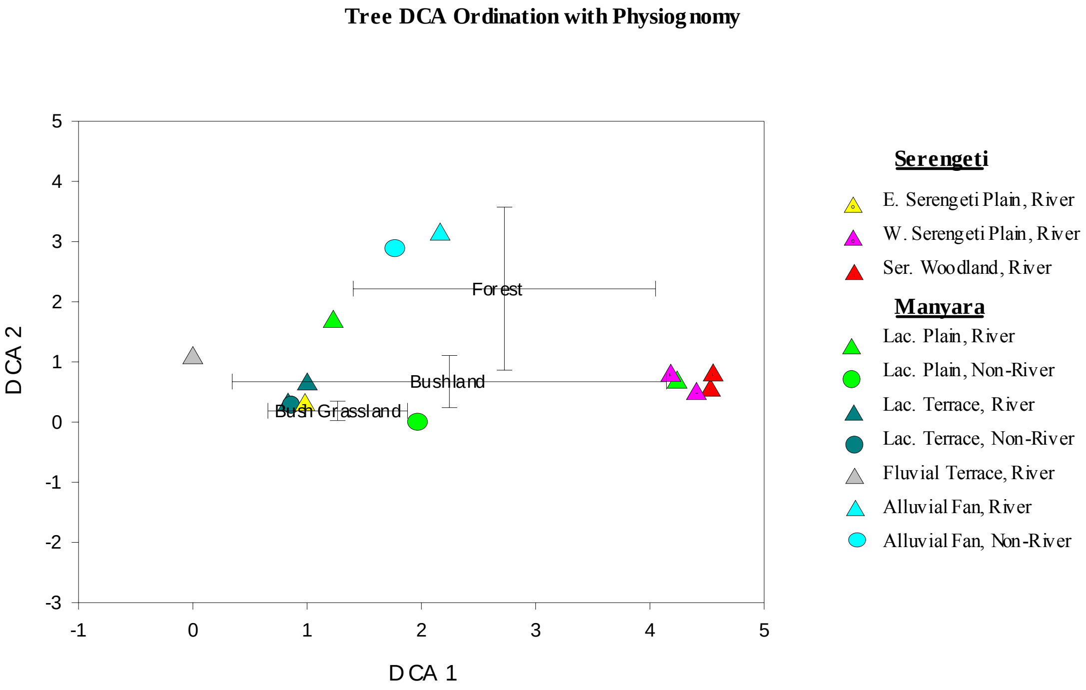


lacustrine plain, and Manyara's alluvial fan (groundwater forest) sites. Manyara's fluvial terrace falls at the left-hand extreme of axis one. As discussed below, axis one may reflect a gradient related to soil drainage, and/or general moisture availability.

The second axis also has a relatively high eigenvalue (λ=0.628). The Serengeti sites are all constrained to similar values along axis two. The Manyara sites are dispersed across axis two, however, which implies that axis two reflects an environmental gradient within the Manyara region. Manyara's alluvial fan sites are at the positive extreme of axis two, followed by an upper lacustrine plain river site (the lower Msasa), and the fluvial terrace river site (Endabash River). The clusters of *Acacia tortilis*-dominated sites and *Acacia xanthophloea*-dominated sites both occur near the low end of axis two, with the non-riverine lacustrine plain site of the Msasa lake flat at its lowest value. With the freshwater dominated alluvial fans at one extreme and the sites more influenced by saline/alkaline lake water at the other, axis two may represent a gradient within Manyara of increasing salinity and alkalinity with decreasing values of axis two.

Physiognomic categories were plotted on the tree ordination as the centroid of all of the site scores of a given physiognomic category, a technique that can be informative regarding the relationship between species composition and vegetation structure (Figure 4-18). Tree cover decreases slightly along axis one and along axis two, but there is a great deal of dispersion along axis one within the bushland and forest categories, and along axis two within the forest category. In general, tree and shrub cover decrease with moisture availability in East African "arid savannas" (Bell, 1982).

Figure 4-18. DCA Ordination of trees in the Serengeti and Manyara modern study areas with physiognomic categories. The word of each habitat type is plotted as the centroid of the values for all study areas in that category. Bars show the range of values for which study areas with each habitat type extend on the DCA 1 and DCA 2 axes.



Tree DCA Discussion

The interpretation of axis one (Figure 4-17) as reflecting soil drainage conditions and general moisture availability is supported by some ecological observations of the important tree species in these sites. The separation of *Acacia tortilis*- and *Acacia xanthophloea*- dominated sites along axis one is consistent with the observation that these species rarely overlap or co-occur in a single landscape facet, although they may occur in close proximity at the ecotone between landscape facets. In general, *Acacia tortilis* likes fairly well-drained soils, while *Acacia xanthophloea* thrives along the often clayey, poorly-drained margins of lakes or rivers. In a study of vervet monkeys at Amboseli National Park, Kenya, a place also dominated by *Acacia tortilis* and *Acacia xanthophloea* trees, Wrangham and Waterman (1981:717) found little overlap in the tree species distribution. *Acacia tortilis* occupied the relatively elevated areas with well-drained soils, while *Acacia xanthophloea* occurred on the edges of water holes or along drainage lines, and was associated with other hydrophytic species. A similar situation is found at the Olbalbal depression on the eastern edge of the modern Olduvai Gorge, where *Acacia tortilis* occupies the slightly elevated well-drained soils, and *Acacia xanthophloea* occupies the lower, periodically flooded swampy area (personal observation). DCA axis one reflects these ecological differences between *Acacia tortilis* and *Acacia xanthophloea*, and represents an environmental moisture gradient related to soil drainage and general moisture availability.

The interpretation of axis two as representing a saline/alkaline gradient within Manyara gains support from the known ecological tolerances of *Acacia xanthophloea* and *Acacia tortilis*. These two species occur together near the lower extreme of axis two, while the alluvial fans/groundwater forest sites are near its upper extreme. *Acacia xanthophloea* and *Acacia tortilis* trees occur in relatively saline/alkaline soil conditions, such as the highly evaporated soils derived from volcanic ash that cover most of the study areas. In these hot and dry savannas, soils have a high evaporative demand that results in a high concentration of salts in their upper horizons. If the salt content is great enough, sodium can go into the soil solution to react with carbonate and bicarbonate ions, thereby raising the pH to 9 or more, and creating a saline-alkaline soil (Lind and Morrison, 1974:174). The soils of Manyara's alluvial fans/groundwater forest are probably less saline and less alkaline than other Manyara soils and Serengeti soils due to their inundation with freshwater from springs at the base of the escarpment.

The DCA ordination (Figure 4-17) also provides a way to assess whether the sites from the three different levels of landscape units (regions, associations, landscape facets) are similar in tree species composition. Regions are mostly separated in the tree ordination, with the majority of Manyara sites to the left on axis one, and most Serengeti sites to the right on axis one. The sites within a given landscape association also remain close together on the tree DCA, with the exception of those belonging to Manyara's lacustrine plain. All four of Manyara's lacustrine plain sites (two are riverine and two are non-riverine, one of which is behind the cluster at DCA 1= 0.85, DCA 2=0.28) are separated from one another along both axes.

Given the environmental gradient interpretations presented above, as well as experience in the field, the soil conditions and moisture availability for trees probably vary within Manyara's upper lacustrine plain landscape association to a greater degree than within other landscape associations. For example, of the two riverine sites, one is along the lower reaches of the perennial Mkindu River (M-MKILF) and was dominated by *Acacia xanthophloea* trees, while the other was along the Msasa River (M-MSALF) in the uppermost part of the lacustrine plain, where the stream was much larger but ephemeral. The Msasa site's tree species included *Acacia tortilis* and *Trichilia emetica*. Landscape facet-level differences in tree species composition were great on the upper lacustrine plain, but small at the alluvial fan, lacustrine terrace, and in the Serengeti facets, as seen by their close proximity in ordination space.

In sum, soil drainage, moisture availability, and saline/alkaline gradients may be the most important environmental factors affecting the species distribution of trees in these sites. The fact that physiognomic categories correspond only moderately well with DCA axis one (Figure 4-18) means that the most important environmental variable(s) relating to tree species composition, represented by axis one, is not the same variable(s) that relates most strongly to structural measures. For example, the cluster of sites in the far right, which are the *Acacia xanthophloea*-lined rivers, include four bushland and one forested site. In this case species composition does not "predict" spatial proximity between landscape units either, as the cluster represents three different landscape associations and two regions. Thus, knowing the vegetation structure of a landscape facet does not necessarily allow for very accurate prediction of its tree species composition in these semi-arid savanna habitats. Tree species composition is not typically unique among regions, but for most landscape associations tree species were similar in adjacent riverine and non-riverine landscape facets. The exception is Manyara's upper lacustrine plain, in which landscape facets varied extensively in tree species composition.

Shrub Species Composition

The number of shrub species per landscape facet is generally greater than the number of tree species, as seen on the graph summarizing shrub species composition (Figure 4-19). In the Manyara region, the landscape associations that are dominated by *Acacia tortilis* trees, the lacustrine terrace and non-riverine landscape facets of the lacustrine plain, tend to have a shrub composition including *Acacia tortilis* in shrub growth form, *Salvadora persica*, *Acalypha fruticosa*, *Maerua triphylla*, and *Capparis tomentosa* (Figure 4-19).

Although the fluvial terrace has a different tree species composition from other Manyara landscape associations, the shrub species that grow there are the same ones that grow on the lacustrine plain and lacustrine terrace. *Acalypha fruticosa* and *Cordia sinensis* are particularly important shrubs in the fluvial terrace.

Most of the shrubs at Manyara are thick, bushy and can grow to three meters tall and three meters across or more, though often they have dimensions of one or two meters. *Acalypha fruticosa* is the exception; it is smaller and thinner and often grows in shady areas. *Capparis tomentosa* has hooked thorns and grows as a climber, sometimes creating massive, impenetrable thickets. *Salvadora persica* has been described as a salt indicator (Mbuya *et al*., 1994; Lind and Morrison, 1974:174), and is often found along rivers or lakes and in dry *Acacia* bushland and wooded grassland (Beentje, 1994). Its leaves are bright green, thick, slightly succulent, and the bark contains an antibiotic that helps prevent tooth decay (Mbuya *et al*., 1994). *Cordia sinensis* is a widespread shrub in semi-arid Africa, can grow on stony or saline soils, and is known to prefer moist river beds (Mbuya *et al*., 1994). Unlike the other shrubs of the lacustrine plain, lacustrine

Figure 4-19. Shrub species composition of the modern analog study areas based on importance values for a) Manyara and Serengeti and b) Ngorongoro.

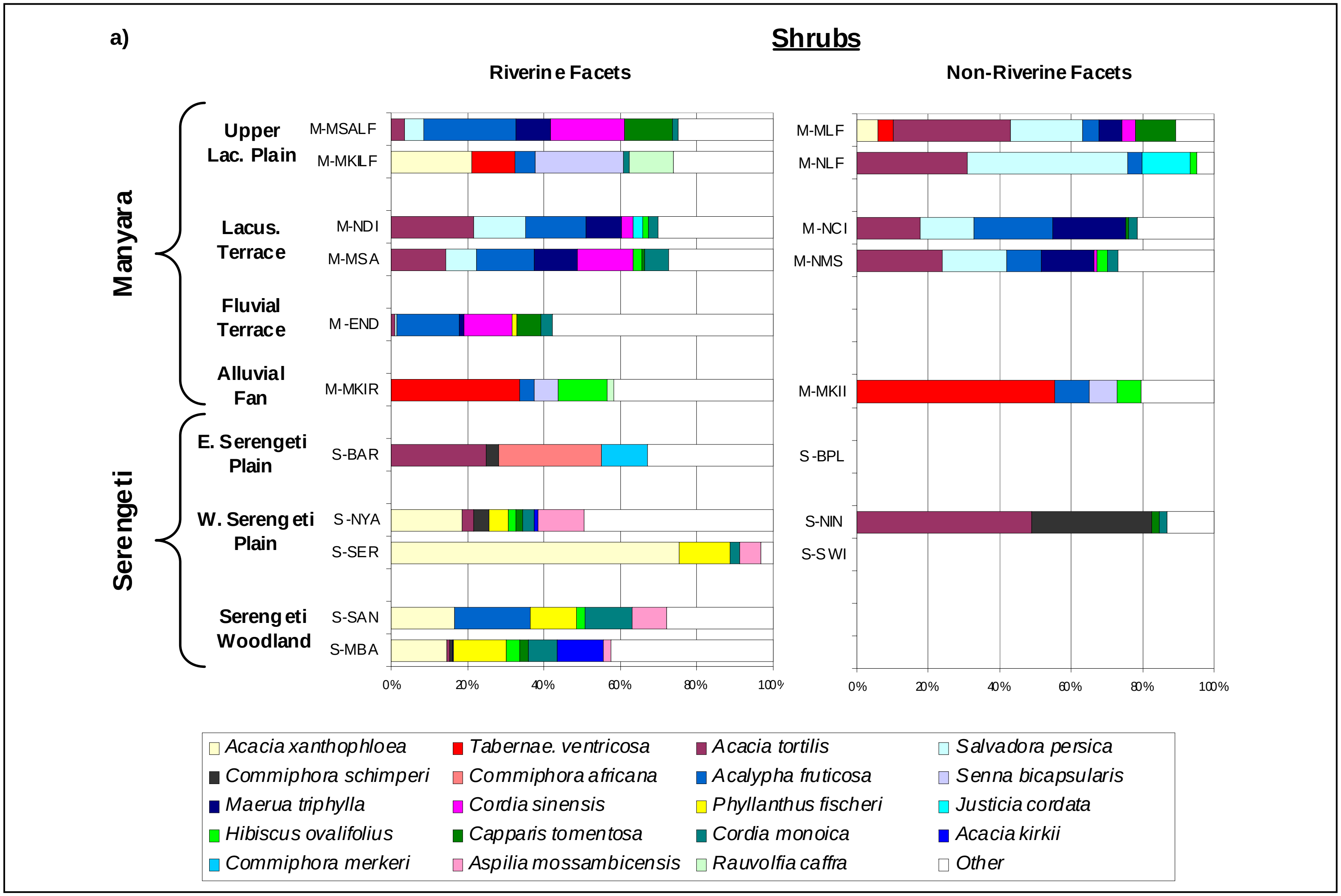
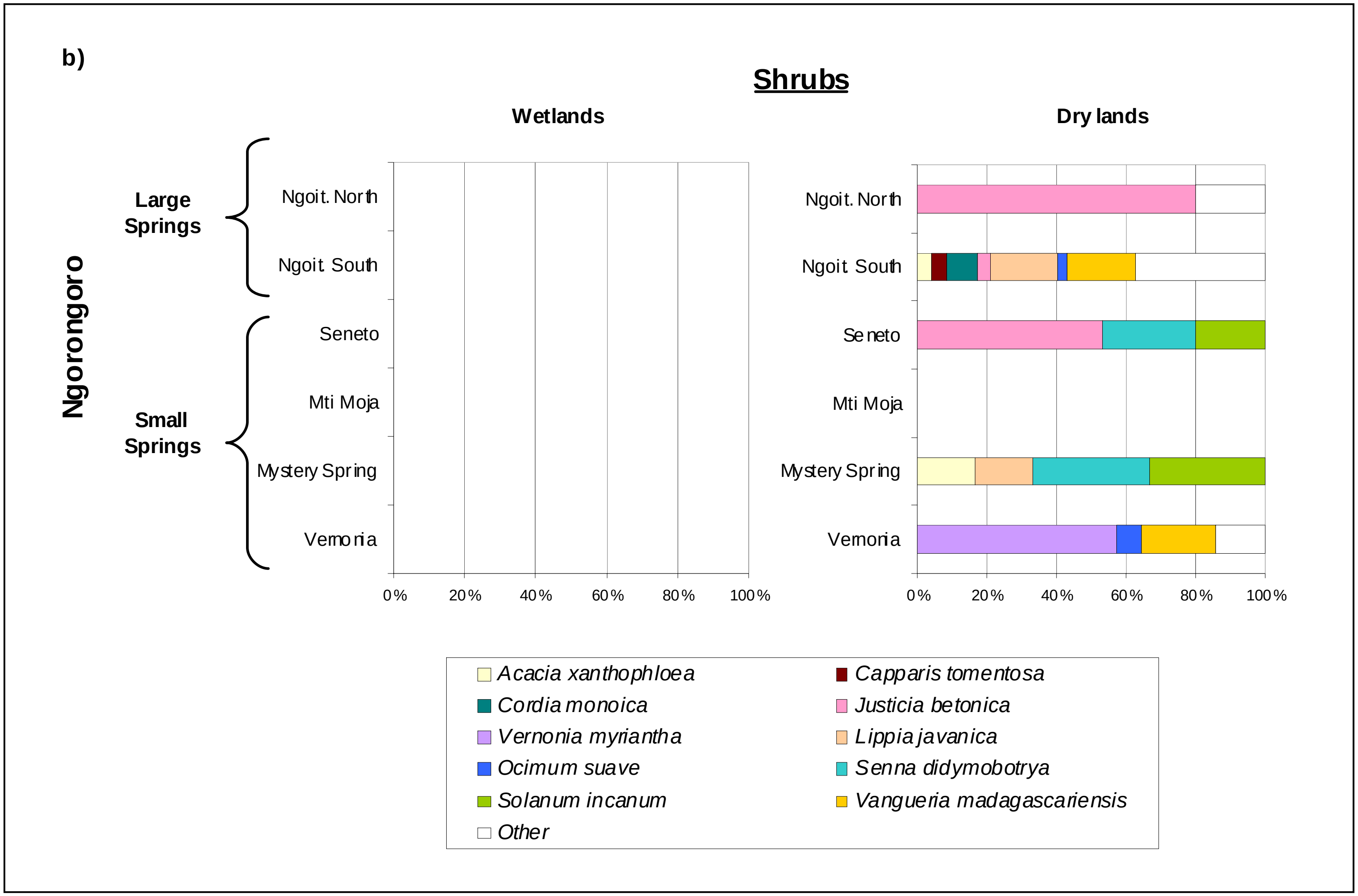


Figure 4-19 (cont.)



terrace, and fluvial terrace landscape associations, *Cordia sinensis* shows a trend of higher importance values in the riverine versus interfluvial landscape facets (Figure 4-19).

On Manyara's upper lacustrine plain, the riverine landscape facet of the lower Mkindu River (M-MKILF) is different in both tree and shrub composition compared to the other upper lacustrine plain sites. The important shrubs along the lower Mkindu are *Acacia xanthophloea*, *Tabernaemontana ventricosa*, and *Senna bicapsularis*. In its shrub growth form, *Acacia xanthophloea* often creates dense, thorny, ground-level thickets. *Senna bicapsularis* is a relatively small, soft, low-growing species that covers much of the shaded ground underneath this narrow strip of riverine forest.

Manyara's alluvial fan has somewhat unique shrub species composed of *Tabernaemontana ventricosa* saplings below a tall canopy of mainly *Trichillia emetica* and *Ficus sycomorus* trees. At maturity, *Tabernaemontana ventricosa* is a tall tree that normally grows in riverine or groundwater forests (Beentje, 1994), but in Manyara's alluvial fan, the species was extremely abundant as saplings and not as mature trees. In this study, its saplings fall within the "shrub" category because although they are single-stemmed, they are less than six meters tall.

Most shrub species in the Serengeti region were different from those at Manyara and Ngorongoro, but *Acacia xanthophloea* was common to all three regions, and *Acacia tortilis* shrubs were common in Serengeti and Manyara. The dominant shrubs in the riverine landscape facet of the Eastern Serengeti Plain and the interfluves of the Western Serengeti Plain were sparsely scattered *Acacia tortilis* shrubs and various *Commiphora* species. The genus *Commiphora* grows in the driest areas of Africa, and is often associated with the arid lands of the Somalia-Masai floristic zone (White, 1983; Figure 2-2), hence the common reference to "*Acacia-Commiphora* savanna". *Commiphora* plants are drought tolerant thorny shrubs or small trees, and most produce a pungent resin.

The riverine landscape facets of the Western Serengeti Plain and the Serengeti Woodland are somewhat similar to each other in shrub species composition. All have *Acacia xanthophloea* shrubs, and these landscape facets are all dominated by *Acacia xanthophloea* trees. Important shrubs at these Serengeti landscape facets that did not grow in Manyara include *Phyllanthus fischeri* and *Aspilia mossambicensis*. *Phyllanthus fischeri* occurs in dry upland forest margins and clearings, and in riverine forest or riverine woodland (Beentje, 1994). *Aspilia mossambicensis* is common throughout East Africa (Blundell, 1987), and has been considered a troublesome species in terms of bush encroachment, as it will spread rapidly into relatively moist areas from which other woody species have been cleared (Pratt and Gwynne, 1977:129). Species that the Serengeti sites have in common with Manyara sites are *Hibiscus ovalifolius*, *Cordia monoica*, and *Capparis tomentosa*. *Cordia monoica*, and *Capparis tomentosa* typically occur in riverine portions of the dry East African habitats.

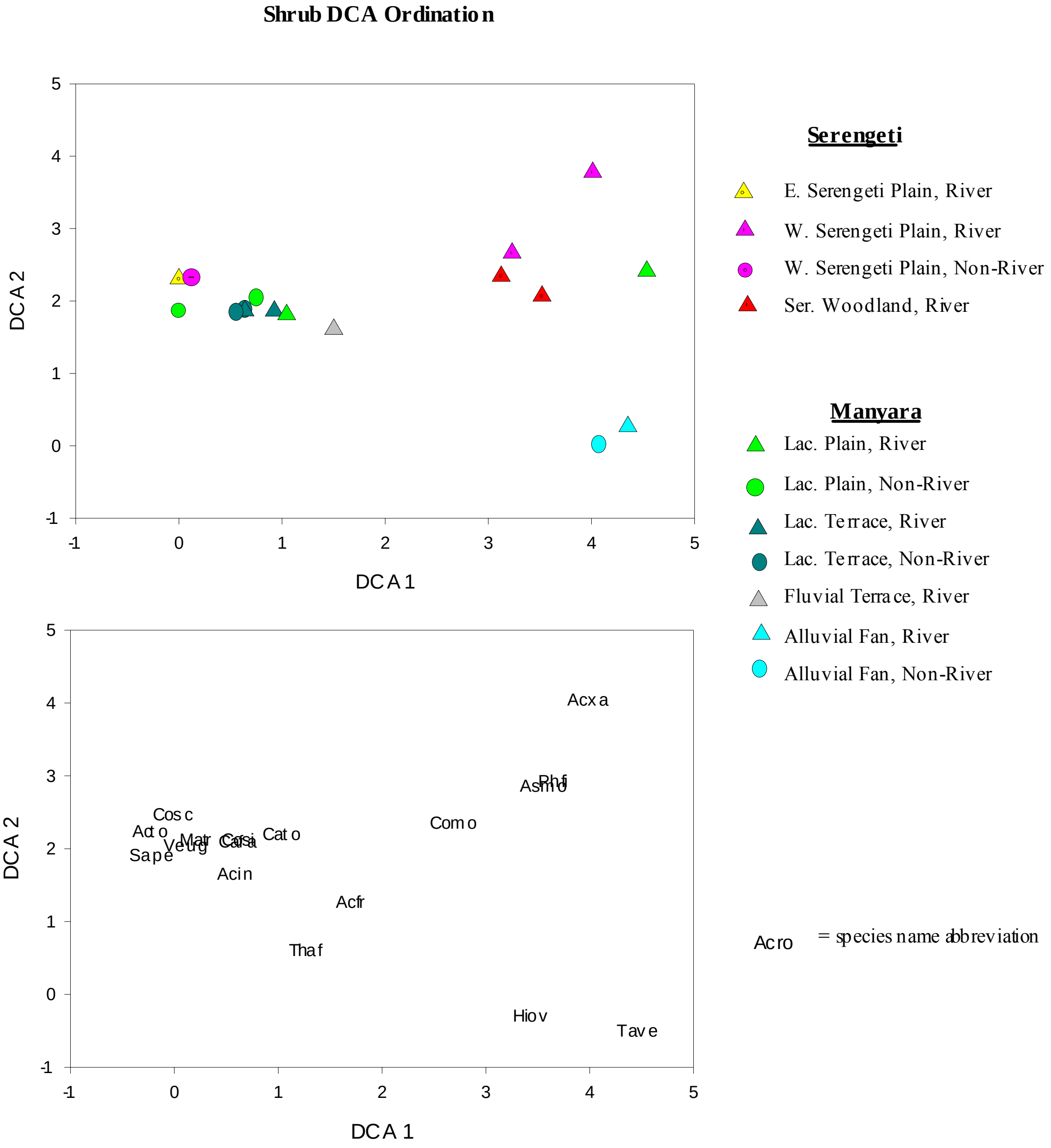
At Ngorongoro, the sites that had shrubs growing were the dry land sites associated with Large Springs and some dry land sites associated with Small Springs. Of the two Large Spring sites, the Ngoitokitok North woodland had a sparse shrub layer dominated by *Justicia betonica*. *Justicia betonica* is a variable and widespread plant that comes in both a wet forest form and the "drier" form that grows in Ngorongoro, which typically grows along rivers in semi-arid habitats (Agnew and Agnew, 1994). The Ngoitokitok South woodland contained *Justicia betonica* as well as a variety of shrubs similar to those at Manyara, including *Cordia monoica*, *Vangueria madagascariensis*, and *Capparis tomentosa*.

The Small Springs had a diversity of shrub species including *Acacia xanthophloea* shrubs, *Senna didymobotrya, Justicia betonica,* and S*olanum incanum*. The Vernonia spring, tucked up in a crevice at the edge of the Crater Wall, was so-named due to the presence of *Vernonia myriantha* shrubs.

Shrub DCA

In a DCA ordination of shrub species at the Serengeti and Manyara sites (Figure 4-20), the first axis ($\lambda = 0.776$) may reflect a salinity gradient, and/or other aspects of soil chemistry and mineral composition. The more saline end of the axis is the left one, confirmed by the presence of the two saline-tolerant shrubs, *Salvadora persica* and *Cordia sinensis*. The more saline sites are those on the evaporative non-riverine lacustrine plain (M-NLF). Also at this extreme are some of the sites from the Western and Eastern Serengeti Plain: the Nyamara interfluve (S-NIN) and the Barafu Valley (S-BAR). Manyara's lacustrine terrace and fluvial terrace sites also cluster toward the possibly saline end of axis one, with *Acacia tortilis* being the shrub that all of these sites have in common. At the opposite, right-hand end of axis one are the groundwater forest and *Acacia xanthophloea*-dominated rivers. Although *Acacia xanthophloea* grows in what are overall "saline-alkaline soils", massive die-offs of the species occur when the roots are saturated with saline water, and the plant dies from physiological drought (Western and Van Praet, 1973). In a relative sense then, *Acacia xanthophloea* may not be very saline tolerant. Axis one may also be influenced by moisture availability, with the

Figure 4-20. DCA Ordination of shrubs in the Serengeti and Manyara modern study areas. The top figure shows the study areas and the bottom shows species. Full species names can be found in Appendix 1.



drier sites in the left part of the graph, and the wetter sites to the right. The groundwater forest and perennial river sites are at the far right of axis one.

On the second axis ($\lambda = 0.607$) the majority of sites cluster together near the center, but Manyara's alluvial fan (groundwater forest) sites are at the lower extreme, and the Seronera river of the Western Serengeti Plain is at the upper extreme. This separation is related to the environmental preferences of *Tabernaimontana ventricosa* (Tave) and *Hibiscus ovlifolius* (Hiov) on the one hand, and *Acacia xanthophloea* (Acxa) on the other. Axis two may represent an alkalinity gradient, with low alkalinity at the groundwater forest and high alkalinity at the Seronera River.

To figure out which environmental variables are actually important will require quantitative soil analyses and other environmental measurements to be taken at the sites, and will require more sites to be sampled. Regardless of the environmental variables involved, however, the shrub ordination makes clear the relative importance of landscape scale with regard to shrub species composition.

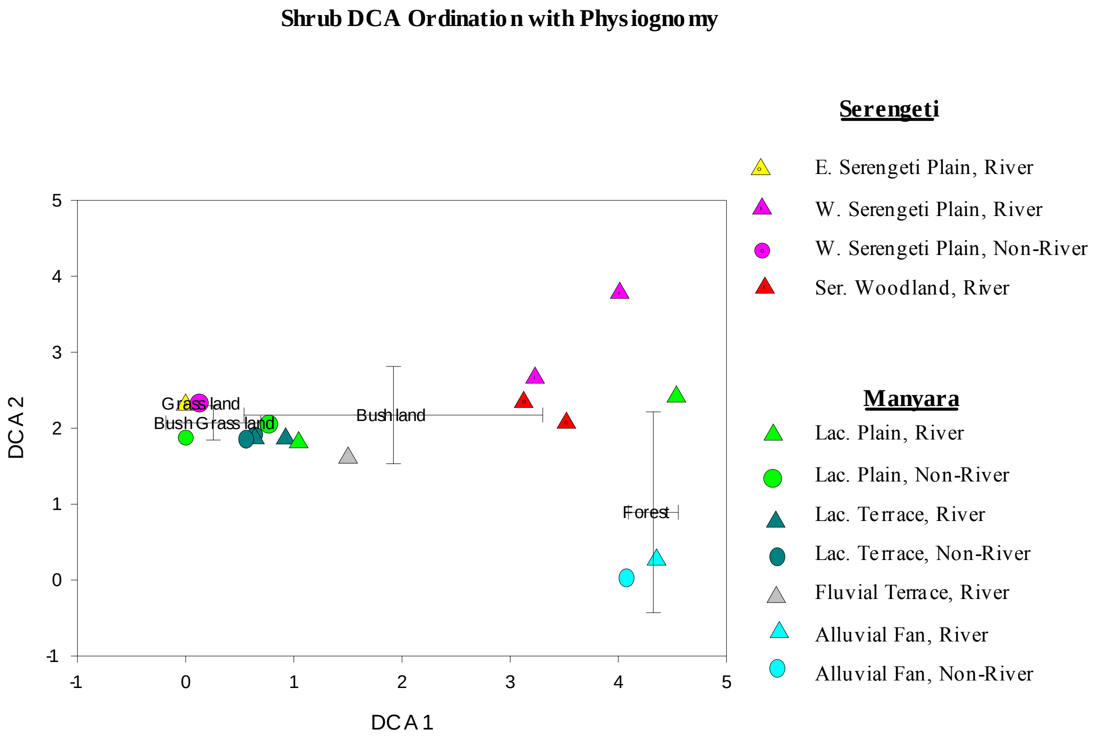
Sites from most landscape associations cluster together, implying that the sites within each of those landscape associations are similar in shrub species composition regardless of whether they are in a riverine or non-riverine landscape facet. However, there are two exceptions: Manyara's upper lacustrine plain and the Western Serengeti Plain. Manyara's upper lacustrine plain sites are spread across axis one broadly, indicating that the important environmental variable(s) represented by that axis varies between the landscape facets of that single landscape association, as was the case for trees. This may reflect differences in moisture availability between the one perennial river site that falls at the extreme right of axis one, and the other non-riverine and ephemeral river sites that fall near the left end of axis one.

In regard to the Western Serengeti Plain sites, the single non-riverine landscape facet is at the opposite extreme along axis one from the riverine landscape facets. Although the sample size is low, this again suggests that strong contrast exists in shrub species composition between riverine and non-riverine landscape facets, reflecting differences in moisture availability.

When physiognomic categories are plotted in the shrub ordination based on site score centroids (Figure 4-21), there is a clear trend of increasing tree and shrub cover along axis one. This implies that the most important environmental variable affecting shrub species composition (represented by DCA axis one) also correlates to physiognomic structure, which was not the case for trees. That could be important in terms of using physiognomic categories to predict shrub species composition and/or hominin resource availability.

On the other hand, the “bushland” category in Figure 4-21 covers a very wide range; the main separation is in forest sites at one extreme and grassland and bush grassland sites at the other extreme. In the tree ordination, bushland sites were also spread widely across axis one (Figure 4-18). This reflects the particularly wide variety of habitat locations and species compositions that can combine to form the physiognomic structure designated as “bushland”. Predicting the specific types or species of hominin plant resources available in bushland habitats therefore may be more tenuous than for other physiognomic categories.

Figure 4-21. DCA Ordination of shrubs in the Serengeti and Manyara modern study areas with physiognomic categories. The word of each habitat type is plotted as the centroid of the values for all study areas in that category. Bars show the range of values for which study areas with each habitat type extend on the DCA 1 and DCA 2 axes.



In sum, the most important environmental variables controlling shrub species composition are not obvious from this DCA, but may be related to soil properties such as salinity and alkalinity. Most landscape associations have a consistent shrub species composition among all of their landscape facets. Exceptions are Manyara's lacustrine plain and the Western Serengeti Plain. The shrub composition along the Mkindu River of the lowermost upper lacustrine plain is unique, while the higher upper lacustrine plain sites, one riverine and two interfluvial, are more similar to one another. At the Western Serengeti Plain the riverine sites are similar to one another, but very different from the interfluvial site. The environmental factor(s) controlling shrub species composition also correspond to physiognomic structure, particularly for grassland and bush grassland versus forest sites. Bushland sites have a wide variety of shrub species compositions.

Herbaceous Species Composition (Forbs and Grasses)

Comparing herbaceous species composition (forbs and grasses) among sites, the most fundamental level of differences is at the regional level, between all Manyara sites, all Serengeti sites, and all Ngorongoro sites (Figures 4-22 and 4-23). In other words, sites at Manyara tend to have similar herbaceous species composition among themselves, while most of those species are not present at Serengeti or Ngorongoro. The same applies to most herbs at Serengeti and Ngorongoro, though there are a few exceptions.

Some of the common herbaceous species at Manyara are *Achyranthes aspera, Monechma debile, Peristrophe bicalyculata,* and *Digitaria velutina*. *Achyranthes aspera* is extremely variable in ecological tolerances, though it has been considered a shade-loving species (Bonnefille, 1984a). *Achyranthes aspera* is the most frequently occurring

Figure 4-22. Forb species composition of the modern analog study areas based on relative frequency for a) Manyara and Serengeti and b) Ngorongoro.

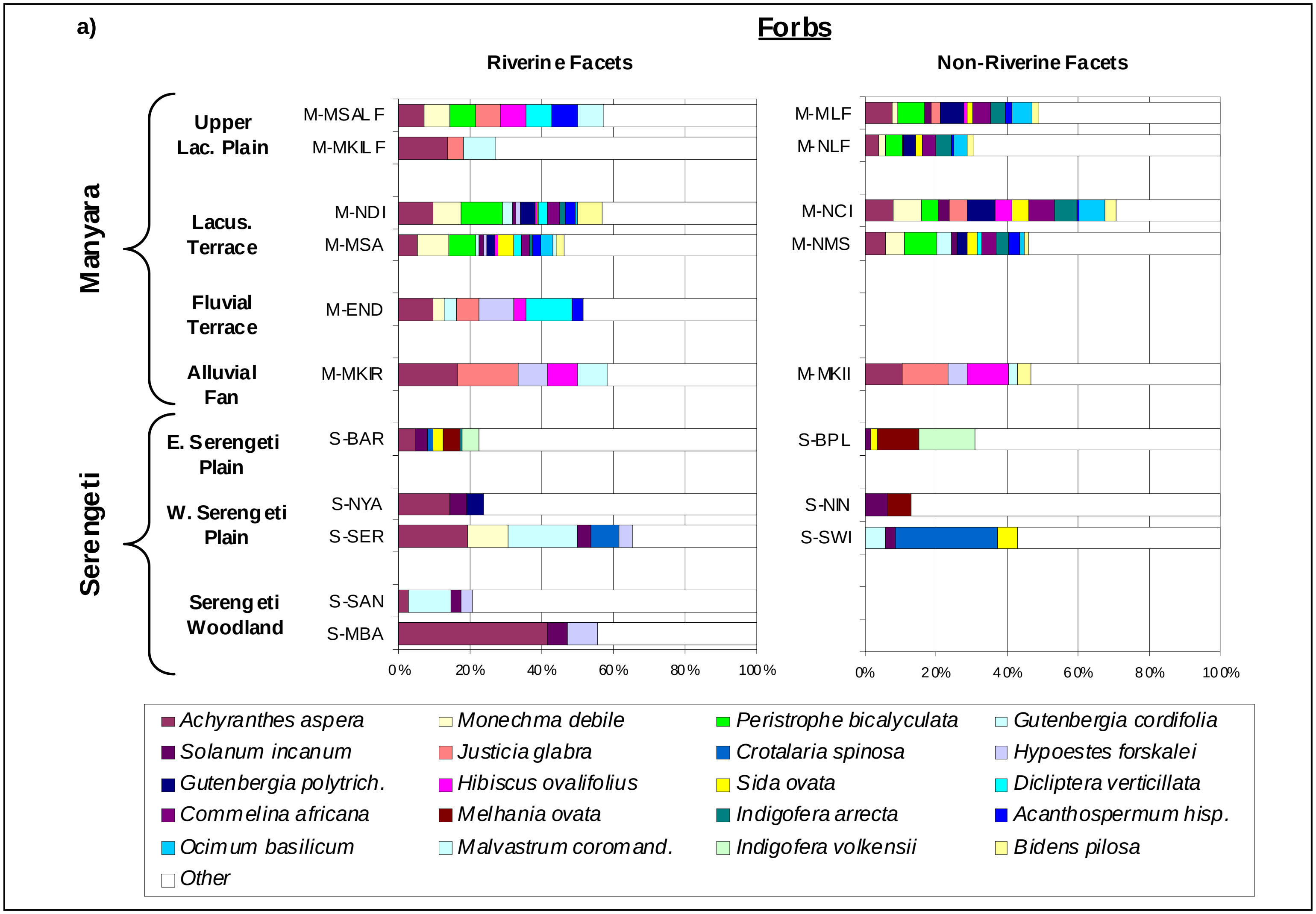


Figure 4-22 (cont.)

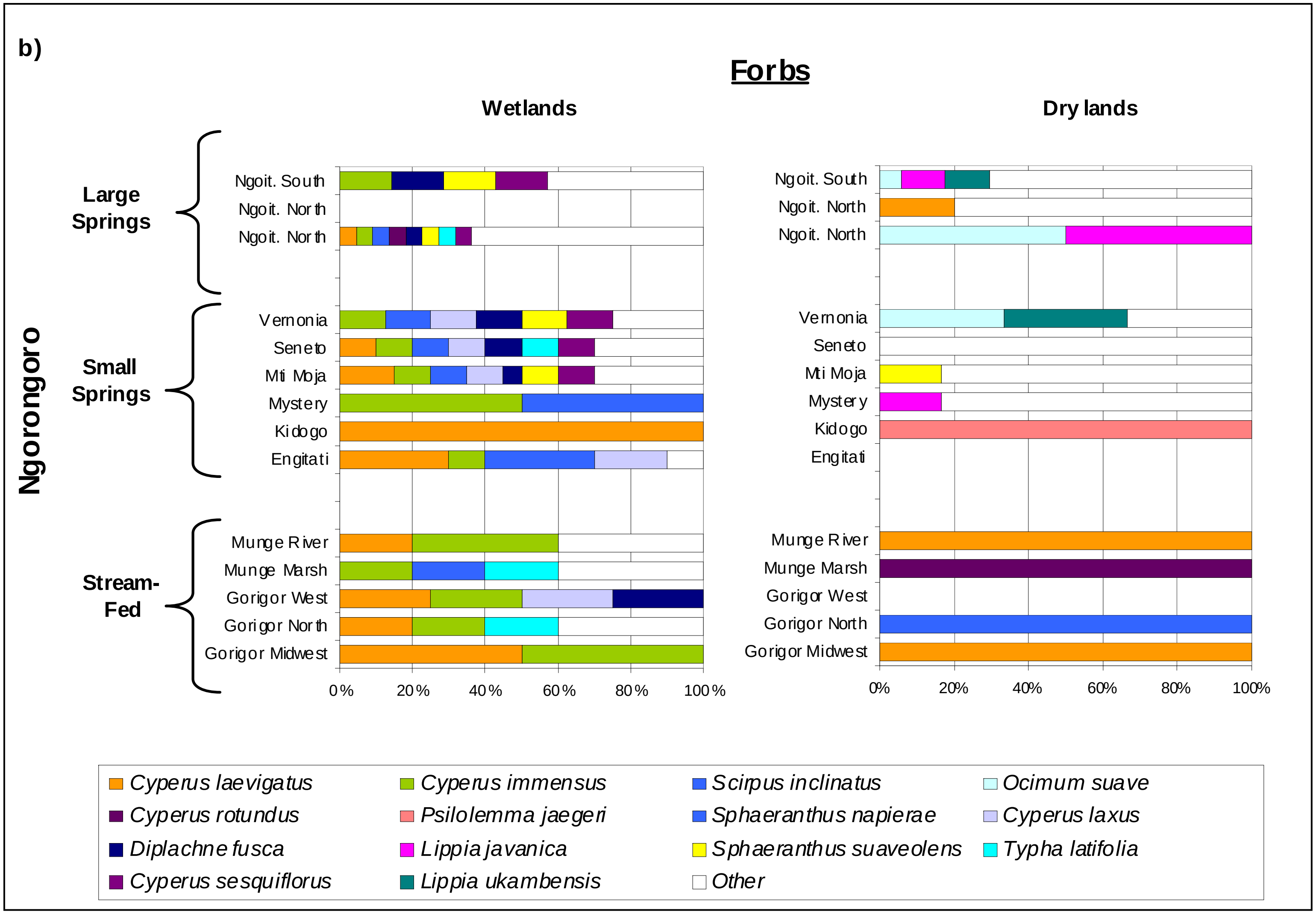


Figure 4-23. Grass species composition of the modern analog study areas based on relative frequency for a) Manyara and Serengeti and b) Ngorongoro.

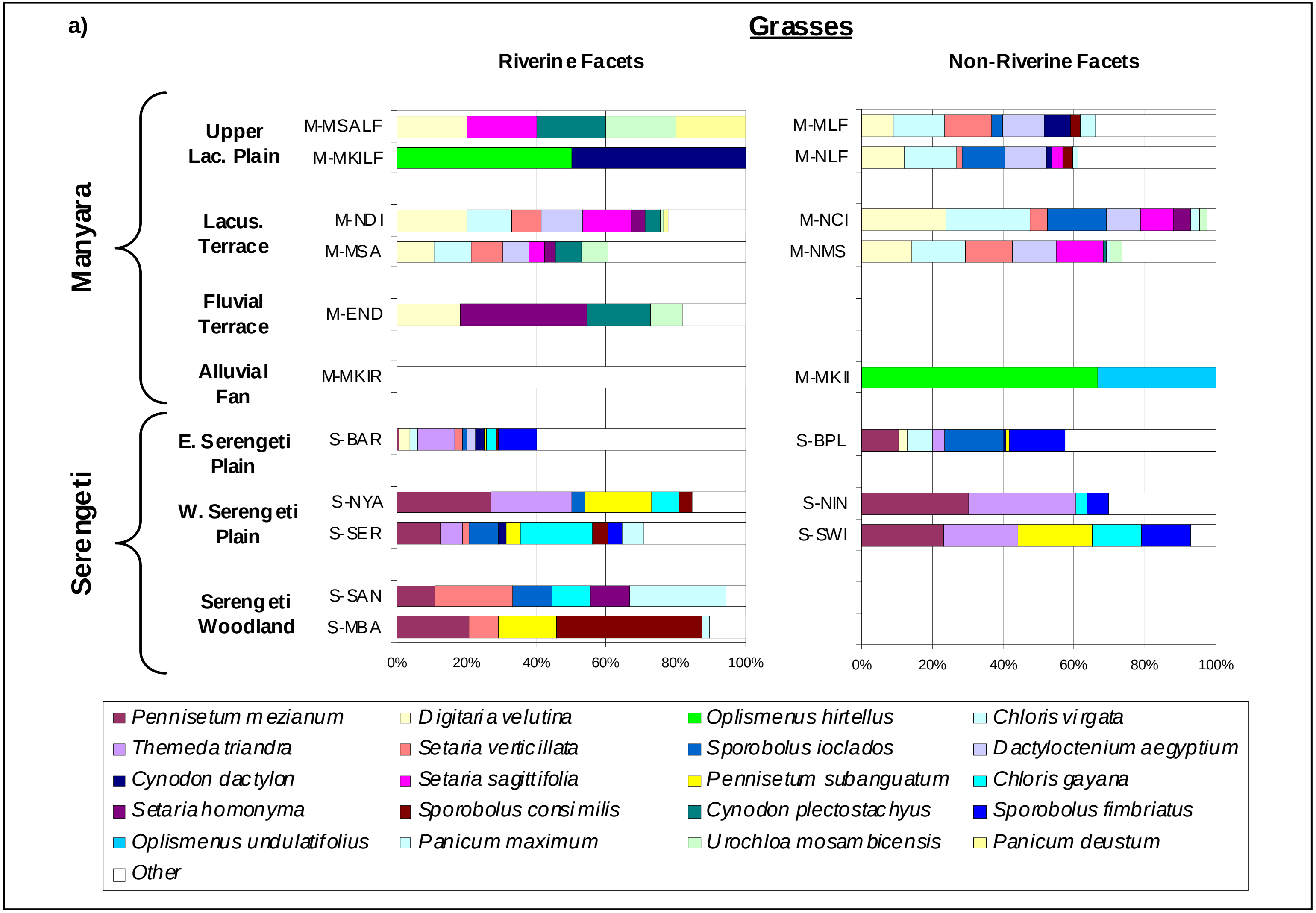
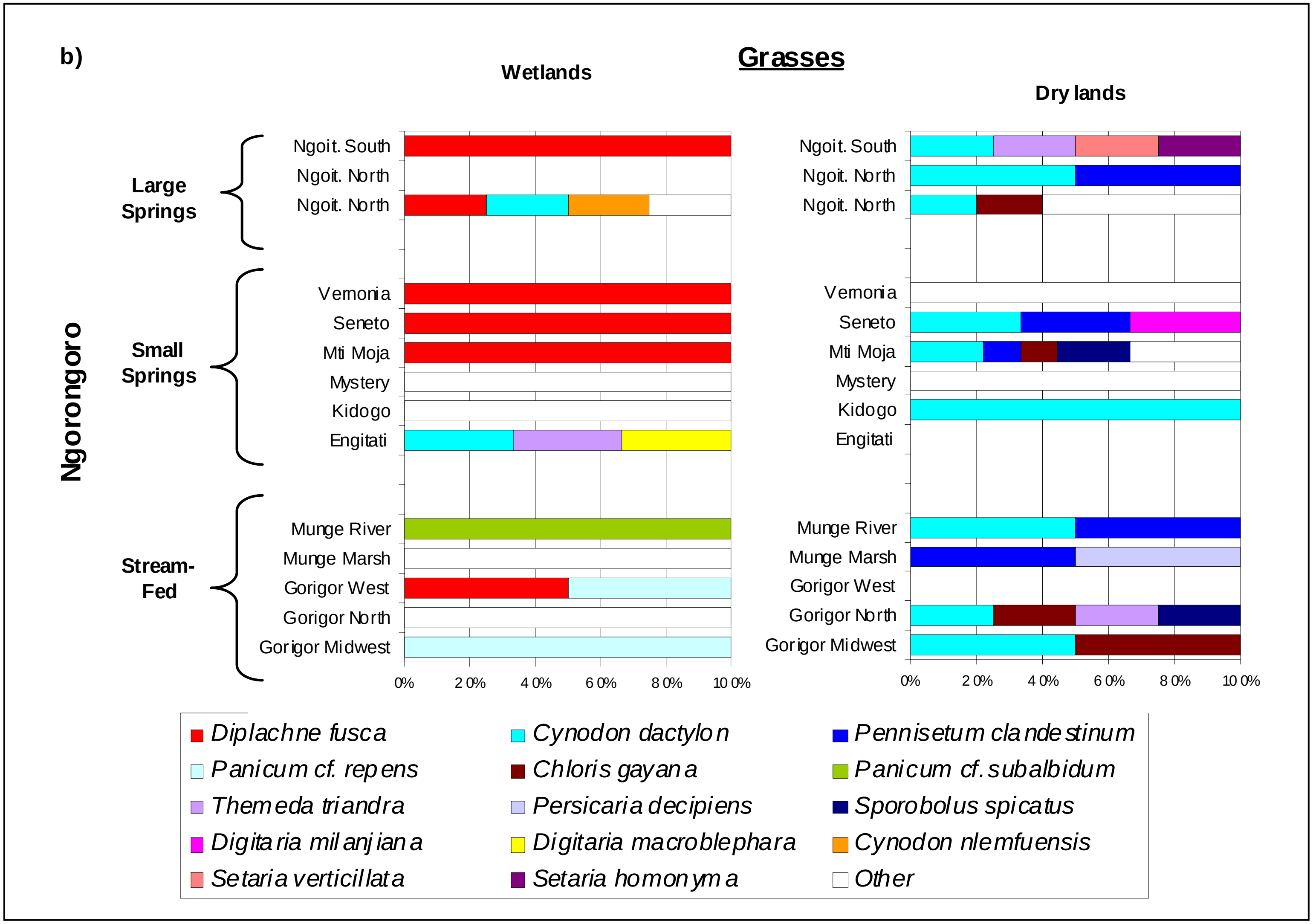


Figure 4-23 (cont.)



of all forbs, and can be found not only in Manyara, but also in Serengeti and Ngorongoro. *Monechma debile* is an annual or perennial, and is common in dry, disturbed areas including *Commiphora* bushland and semi-desert (Agnew and Agnew, 1994; Lind and Morrison, 1974:68). *Peristrophe bicalyculata* is an annual that occurs under trees in open bushland and on dry rocky soils (Agnew and Agnew, 1994). In this study *Peristrophe bicalyculata* is found exclusively on Manyara's lacustrine plain and lacustrine terrace. *Oplismenus hirtellus*, a grass which prefers shade and is not good for grazing (Ibrahim and Kabuye, 1987), only occurred in the forested sites of the groundwater forest/alluvial fan.

In Serengeti, common forbs include *Indigofera volkensii*, *Melhania ovata*, and *Crotalaria spinosa*, and some common grasses are *Pennisetum mezianum*, *Themeda triandra*, and *Chloris gayana*. The grass *Sporobolus fimbriatus* is typical in the Eastern Serengeti Plain around the Barafu Valley. All of these Serengeti forbs and grasses are adapted to withstand the impact of migrating herds of grazing wildebeest, zebra, gazelles, and other animals. Only riverine sites in Serengeti had *Sporobolis consimilis*, a tall, thick grass that grows on well-drained soils near access to water. *Sporobolis consimilis* also occurs on the lacustrine plain at Manyara and near springs on the lacustrine plain of Ngorongoro Crater.

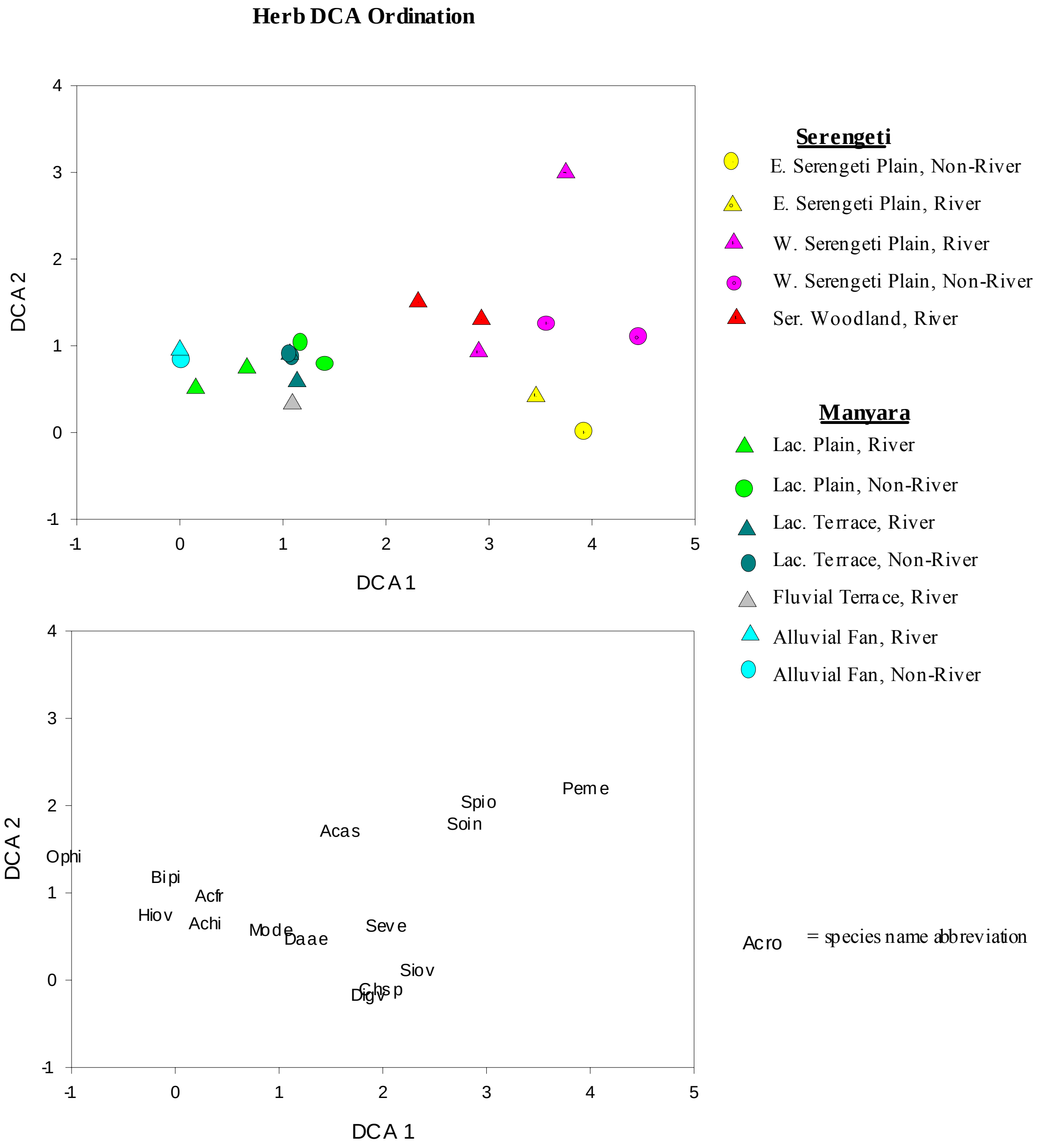
At Ngorongoro, a fundamental division of herbaceous species composition occurs between all wetland versus all dry land sites (Figures 4-22 and 4-23). Whether associated with Large or Small Springs or stream-fed areas, the wetlands support marsh plants – rushes and sedges. The most common marsh plant is the sedge *Cyperus laevigatus*, a typically low-growing sedge with a high tolerance for salinity (Ellery and McCarthy, 1993). *Cyperus immensus* and *Scirpus inclinatus* sedges can grow to one or two meters, and were found often growing in the wetter, less saline parts of the marshes. *Typha latifolia*, the cattail, shows up in four of the wetland samples, including the diverse wetland at Ngoitokitok North. Other marsh species at Ngoitokitok which were not represented in my sample plots because of logistics– they were not located near the accessible marsh edge - are *Cyperus papyrus* and *Phragmites mauritianus* (Herlocker and Dirschl, 1972:32).

The grass *Diplachne fusca* is most common at Ngorongoro's wetland sites, as it is typical along the margins of lakes, rivers and seasonally flooded plains, and can withstand alkaline situations (Ibrahim and Kabuye, 1987). The most common grass at Ngorongoro's dry land sites is *Cynodon dactylon*, typically found in areas that are not periodically flooded, but where soils have a low sodium concentration (Ellery and McCarthy, 1993).

Herb DCA

A DCA ordination of herbaceous species was performed using species relative frequency at landscape facets in Serengeti and Manyara (Figure 4-24). The ordination confirms that the most fundamental difference in herbaceous species composition occurs at the regional level, between all Manyara sites and all Serengeti sites. DCA axis one (λ=0.633) represents the most important environmental variable(s) controlling species composition, and since this axis corresponds to a regional division, the important environmental variable(s) must change by regions as well.

Figure 4-24. DCA Ordination of herbs (forbs and grasses) in the Serengeti and Manyara modern study areas. The top figure shows the study areas and the bottom shows species. Full species names can be found in Appendix 1.



At the level of landscape associations, it is difficult to distinguish Manyara's lacustrine plain, lacustrine terrace, and fluvial terrace from one another based on species composition, and the alluvial fan also shares species in common with those other landscape associations (Figure 4-24). This is reflected in the ordination by the close spatial proximity of all Manyara sites on the left-hand side of the graph.

Landscape facet-level differences in species composition at Manyara are most pronounced within the lacustrine plain based on both the visual comparison of species composition (Figure 4-22, 4-23), and the fact that within each Manyara landscape association, landscape facets within the lacustrine plain are dispersed most widely by DCA axis one. Sites from other landscape associations are close to each other regardless of whether they are riverine or non-riverine.

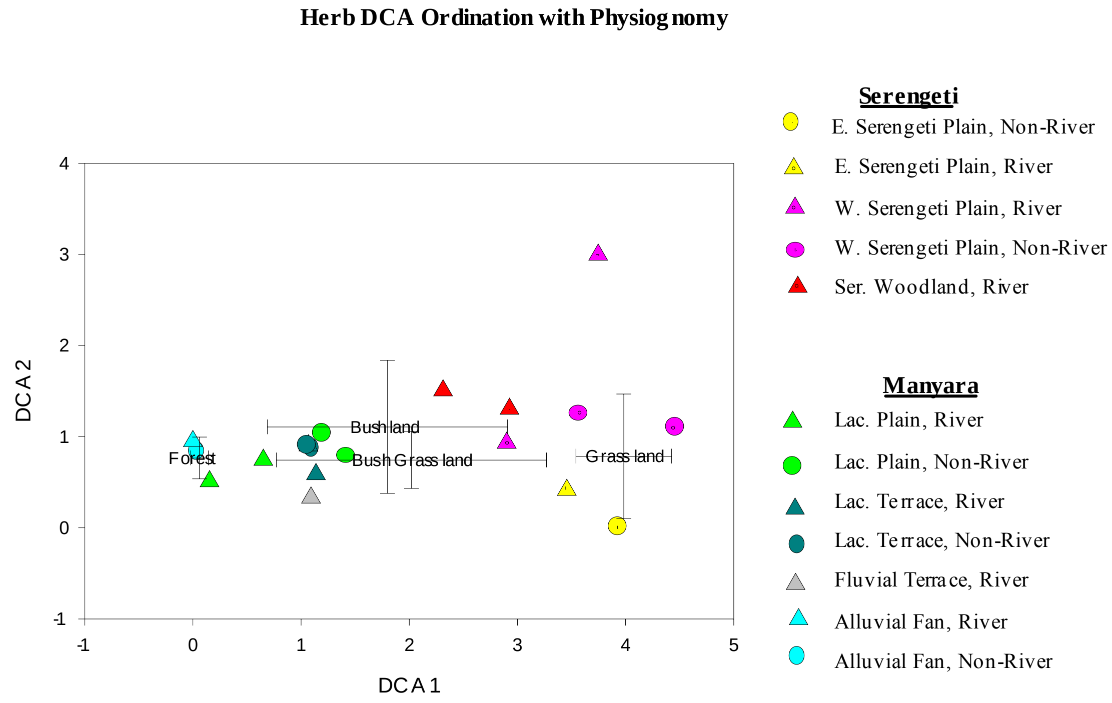
The Serengeti sites are more dissimilar overall than are the Manyara sites, as evidenced by the fact that they are spread across a larger area of ordination space (Figure 4-24), and by a visual comparison of species composition (Figure 4-22, 4-23). In general at Serengeti, landscape facets within a given landscape association are more similar to one another than they are between landscape associations. The Western Serengeti Plain sites are slightly more dispersed across the ordination, suggesting that environmental factors affecting species composition vary more strongly between the landscape facets of that landscape association. In environmental terms, axis one may reflect a moisture gradient. Within the Serengeti sites, the drier, grassland non-riverine sites are towards the right and the wetter, more shaded riverine sites are towards the left. Similarly, within the Manyara sites, the wettest, forested and well-shaded sites are on the far left, as is the forest shade-loving grass species *Oplismenus hirtellus*.

When the physiognomic categories are plotted onto the herbaceous DCA ordination, they are dispersed along axis one (Figure 4-25). In order to evaluate a possible relationship between woody and herbaceous species, I ran a linear regression of the herb DCA axis one scores versus percentage woody cover values (visually-estimated tree plus shrub cover values). The results (R^2=0.505, p=0.001) show a moderate correlation between physiognomy and herbaceous species composition.

Physiognomic categories are not dispersed along axis two. The Nyamara river site (S-NYA) within the long grasslands of the Serengeti Plain is separated from all other sites along the second DCA axis, but the significance of this cannot be explained based on current data.

In sum, for herbaceous species, regional level differences are fundamentally important. The landscape facets within most landscape associations are similar in herbaceous species composition, whether they are riverine or interfluvial. The exception is Manyara's lacustrine plain landscape facet, as was the case for trees and shrubs. In general, Serengeti landscape facets and landscape associations differ more from one another in herbaceous species composition compared to Manyara, and the Western Serengeti Plain shows the greatest difference within a single Serengeti landscape association between riverine and non-riverine landscape facets, as was the case for shrubs. At Ngorongoro, herbaceous species differ strongly between wetland versus dry land sites. Vegetation structure or physiognomy correlates somewhat well with the latent environmental variable(s) controlling herbaceous species composition represented by axis one of the DCA. When each region is considered separately, physiognomic structure

Figure 4-25. DCA Ordination of herbs in the Serengeti and Manyara modern study areas with physiognomic categories. The word of each habitat type is plotted as the centroid of the values for all study areas in that category. Bars show the range of values for which study areas with each habitat type extend on the DCA 1 and DCA 2 axes.



seems to be as good a predictor of herbaceous species composition as landscape associations or landscape facets.

Comparing Tree, Shrub, and Herbaceous DCA Ordinations

There are several differences in the patterns of the DCA ordinations for trees, shrubs, and herbaceous plants. Both trees and herbs are divided at the regional level along axis one, but for shrubs it is axis two that divides the sites by regions. For trees, axis two disperses Manyara sites, whereas for herbs axis two disperses Serengeti sites. Axis one corresponds to a trend of increasing cover in physiognomic sites for shrubs and herbs, while for trees both axes one and two are only moderately correlated to physiognomic categories.

These patterns mean that the most important environmental variable(s) controlling tree species distribution (represented by axis one) does not relate to physiognomic structure, while for shrubs and herbs it does. Trees and herbs are most sensitive to regional gradients (that differentiate regions), while shrubs are less so (because regional separation in ordination space only occurs along axis two). Within Manyara, tree species vary according to axis two, which probably represents a salinity/alkalinity gradient. Within Serengeti, and to a lesser degree within Manyara, herbs vary according to an unknown environmental gradient (represented by axis two) that is probably secondary to a moisture gradient (represented by axis one).

The interpretations of which environmental variables were the most important influencing factors on axes one and two for the various plant growth forms are somewhat tenuous, but overall conditions such as well-drained versus poorly-drained soils, soil chemistry such as salinity and alkalinity, and moisture gradients seem to be most important for all growth forms. For trees especially, the redistribution of groundwater, as opposed to surface water run-off, is an important factor affecting species distribution.

Relating Physiognomy, Landscape Units, and Species Composition

Below I summarize the main findings in terms of the relationships between physiognomic structure, landscape units, and plant species composition. As outlined in Figure 1-1, physiognomic structure has been theorized to play an important, and possibly even central role in the understanding of early hominin ecology based on a combination of actualistic studies and paleoenvironmental evidence. What has been missing in paleoanthropology is a clear understanding of how plant species composition and other factors relate to vegetation structure, and whether landscape units, however defined, have consistent or predictable vegetation structure and plant species types that would have been relevant to early hominin ecology.

Summary of Vegetation Characteristics By Physiognomic Categories

There were three forest study areas in this thesis, all of which were in the Manyara region. Since they were in the same region, they were similar in shrub and herbaceous species composition. Tree composition was similar in the two alluvial fan sites, but differed completely on the forested, *Acacia xanthophloea*-dominated Mkindu River on the upper lacustrine plain.

The nine bushland sites of the Serengeti and Manyara regions hosted a broad range of tree, shrub, and herbaceous species. Within each region, trees, shrubs, and herbs were more alike among bushland sites than they were between bushland and other physiognomic types in that region. However, this does not apply between regions. For example, bushland sites in Serengeti were mostly dominated by *Acacia xanthophloea* trees, while bushland sites in Manyara were mostly dominated by *Acacia tortilis* trees.

Three of Ngorongoro's sites are classified as woodland, and two as shrubland, but no sites in Serengeti and Manyara fell into these categories. The woodland sites all were dominated by *Acacia xanthophloea* trees, and were similar in shrub and herb constitution. The two shrubland sites, the Mystery Spring and Vernonia dry lands, had no overlap in shrub species composition, though the forbs were similar in both.

Of the bush grassland sites, two were in Manyara and one was in Serengeti. All were dominated by *Acacia tortilis* trees, and had *Acacia tortilis* shrubs, but otherwise the shrubs differed by region. Forbs and grasses in bush grassland sites mostly differed by region.

Of the grassland sites, three were in the Serengeti Plain, while the other eight were in Ngorongoro. Most did not have trees and shrubs, so species composition cannot be compared for those growth forms. There is only moderate overlap of forb species between sites within each single region, in part because the number of forbs per site tended to be very low in these grassland sites. There is almost no overlap of forb species composition between regions. Grass species composition was fairly consistent among grassland sites within each region, but again there was very little overlap between regions.

Summary of Vegetation Characteristics by Landscape Units

Regions are characterized by diverse physiognomic types and tree species, and share tree species in common with other regions. Shrub species within a region are diverse, but there is limited overlap of species between regions. Similarly, herbaceous species are diverse, with very little overlap between regions.

Landscape associations vary a great deal by type. In the case of Manyara's lacustrine terrace and alluvial fan, they are characterized by relatively consistent internal physiognomy and species composition, regardless of landscape facet. In Manyara's lacustrine plain and in the Eastern and Western Serengeti Plain, riverine versus non-riverine landscape facets have distinctive physiognomies and species compositions. The physiognomy and species composition of the Ngorongoro Crater Floor landscape association varies dramatically by landscape facet, such as the differences between marshy Large Spring wetlands and the woodlands on the dry land adjacent to those springs.

Most landscape facets are fairly homogeneous in terms of their internal physiognomy and species composition. This is consistent with the fact that landscape facets are defined as ecological units that are relatively homogeneous throughout, with the exception of very localized elements within them such as a shade tree (Gerrescheim, 1974). Other exceptions to homogeneity within landscape facets might be found among herbaceous plants such as those at the Barafu Valley, in which microtopography varies and the spatial distribution of herbs varies as well (although this was not tested directly in this study). Also, along ephemeral rivers such as the Seronera, tree cover of *Acacia xanthophloea* is patchy. For example it may have 90% cover along a 100 meter stretch of the river, and then be open grass- or shrub-land for the next 100 meters. At Ngorongoro, the dry lands directly adjacent to Large Springs often consisted of some areas of woodland and other areas of grassland.

The degree of contrast between adjacent landscape facets in terms of plant structure and species composition is of central importance for modeling hominin use of and archaeological signatures across paleolandscapes. In the Serengeti, the riverine versus adjacent interfluvial landscape facets of the Eastern and Western Serengeti Plain differ strongly in both structure and composition. Although I did not make quantitative collections in the interfluves of the Serengeti Woodland, casual observations suggest that vegetation structure does not vary greatly between riverine and non-riverine - both are bushland - but species composition does differ for shrubs and trees.

At Manyara, the upper lacustrine plain shows a high contrast in physiognomy and species composition between riverine and non-riverine landscape facets. On the other hand, the lacustrine terrace, alluvial fan, and probably the fluvial terrace are very similar in their riverine and interfluvial landscape facets. Some landscape facets at Manyara are adjacent that are in different landscape associations (Figure 3-2). The forested alluvial fan, for example, is adjacent to and contrasts greatly with the lacustrine terrace bushland and lacustrine plain bush grassland landscape facets. The bush grassland upper lacustrine plain also contrasts with the adjacent bushland lacustrine terrace.

At Ngorongoro, nearly all adjacent landscape facets show some structural and species contrasts, such as the wetland marsh areas versus adjacent grassland or woodland landscape facets.

Discussion

Vegetation Structure in East African Savannas (Tree/Grass Ratios)

I have emphasized the fundamental importance of gross physiognomic structure for paleoenvironmental reconstructions, since it is an aspect of vegetation that is most likely to be evidenced based on fossil clues. There is a body of literature that discusses the controls of herbaceous to woody ratios in modern semi-arid habitats, and this untapped resource is highly relevant for landscape paleoanthropology.

Walker's (1987) theory holds that the ratio of woody to herbaceous biomass is related to the plant rooting depths of those categories. Herbaceous plants have a denser root distribution in the upper soil layer, and woody plants have sole access to the lower soil layer. The woody:herb ratio therefore depends on the relative amount of moisture in the two soil layers.

In order to understand herb distribution in my study areas, I tested the possibility that forb species diversity was greater in areas with less tree and shrub cover, but the relationship was not significant. One of the processes known to influence species diversity, habitat heterogeneity, may account for higher herbaceous species diversity in some landscape facets. For example, the Eastern Serengeti Plain has a broad range of microhabitats within its riverine landscape facets. The sloped sides of the Barafu Valley have patches in which basement rock is exposed, forming local soils that are different in nutrient and mineral composition from the dominant volcanic ash-derived soils of the greater Serengeti Plain (Anderson and Talbot, 1965). Those patches, and the marshy areas at the base of the valley, support a wider variety of herbaceous plants than the more homogeneous areas of rolling plains away from drainage lines (personal observation).

Thus the contrast of herbaceous species richness between the valley and the surrounding plains of the Eastern Serengeti is high.

Breshears and Barnes (1999) have added to Walker's theory concerning woody to herbaceous biomass by distinguishing two types of woody plants, those that extract water from deep layers and those that extract water from shallower layers. This allows them to account for short term changes in savanna structure that cannot be explained when all woody plants are grouped into a single type. It also allows them to account for the fact that horizontal heterogeneity, not just vertical, is important, such as the differences in soil moisture between canopy and intercanopy locations on the landscape.

Breshears and Barnes' (1999) model provides a possible theoretical basis to explain some of the differences between shrub and tree distribution in this study. If in general, trees extract moisture from deep layers and shrubs extract moisture from shallower layers, then differences in how groundwater is distributed across deep and shallow layers in a particular landscape should be reflected in differences in tree and shrub cover as shown in Figures 4-1 and 4-2. For example, in the alluvial fan, tree cover (Figure 4-1) is similar in the riverine and non-riverine landscape facets, suggesting that the deep groundwater is ubiquitous. Shrub cover (Figure 4-2), on the other hand, is higher in the riverine landscape facets, reflecting the fact that the presence of the river at the surface also causes there to be more groundwater at shallower layers near the river, but not away from it in the non-riverine landscape facets.

The bottom line is that the ratio of herbaceous to woody biomass in semiarid landscapes depends largely on the amount and spatial distribution of soil moisture that is available to plants. That is not necessarily directly related to local annual rainfall, nor to surface features such as rivers versus interfluves. Groundwater appears to be most important in semi-arid savannas. Any paleoenvironmental reconstructions based on landscape units and geomorphological features should therefore emphasize not just surface features like rivers and interfluves, but also potential groundwater resources.

Coughener and Ellis (1993) conducted a landscape ecological study of semi-arid habitat in northern Kenya and found that woody cover was strongly influenced by water availability, but not in a straight-forward manner. They found that *within riparian zones*, or along rivers, rainfall had no effect on woody canopy cover, rather, redistribution of water was most important. *Within non-riparian zones*, or interfluves, rainfall did effect woody canopy cover. Presumably the riverine trees tapped the perennial subterranean water that followed the river bed, but the non-riverine trees depended on a water source that was more directly related to local rainfall.

Interestingly, Coughener and Ellis (1993:392) also found that degree of woody cover was not strongly related to dominant tree species. Thus, as I found in this study, nearby woodland or bushland landscape facets within a single region can have very different tree species, while a woodland or bushland landscape facet in a different distant region may have the same tree species composition. This was not generally the case for shrubs and herbaceous species.

Greenway and Vesey-Fitzgerald (1969) also found the extent and compositional complexity of *Acacia* dominated riverine woodlands in East Africa to be independent of rainfall and dependent on groundwater availability and disturbance factors. In Whittaker's (1975, cited in Belsky, 1990) model for explaining tree/grass ratios, physiognomy depends on soil characteristics and fire, rather than rainfall. Belsky

(1990:485) concludes that "tree/grass ratios in East Africa are determined by fire, soil and herbivory, not by rainfall."

In my modern study areas, the importance of groundwater distribution as a controlling factor of physiognomy is also clear. At Manyara, for example, the rainfall is similar across the entire region, as the Manyara region is relatively small compared to Serengeti. But since the alluvial fans are underlain by a high and perennial groundwater table at Manyara, a lush groundwater forest is supported. The nearby lacustrine terrace only supports an *Acacia tortilis*-dominated bushland, which may also be dependent upon groundwater, but the plant-available water there must be less than that available to the alluvial fans, perhaps due to a lower or more ephemeral groundwater table. At Ngorongoro, the distribution of woodlands across the Crater Floor probably corresponds closely to the distribution of near-surface fresh groundwater. Rainfall is similar across the Crater Floor, but trees are only supported near large springs where more fresh water is reliably available below the surface.

Short- and Long-term Dynamics in East African Savannas

Another important question is: how stable are these physiognomic units over short and long time scales? Inter-annual variability in seasonal rainfall is always present, and several lines of evidence suggest that local vegetation structure in woodland/savanna ecosystems can vary at decade- and century-level time scales (e.g., Norton-Griffiths *et al*., 1975; Prins and Loth, 1988). A growing body of literature is helping us begin to understand the short- and long-term dynamics of East African savannas, which will enable us to put our current, snap-shot view of the world into a broader perspective that is more useful for paleoenvironmental reconstructions.

Evidence from the Serengeti and other areas suggests that cyclical changes from woodland to grassland, with various intermediate stages of bushland, are a fundamental feature of semi-arid savannas in East Africa (e.g., Dublin, 1995; Pellew, 1983; Lamprey *et al.*, 1967). Historical documents show that much of what is now woodland in the Serengeti National Park northern and western areas was open grassland at the beginning of the twentieth century (Sinclair, 1979a). This change was traced back to the rinderpest epidemic that swept through East Africa beginning in the 1890's, brought by cattle from Asia. The domestic cattle of the Masai became infected, as did many of the wild ungulates. A complex chain of events transpired, and ninety percent of wildebeest died. This drastic reduction in grazing pressure led to bush encroachment and the appearance of tse-tse flies. Woodlands then developed where grasslands had been before. The rinderpest epidemic was finally ended in the 1950's after which grazing ungulates, particularly wildebeest, began a population explosion, eventually numbering two million wildebeests, a level that seems relatively stable since the 1980's. The grazing of wildebeest, and the appearance of elephants in the park in the 1970's then led to woodland decline and the reappearance of grasslands.

The rinderpest epidemic and its far-reaching consequences for the vegetation were induced by modern humans and their movements with domestic animals. However, it is possible that disruptions in ecosystems are typical, whether human-induced or not.

At Amboseli National Park in southern Kenya, a die-off of *Acacia xanthophloea* trees occurred in the mid-1900's, and was originally attributed to damage by elephants and overgrazing by domestic livestock (Laws, 1970). A study by Western and Van Praet (1973), however, concluded that the ultimate cause of the die-off was a change in climate, particularly the very wet years 1961-1964, which caused the ground water table to rise by 3.5 m. This rise caused the capillary fringe to bring soluble salts into the rooting level of the trees, thereby causing death through physiological drought. At that time, halophytic plants such as the shrub *Suaeda monoica* took over and flourished, changing the basin from a woodland to a bush grassland (Western and van Praet, 1973). In this case, natural short-term climatic changes resulted in vegetation change within a lake basin. This example also points out important links between soil characteristics and moisture availability for plants. Ironically, it is during higher rainfall times when a more salt-tolerant, xerophytic plant community is to be found at places closest to the lake, while *Acacia xanthophloea* woodlands dominate in times of more arid climate.

The die-offs at Amboseli may also have been related to the relatively even-aged stand of *Acacia xanthophloea* trees that existed there. Even-aged stands are a typical characteristic of East African savannas, and are strong evidence that certain landscape facets undergo natural cycles that involve major structural changes. Young and Lindsay (1988) found that *Acacia xanthophloea* trees in Kenya occur in even-aged stands at Lake Naivasha, Lake Nakuru, and Amboseli National Park. They argue that the *Acacia xanthophloea* deaths at Amboseli in the 1960's (Western and van Praet, 1973) were at least partially due to the fact that the trees are an even-aged stand. Since the large trees near the spring were all approximately the same age, they all started to senesce at the same time, and therefore were more susceptible to any immediate cause, be it elephant damage, groundwater level changes, or size-specific stressors like wind. Lamprey *et al.*

(1967) surveyed *Acacia xanthophloea* trees along the Seronera River just downstream (northwest) of where I surveyed in this study. They found the trees to fall into four diameter classes which they interpreted as representing ages of 8-9, 32, 63, and 84 years.

Prins and Van der Jeugd (1993) determined the ages of large *Acacia tortilis* trees at Manyara's lacustrine terrace based on their dbh (diameter at breast height) measures, and others' estimates of annual diameter increase. They concluded that in the mature woodlands area of the lacustrine terrace, 25 old trees were established in 1887. This corresponds to the afore-mentioned rinderpest epidemic, which affected all of East Africa. Prins and Van der Jeugd (1993) also found evidence for similar aged stands of trees in Tarangire National Park (near Lake Manyara) and Ndutu in the eastern Serengeti Plain.

Baobab trees (*Adansonia digitata*) in Manyara have a peak establishment between 1870-1880 (Weyerhaueser, 1982), and in Ruaha National Park, there is an over-representation of baobab trees established between 1860-1870, assuming a trunk girth increase of one meter per 40 years (Barnes, 1979).

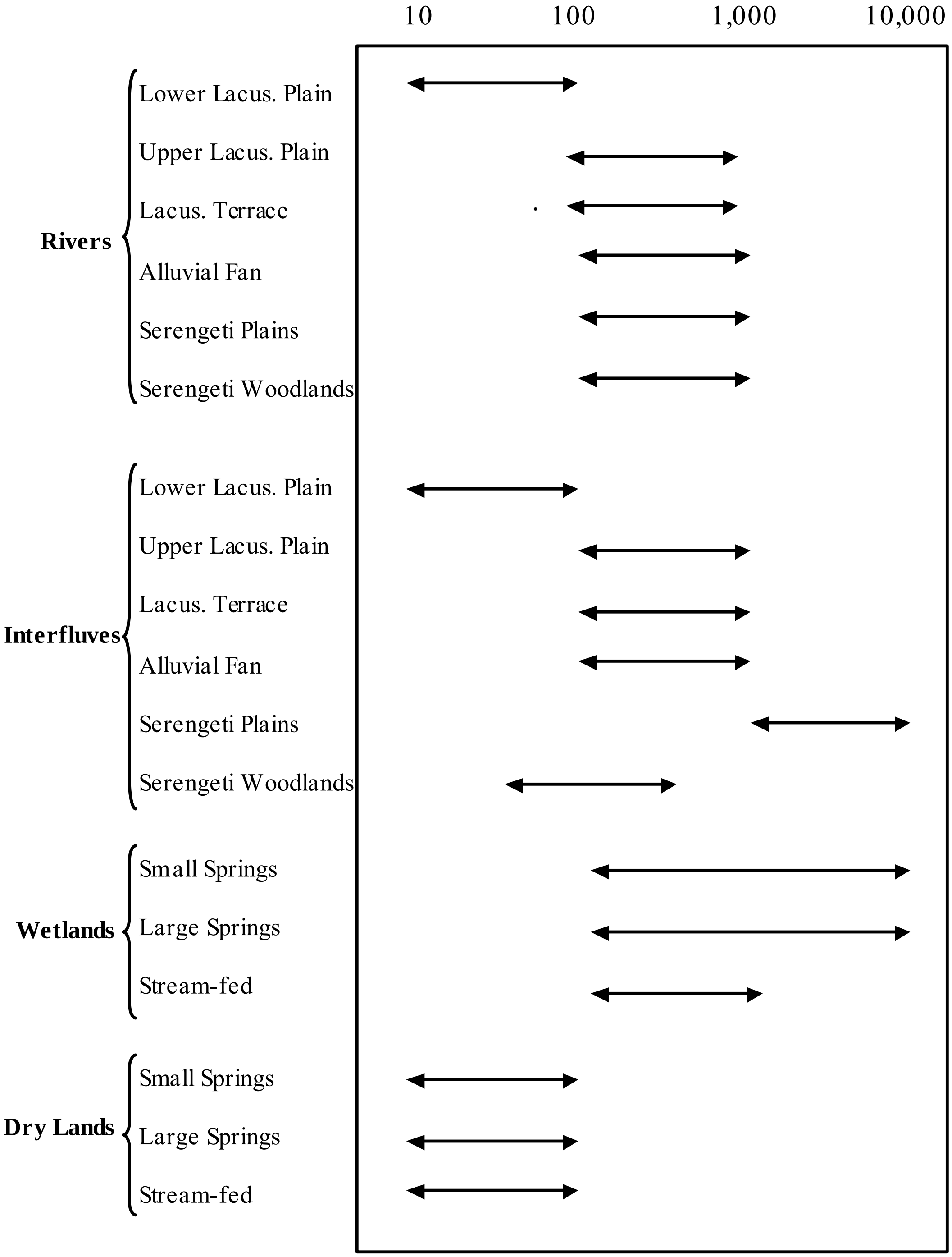
In Dublin *et al*.'s (1990) multiple stable states hypothesis based on research in the Serengeti ecosystem, certain areas are thought to cycle through stages of woodland, bushland, and grassland in response to factors such as fire, herbivory, and climate fluctuations. This does not apply to all landscape units within the ecosystems, however. Certain landscape facets are more permanent over the long-term, while others fluctuate on a shorter time scale. Within the Serengeti region, Belsky (1990) concluded that grasslands, riverine evergreen forest, and inselberg vegetations are climax, but wooded grasslands, bushlands, and woodlands are dynamic and convert to one another over time.

These generalizations can be made more specific when landscape facets are added to the equation.

Since the duration of landscape facet structural homogeneity has important implications for landscape paleoanthropology and for OLAPP, I have developed a model that estimates the duration of stability in vegetation structure for my modern landscape facets, ranging from 10 to 10,000 years (Figure 4-26). Landscape facets with the shortest duration of stability are the rivers and interfluves of the lower lacustrine plain, and the dry lands directly adjacent to the Ngorongoro wetlands. They are expected to vary in structure within 10 to 100 year time periods as rainfall varies and climatic cycles such as El Niño cause lake levels and wetlands to expand and recede. For example, when an *Acacia xanthophloea* tree-lined river or woodland is inundated with saline lake water, it can quickly revert to bush grassland, as was the case for the *Acacia xanthophloea* die-off at Amboseli (Western and Van Praet, 1973) and at Manyara after 1998. At lower lacustrine plain interfluves, grassland can quickly change to bare mudflats or marshes. These are the landscape facets closest to groundwater level, and therefore the most sensitive to small climatic changes.

At the opposite extreme are landscape facets whose vegetation structure persists for thousands of years. In my study areas, these are the Serengeti Plain grasslands and possibly the wetlands association with Small and Large Springs in Ngorongoro Crater. Earlier researchers (Bell, 1982; McNaughton, 1983) claimed that species composition and physiognomy in the Serengeti Plain was controlled by grazing intensity. However, it is ultimately the soil type – alkaline, sodic and with a shallow layer of calcrete – that prevents the growth of trees and maintains a grassland (Belsky, 1990). Enclosures in the

Figure 4-26. Estimated duration of stability (in years) for vegetation structure in various landscape facets.



Plains protected from fire and herbivory still do not grow trees. Thus in a sense the Serengeti Plain grasslands are a climax vegetation, and persist for thousands of years (Belsky, 1990).

Wetlands also have the potential to persist for thousands of years if they are in a stable geomorphological setting. Most stream-fed wetlands are apt to migrate over space as the river channel changes course, but some spring-fed wetlands such as those near the Crater wall exist due to particular locations of geological structures that allow for the groundwater to seep to the surface. Those localities could change with geological movement or if inundated by high lake levels, but otherwise they have the potential to be stable for thousands of years or more.

Other landscape units that I did not sample, but that would be expected to persist for thousands of years, are riverine evergreen forests (Belsky, 1990), inselberg vegetation such as that on the kopjes of Serengeti (Belsky, 1987) and montane forests (Bonnefille, 1984a). Examples of riverine evergreen forest are those growing along the lower Grumeti and lower Mbalageti Rivers in Serengeti National Park. Pollen evidence (Bonnefille, 1984a) suggests that the montane forest of the Crater Highlands has persisted over thousands or even millions of years, despite its fluctuations in size with Milankovich cycles and other global climatic events.

The alluvial fan groundwater forest that I sampled is not a long-term or climax forest, as the tall trees are all quick-growing (Greenway and Vesey-Fitzgerald, 1969), and the understory of saplings are of a completely different species composition than the upper canopy. It falls into the 100 to 1000 year category, as do most of my study areas. The rivers and interfluves at Serengeti and Manyara have persisted as bushland or bush grassland vegetation for most of this century, but could be expected to fluctuate between woodland, bushland, and grassland over the time period of 1000 years, as climate changes, natural disturbances such as fires occur, and large herbivore populations fluctuate.

Conclusion

By conducting a detailed analysis of the vegetation in the modern analog study areas, I have addressed the central question of this chapter: what is the nature of the relationships between physiognomy, plant species composition, and landscape units in the modern analog settings? The answer is complicated, as would be expected for ecological processes. In the section "Relating physiognomy, landscape units, and species composition," I summarized those aspects for the various units in the modern study areas. What emerges is a sense that each land unit has unique properties, and contrasts between different landscape facets, landscape associations, and regions vary according to the particular land unit is in question. For example, physiognomic structural categories cross-cut many different land units, but on the whole are predictable for a particular landscape facet. Species composition varies a great deal across regions, particularly for shrubs, forbs, and grasses, but the importance of species composition is more closely tied to hominin plant food resources, a subject which is explored in Chapter Five.

For paleoanthropology in general, a landscape approach to paleoenvironmental reconstruction that identifies particular landscape units such as landscape facets from the fossil/geological record has great potential to enrich our paleoecological understanding of early hominin sites. Each hominin site has its own unique geological and ecological settings such that modern analogs that are pertinent to that particular setting will have to be examined for each site, just as the modern analogs studied here are particularly relevant to the paleo-Olduvai basin and its surroundings. In other words, the relationships between vegetation structure, land units, and species composition that were investigated here cannot be summed up into simple generalizations that will be applicable to all fossil hominin settings. The key for each situation will be to understand how environmental variables control physiognomy and plant species composition, to identify those environmental variables in a paleolandscape, and therefore to be able to develop strong relational analogies (Gifford-Gonzalez, 1991) which will allow us to predict the ecological characteristics of the ancient setting. This chapter and the next make a strong beginning toward that goal for the Olduvai case study.

CHAPTER 5. PLANT RESOURCES FOR HOMININS IN THE MODERN ANALOG ENVIRONMENTS

Introduction

In this chapter, I address the issue of how plant resources for hominins are distributed in the modern analog study areas at Manyara, Serengeti, and Ngorongoro. In Chapter Four I focused only on the relationships between vegetation physiognomy, species composition, and land units, without regard to how the vegetation might be relative to hominin ecology. Here I focus on plant foods and refuge trees, and how those resources relate to vegetation physiognomy, species composition, and land units.

In this landscape approach to paleoanthropology, the distribution of hominin affordances, including all resources and hazards, is used to create models of hominin land use, which in turn is used to predict the archaeological residues that will be left behind. Blumenschine and Peters (1998) highlight the importance of animal foods in the form of scavengeable carcasses as the resource whose use by hominins will leave the majority of archaeological traces. While that is true, it is also possible that plant foods formed the staple diets of hominins, so that their ranging patterns were to a large degree dependent upon the distribution of plant foods and arboreal refuge for nighttime sleeping. Thus any interpretation of hominin land use and scavenging of carcasses must be made with an understanding of what hominins' daily foraging routine most likely encompassed, which was the exploitation of wild plant foods.

In this chapter, I focus on the types and abundance of plant foods and refuge trees in the modern analog study areas, and in Chapter Six I apply this information to the

Olduvai case study and create models of hominin plant food and refuge tree distribution across that paleolandscape. To characterize plant resources in the modern analog settings, I first describe the nature, habitats, and other anecdotal attributes of many of the wild plant food species that I encountered in my study areas. I then begin the quantitative analysis by comparing the calculated cover values of edible trees and shrubs, and the species richness values for edible forbs and grasses, in the different physiognomically-defined categories of the modern study areas. Next, I do a similar quantitative analysis of plant foods according to land regions, landscape associations, and landscape facets. In order to have a relatively simple means by which to compare the relative abundance of particular plant food parts (e.g., fruit, seeds/pods, etc.) among different landscape facets, I transpose all of the data to an ordinal scale ranging from the lowest value, 0 to a highest value of four plus signs (0, +, ++, +++, and ++++), following Peters and Blumenschine (1995; 1996). This information is later used in Chapter Six to model the relative distribution of plant foods across the Olduvai paleolandscape.

In the latter portion of this chapter, I discuss refuge tree density in the modern study areas. As with plant foods, I first look at the abundance of refuge trees by physiognomic categories, and then by land regions, landscape associations, and landscape facets. Finally, I transpose the data to the simple abundance scale of 0, +, ++, +++, and ++++, following Peters and Blumenschine (1995; 1996), so that all landscape facets can be easily compared in terms of refuge tree density, and the results can be applied to a resource model of the Olduvai paleo-basin in Chapter Six.

Methods

The abundance of edible trees and shrubs are expressed as calculated cover values, that is, the sum of crown areas of the species in question. As described in Chapter Three, this method can lead to larger numbers than that of overall visual cover estimates for trees or shrubs, for example, because of the overlap of individual crowns. However, for the purpose of estimating the relative contribution of a particular species to its plot, the calculated cover values are more appropriate because they take into account each plant, regardless of whether it is overlapped by the crown of another. Edible tree and shrub cover values presented in this chapter therefore will differ from the visually estimated, overall cover values used to describe physiognomic categories in Chapter Four.

Plant food and refuge tree data are compared by the mean abundance of the study areas in each landscape facet. Since there is a maximum of two study areas per landscape facet, and in some instances only one study area per landscape facet, it is not possible to compare those means statistically. However, it is informative to compare patterns between the different landscape facets.

Study areas are grouped according to their physiognomic categories following Pratt and Gwynne (1977), as described in Chapter Three (Table 3-3). The total number of study areas in marsh, grassland, bush grassland, bushland, and forest are low, so again it is not possible to compare those means statistically. It was necessary to exclude the shrubland and woodland data from the overall edible plant and refuge tree analyses because those physiognomic types were sampled only in Ngorongoro Crater.

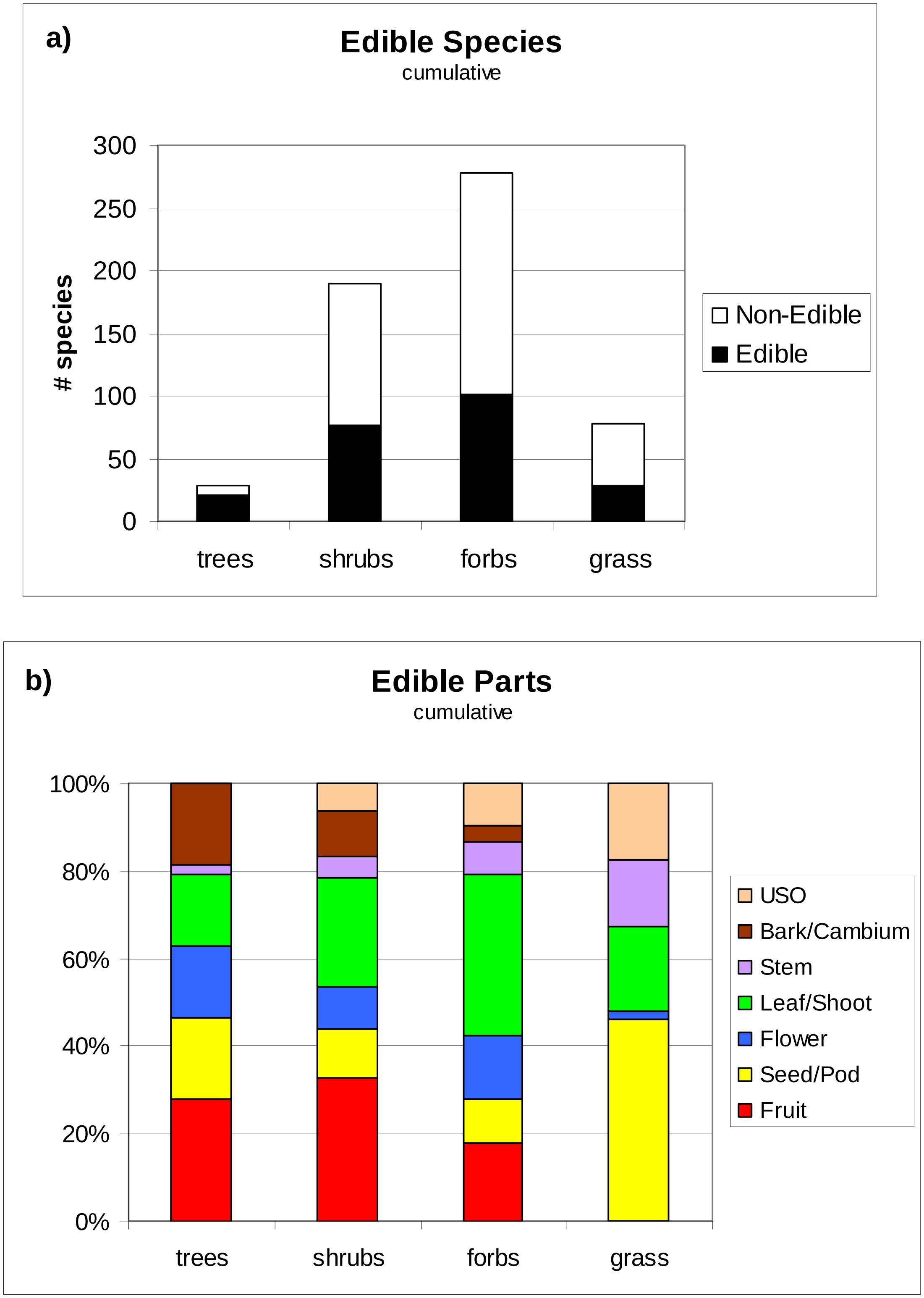
Edible Plants

Of the total of 476 species encountered in the Manyara, Serengeti, and Ngorongoro study regions, 181, or 38%, had one or more edible parts, that is, parts that have been recorded to be eaten by humans, chimpanzees, or baboons in a natural setting (Peters *et al*., 1992). By growth form, the proportion of all shrub, forb, and grass species that are edible are 41%, 36%, and 37% respectively, while the proportion of trees that are edible is higher at 72% (Figure 5-1a).

The proportion of edible plant parts, e.g., leaves, fruits, etc., differs for each growth form (Figure 5-1b). Trees have a high proportion of edible bark/cambium, shrubs are high in edible fruits, forbs have relatively more edible leaves/shoots, and grasses have especially high proportions of edible seeds, edible underground storage organs (USOs), and edible stems. No grasses are noted to produce edible fruits because their reproductive parts were always classified as seeds.

A complete list of all plant species, including information on which species are edible, what parts of the plant are edible, and the study areas in which those species are found is given in Appendix 1. Appendix 2 contains a detailed summary of the edible plants that were found in each study area. In the next section I give an overall description of the more common edible plants, followed by quantitative comparisons of edible plant abundance by physiognomic categories and landscape units.

Figure 5-1. Edible species from the modern study areas at Manyara, Serengeti, and Ngorongoro grouped by growth form. Results are shown as a) count of species and b) proportions of edible plant parts. USO = underground storage organs.



Description of Edible Species in the Modern Study Areas

Trees

The Somalia-Masai floristic zone, which includes northern Tanzania, Kenya, and Somalia (Figure 2-7), has 30 endemic species of *Acacia* (White, 1983), and the two most common trees in the Serengeti, Manyara, and Ngorongoro sites of this study were *Acacia tortilis* and *Acacia xanthophloea*. Five other species of *Acacia* were encountered less frequently. Since they are legumes, mature *Acacia* trees produce “beans” whose pods and seeds have varying degrees of edibility.

Many *Acacia* species have parts that are eaten by primates, particularly baboons, vervets, and patas monkeys. Humans have been observed to eat the pods (not the seeds) of *Acacia tortilis*, for example, by pounding them into a flour and mixing that with milk for porridge (Birnie, 1997). Most humans living around *Acacia tortilis* trees today do not consider them edible. Rather, the trees provide firewood, food for domestic stock, and shade in otherwise relatively open habitats.

Acacia xanthophloea pods and seeds are eaten by baboons, but only rarely, and *Acacia xanthophloea* trees full of fruits are often ignored by baboons (Wrangham and Waterman, 1981). *Acacia xanthophloea* flowers, which appear in the late dry season, are not consumed by baboons, and only rarely by vervet monkeys, and therefore are not considered as potentially edible to hominins. On the other hand, the flowers of *Acacia tortilis*, which also appear in the late dry season, are eagerly consumed by primates during this time of general resource scarcity. Nutritional analyses show that both flowers and pods of *Acacia xanthophloea* have higher levels of tannins and phenolics than those of *Acacia tortilis* (Wrangham and Waterman, 1981; Hausfater and Bearce, 1976).

Almost all *Acacia* species tend to ooze gum from wounds in their trunks. *Acacia* gums can be a valuable resource, and most are non-poisonous (Story, 1958). Vervet monkeys and baboons are particularly fond of eating *Acacia xanthophloea* gum, which contains over 50% carbohydrates (sugars), and less than 3% (dry weight) total phenolics and condensed tannins (Wrangham and Waterman, 1981; Hausfater and Bearce, 1976). In contrast, these primates only rarely eat *Acacia tortilis* gum, which contains less than 1% carbohydrates, and greater than 27% total phenolics and condensed tannins (Wrangham and Waterman, 1981; Hausfater and Bearce, 1976).

In sum, the main potential hominin foods provided by *Acacia tortilis* are pods and flowers, although the leaves, gum, and bark are also technically edible (Peters *et al*., 1992). The main resource provided by *Acacia xanthophloea* is an edible gum, though its pod, seed, and bark have been known to be eaten rarely by baboons.

Acacia sieberiana, which occurred only in Manyara's fluvial terrace in this study (along the Endabash River), produces seeds that are eaten by chimps and baboons, and baboons also eat the flowers and gum (Peters *et al*., 1992). For the species *Acacia robusta*, which occurs in Manyara's groundwater forest and in the Serengeti Woodland, humans and baboons have been recorded to eat the gum, while baboons also eat the seeds, shoots, and flowers (Peters *et al*., 1992). The only recorded uses of *Acacia kirkii*, which in this study occurs exclusively along the Serengeti Woodland's Mbalageti River, are by humans who make tea and rope from the bark, medicines from the gum, and use the wood for fuel (Marcan, 1998).

Trichilia emetica, the most common tree in Manyara's alluvial fan/groundwater forest, has edible seed arils known to be eaten by humans and baboons (Peters *et al*.

1992). The bright red arils can be peeled or bitten off the black seeds, but the seeds themselves may be poisonous to humans (Mbuya *et al*., 1994). Although the fruits typically grow at heights of greater than 20 meters in the canopy, many fall to the forest floor where they can be eaten on the spot or collected for later consumption.

Balanites aegyptiaca trees are known as the "desert date" in reference to their date-like fruits, which are eaten by humans and baboons (Peters *et al*., 1992). These trees occur in Manyara and at the present day setting of Olduvai Gorge, and in this study were found along the Ndilana River of the Lacustrine Terrace and in the western Serengeti Plain in the interfluve near the Nyamara River. The leaves of *Balanites aegyptiaca* are also eaten by humans as a cooked vegetable (Marcan, 1998). The wood can be made into charcoal. The fruits, seeds, or bark ground up in water serve as a poison to fish and snails, including those snails that host bilharzias (Coates Palgrave, 1993; Birnie, 1997).

The genus *Ficus* has several species endemic to East Africa's Somalia-Masai floristic zone, and many more *Ficus* species occur throughout the Old and New World tropics (White, 1983). *Ficus* species tend to produce copious amounts of nutritious fig fruits on the tree when they bear. Each individual tree bears fruits at a different time of year, so that in an area of many fig trees, at least one or more are likely to be fruiting (Wrangham *et al*., 1991). Fig fruits are usually high in carbohydrates and have high food value, so figs are considered keystone species for many frugivores, including various primates. In some *Ficus* species, the leaves are edible as well (Peters *et al*., 1992).

Ficus sycomorus, which occurs on well-drained soils close to underground water sources throughout the study regions, has fruits and young leaves/shoots that are eaten by humans and baboons (Peters *et al*., 1992). Other edible fig tree species that have been recorded inside Manyara National Park, but were not in any of my sampling plots, are *Ficus vallis-choudae*, *Ficus thonningii*, and *Ficus wakefieldii* (Snelson, 1986).

Ziziphus species are thorny trees or shrubs common throughout the drier parts of Africa, and most species produce edible fruits. Along Serengeti's Nyamara and Mbalageti Rivers, *Ziziphus mucronata* occurred as a riverine shrub. The round, brownish-red fruits, about 1 cm diameter, have a rather dry, mealy substance surrounding a large stone. The mealy flesh is known to be eaten by humans, chimps, and baboons (Peters *et al.*, 1992), but I and the Bushmen of southern Africa consider it unpleasant tasting (Story, 1958). *Ziziphus pubescens* is a common tree in Manyara's fluvial terrace along the Endabash River, and its fruits are similar: reddish, round, and edible to humans, and described as "sickly bitter" in taste (Markan, 1998).

A variety of palm trees are native to sub-Saharan Africa. Of those, at least 17 species in six genera produce edible fruits (Peters *et al.*, 1992). The palm *Hyphaene petersiana*, which occurs on the lacustrine plain at Manyara, has fruits that are known to be eaten by the Bushmen of southern Africa (Story, 1958) and the Gwembe Tonga of Zimbabwe (Scudder, 1962). The fruits are slightly smaller than a tennis ball, and have a two to three cm thick edible mealy layer between the skin and the inner kernel (Story, 1958). Humans also eat the seed (raw), the flower nectar, and the pith, otherwise known as the palm heart (Peters *et al.*, 1992). Baboons also eat the fruits of these palms (Peters *et al.*, 1992).

Shrubs

Individual plants of the genus *Acalypha* usually come in the form of small shrubs, typically less than two meters tall in this study. Several of the species of *Acalypha* provide edible leaves for humans (Marcan, 1998). *Acalypha fruticosa* has the third highest importance value for shrubs over all Serengeti and Manyara sites, behind *Acacia tortilis* and *Acacia xanthophloea* shrubs. Baboons are known to eat the small (2 x 3 mm), dehiscent fruits and the pith of *Acalypha fruticosa* (Peters *et al*., 1992). Also occurring at most of the Manyara sites was *Acalypha indica*, which has leaves that are edible to humans, and *Acaclypha ornata*, of which chimpanzees in western Tanzania eat the fruits and leaves (Nishida and Uehara, 1983; Van Lawick-Goodall, 1968).

The Capparaceae family is common in dry areas of Africa, particularly in bushland (Kokwaro, 1994; Lind and Morrison, 1974:60). Capparaceae plants can be recognized by showy flowers with many stamens, and succulent, berry-like fruits on long stalks (Lind and Morrison, 1974:60). Six genera and ten species are represented in this study, including *Maerua*, *Capparis*, *Cadaba*, *Thilachium*, and *Cleome*. Most have edible parts, and all are either shrubs or small trees not suitable for arboreal sleeping refuge.

Several species of the genus *Maerua* have fruits that are edible to humans or baboons (Peters *et al*., 1992). *Maerua triphylla* has one of the highest importance values for shrubs at Manyara, although it is not found in the groundwater forest, and it has long, cylindrical edible fruits (2-7 cm) and edible roots. Both parts are labeled “may be poisonous” from East African herbarium records (Peters *et al*., 1992), and therefore may need treatment such as cooking or soaking before they are edible to modern humans.

Of the genus *Capparis* (which includes the caper, a spice known from Mediterranean cuisine), a species found at many of the Manyara and Serengeti sites was *Capparis tomentosa*. Baboons eat the relatively large (2-6 cm), round fleshy fruit, and humans are known to eat it cooked as a famine food, although many accounts regard it as poisonous (Peters *et al*., 1992). *Capparis tomentosa* can form an almost impenetrable thicket, as it grows like a woody climber, intertwining with other shrubs, and its stems are covered with sharp, hooked thorns. Its relative, *Cadaba farinosa,* which also occurs in this study at many Serengeti and Manyara sites, looks similar but has no thorns, and humans eat the leaf and stem (Peters *et al*., 1992).

Also in the Capparaceae family, *Thilachium africanum* has roots that can be boiled and eaten. *Thilachium africanum* was used as a famine food by the foraging/agriculturalist Sandawe of Tanzania in years of low crop production (Newman, 1975). *Cleome gynandra* (formerly known as *Gynandropsis gynandra*) is a common vegetable in East Africa, and is occasionally semi-cultivated (Kokwaro, 1994). Humans eat the leaf, young shoots, stems and flowers cooked as potherbs (Peters *et al*., 1992).

The Hadza foragers live today in Tanzania within 200 km of Olduvai Gorge, so their diet is of particular interest here. Two of the three most important wild fruit species in their diet come from shrubs that were found at my modern study area sites in relatively high abundance, *Salvadora persica* and *Cordia sinensis* (Vincent, 1985b:39). The third is the fruit of the baobab tree, *Adansonia digitata* which, though not present inside any of my plots, does grow at Manyara along the rift escarpment.

Salvadora persica shrubs were found at almost all Manyara sites except in the groundwater forest and Mkindu River of the lacustrine plain. It produces clusters of tiny, juicy, sweet edible fruits during the dry season. *Salvadora persica* is also one of the most desired "supplement" foods of the Sandawe, being eaten in significant quantities by individuals who are in pursuit of other activities such as livestock herding or collecting firewood (Newman, 1975). Stems of *Salvadora persica* can be broken off and used to clean the teeth, hence the shrub's common name, the tooth brush tree (Beentje, 1994). Baboons also eat the sweet fruits of *Salvadora persica* (Peters *et al*., 1992).

At least five East African *Cordia* species have fruits that are edible to primates (Peters *et al*., 1992). *Cordia sinensis*, mentioned above as an important food for the Hadza, grows as a shrub or small tree in Manyara's lacustrine and fluvial terraces, and produces a tasty, ovoid yellow/orange fleshy fruit (1 cm diameter). The root is also reported to be edible raw by humans (Peters *et al*., 1992). *Cordia monoica*, which occurred in most sites at Serengeti and Manyara, also has fruits that are edible to humans and baboons (Peters *et al*., 1992). The leaves of *Cordia monoica* are used as sandpaper, hence it's common name, msasa, the Swahili word for sandpaper.

The small shrub *Aspilia mossambicensis* has leaves that are eaten by chimpanzees. These leaves might serve more of a medicinal purpose than one of sustenance for the chimpanzees. Instead of quickly consuming the leaves as was done with other plant species, chimpanzees at Gombe took the leaves of *Aspilia mossambicensis* one at a time, after careful inspection, and sometimes swallowed the leaves whole (Wrangham, 1977; McGrew, 1992). Biochemical analyses revealed the leaves to contain a potent antibiotic, hiarubine A, with anti-fungal, -viral, -bacterial, and -parasitic properties (McGrew, 1992:183).

Shrubs of the genus *Commiphora* are common in the Somalia-Masai floristic zone, are typically thorny, and most produce a pungent resin. *Commiphora africana*, for example, is the African myrrh tree, referring to the valuable spice that derives from its resin (Marcan, 1998). *Commiphora africana* occurred in the Eastern Serengeti Plain, and is one of the most common shrubs around Olduvai Gorge today. Humans eat the fruit, leaf, and stem (Peters *et al*., 1992). The gum of *Commiphora africana* is a chewing gum, and the roots can be eaten like a cassava substitute (Marcan, 1998). Baboons eat the fruit as well.

Forbs

Because there were so many forb species identified in the modern study areas, I describe some of the more common edible ones grouped according to family.

The most common forb in the modern sites is *Achyranthes aspera*, of the family Amaranthaceae. This forb often grows in the shade of a tree, and is easily recognized by the long stalks of pink/purple fruiting flowers, the seeds of which attach to the clothing or fur of passers-by. Like several other African members of the family Amaranthaceae, *Achyranthes aspera* has edible leaves, observed to be consumed by humans and baboons (Peters *et al*., 1992).

The family Acanthaceae is a large, pantropical family of mostly herbs and some shrubs, and in this study is the third most species rich family with 29 species, behind Gramineae (grasses) with 78 species, and Compositae with 40 species. Two of the most common species of Acanthaceae in these study areas are *Monechma debile* and *Hypoestes forskalei*. Humans eat the leaves of both of these species as a vegetable, and baboons are known to eat the leaf and flower of *Monechma debile* (Peters *et al*., 1992). Also in the Acanthaceae family, the genus *Justicia* was represented by 12 different species in this study, all forbs or small shrubs, and four of which have edible parts. *Justicia flava* has edible leaves, *Justicia caerulea* has edible flowers (eaten by children), *Justicia striata* has edible leaves, young shoots, and flowers, and humans eat the whole plant of *Justicia matamensis* (Peters *et al*., 1992)

Another commonly occurring family is Solanaceae, the tomato, potato, tobacco, and deadly nightshade family. Although most species of this family are found in tropical America, there are also species indigenous to Africa, many of which are poisonous. Of the six forbs and one shrub species of this family that are present in these study sites, only the woody herb *Solanum incanum* is edible. Humans eat the leaf, and baboons eat the round, yellow tomato-like fruits (Peters *et al*., 1992). These plants occur around the antiquities camp at Olduvai Gorge, and the local Masai regard the fruits as poisonous.

The Malvaceae or cotton family was most commonly represented in my study areas by the genera *Hibiscus*, *Sida*, and *Abutilon*. These plants often have showy flowers and tend to be part of the ground or shrub layer, small but with woody stems, making it difficult to determine whether they should be classified within the shrub or herb category. Of the six species of *Hibiscus* present, four are known to be edible: *Hibiscus ovalifolius*, *Hibiscus micranthrus*, *Hibiscus cannabinus*, and *Hibiscus aponeurus* (Peters *et al*., 1992). Fruits, leaves, flowers, and other parts are recorded as being eaten by chimpanzees, humans, and baboons.

Two of the eight species of *Abutilon* are edible. *Abutilon mauritianum* has edible seeds and flower buds, and *Abutilon hirtum* has seeds edible to humans. All three species of *Sida* have edible parts; *Sida alba* and *Sida acuta* have edible seeds and flower buds, and *Sida alba* and *Sida ovata* have leaves that are edible to humans.

The monocot family Commelinaceae is composed of mostly tropical herbs with jointed stems, alternate sheathing leaves, and small, blue, bisymmetrical flowers. Three of the six *Commelina* species found in these study areas are edible. Humans are known to eat the whole plants of *Commelina africana* and *Commelina benghalensis* boiled as potherbs, and the flowers and pith of *Commelina erecta* are eaten by baboons (Peters *et al.*, 1992).

Within the legume superfamily, Leguminosae, there are three subfamilies: the Mimosoideae which includes *Acacia*, the Caesalpinnioideae which includes *Brachystegia*, a dominant tree in miombo woodland, and the Papilionoideae which includes *Indigofera* and several other forbs and woody herbs found in my study areas. Legumes have special associations with nitrogen-fixing bacteria in or around their roots. Several common forbs in my sites belong to Papilionoideae. At Manyara and in the Eastern Serengeti plain was *Indigofera arrecta*, reported by the East African Herbarium to have roots edible to humans (Peters *et al.*, 1992). Baboons are known to eat the pods of another common species in this study, *Indigofera colutea*, but the other six species of *Indigofera* are not recorded to be edible. Baboons eat the seeds of *Tephrosia pumila*, found in the Western Serengeti Plain grassland, and baboons also eat the pod of *Rhynchosia minima*, a small, ground-level forb found in all Serengeti landscape associations (Peters *et al.*, 1992).

Compositae is the largest family of flowering plants in the world, and is represented by more species than any other except for Gramineae in these study areas

(Kokwaro, 1994). Compositae includes daisies and sunflowers, whose “flowers” are actually a composite of many tiny flowers in the central disc. Of the Compositae species in this study, 31 of the 40 species are herbaceous, and 10 of the 40 species are edible. A common forb in the Manyara sites was *Bidens pilosa*, whose leaves and young shoots are cooked and eaten as a side dish or relish in Tanzania (Peters *et al*., 1992; Marcan, 1998). *Emilia conninea* is a small forb with a bright orange flower that grows amidst the grasslands of the Western Serengeti Plain, and has leaves that are eaten raw by humans (Peters *et al*., 1992).

Many of the edible herbaceous species from Ngorongoro were marsh plants. *Typha latifolia*, the cattail, has large, pleasant tasting edible rootstocks and nutritious edible pollen (Prendergast *et al*., 2000). *Cyperus immensus* and *Cyperus laevigatus*, the two most common sedges in the smaller wetlands of the Crater Floor, both have edible underground bulbs. Of all twelve sedge species (of the family Cyperaceae) that were encountered in these study areas, five had edible underground storage organs such as rhizomes or bulbs.

Grasses

There were 78 grass species in the Serengeti, Manyara, and Ngorongoro study areas, and 28 (36%) of them are edible. Nineteen of the edible grass species have been recorded to be eaten by humans, 22 are consumed by baboons, and only two are consumed by chimpanzees. Of the edible grass plants, 86% had edible seeds, 68% had edible leaves, 29% had edible stems, and 29% had edible underground parts.

Common edible grasses in Manyara were *Digitaria velutina* and *Dactylotenium aegyptium*. In Serengeti, important edible grasses included *Themeda triandra* and

Sporobolus ioclados. The widespread Serengeti grass *Pennisetum mezianum* is not known to be edible to humans, chimps, or baboons. The most common edible grass at Ngorongoro was *Cynodon dactylon*, of which humans eat the grain and baboons eat the entire plant (Peters *et al*., 1992).

Physiognomic Categories: Quantitative Analysis of Edible Plants

When sites are grouped according to their physiognomic categories, the proportions of all species which are edible for marsh, grassland, bush grassland, bushland, and forest are 42%, 41%, 50%, 53%, and 49%, respectively (Figure 5-2a). Edible species are broken down into proportions of edible plant parts in Figure 5-2b. The marsh habitat has by far the highest proportion of edible underground storage organs. With progressively more woody cover from grassland to forest, there is an increasingly higher proportion of edible fruits, and decreasing proportions of edible seeds/pods and stems. In the following paragraphs, I discuss edible plants in each of the physiognomic categories, broken down by trees, shrubs, forbs, and grasses.

Trees

Both total and edible tree cover increase dramatically as habitat types become more wooded (Figure 5-3a). Edible tree species comprise 98% of all tree cover in bush grassland; the edible trees are *Acacia tortilis* and *Acacia xanthophloea*. In bushland, 90% of tree cover derives from edible species, and those include *Acacia tortilis*, *Acacia xanthophloea*, *Trichilia emetica*, and several others. In forested sites, total tree cover is about ten times greater than in the bushland sites, and 88% of the tree cover in forest

Figure 5-2. Edible species from modern Manyara, Serengeti, and Ngorongoro, by physiognomic categories. Results are a) the mean number of species with one standard error and b) the proportions of edible plant parts. USO = underground storage organs.

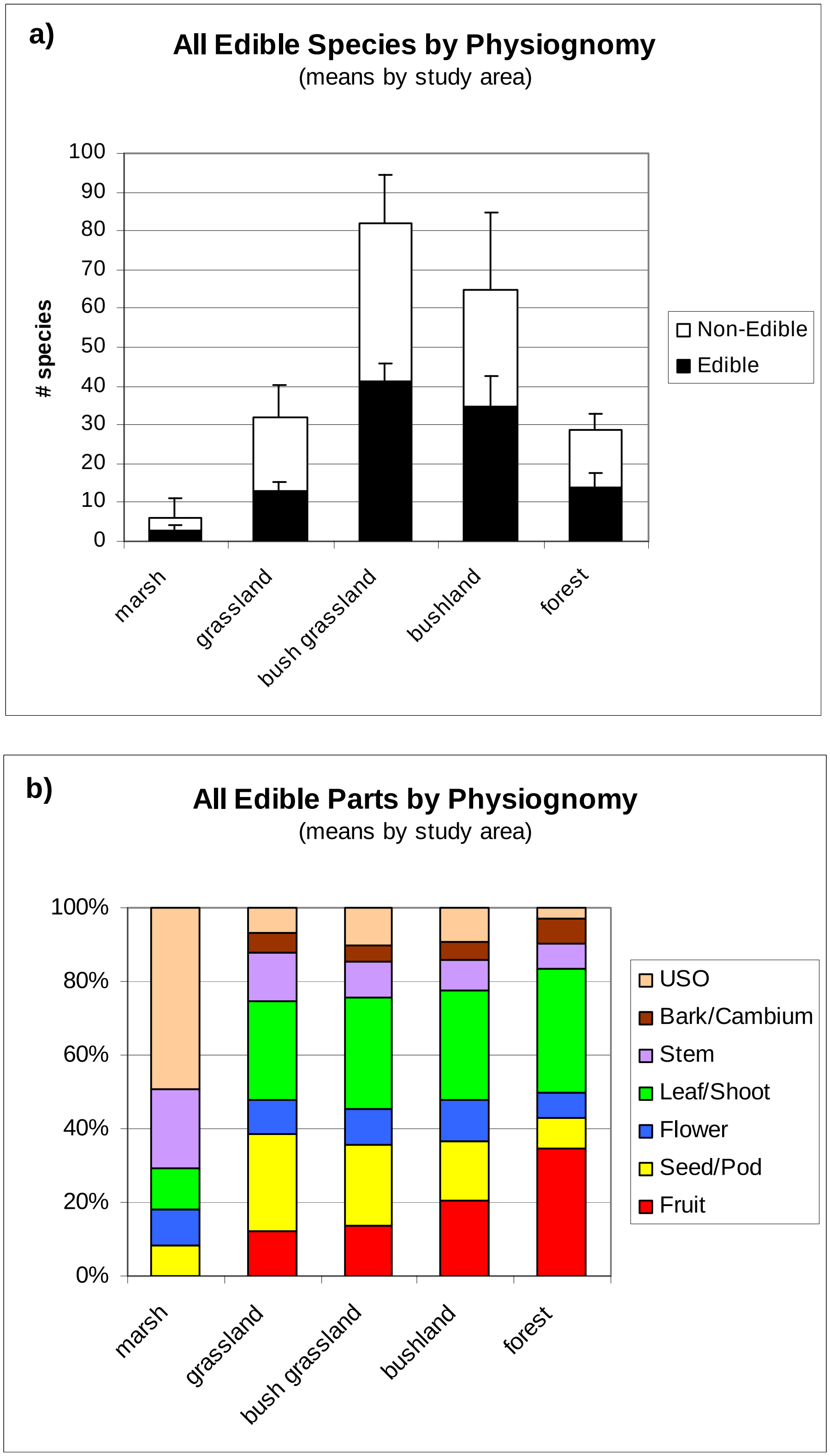
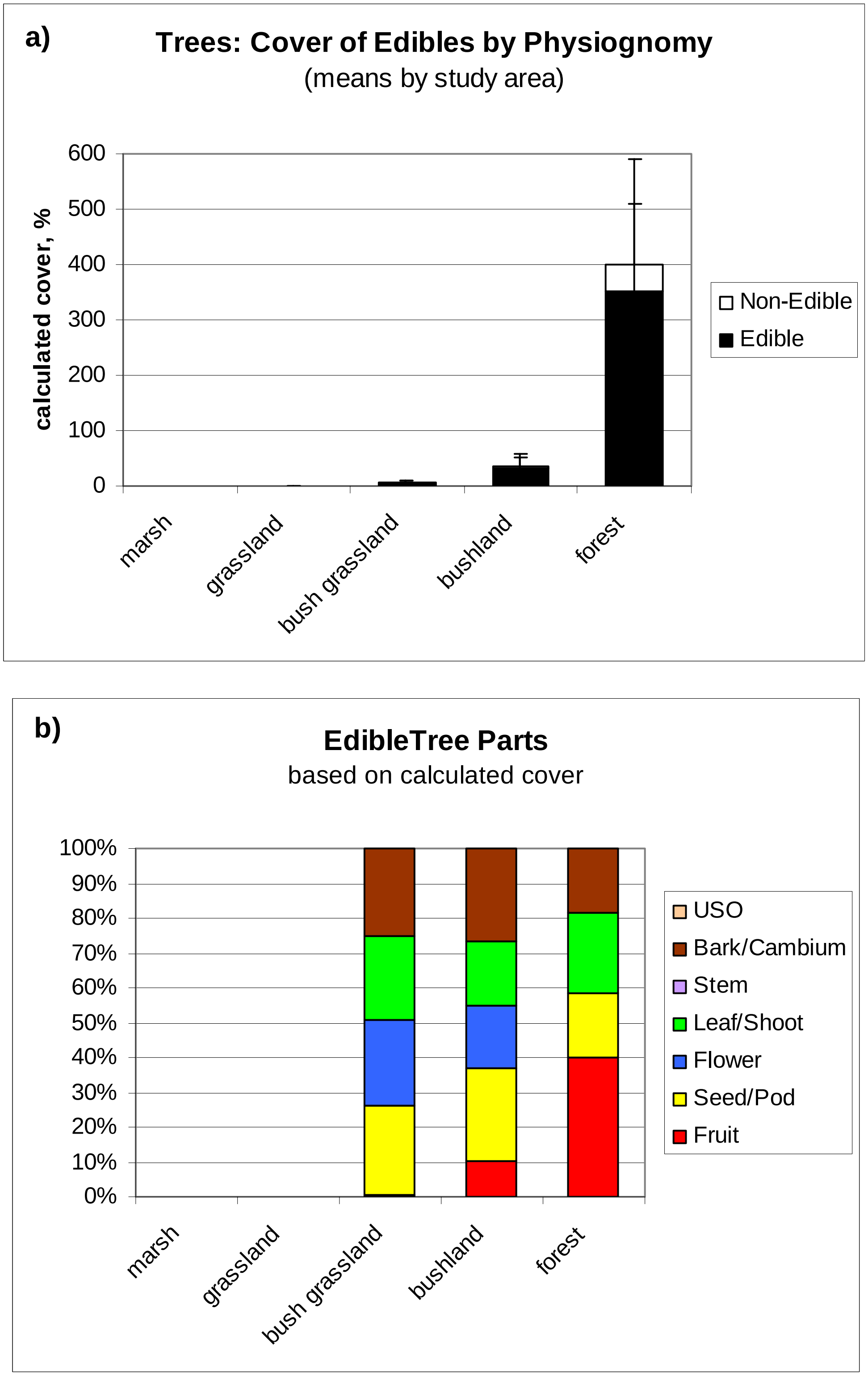


Figure 5-3. Calculated cover values for edible trees encountered in the modern study areas and the proportions of edible plant parts, grouped by physiognomic categories. Bars show the mean with one standard error.



comes from edible species. In these modern study areas I found that forested sites from two adjacent landscape facets sometimes have completely different edible tree species composition from one another. The edible tree species on Manyara's upper lacustrine plain Mkindu River were mainly *Acacia xanthophloea*, while edible tree species in Manyara's alluvial fan/groundwater forest were *Trichilia emetica*, *Ficus sycomorus*, and *Ekebergia capensis*.

In terms of the plant parts that are edible from trees, edible flowers disappear altogether in the forested sites, and edible seeds/pods and bark/cambium are slightly less in the forest. Edible tree fruits show a trend of increasing proportions from bush grassland to bushland to forest (Figure 5-3b).

Using a different definition of edibility, trees may be categorized as potential food for primates according to whether the fruits are dry or fleshy, regardless of whether they have been shown to be edible by primates. This technique was used by Balcolm *et al.* (2000), who suggested the density of fleshy fruit producing trees as a measure of chimpanzee density in a given area, since chimpanzees rely heavily on fleshy fruits for their sustenance (Goodall, 1986; Suzuki, 1969; Wrangham *et al*., 1998). The fruits from East African dry woodlands are mainly pod and seeds from the legume family (e.g., *Acacia*, *Brachystegia*), and these are nutritionally different than fleshy fruits produced in moister habitats (Suzuki, 1969). In general, legume pods and seeds are protein-rich, while fleshy fruit pulp is high in water, simple sugars, and other carbohydrates (Waterman, 1984).

In all of the Serengeti, Manyara, and Ngorongoro modern vegetation plots, I encountered a total of 29 tree species. Of those, 14 tree species produce fleshy fruits, and

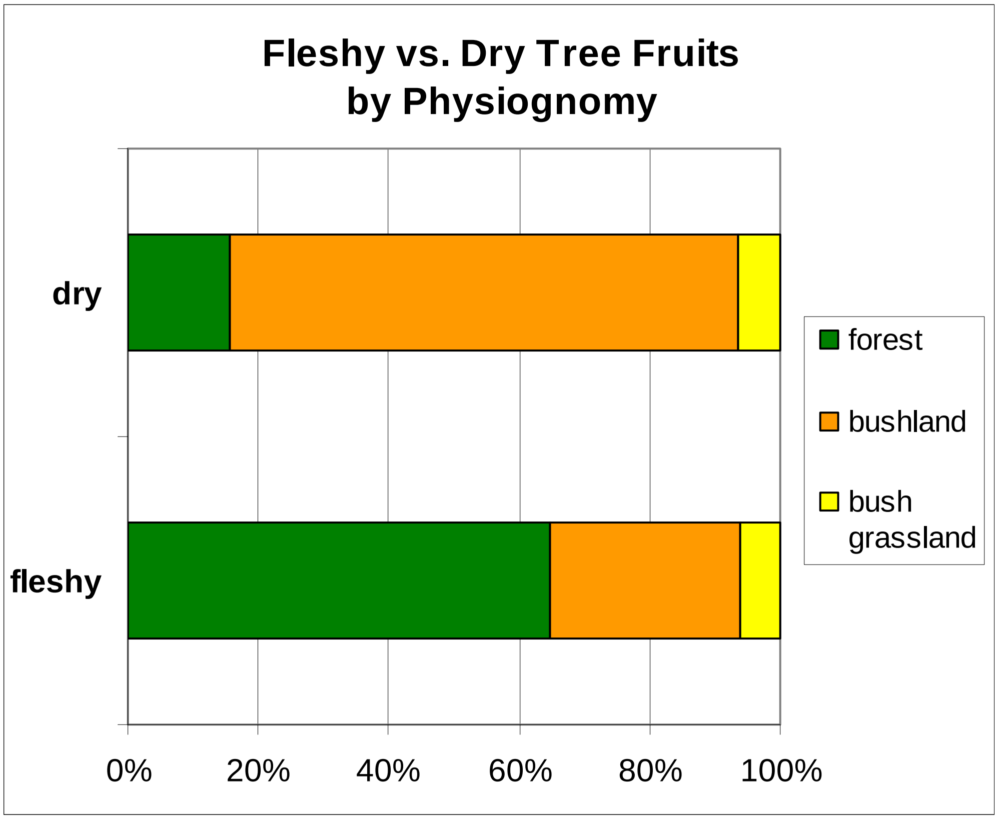
16 produce dry fruits (see Appendix 1). In terms of numbers of individuals, I encountered a total of 898 dry-fruit-producing trees and 83 fleshy-fruit-producing trees, which together account for 97% of the total 1015 trees recorded in all of the modern study areas. As shown in Figure 5-4, the majority of the fleshy fruits can be found in the forest, while bushland and bush grassland have most of the dry-fruit-producing trees. This is consistent with Suzuki's (1969) earlier observation about chimpanzee food resource distribution in western Tanzania. He found that dry fruits are produced in dry woodlands, and juicy fruits (fleshy fruits) are produced in "wet habitats," referring to riverine forest.

The chimp habitats studied by Balcolm *et al*. (2000: Figure 1) at Kibale National Park, Uganda, ranged in density from approximately 27 to 190 fleshy-fruit trees per hectare. In Manyara's alluvial fan/groundwater forest of this study, the average density is 32 fleshy-fruit trees per hectare, while the average density of fleshy-fruit trees in my bushland sites was only two per hectare, and bush grassland had less than one fleshy-fruit tree per hectare. According to my samples, bushland, bush grassland, or other open habitats would not be ideal foraging areas for a primate dependent on fleshy fruits from trees. The potential implications of this distribution to early hominins are taken up in Chapters Six and Seven.

Shrubs

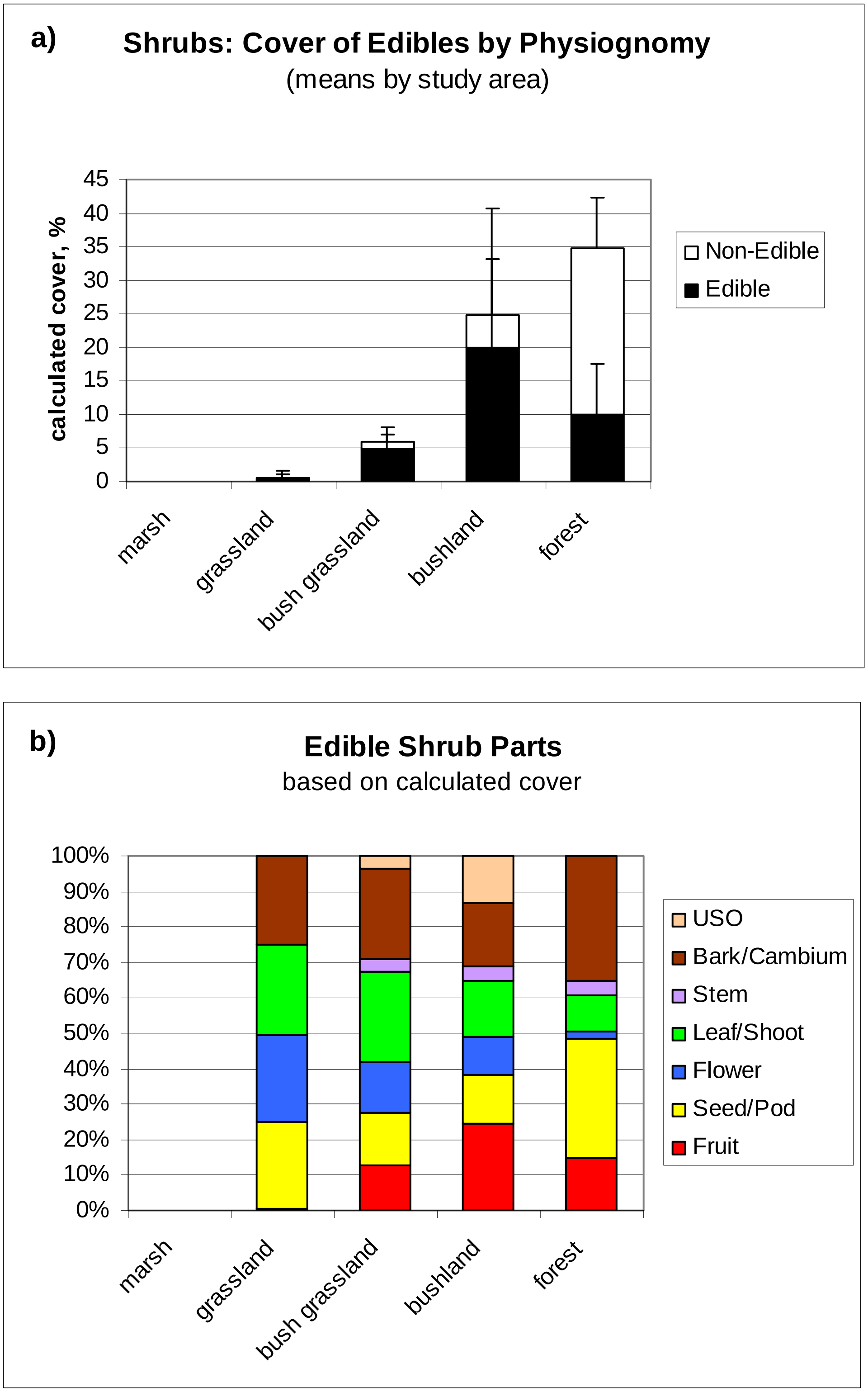
While total shrub cover increases from grassland to forest, edible shrub cover has both a higher proportion and a higher absolute value in bushland compared to forest sites (Figure 5-5a). In the forest, only 29% of shrubs are edible, compared to 81% in bushland, 84% in bush grassland, and 74% in grassland.

Figure 5-4. Proportion of individual trees encountered in the modern study areas with fleshy fruits versus dry fruits, grouped by physiognomy.



The dominant shrubs from the forested sites in this study are inedible, such as *Senna bicapsularis*, *Rauvolfia caffra*, and saplings of *Tabernaemontana ventricosa*. The edible shrub species in bushland include *Acacia xanthophloea*, *Acacia tortilis*, *Salvadora persica*, *Maerua triphylla*, *Cordia sinensis*, *Cordia monoica*, and others. Overall, bushland shrubs have the highest proportion of edible fruits and edible underground parts (USOs) compared to other physiognomic categories (Figure 5-5b). The edible USOs from shrubs in bushland are mainly woody roots, and are unlike the edible rootstocks and bulbs from forbs that prevail in marsh habitats.

Figure 5-5. Calculated cover values for edible shrubs encountered in the modern study areas and the proportions of edible plant parts, grouped by physiognomic categories. Bars show the mean with one standard error. USO = underground storage organs.



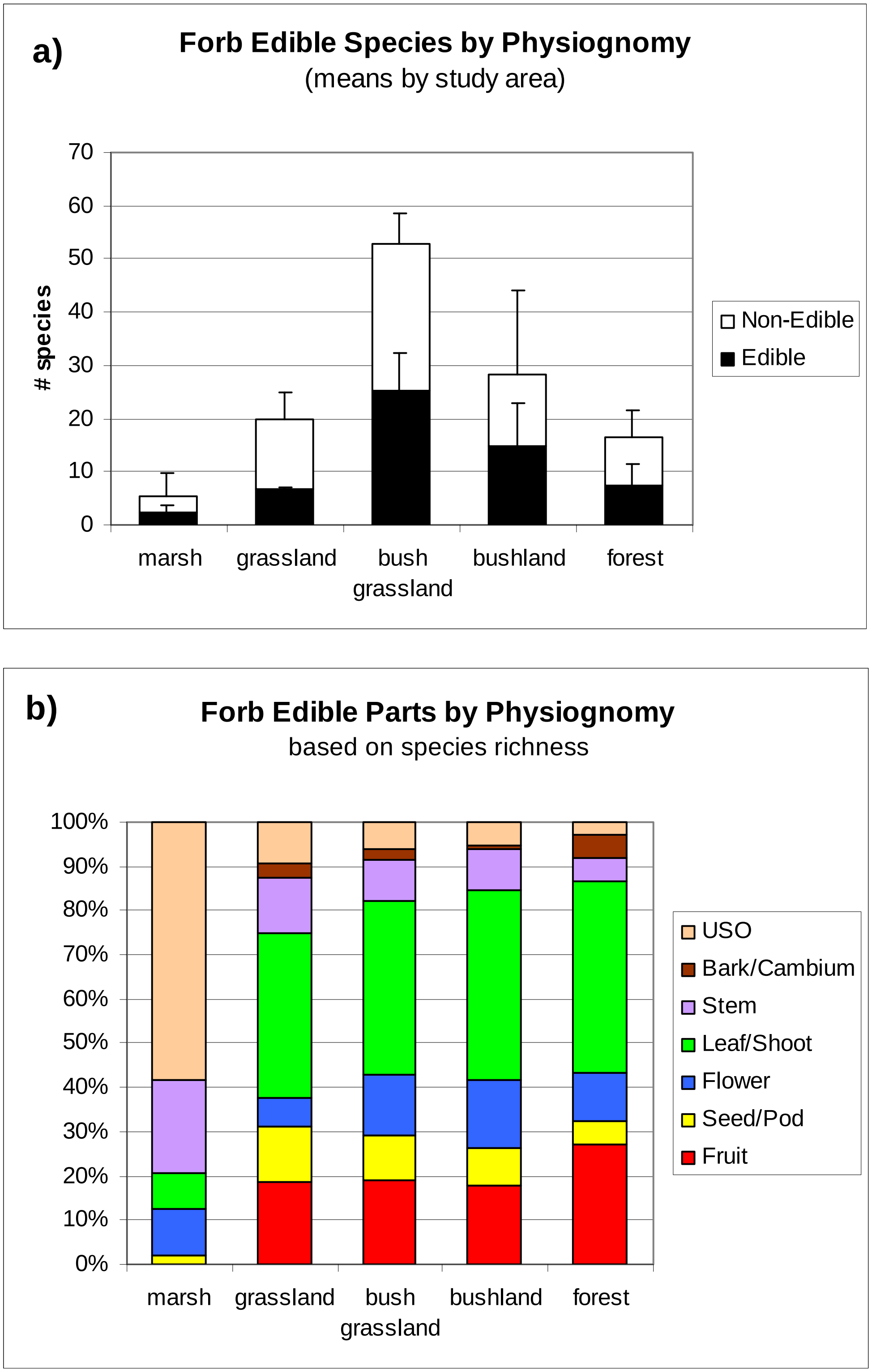
In bush grassland, the main edible shrub species are *Acacia tortilis*, *Salvadora persica*, and *Commiphora africana*. Only one of the three grassland sites actually had shrubs, and the edible shrub species there were *Acacia tortilis* and a small area of *Capparis tomentosa*. The edible plant part proportions in grassland sites thus reflect mainly the edible parts provided by *Acacia tortilis* (Figure 5-5b). There were no shrubs in the marsh habitats.

Forbs

Edible forb species richness follows a pattern close to that of overall forb species richness by physiognomic categories (Figure 5-6a). The highest edible forb values are found in bush grassland, followed by bushland, with forest, grassland, and marsh sites relatively low. Common edible species in bush grassland sites are *Achyranthes aspera*, *Solanum incanum*, and *Sida ovata*. Grassland sites also have *Solanum incanum*, *Sida ovata*, and *Melhania ovata* with unspecified edible parts. There are many edible forb species in bushland, often including *Achyranthes aspera*, *Monechma debile*, *Solanum incanum*, and *Hypoestes forskalei*. Edible forb species in forest were *Achyranthes aspera*, *Hibiscus ovalifolius*, and *Hypoestes forskalei*. The main edible components of forbs in non-marsh habitats are leaves (Figure 5-6b).

The marsh habitat is completely different in edible forb species composition, and has notably more edible underground parts (USOs) (Figure 5-6b). Typical marsh forbs are sedges, usually *Cyperus immensus* and *Cyperus laevigatus*, and cattails, *Typha latifolia*, all three of which have edible rootstocks or bulbs.

Figure 5-6. Number of edible forb species from the modern study areas and the proportions of edible plant parts, by physiognomic categories. Bars show mean number of species per study area with one standard error. USO = underground storage organs.



Grasses

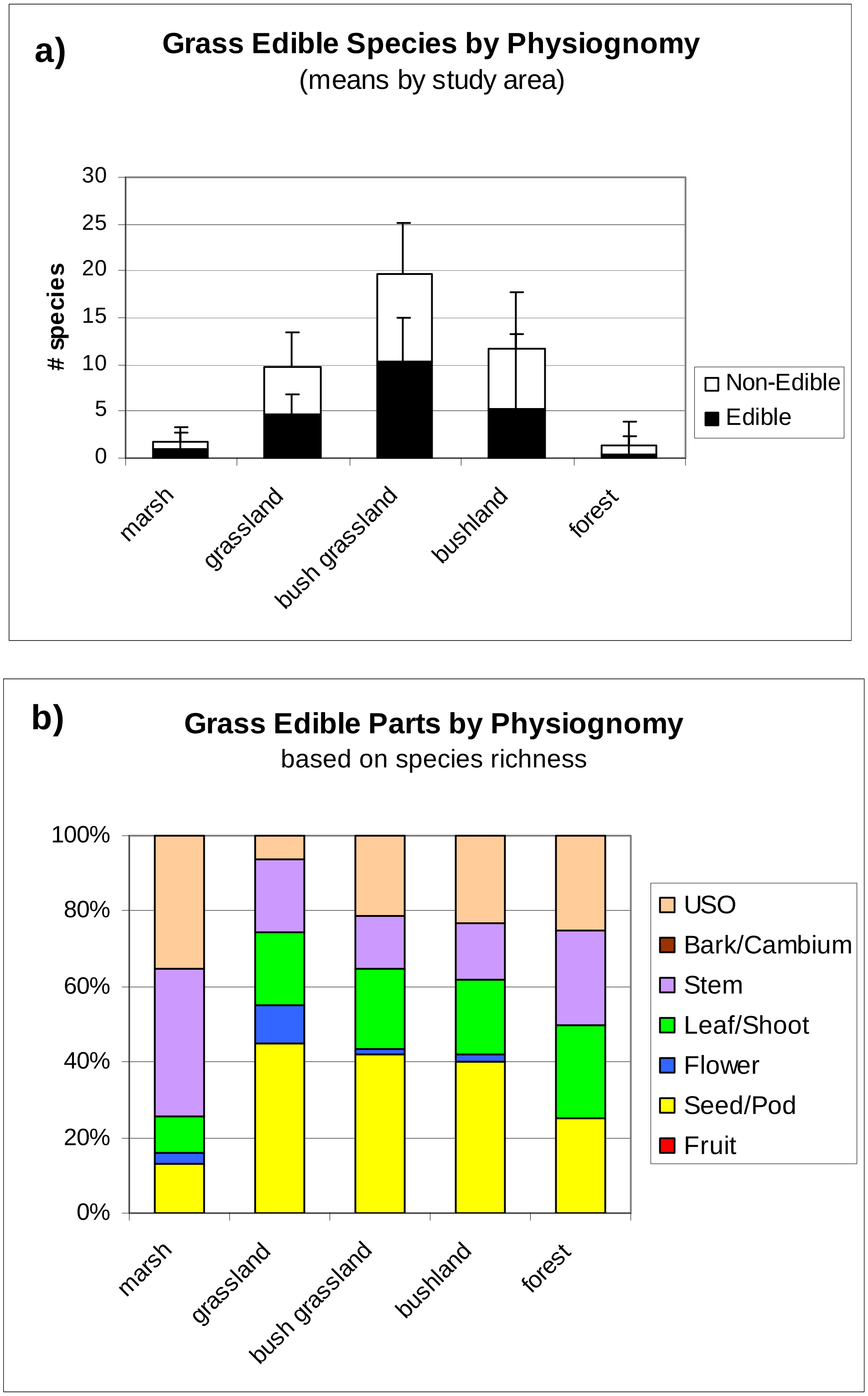
Grass species richness, like that of forbs, is highest in bush grassland sites (Figure 5-7a). Grassland and bushland have about the same numbers of edible grass species, while forest and marsh average less than one edible grass species per study area. Some common edible grass species in grassland are *Themeda triandra* and *Sporobolus fimbriatus*, in bush grassland are *Digitaria velutina*, *Sporobolus ioclados*, *Dactylotenium aegyptium*, and in bushland edible grass species include *Digitaria velutina*, *Dactylotenium aegyptium*, *Themeda triandra*, and *Sporobolis consimilis*.

In grassland, bush grassland, and bushland, a large proportion of edible grass parts are seeds. Marsh habitats have a very high proportion of edible underground parts, as did forbs in the marsh. One grass with edible underground parts that commonly grows at the edges of marshes is *Cynodon dactylon*.

Summary of Edible Plants by Physiognomic Categories

In sum, the forested sites of the Manyara, Serengeti, and Ngorongoro modern study areas can be characterized as having many edible trees, especially trees with edible fruits (except in an *Acacia* forest), a fair amount of shrubs, very few of which are edible, and few edible forbs and grasses. In bushland sites, although overall tree cover is lower than in forest, a higher proportion of bushland trees provide edible parts, especially seeds/pods and bark/cambium/gum. Bushland sites have the highest proportion of edible shrubs, and those shrubs often bear edible fruit. Bush grassland has some edible trees and shrubs, but less than a quarter as much (in terms of cover) as bushland. Bush grassland sites are by far the highest in forb and grass edible species richness, with forbs generally

Figure 5-7. Number of edible grass species from the modern study areas and the proportions of edible plant parts, by physiognomic categories. Bars show mean number of species per study area with one standard error. USO = underground storage organs.



providing edible leaves and grasses providing edible seeds. Grassland sites have only a moderate abundance (lower than bush grassland) of edible herbaceous plants, and no edible trees or shrubs. Marsh habitats are unique in plant species composition, and have a very high proportion of edible underground parts available from sedges, cattails, and grasses.

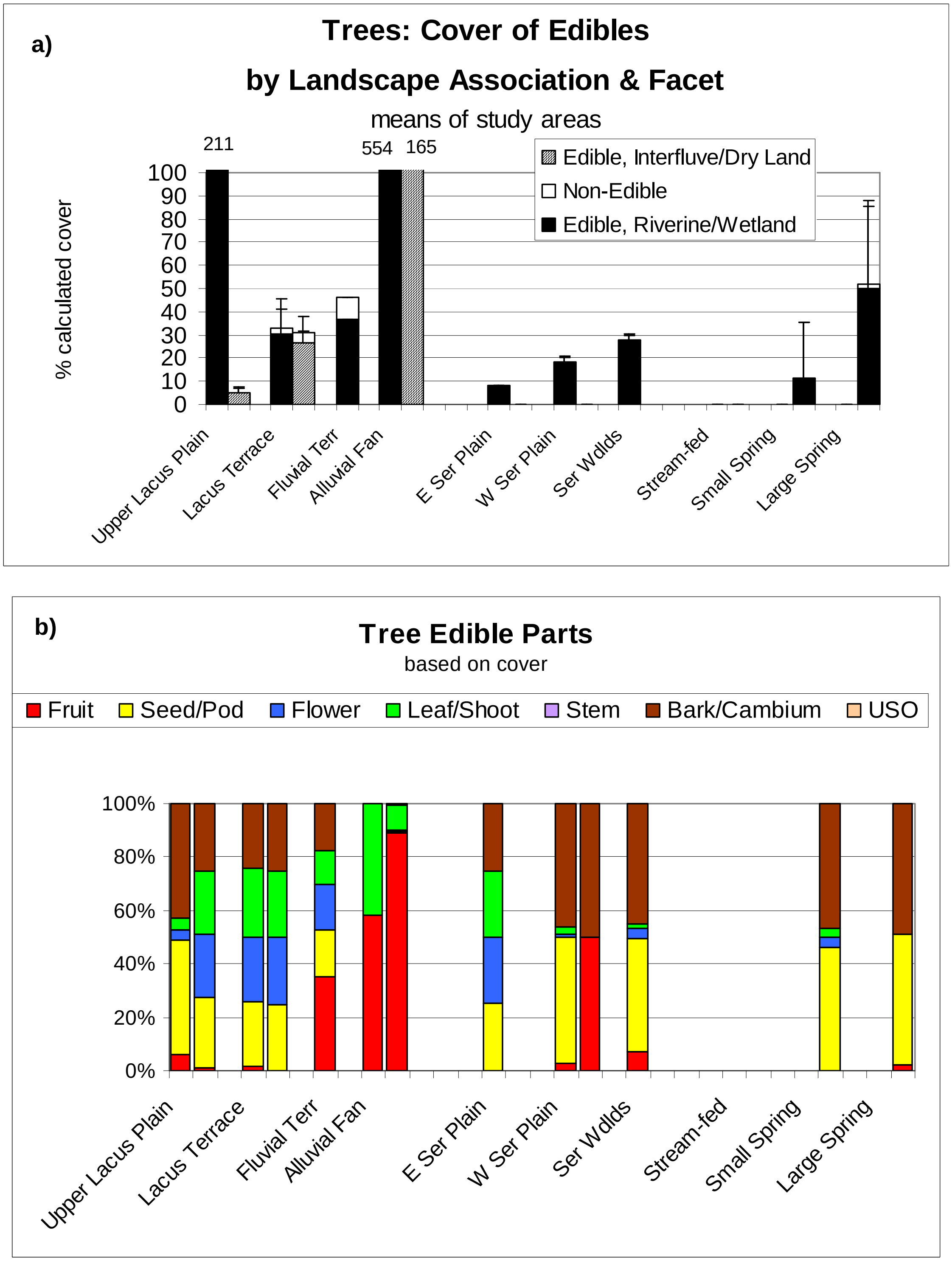
Landscape Units: Quantitative Analysis of Edible Plants

In this section I discuss quantitative measures of plant food availability grouped according to landscape units: land regions, landscape associations, and landscape facets. As in the above section, I have divided the discussion according to plant growth forms. Ultimately, I summarize the results of edible plant foods by landscape units with a table that shows the relative abundance of each edible plant part across all landscape facets.

Trees

Edible tree cover closely follows the pattern of total tree cover, as shown in Figure 5-8a. Manyara has more overall tree and edible tree cover than the other regions, likely a result of higher plant-available water for Manyara trees, as discussed in Chapter Four. At a finer landscape scale, the most striking features of Figure 5-8a are the very high edible tree cover at Manyara's alluvial fan landscape association, and along the riverine landscape facet of the lacustrine plain. These are the three forested landscape facets along and near the Mkindu River. Other landscape facets are almost an order of magnitude lower in edible (and non-edible) tree cover values.

Figure 5-8. Calculated cover for edible trees in the modern study areas and proportions of edible plant parts, by landscape units. Bars show mean with one standard error. The double bars in b) correspond to double bars in a). USO = underground storage organs.



The cover of edible tree species varies a great deal within landscape associations and among landscape facets. Only the lacustrine terrace has similar edible tree cover values in its riverine versus adjacent interfluvial landscape facets. Manyara's upper lacustrine plain has the greatest difference between riverine and interfluvial landscape facets; the former are forested while the latter are bush grassland. There, the edible trees in the riverine forest are *Acacia xanthophloea*, with mainly edible gum, and the edible trees in the interfluve are scattered *Acacia tortilis*, with edible seeds, pods, leaves, gum, bark, and flowers. Adjacent landscape facets in the Serengeti Plain and Ngorongoro Springs contrast highly in terms of edible tree cover simply because there are no trees, edible or non-edible, in the interfluves and wetlands, while the riverine landscape facets and dry lands are dominated mainly by edible *Acacia* trees.

The proportions of edible tree parts are strikingly higher in edible fruits at the alluvial fan (Figure 5-8b). Fruit abundance is highest at the non-riverine alluvial fan sites because they are dominated by *Trichilia emetica* trees, which have an edible red aril (=fruit) surrounding the black seed. Also important in both riverine and non-riverine landscape facets of the alluvial fan are fig trees with edible fruits. The fluvial terrace has several trees with edible fruits as well: *Trichilia emetica*, *Ziziphus pubescens*, and *Kigelia africana* (the sausage tree). The high proportion of edible tree fruits at the interfluve of the Western Serengeti Plain reflects a single specimen of *Balanites aegyptiaca,* which happened to be the only tree that occurred inside one of the sample plots in that grassland landscape facet. The landscape facets dominated by *Acacia* trees conspicuously lack edible tree fruits because *Acacia* "fruits" count in the seed/pod category since they are legumes.

Shrubs

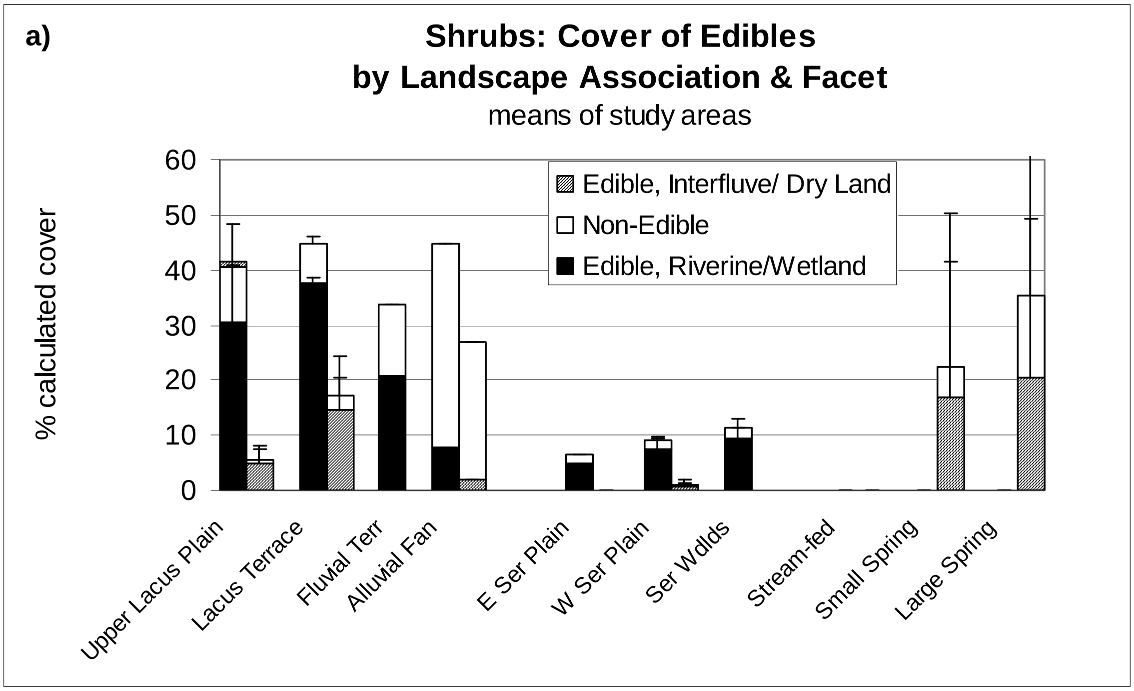
At a regional level, edible shrub cover is higher at Manyara and Ngorongoro than it is in Serengeti (Figure 5-9a). Landscape associations in Manyara and Ngorongoro are also generally higher in edible shrub cover abundance than Serengeti, but the most important degree of contrast is at the landscape facet level.

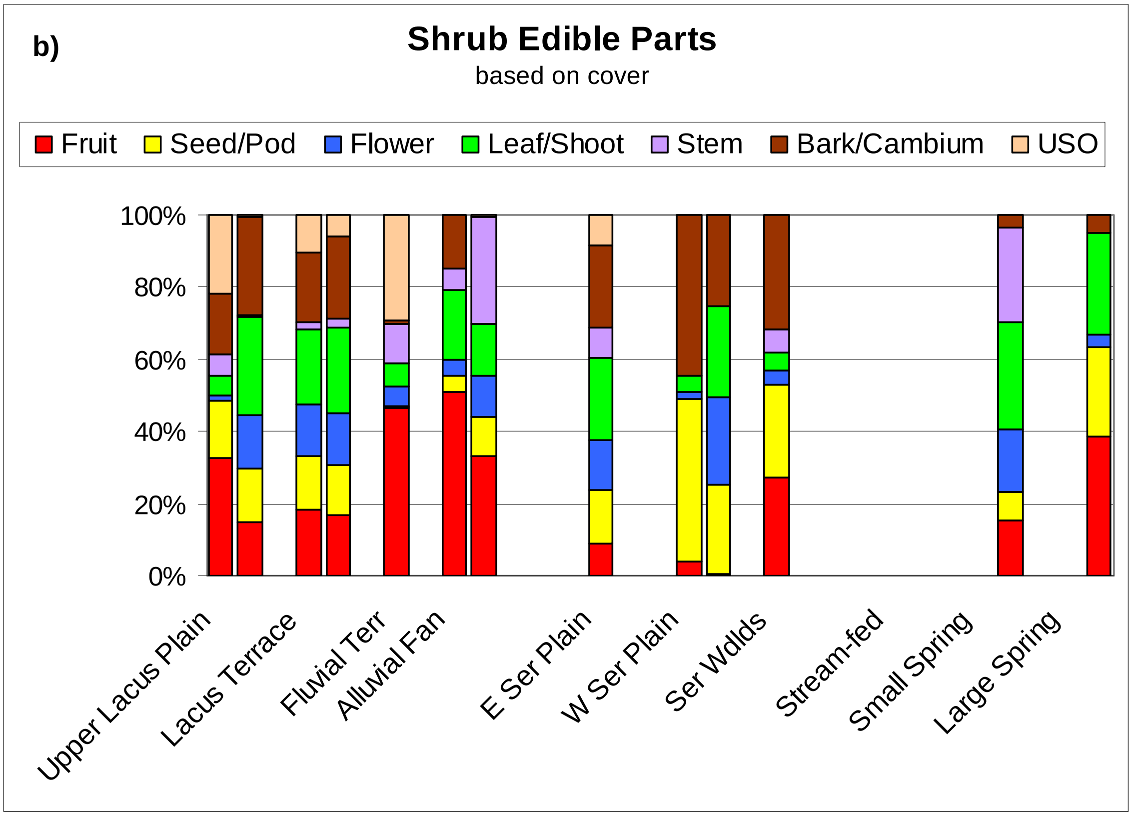
Riverine values of edible shrub abundance are high compared to non-riverine values in all landscape associations in which both riverine and non-riverine sites were sampled. At Ngorongoro, only dry lands associated with Springs had shrubs, many of which were edible.

In terms of the proportion of edible plant parts for shrubs, the main regional differences are higher proportions of edible shrub fruits at Manyara and Ngorongoro, and higher proportions of edible shrub seeds/pods at Serengeti (Figure 5-9b). At the level of landscape associations in Manyara, the proportion of edible shrub fruits is high in the alluvial fan, due to *Acalypha fruticosa* and *Hibiscus ovalifolius*. The fluvial terrace, lacustrine terrace, and some of the lacustrine plain landscape facets have similar edible shrub species among themselves, such as *Acalypha fruticosa*, *Salvadora persica*, *Maerua triphylla*, *Capparis tomentosa* and *Cordia monoica*, and in the riverine landscape facets, *Cordia sinensis*. The relatively large proportion of edible USOs in the fluvial terrace reflects the importance of *Cordia sinensis* (with edible roots) in that landscape facet.

In Serengeti, the proportions of edible parts reflect mainly the contribution of *Acacia tortilis* and *Acacia xanthophloea* shrubs. It is important to take into consideration the fact that normally only mature individuals, i.e. trees, of *Acacia xanthophloea* and

Figure 5-9. Calculated cover for edible shrubs in the modern study areas and proportions of edible plant parts, by landscape units. Bars show mean with one standard error. The double bars in b) correspond to double bars in a). USO = underground storage organs.





Acacia tortilis flower and produce pods, thus the actual amount of edible parts provided by those shrubs is minimal. The edible shrub fruits that appear at the riverine Serengeti Woodland landscape facets include *Acalypha fruticosa* and *Cordia monoica*.

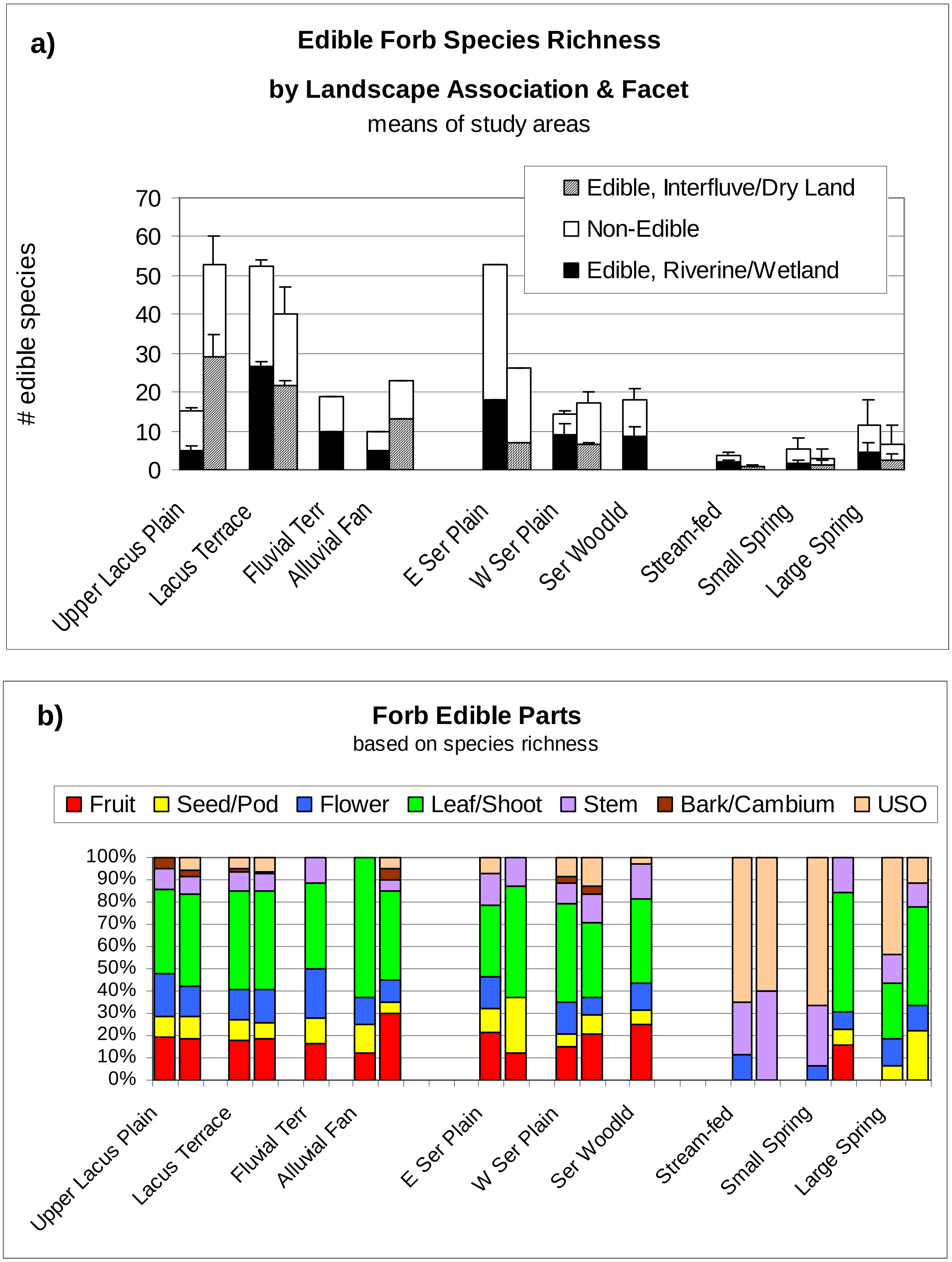
In Ngorongoro, the edible shrubs near the Large and Small Springs include *Cordia monoica* and *Vangueria madagascariensis* with edible fruits.

Forbs

At a regional level, Manyara has more edible forb species per facet (5-30 species) than Serengeti (7-18 species) and Ngorongoro (1-5 species) (Figure 5-10a). The contrast between landscape facets varies by landscape associations. Along rivers at Manyara's lacustrine terrace and the Serengeti Plain, there are slightly more edible forbs than in the adjacent interfluves. In contrast, at Manyara's lacustrine plain and alluvial fan, interfluvial sites have more edible forb species than riverine sites. At Ngorongoro, there is not much difference in edible species richness between wetland and dry land sites, but edible species composition is quite different, with edible sedges (*Cyperus* spp.) and cattails (*Typha latifolia*) in the wetland marshes.

The relative contributions of different edible forb plant parts to Manyara, Serengeti, and the dry land sites of Ngorongoro are quite similar despite the fact that species composition differs markedly by regions (Figure 5-10b). Compared to the edible parts available from other growth forms, there is a particularly high proportion of edible leaves among the non-marsh forbs. For example, the species that was common to almost all sites, *Achyranthes aspera*, has edible leaves.

Figure 5-10. Number of edible forb species in the modern study areas and proportions of edible plant parts, by landscape units. Bars show mean with one standard error. The double bars in b) correspond to the double bars in a). USO = underground storage organs.



At Ngorongoro's wetland sites, edible forb parts are dominated by underground storage organs because sedges and cattails have edible rootstocks or bulbs.

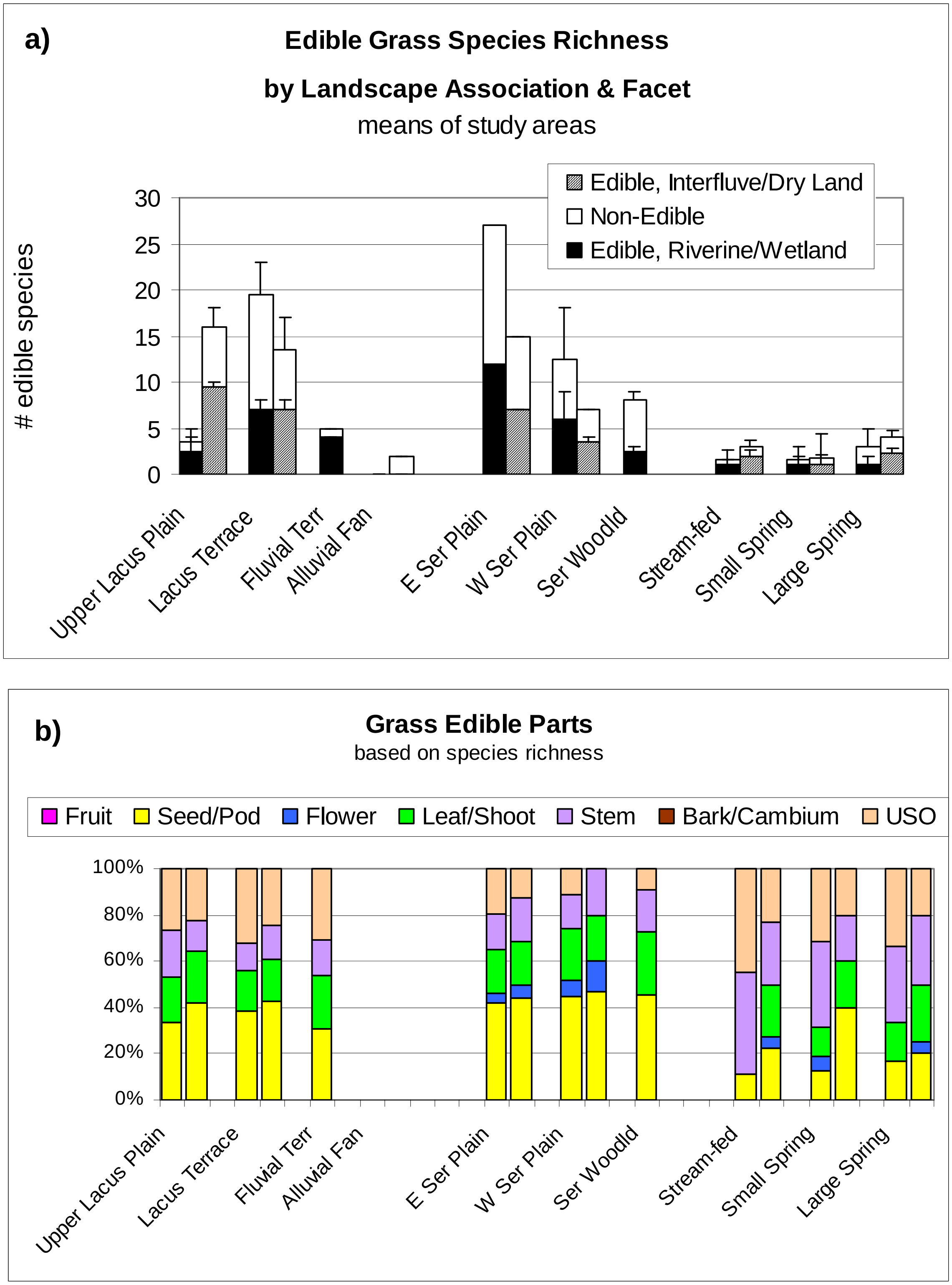
Grasses

Since grass is the main food of many herbivores in East African savanna habitats, grass composition is important regarding habitat use by many animals. Whether or not hominins ate many grass foods themselves, grass composition would likely have affected hominin behavior and land use due to the presence of other grazing animals and their predators.

At Manyara, edible grass abundance varies greatly by landscape facet, being absent altogether at the alluvial fan, and abundant in the interfluves of the lacustrine plain (Figure 5-11a). There is a notable lack of contrast in edible grass richness at the lacustrine terrace landscape facets. In the Serengeti region, edible grass species richness (and total grass species richness) is actually higher in and around the slightly wooded rivers, as opposed to out in the "open grassland". The Ngorongoro Crater sites were smaller in area, which probably accounts for the low number of total and edible grass species recorded there.

In terms of the proportions of edible grass parts, there is a greater proportion of edible grass USO parts in Manyara and the Ngorongoro wetland sites as compared to sites in the Serengeti region (Figure 5-11b). Ngorongoro sites also tend to have higher proportions of edible stems. The Serengeti and Manyara grasses have high proportions of edible seeds.

Figure 5-11. Number of edible grass species in the modern study areas and proportions of edible plant parts, by landscape units. Bars show mean with one standard error. The double bars in b) correspond to double bars in a). USO = underground storage organs.



Summary of Edible Plants by Landscape Units

At the regional level, Manyara has the greatest abundance of tree foods. Edible shrubs have their lowest abundance in Serengeti, where most are *Acacia* spp., and neither edible shrubs nor edible trees are found at the Ngorongoro wetland sites, though they are locally present at Ngorongoro's "dry land" sites adjacent to some of the wetlands. Edible forbs and grasses differ in species composition by region.

In terms of landscape associations, Manyara's forested alluvial fan provides the majority of the fleshy tree fruits to be found in the study areas. The degree of contrast in plant food availability between adjacent landscape facets varies a great deal according to the landscape association and plant growth form in question. There are more edible trees and shrubs at riverine versus non-riverine landscape facets except in the lacustrine terrace, where edible tree abundance is the same in riverine and non-riverine landscape facets. In Ngorongoro, only dry land landscape facets adjacent to large or, in some cases, small springs have edible (or non-edible) woody plants, so there is contrast in woody plant food availability between some adjacent spring landscape facets.

Within a given landscape association in Manyara or Serengeti, edible forbs and grasses are usually similar in riverine versus interfluvial landscape facets. The most notable exception is in the upper lacustrine plain, where bushed or forested rivers contrast in terms of structure and herbaceous species composition with the bush grassland interfluves. In the Ngorongoro wetland (marsh) habitats, sedges, cattails, and grasses provide edible rhizomes, bulbs, and stem bases, which contrast greatly in type with the foods available in adjacent dry land sites.

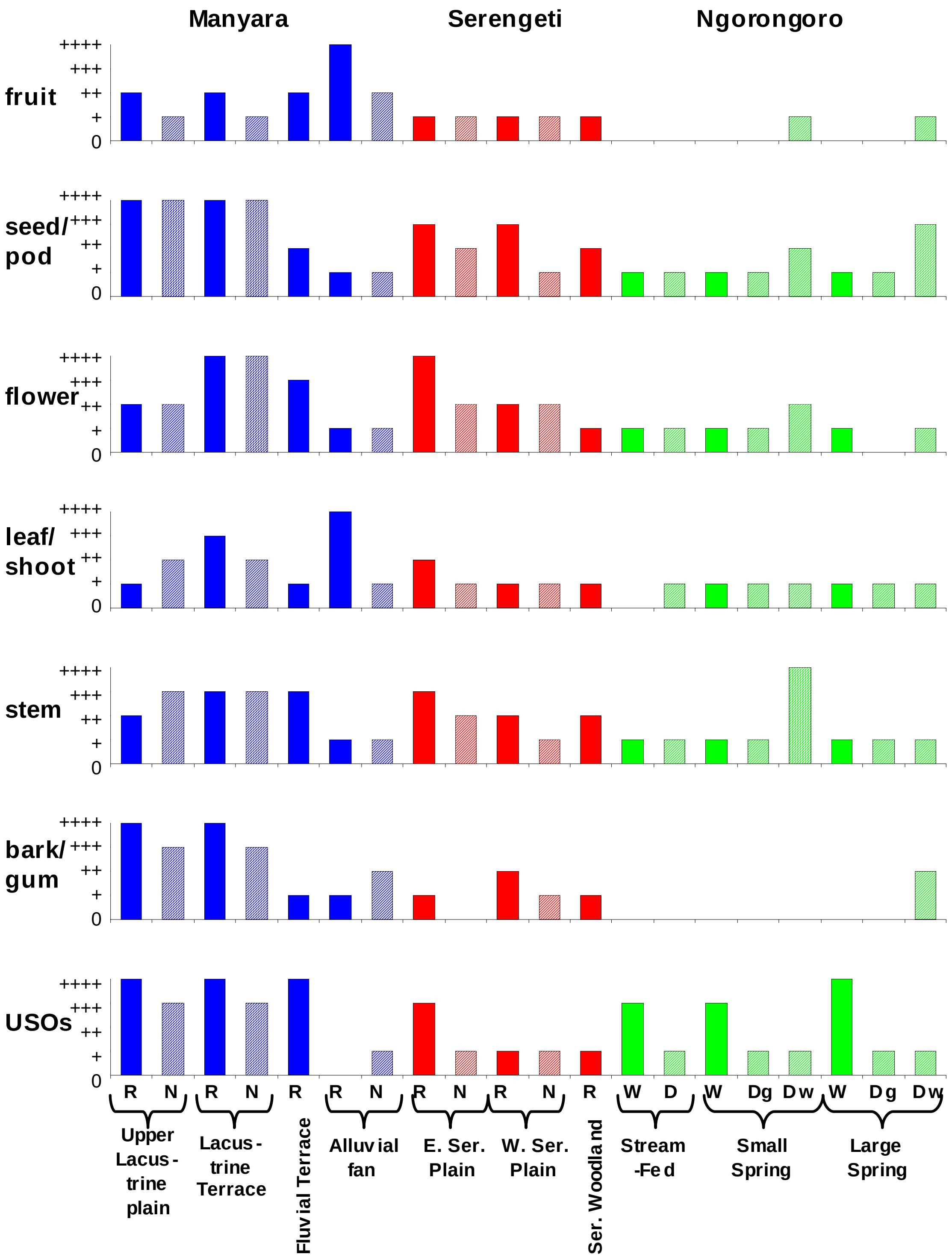
In very general terms, trees tend to provide a high proportion of edible bark/cambium and either seeds/pods or fruits, shrubs often produce edible fruits, forbs often provide edible leaves, or, for marsh plants, edible USOs, and grasses provide edible seeds and sometimes underground parts.

Relative Proportions of Edible Plant Parts by Landscape Units

A useful way to summarize the *relative* abundance of particular edible plant parts in adjacent landscape facets is to use a format comparable to Table 2 in Peters and Blumenschine (1995; 1996), in which they presented the hypothetical abundance of resources across the paleo-Olduvai lowermost Bed II landscape facets. They used five classes to represent increasing quantities, from zero to four plus signs (0, +, ++, +++, ++++). Here I use the same classifications, but instead of presenting the values in a table, I show the results in bar graphs (Figure 5-12).

In order to obtain relative values for each plant part in each landscape facet, I first added the species richness value of, for example, forbs with edible flowers in all study areas. I then divided the richness of forbs with edible flowers at each study area by the sum of all forbs with edible flowers in all study areas. That resulted in a percentage value that reflects relative abundance of edible forbs among the study areas. Similar calculations were done with grasses with edible flowers. For trees and shrubs, however, I used calculated cover instead of species richness, because calculated cover better reflects actual plant food abundance for trees and shrubs. Calculated cover values were not available for forbs and grasses, which is why I had to use richness.

Figure 5-12. Relative plant food abundances in the modern study areas. The scale follows Table 5-1 and is described in the text. R=riverine, N=non-riverine, W=wetland, D=dry land adjacent to a wetland, Dg= grassland dry land, Dw= woodland dry land.



Now that I had a percentage value for the relative abundance of flowers for trees, shrubs, forbs, and grasses, I needed to combine those to create a simple measure of overall relative edible flower abundance for each study area. Thus, I simply added the relative percentages of edible flowers from trees, shrubs, forbs, and grasses to obtain the final relative abundance of edible flowers for each study area. I translated this final number into the five classes (0 through ++++) by dividing the landscape facet edible flower value that was the maximum of all landscape facets into 5 equal parts. Each landscape facet was then assigned a relative value as shown in Table 5-1.

Table 5-1. Scale used for relative edible part abundance by facet in Figure 5-12.

Scale	Relative proportion of edible part abundance based on the sum of the relative abundance values for trees, shrubs, forbs, & grasses.
0	0%
+	>0-20%
++	>20%-40%
+++	>40%-60%
++++	>60%

Since the relative values of each plant part were calculated separately, only the values of a given plant part are comparable between landscape facets. Calculated in this manner, it would not be meaningful to compare the relative amount of, for example, edible fruits to edible seeds within a single landscape facet. That information has already been discussed in previous figures showing relative edible plant part abundance for physiognomic categories and landscape units. It is important to note that the final abundance values assign equal weight to the relative contribution of trees, shrubs, forbs, and grasses. This may not always be the case in reality, but it is the closest estimate available with the current data. The results, depicted in Figure 5-12, are summarized by plant food part below.

Fruits: Fruit abundance is higher at rivers compared to their adjacent interfluvial landscape facets within Manyara, but not in Serengeti. In Ngorongoro Crater fruits only occur in the large and small spring woodlands, and there they have relatively low abundance.

Seeds/pods: Seeds and pods show an opposite distribution from fruits in that seed and pod abundance is higher at rivers than adjacent interfluves in Serengeti, but not in Manyara. In the Crater, all landscape facets have edible seeds, but the large and small spring woodlands have slightly more.

Flowers: At Manyara, edible flower abundance differs between landscape associations, but not between landscape facets within any single landscape association. In Serengeti, the river of the Eastern Serengeti Plain has the highest edible flower abundance, and this abundance diminishes in landscape units as one moves west toward the Serengeti Woodland.

Leaves/shoots: Leaves and shoots show an interestingly high degree of contrast between adjacent landscape facets at Manyara, but there is little difference among Serengeti and Ngorongoro landscape facets.

Stems: As with leaves, edible stems are more abundant in the interfluves of Manyara's upper lacustrine plain than along the river. Other Manyara landscape facet pairs show no contrast, but in Serengeti, riverine landscape facets have slightly more edible stems than interfluvial landscape facets. The uniformity at Ngorongoro is interrupted only by the surprisingly high value of edible stems in the small spring shrublands.

Bark/gum: Edible bark and gum is high in the upper lacustrine plain and lacustrine terrace at Manyara, but low in the alluvial fan and fluvial terrace. In Serengeti, riverine landscape facets have slightly more edible bark/gum than adjacent interfluves.

USOs: Underground storage organs are higher overall at Manyara's sites except in the alluvial fan. These are mainly edible shrub roots. In Serengeti there are many edible USOs near the Barafu river of the Eastern Serengeti Plain, and at Ngorongoro there are large amounts of marsh plant USOs available in the wetlands.

In summary, of the interesting patterns that can be seen in Figure 5-12, one is that fruits are higher in riverine versus interfluvial landscape facets in Manyara's lacustrine plain and lacustrine terrace, whereas seed/pod abundance is equivalent in those adjacent landscape facets. At Ngorongoro, fruits are only available in the dry land woodlands/shrublands near springs, whereas seeds/pods are present there and in lower amounts in adjacent wetlands and dry grasslands. Underground edible parts are highest at the spring wetlands due to marsh plants, but are also moderately high in Manyara landscape facets where edible shrub roots are available. Bark/gum has a high concentration along the rivers of the upper lacustrine plain and lacustrine terrace due to the high density of *Acacia xanthophloea* and *Acacia tortilis* trees there.

It is enlightening to view these results in terms of the idea that riverine landscape facets in savanna habitats are resource-rich corridors for hominins, surrounded by resource-poor interfluves. In the Serengeti, there are nine cases of paired (adjacent) landscape facets in which the rivers have higher abundance of an edible part than the interfluves. In five cases at Serengeti, abundance is equal in adjacent rivers and interfluves. At Manyara, in nine cases rivers have higher edible part abundance than interfluves, in seven cases river and interfluve abundance are equal, and in four cases interfluves are higher than rivers.

Thus, while riverine corridors more often have a greater abundance of any given plant food type, adjacent interfluves are not necessarily “non-habitat” for hominins in terms of plant food availability. (Predation hazards and a lack of resources like refuge trees and water may make some interfluves less appealing, however). Interfluve or non-riverine landscape facets in general are more resource-rich at Manyara than Serengeti. Vegetation structure at Manyara does not differ as dramatically between riverine and non-riverine landscape facets as it does in the Serengeti. For example, in the Serengeti Plain, tree- or shrub-lined rivers are typically surrounded by open grassy plains.

At Ngorongoro, overall food abundance is relatively low. The notable exceptions are the woodlands adjacent to small and large springs, and the plentiful edible underground parts in the wetlands. In this sense, the localized woodlands near springs and the springs and stream-fed wetlands themselves are somewhat like islands of resource density in an otherwise resource-poor open, grassy lacustrine plain.

Seasonal variations in plant resources

I did not systematically record seasonal differences in plant resources in the modern analog settings, but I did notice some general patterns. Many *Acacia* trees produce flowers and pods during the dry season, providing an edible resource that is concentrated in the lacustrine terrace and eastern upper lacustrine plain. The rootstocks and edible underground parts of sedges and *Typha* are available year-round, but might be more accessible during the dry season when the water levels in wetlands recede. In the modern analog lacustrine terrace at Manyara, the common edible fruits from the *Salvadora persica* shrubs are available during the dry season. Most of the other bushland shrub fruits of the lacustrine terrace are available during the wet season. Edible underground parts from shrubs, also common in the lacustrine terrace, are probably available at any time of year.

The alluvial fans as modeled here support a forest due to the presence of a high groundwater table. The most common tree in Manyara's alluvial fan, *Trichilia emetica*, produces its edible fruits during the wet season, and the tree *Ekebergia capensis* also has edible fruits during the wet season. Individual trees of the fig species *Ficus sycomorus* produce figs at different times throughout the year (Coates Palgrave, 1993). Edible parts from herbaceous plants in the modern analog alluvial fans are available mainly in the wet season.

Grass seeds and flowers were likely the main edible plant foods for hominins available in the western side of the lowermost Bed II Olduvai basin. The edible parts of grasses and other herbaceous plants exist almost exclusively during the wet season. On the other hand, the flowers and pods of *Acacia* trees that might grow along the rivers in the western basin would appear for a few weeks during the dry season.

In sum, different edible plants would have been available at different times of year across of the paleo-Olduvai basin. The Eastern Lake Margin provides edible *Acacia* seeds, shrub roots, marsh plants, and some shrub fruits during the dry season, and during the wet season the rootstocks of marsh plants and more edible shrub fruits. The lower alluvial fans, if forested, provide some edible tree fruits during the dry season, and most edible tree fruits and herbaceous plants during the wet season. The western side of the basin provides edible *Acacia* seeds along rivers during the dry season, and edible grasses and herbaceous plants during the wet season.

Refuge Trees

Background

Humans' closest relatives, the four great ape species, all use nests for sleeping, and all build day nests. Chimpanzees, bonobos, and orangutans build tree nests by creating a foundation with strong branches by bending and interweaving them. They finish off the circular nest by bending most of the smaller leafy branches over the rim to create a bed (Fruth and Hohmann, 1996). Because of the large size and weight, gorillas often build nests on the ground, but the construction is similar. Gorillas arrange herbaceous foliage into a nest form with a rim by pulling, bending and breaking stems to fit around and underneath their bodies (Fruth and Hohmann, 1996).

The location in which great apes build their nests relates to both environmental features and social phenomena. Chimpanzees and bonobos living in rainforest sites prefer to build nests in primary forest and gallery forest. In savanna woodland habitats at Assirik, Senegal nests were found in equal proportion in woodland and gallery forest (Baldwin *et al*., 1981), and at Ugalla, Tanzania, most chimpanzee nests were found in dry open woodland but not in gallery forest (Itani, 1979).

Chimpanzees and bonobos seem to prefer particular tree species for nest building, though why particular species are preferred is not known. Chimpanzees and bonobos will build day nests in fruiting/feeding trees, but rarely will sleep in trees that are currently bearing ripe fruit.

Gorillas build nests on the ground or low in trees, with an average nest height of below 10 meters (Fruth and Hohmann, 1996). The average nest height for the other three great ape species is between 10 and 20 meters. Chimpanzee nests in rain forest habitats had average heights of 23, 9, 12, 12, and 10 meters, while chimp nests in savanna woodland had median heights of 11 meters at Assirik, Senegal, and 12 meters at Sapo, Liberia, and an average height of 12 meters at Guinea (Fruth and Hohmann, 1994).

Given the information on modern ape nesting behavior, it is parsimonious to assume that early hominins such as those living in the Plio-Pleistocene Olduvai basin used trees to build nests for sleeping refuge at night. The body size of early hominins was much closer to that of a chimpanzee than a gorilla (McHenry, 1992), and many Plio-Pleistocene hominins retained arms and hands with good tree-climbing capabilities (Susman and Stern, 1982). Although the details of their preferred trees are not known, a reasonable and measurable characteristic for a sleeping tree is a minimum height of 10 meters. Trees and shrubs also provide refuge in the form of shade during the day. For the purpose of analyzing the modern data in this project, I assume that shrubs or trees greater than or equal to three meters in height constitute substantial shade for a hominin.

It is likely that factors other than height were important to hominins choosing sleeping or resting trees. For example, thorny trees would probably propose a problem. Easy escape routes would also be a factor when predators were lurking. Seasonality can be important, since some trees lose their leaves during the dry season, and that might make them less suitable candidates for nesting trees. There are also considerations about the ease with which a tree could be climbed. Given the complicated and subjective nature of these other considerations, in this analysis I use height as a single quantitative measure for sleeping and shade refuge tree quality. In addition, I discuss the other characteristics of the trees in my modern study areas in terms of thorniness, escape routes, etc. in the text.

Refuge Tree Results from the Modern Study Areas

By Physiognomic Categories

The average densities of potential “sleeping” refuge trees for hominins, that is trees greater than 10 meters in height, are grouped by physiognomic categories in Figure 5-13. Tree density increases by an order of magnitude per physiognomic category, from one per hectare in bush grassland, to 14 and 148 in bushland and forest, respectively. Fourteen sleeping trees per hectare in bushland would probably suffice as a sleeping place, but in bush grassland, a tree is likely to be fairly isolated, with little in the way of escape routes to other trees. Tree species that grow in bush grassland also tend to be thorny. Trees over 20 meters in height occur almost exclusively in the forest, with a few in bushland sites (Figure 5-14).

Shade trees/shrubs greater than three meters tall are found in increasing densities from bush grassland to bushland to forest (Figure 5-15). Of these modern study areas, the only ones in which hominins would not find shade are marsh or grassland habitats. Note that grassland sites have no trees or shrubs in either the sleeping or shade categories. Physiognomy is a good predictor of tall tree density, and the taller the tree, the more likely it will be found in a forest.

Figure 5-13. Density of potential hominin refuge trees greater than ten meters height in the modern study areas, grouped by physiognomy. Bars show the mean with one standard error.

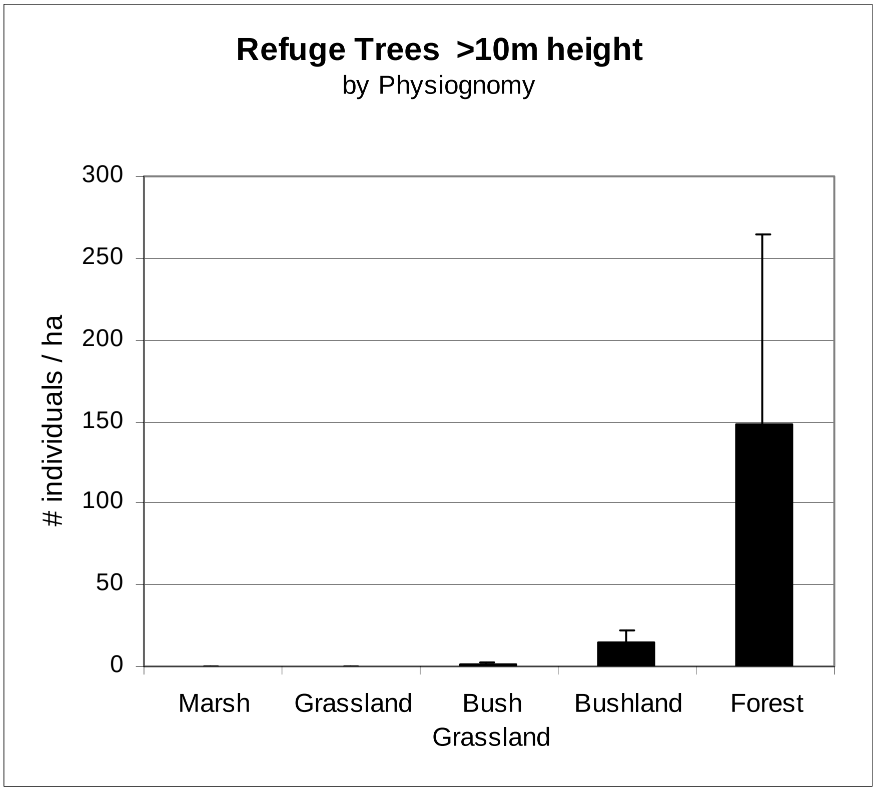


Figure 5-14. Density of potential hominin refuge trees greater than 20 meters height in the modern study areas, grouped by physiognomy. Bars show the mean with one standard error.

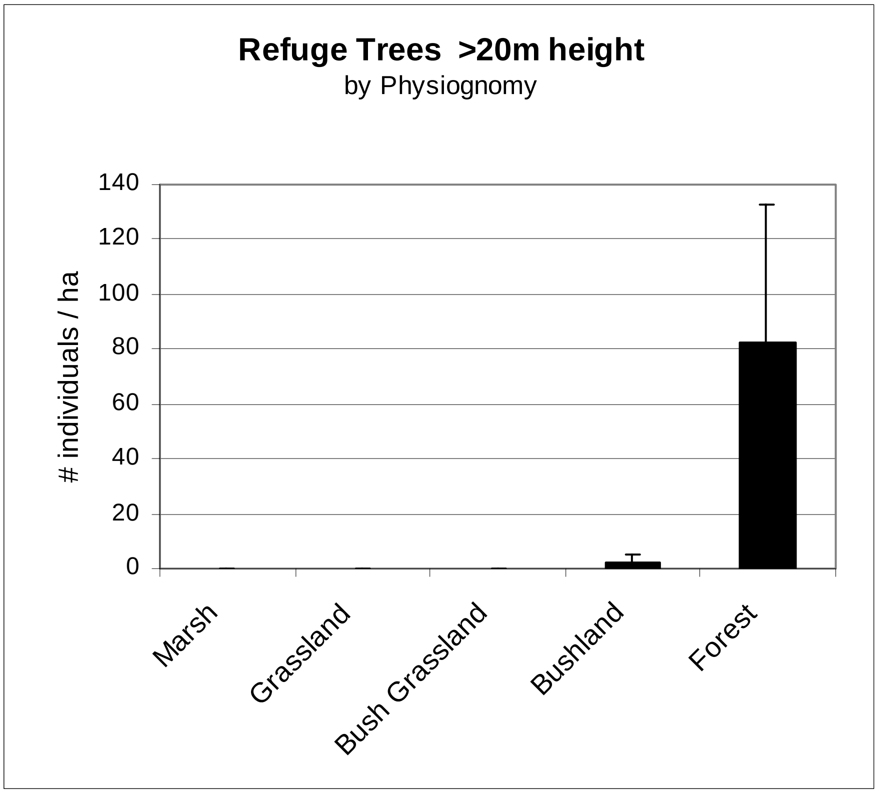
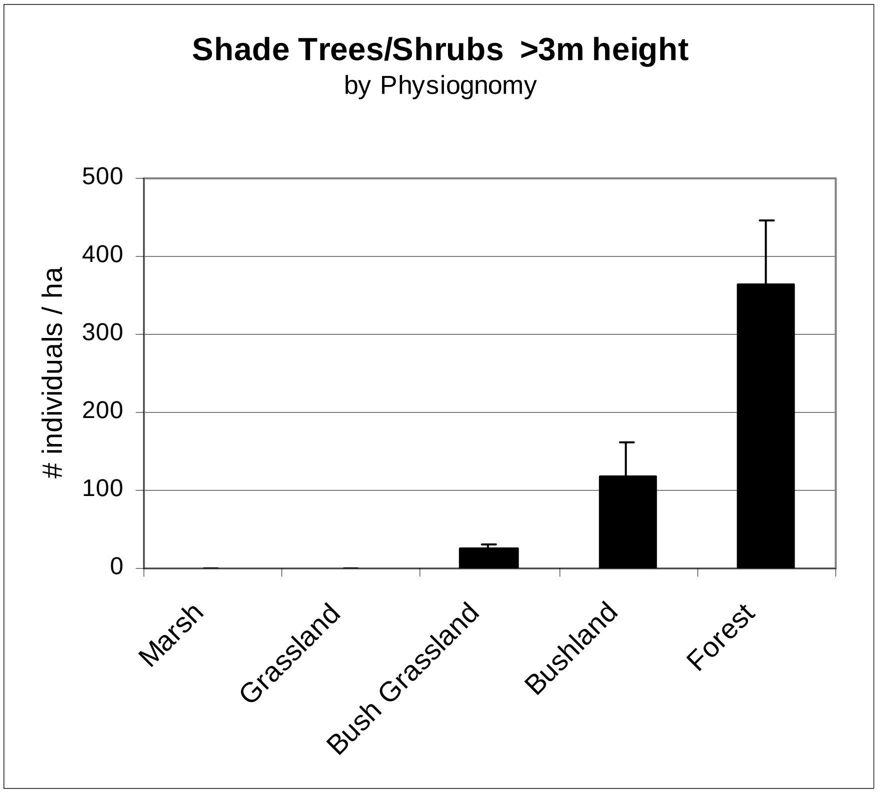


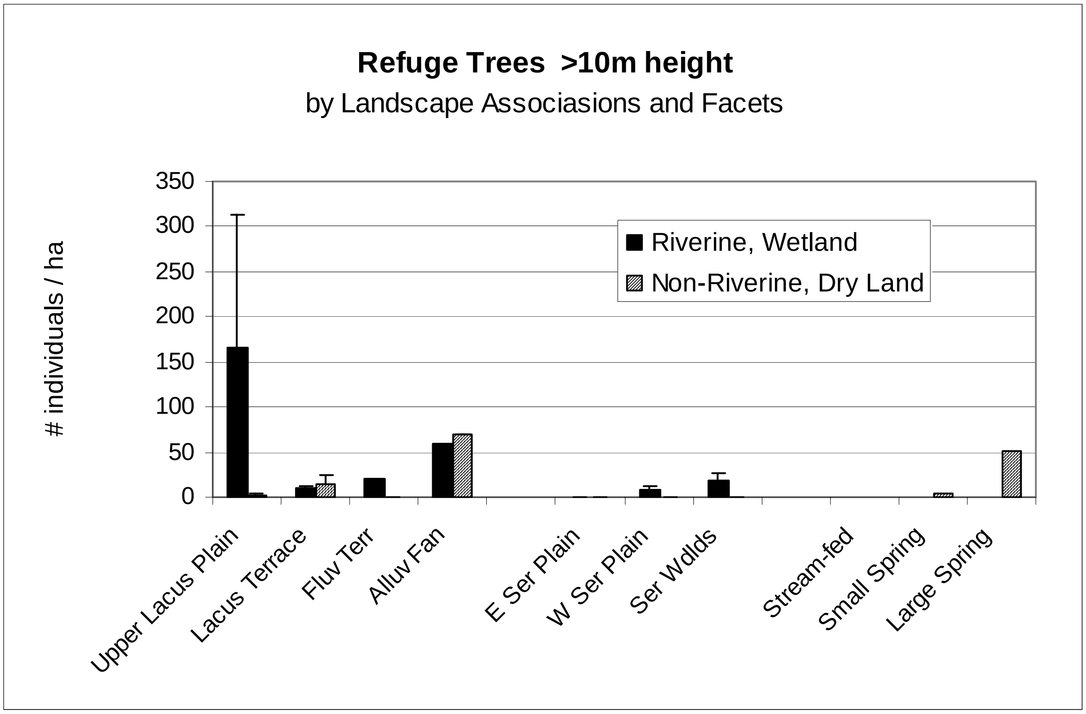
Figure 5-15. Density of shade trees and shrubs greater than three meters height in the modern study areas, grouped by physiognomy. Bars show the mean with one standard error.



By Landscape Associations

The variation of sleeping tree density is large within regions and within some landscape associations (Figure 5-16). The upper lacustrine plain riverine landscape facet has the highest average density of sleeping trees greater than 10m tall, although there is a great deal of variation, but notice that its adjacent interfluve has almost no sleeping trees. There is little contrast in sleeping tree density between adjacent landscape facets at Manyara's alluvial fan and lacustrine terrace. In the Serengeti, only along some riverine landscape facets are there any sleeping trees. Those in the Western Serengeti plain tend to be thorny, and are surrounded by open landscape facets that might make escape routes difficult. At Ngorongoro, the only place with substantial sleeping tree density is in woodlands associated with Large Springs.

Figure 5-16. Density of potential hominin refuge trees greater than ten meters height in the modern study areas, grouped by landscape units. Bars show the mean with one standard error.



If 20 meters is considered the minimum criteria for sleeping tree height (although based on modern ape comparisons shorter trees can be used for sleeping), then the only landscape facets of my modern study areas to be worthy sleeping areas would be in riverine upper lacustrine plain sites and along both rivers and interfluves of the alluvial fan (Figure 5-17).

Shade trees or shrubs (greater than three meters height) are found in all of the Manyara landscape facets, with even the lowest density of 28 per hectare in the interfluve upper lacustrine plain being quite substantial (Figure 5-18). In Serengeti, on the other hand, only the riverine landscape facets have any density of shade at all. Hominins in the interfluves of the Serengeti Plain would have to suffice with no shade and no escape trees in those landscape facets. Data on shade tree/shrub density is not available for Ngorongoro because shrub density information was not collected there.

Figure 5-17. Density of potential hominin refuge trees greater than 20 meters height in the modern study areas, grouped by landscape units. Bars show the mean with one standard error.

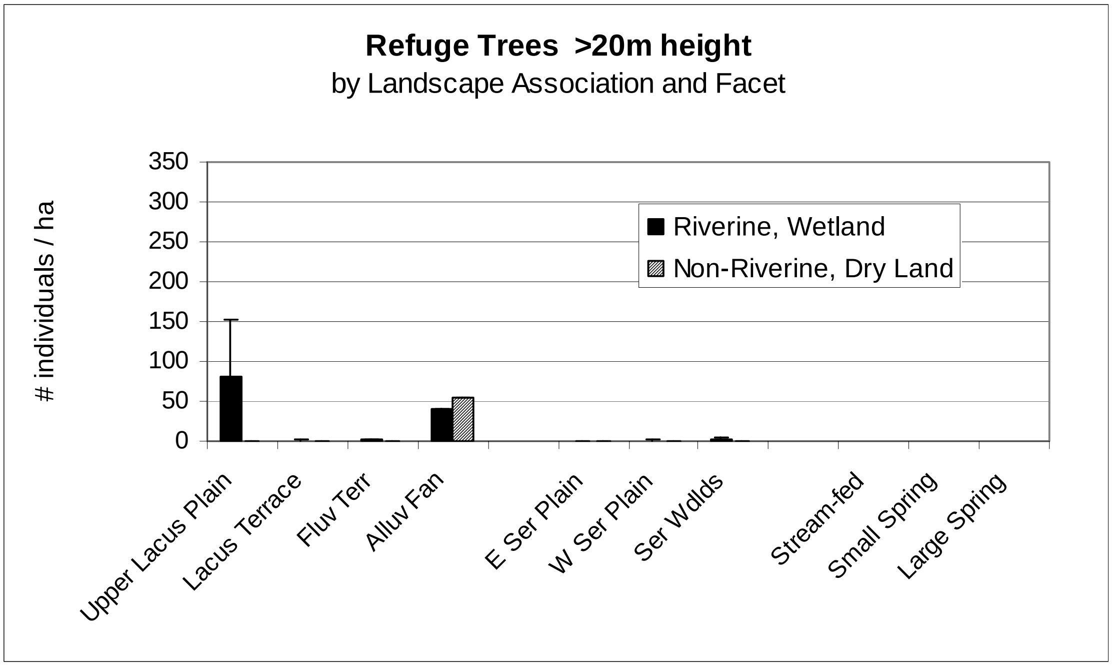
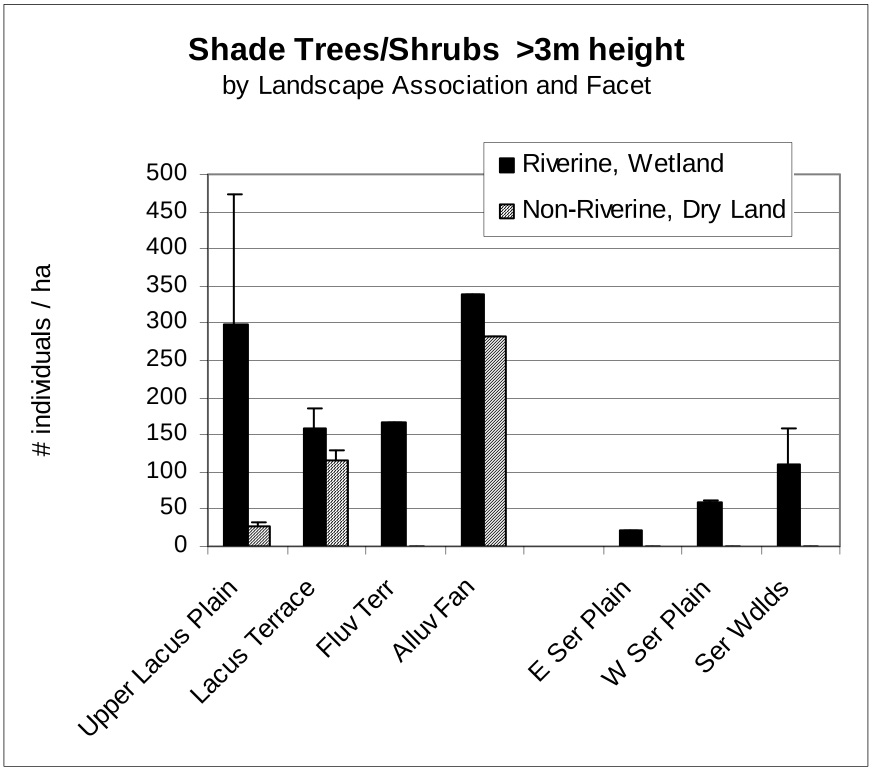


Figure 5-18. Density of shade trees and shrubs greater than three meters height in the modern study areas, grouped by physiognomy. Bars show the mean with one standard error. Ngorongoro data was not available because shrub density was not measured there.



Relative Density of Refuge Trees by Landscape Units

As in the case for edible plant foods, I calculated relative values of sleeping and shade refuge tree density by landscape facet, so that they can be compared to the predictions of Peters and Blumenschine (1995, 1996). Relative values of adjacent landscape units are also the preferred type to be used when reconstructing paleo-landscapes, as is done in Chapter Six.

I calculated relative refuge tree values similar to the way in which relative values of edible plant food abundance were calculated. The average number of trees per hectare in the appropriate height category, e.g. taller than 10 meters, was acquired for each landscape facet. I took the maximum landscape facet density value and divided that number into six equal parts. Each landscape facet was then assigned a relative value (0, +, ++, +++, or ++++) based on whether its density fell into the zero, first sixth, second sixth, third sixth, or greater than the third sixth categories. The relative rankings are defined in Table 5-2. Unlike the case of edible plant parts, the relative densities of refuge trees are comparable between the >3 meter, >10 meter, and >20 meter categories. I assigned values to the >3 meter and >20 meter refuge tree densities using the scale based on proportions of trees greater than 10 meters. In other words, the >3 meter category will always have the highest values because that category inherently includes any trees that are >10 meters and >20 meters.

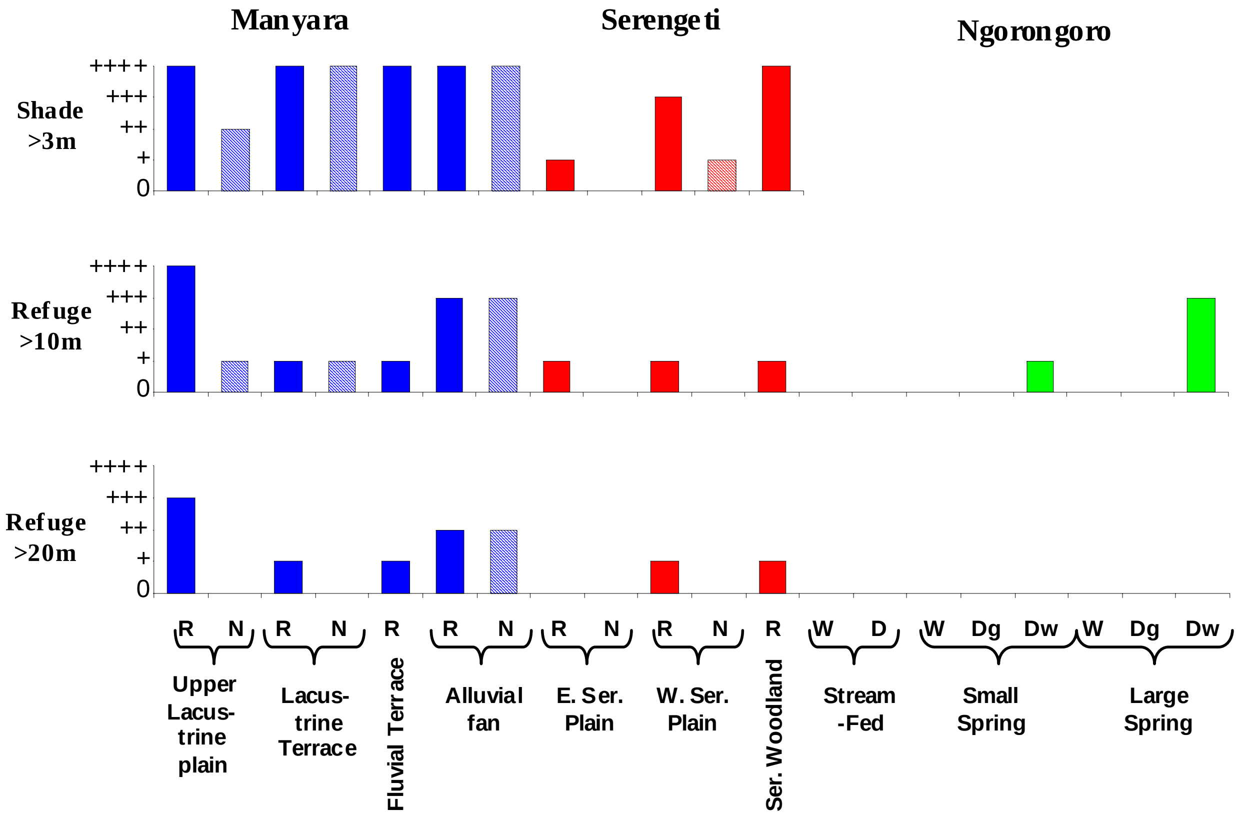
Table 5-2. Scale used for relative refuge tree/shrub abundance by facet in Figure 5-19.

Scale	Relative proportion of “sleep” or “shade” refuge trees, based on the proportion of trees >10 meters in height as follows.
0	0%
+	>0-17%
++	>17%-33%
+++	>33%-50%
++++	>50%

In the case of shade tree/shrub density (>3meters) (Figure 5-19), the Manyara region has much higher concentrations overall than Serengeti. Ngorongoro cannot be compared due to a lack of comparable field data.

The distribution of likely sleeping tree density, defined as trees ten meters tall or greater, is highest along the rivers of the upper lacustrine plain, across the alluvial fan, and in the woodlands associated with large springs (Figure 5-19). In Ngorongoro, the woodlands associated with springs stand in stark contrast to surrounding wetland and

Figure 5-19. Relative shade tree/shrub and refuge tree density in the modern study areas. The scale follows Table 5-2 and is described in the text. R=riverine, N=non-riverine, W=wetland, D=dry land adjacent to a wetland, Dg= grassland dry land, Dw= woodland dry land. Shade data was not available for Ngorongoro because shrub density was not measured there.



grassland landscape facets there. Similarly, in Serengeti, although the concentration of sleeping trees is not very high along rivers of the Eastern and Western Serengeti Plain, their presence is in sharp contrast to the bareness of adjacent interfluves. At Manyara, contrast between adjacent landscape facets in terms of sleeping tree density is found only at the upper lacustrine plain. At the lacustrine terrace and alluvial fan, the density of sleeping trees along rivers and in interfluves was the same.

Refuge trees greater than 20 meters tall are found only in Manyara and Serengeti, not in Ngorongoro (Figure 5-19). This class of trees occurs only in the riverine and not in the interfluve landscape facets of the lacustrine terrace, whereas in the alluvial fan, the concentration of trees is slightly higher in the interfluve as opposed to riverine landscape facets.

Summary of Edible Plants and Refuge Tree Distribution in the Modern Study Areas

In this section I summarize the findings on how plant foods and refuge trees were distributed according to physiognomic categories and land units.

Physiognomy

Although roughly the same percentage of edible fruit parts is produced by trees and shrubs (Figure 5-1b), the majority of edible fruit producing plants, and specifically edible fruit producing trees, occur in forests (Figures 5-2b and 5-3b). Furthermore, of the forest trees most produce “fleshy” as opposed to “dry” fruits (Figure 5-4). The exception to this are *Acacia xanthophloea* “forests” that typically line rivers in the lacustrine plain zone. Forests also have the highest abundance of sleeping and shade refuge trees (Figure

5-13, 5-14, and 5-15), and might have been preferred sleeping areas for hominins due to the high density of trees and the closed canopy.

In contrast to forest, bushland habitats harbor abundant shrub species (Figure 5-5a), a high percentage of which are edible. There are notably abundant edible fruits and edible roots produced by the bushland shrubs (Figure 5-5b). Bushland areas do have tall trees that might be used for sleeping, but they are often widely dispersed isolated trees surrounded by shrubs. The bushland trees encountered in these modern habitats were often *Acacia* species, which provide marginally edible seeds and pods, flowers, and gum.

Bush grassland sites have the highest numbers of edible and non-edible forb and grass species by far compared to other physiognomic units (Figures 5-6a and 5-7a). The forbs tend to have edible leaves (Figure 5-6b), while grasses tend to have edible seeds and underground parts (Figure 5-7b). Bush grassland and grassland sites do not provide sleeping refuge trees, but shade can be found in bush grassland.

The wetland marsh habitats offer food for hominins in the form of rootstocks, bulbs, and stem bases of sedges, cattails, and grasses. Some wetlands have nearby woodlands with refuge trees, while others are adjacent only to open grassland.

Landscape Units

Landscape facets with the most abundant and perennial plant-available water tend to have the most tree cover, and the most edible trees and sleeping refuge trees. In these modern examples those were the alluvial fan of Manyara, and the perennial stream on the upper lacustrine plain. Alluvial fan forests produced the majority of the trees with fleshy fruits, while the upper lacustrine plain forest was nearly all *Acacia xanthophloea* trees whose main edible component is gum. *Acacia xanthophloea* forests might be undesirable sleeping areas despite their tall trees because the trees are thorny, and the forest is a narrow strip adjacent to open interfluvial areas.

In areas where groundwater is the main source of tree and shrub water, such as Manyara's alluvial fan and lacustrine terrace, edible plants and refuge trees are relatively ubiquitous across landscape associations, and little difference can be found between adjacent riverine and non-riverine landscape facets. In the Serengeti Plain, on the other hand, there is a large contrast in terms of structure, refuge trees, and the types of plant foods available in riverine versus non-riverine landscape facets. The upper lacustrine plain, modeled at Manyara, is also an area of strong contrast between riverine and non-riverine landscape facets. On the Ngorongoro Crater lacustrine plain, in wetland versus adjacent dry land sites, there was always high contrast in edible plant types and abundance and refuge tree availability between the wetland marsh and either the grassland or shrubland or woodland adjacent to it.

Conclusion

In this chapter I have addressed the issue of how plant foods and refuge trees relate to vegetation physiognomy, species composition, and land units in the Manyara, Serengeti, and Ngorongoro modern analog study areas. The different physiognomic categories each have a suite of resources that are characteristically found there, as summarized above. I would expect that pattern to be characteristic of semi-arid East African savannas in general, as other studies also confirm some of these findings. For example, Sept's (1990) study also concludes that in bushland, shrubs tend to provide many edible fruits, and studies of primate food availability have found abundant availability of grass seeds in grassland (e.g., Barton *et al*., 1992), and tree fruits in groundwater forests (e.g., Rowell, 1966). It might be premature to extrapolate these patterns beyond the Somalia-Masai phytochoria (Figure 2-2), however, or at least beyond the Sudano-Zambezian Region (Figure 2-3) that encompasses African savannas in general. A forest in an Afromontane or Guineo-Congolian setting (Figure 2-2), for example, is likely to have a different floristic composition than the groundwater forest at Manyara, so the types of edible plant foods may be of a different type, abundance, or quality.

As described in the first chapter, the methodology that I developed for this study is aimed at identifying all *potential* hominin plant foods and refuge trees among the various physiognomic types and landscape units in the modern habitats. In other words, I am identifying the fundamental as opposed to the realized niche of hominin plant foods for the paleo-Olduvai basin (cf. Peters and O'Brien, 1981). Factors such as predation and competition would have narrowed the actual hominin plant food diet to fewer species than the entire list of theoretically edible species that grew near Olduvai in the past. There are several potential hominin predators on the African continent, and there were others during Plio-Pleistocene times, such as saber tooth cats and giant hyenas (Turner, 1985). Predators may have influenced hominins' plant food diet, for example, by preventing hominins from exploiting all of the edible marsh plants on the Eastern Lacustrine Plain if that was a favorite location for those predators to ambush prey. Competition for plant foods can be severe and hominins may have had to compete with monkeys, suids, and many other animals for edible resources. For example, monkeys tend to be able to eat unripe fruits, and thereby could decimate potential ripe fruit foods for hominins by getting to those resources earlier in the season.

Ultimately, to find out the realized niches of hominins requires independent means of testing such as studies of the tooth wear on hominin fossils, isotopic analyses of bone, and analyses of butchery remains. The results of some of those studies are discussed in Chapter Seven and are used to speculate on the actual diets of Olduvai hominins.

In the next chapter, I use the results presented here regarding the plant resources for hominins in modern analog settings to model what types of plant foods and refuge trees were available to hominins in the past, and how those resources were distributed across the Olduvai paleolandscape. I then develop models of potential hominin land use for hominins with different dietary preferences.

CHAPTER 6. APPLYING THE MODERN ANALOG-DERIVED INFORMATION TO THE PLIO-PLEISTOCENE OLDUVAI GORGE CASE STUDY

Introduction

In this chapter I apply the results of the modern analog vegetation studies presented in Chapters Four and Five toward reconstructing the vegetation across the 1.75 million-year-old lowermost Bed II, Olduvai paleolandscape. I apply both quantitative and qualitative results regarding vegetation composition, structure, and resource distribution from modern landscape units to similar landscape units reconstructed for the paleo-Olduvai basin. Some of the chapter deals directly with comparisons of my results to those of Peters and Blumenschine (1995, 1996; Blumenschine and Peters, 1998), who made the first attempt to systematically describe the landscape-scale distribution of Olduvai's resources, how early hominins exploited them, and the potential archaeological traces of those hominin activities.

I take five different but complementary approaches toward using the modern analog results to understand more about the ancient Olduvai vegetation. I begin by comparing the taxonomic list of fossil pollen data from Olduvai (Bonnefille, 1984a) with the taxonomic list of plants I encountered at Serengeti, Manyara, and Ngorongoro Crater. Next, I summarize what the vegetation of the paleo-Olduvai basin landscape units might have been like in terms of physiognomy, species composition, and hominin plant affordances. I then use the relative abundances of different plant food types in particular landscape units to reconstruct hominin resource distribution across the paleo-Olduvai basin. Based on the predictive plant resource distribution maps, I model how hominins with different dietary preferences might have exploited resources across the basin. Finally, I comment on how my reconstructions of vegetation structure would change the archaeological predictions made by Blumenschine and Peters (1998).

Throughout the chapter I am addressing the questions: What are the major interpretive changes to previous models of vegetation and resource distribution, hominin land use, and archaeological predictions based on the results of this thesis? What are the major implications for hominin ecology at Olduvai and hominin niche differentiation?

Fossil pollen at Olduvai versus plants in the modern study areas

The fossil pollen data for Plio-Pleistocene Olduvai that was collected by Bonnefille (1984a) provides valuable information about the actual plant taxa that grew in the paleo-Olduvai basin. Here I compare her list of fossil pollen with the plants that I encountered in the modern study areas in order to get a sense of how well the floristic composition of the modern study areas matches that of the paleolandscape. The comparison is also relevant for assessing whether the ancient habitats were more akin to moist/dystrophic or arid/eutrophic savannas.

Of the 54 plant *families* identified by Bonnefille (1984a) in the fossil pollen from Bed I and Lower Bed II, 34 of those, or 63%, occurred in my modern study areas at Serengeti, Manyara, and Ngorongoro Crater. Thirty-five of 74, or 47% of the *genera* in Bonnefille's fossil pollen list (including "type" genera) were also encountered in at least one of my plots. Five of 21, or 24% of *species* in Bonnefille's fossil pollen list (plants identified to species, including "type" species and "type" genera species) were encountered in at least one of my modern vegetation plots.

The plants in common between Bonnefille's (1984a) fossil pollen study from Olduvai and my modern vegetation studies at Serengeti, Manyara, and Ngorongoro are listed in Table 6-1. A substantial portion of the pollen identified by Bonnefille is associated with Afromontane elements as opposed to the Sudano-Zambezian component, as discussed in Chapter Two. The Afromontane pollen is presumed to have been washed down and blown into the basin from the nearby Crater Highlands, as we know it does today based on modern pollen rain studies (Bonnefille, 1984a). Therefore the Afromontane pollen does not represent plants growing in the immediate vicinity of Olduvai during lowermost Bed II times. Since my vegetation studies were only meant to model the vegetation growing within the Olduvai basin itself, the Afromontane elements from Bonnefille's analysis can be subtracted from her total list for the purpose of comparison. Subtracting the Afromontane elements from the fossil pollen from Bed I and Lower Bed II then suggests that 68%, 54%, and 31% of those plant families, genera, and species, respectfully, are present in my modern study areas.

The fact that plant species lists for the fossil pollen from Olduvai and the modern study areas have differences is expected for at least two reasons. First, the fossil pollen represent only a subset of all of the plant taxa that were growing in and around the paleo-Olduvai basin. Similarly, my sampling in selected landscape facets at Serengeti, Manyara, and Ngorongoro represents only a subset of the modern vegetation, and can by definition only be a sample of the range of potential vegetation types for Olduvai. A second reason to expect differences between the modern and ancient vegetation is that paleobotanical studies have found that particular plant communities, or species associations, that exist today did not necessarily exist as similar ecological units in the

Table 6-1. Pollen taxa recovered by Bonnefille (1984a:Table 2) from Bed I and Lower Bed II Olduvai deposits that are in common with plants identified in this modern vegetation study at Serengeti, Ngorongoro, and Manyara.

- Acanthaceae
    - type *Asystasia*
    - type *Hypoestes*
    - type *Justicia* (*J. anselliana* and *J. odora* are not in the modern sites)
- Amaranthaceae type *Achyranthes*
    - type *Aerva persica*
    - type *Digera muricata*
    - type *Pupalia*
- Amaranthaceae/Chenopodiaceae
- Anacardiaceae type *Rhus*
- Apocynaceae type *Carissa*
- Boraginaceae *Heliotropium*
    - type *steudneri*
- Burseraceae *Commiphora*
- Capparaceae (formerly Capparidaceae)
- Capparaceae type *Boscia*
    - type *Cleome gynandra* (formerly *Gynandropsis gynandra*)
- Combretaceae
- Commelinaceae type *Commelina benghalensis*
- Compositae *Hirpicium* type *diffusum*
- Compositae type *Vernonia*
- Cyperaceae
- Ebenaceae *Euclea*
- Euphorbiaceae *Acalypha*
    - type *Croton*
    - type *Euphorbia*
- Flacourtiaceae
- Gramineae
- Labiatae type *Plectranthus*
- Leguminoseae subfam. Mimosoideae
    - *Acacia albida*
    - *Acacia*
    - type *Dichrostachys*
- Leguminoseae subfam. Papilionoideae
    - type *Ormocarpum*
    - type *Rynchosia*
- Nyctaginaceae type *Boerhavia*
- Palmae type *Phoenix*
- Polygonaceae
- Rhamnaceae
- Rubiaceae
    - type *Oldenlandia*
    - type *Pavetta*
- Salvadoraceae *Salvadora*
- Sapindaceae
- Solanaceae
    - type *Solanum*
- Sterculiaceae type *Dombeya*
- Tiliaceae type *Grewia*
- Typhaceae *Typha*
- Ulmaceae *Celtis*
- Umbelliferae
- Verbenaceae
- Vitaceae
- Zygophyllaceae *Tribulus*

past (e.g., Webb, 1987; 1988; Delcourt and Delcourt, 1987). In a taphonomic and taxonomic study of the rodents from Olduvai, for example, Fernández-Jalvo *et al*. (1998) concluded that the environments that existed during middle Bed I times have no modern counterparts, as they were structurally complex dense canopy woodland with a more species-rich bush and ground vegetation than is found anywhere today.

Plant taxa with high frequencies or importance values in my modern study areas that are in evidence for lowermost Bed II are as follows. There is fossil pollen evidence for *Acacia*, the genus of trees that was most common overall in the modern study areas. Fossil pollen also indicates the presence of shrubs that had high importance values in the modern study areas such as *Commiphora*, *Salvadora*, *Grewia*, *Acalypha*, and *Justicia*. Among herbaceous species, the fossil pollen represents *Achyranthes*, *Hypoestes*, *Typha*, Commelinaceae, Cyperaceae (sedge), and Gramineae (grasses).

Bonnefille identified the non-Afromontane arboreal pollen from Olduvai as Sudano-Zambezian, but White’s (1983) phytochoria split the Sudano-Zambezian Region as defined by LeBrun (1947) into several separate (but closely related) categories (Figures 2-2 and 2-3). Is it possible to say with which of White’s phytochoria the Olduvai pollen have the most in common? The taxa found among Olduvai’s fossil pollen imply an alliance with the Somalia-Masai phytochoria, which is the arid/eutrophic savanna and currently dominates arid northern Tanzania, Kenya, and Somalia. It is often characterized by the woody plants *Acacia* and *Commiphora*. This is opposed to the Zambezian “moist savanna” or miombo woodlands that exist in southern Tanzania and much of central and southern Africa and are characterized by *Brachystegia* and *Julbernardia* tree species (Bell, 1982; Bonnefille, 1984a; Huntley, 1982; White, 1983).

According to Hamilton (1982:107), it is possible to differentiate *Brachystegia*-dominated miombo woodland from *Acacia*/*Commiphora* woodland in modern pollen rain samples by their pollen percentages. *Acacia*/*Commiphora* woodland, typical of arid savanna, has high percentages of Chenopodiaceae/Amaranthaceae, as is often the case in dry environments worldwide (Livingstone, 1971). The pollen of *Acacia* and *Commiphora* trees themselves are poorly represented in modern pollen assemblages, but nonetheless there are some *Acacia* pollen preserved in the lowermost Bed II fossil assemblage (Bonnefille, 1984a). *Brachystegia* percentages can be as high as 21% in modern assemblages of southern East African miombo woodland, or moist savanna, as they produce fair amounts of pollen (Livingstone, 1971). However, no samples of pollen belonging to the Caesalpiniodeae subfamily of Leguminoseae, to which *Brachystegia* belongs, were found in the lowermost Bed II fossil pollen assemblage (Bonnefille, 1984a).

Thus, while there are inevitable differences in the actual species composition of the modern East African habitats used as modern analogs for this thesis versus the ancient savannas in the vicinity of Olduvai, the similarities in pollen assemblages suggest that the modern analogs used here are among the best that could be found today. The ancient and modern ecosystems may have ecological similarities in terms of the importance of grasses, the dominance of microphyll-leaved trees like *Acacia*s, the many large herbivores, and in the fact that both are highly productive ecosystems in lake margin environments. For the purpose of this study, their similarities are assumed to be great enough to allow us to use slightly different modern analogs to predict the relative abundance of plant resources for hominins in different landscape units. In the future, new fossil evidence of particular plant taxa from Olduvai could help to test this assumption and incorporate into models of the ancient plant distribution the concept that novel plant species associations may have existed in the past.

Hypothetical landscapes and plant affordances for lowermost Bed II, Olduvai

Peters and Blumenschine (1995, 1996) outlined a conceptual approach for "landscape paleoanthropology," and elaborated on specific reconstructions of Olduvai paleolandscapes during lowermost Bed II times. Their reconstructed landscape units, including land regions, landscape associations, and landscape facets, were based on a compilation of previously conducted geological and paleoenvironmental studies, Peters' and Blumenschine's own observations of modern analog environments in East and southern Africa, and the results of several field seasons at Olduvai in 1989 and the 1990s. I described the multiple lines of paleoenvironmental evidence that have been collected from Olduvai Gorge, including Peters and Blumenschine's reconstructed paleolandscape units, in Chapter Two (see references in Table 2-1). I use these theoretical paleolandscape units as a basis for the application of my modern analog-derived vegetation information to the Olduvai case study. Table 2-2 describes the paleo-landscape associations and landscape facets, and Figure 2-7 shows them depicted on a map of the lowermost Bed II Olduvai basin.

In Table 6-2, I summarize which of my modern analog landscape facets are used to model the various theoretical paleolandscape facets of lowermost Bed II, and the particular plant food affordances that I found in those modern settings. The results are placed alongside Peters and Blumenschine's predictions for the same paleolandscape units, which they derived through casual, as opposed to quantitative, observations at modern analog settings. The "modern analog" columns show that some of the places they used to model the paleo-settings were the same places where I conducted quantitative analyses.

Peters and Blumenschine (1995; 1996) presented two different models of the paleo-Olduvai basin. The first was the riparian model (1995: Table 1), in which all of the fresh-water input to the Eastern Lake Margin was assumed to have come as surface drainage in streams from the Crater Highlands. In their 1996 paper, they contrasted that to a spring-oasis/mock aridity model, in which the eastern mountain sides were thought to be largely devoid of vegetation and rivers, and in which groundwater flow from the Crater Highlands emerged as fresh water springs along the Eastern Lake Margin.

More recent geological studies support a riparian model in which an alluvial fan system dominates the area east of the lake for most of the duration of lowermost Bed II times (Blumenschine *et al*., 2000). There may have been freshwater springs emerging near the Eastern Lake Margin as well (Hay, 1996; Ashley and Feibel, 1995). Thus, I incorporated both riparian and spring elements into my reconstruction of lowermost Bed II paleogeography (Figure 2-7 and Table 2-2). In Table 6-2 I compare my landscape units, modern analogs, and plant foods with those reconstructed by Peters and Blumenschine. Their description of the Eastern Lacustrine Plain is based on Peters and Blumenschine, 1996: Table 1, which includes riparian and spring descriptions. Their reconstructions of all of the other landscape associations follow Peters and Blumenschine, 1995: Table 1.

Table 6-2. Hypothetical paleo-Olduvai landscape units, modern analogs, and hominin affordances, comparing the results from Peters and Blumenschine 1995, Table 1 and Peters and Blumenschine 1996, Table 1 to results based on this study.

Landscape Units, as shown in Figure 2-7.		**PETERS & BLUMENSCHINE 1995, 1996**			**THIS STUDY**		
Land-scape assoc-iation	**Landscape locale (P&B, 1995)**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances-Plant Foods**
Serengeti Peneplain	West Lake Olduvai	*Gently rolling open plains: calcareous loams and sandy clay loams overlying weathered tuff; dotted with pans in a wetter climate?*	*West Serengeti Plains*	*Non-habitat*	Interfluves	**Serengeti:** Barafu Plain Nyamara Interfluve Seronera-Wandamu Interfluve	Some edible forb leaves and grass seeds, especially in the wet season. Rare trees/shrubs with edible fruits/pods/seeds.
	West Lake Olduvai (cont.)	*Drainage lines: sparsely wooded streams; stream pools on hard pan (?), pool water slightly alkaline (pH=7.8) with* Typha *patches (?)*	*Wandamu River (West Serengeti Plains)*	*Fruit/seed and gum trees:* Balanites, Acacia tortilis *Arboreal sleeping sites* *Scavenging opportunities* *Drinking H_2O in the wet season*	Rivers -crossing the plains	**Serengeti:** Barafu River Seronera River Nyamara River	Scattered *Acacia tortilis* trees with edible pods, lvs, & flowers at sparsely watered rivers, and *Acacia xanthophloea* trees with edible gum lining rivers further downstream with more water. More edible shrub and forb fruits/seeds/leaves than in nearby interfluves, and more edible grass species than in nearby interfluves.
					-further west in the basement rock zone	**Serengeti:** Mbalageti River Sangare River	Abundant *Acacia xanthophloea* trees with edible gum, and occasional *Ficus* sp. trees with high-quality edible fruits. Frequent shrubs with edible fruits, such as *Cordia monoica* and *Grewia* spp., but only a few edible forbs and grasses.

Table 6-2 (cont.)

Landscape Units, as shown in Figure 2-7.		**PETERS & BLUMENSCHINE 1995, 1996**			**THIS STUDY**		
Land-scape assoc-iation	**Landscape locale (P&B, 1995)**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances-Plant Foods**
Lacustrine Plains	West Lake Olduvai	*Intermittently flooded to intermittently dry zones: alkaline grasslands near the perennial lake*	West Lake Nakuru (Kenya) *Ngorongoro Soda Lake*	*Minor opportunities for scavenging (including drownings) Otherwise=non-habitat*	Interfluve	**Manyara:** Ndala Lake Flat Msasa Lake Flat **Ngorongoro:** dry land sites	On uppermost lacustrine plain: Sparse scattered trees, *Acacia tortilis* with edible pods, lvs, & flowers, *Acacia xanthophloea* with edible gum, *Hyphaene petersiana* palms with edible fruits/seeds. Some shrubs with edible fruits/seeds/leaves. A great variety of edible forbs and grasses in the wet season. Lower lacustrine plain between water sources is alkaline grassland or mudflats with sparse edible sedges and grasses.
	West Lake Olduvai (cont.)				Streams	**Manyara:** Mkindu River on Lacus Plain Msasa River on Lacus Plain **Ngorongoro:** wetland sites	Along upper lacustrine plain rivers may be *Acacia tortilis* trees with edible pods, leaves, and flowers, and a variety of shrubs with edible fruits and roots, and edible forbs and grasses. On the lower lacustrine plain, *Acacia xanthophloea* with edible gum line rivers to form linear patches surrounded by grassland/mudflats. Under the trees are very few, very sparse edible shrub, forb, and grass species.

Table 6-2 (cont.)

Landscape Units, as shown in Figure 2-7.		**PETERS & BLUMENSCHINE 1995, 1996**			**THIS STUDY**		
Land-scape assoc-iation	**Landscape locale (P&B, 1995)**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances-Plant Foods**
Lacustrine Plains (cont.)	East Lake Olduvai	**Mid-Upper Lacustrine Plain** (Intermittently flooded to intermittently dry zones): ***Riparian model*** – minor deltas; some places permanently marshy from fresh water river-mouth flooding and seepage.	*Lake Manyara* *Gorigor Marsh (Ngorongoro Crater)* *East Lake Nakuru (Kenya)*	*Game: migratory birds in the sedge marshes* *Edible rootstocks in the* Typha *marshes.* *Shrubland=non-habitat* *Prime scavenging opportunities at fresh* H_2O *site.* *Hazards include carnivores, crocodiles and exposure.*	Stream-fed wetlands Adjacent dry lands	**Ngorongoro**: Gorigor Midwest Gorigor North Gorigor West Munge Marsh Munge River	Where low velocity creates wetlands (Munge), marsh plants like *Typha* and *Cyperus immensus*, and *Cyperus laevigatus* provide edible rootstocks, rhizomes, and stem bases. Dry lands adjacent to the stream-fed wetlands are typically grassy, bare, and/or have sparse edible sedges. Edible grasses include *Cynodon dactylon*, *Sporobolus spicatus*, and *Themeda triandra*.

Table 6-2 (cont.)

Landscape Units, as shown in Figure 2-7.		**PETERS & BLUMENSCHINE 1995, 1996**			**THIS STUDY**		
Land-scape assoc-iation	**Landscape locale (P&B, 1995)**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances-Plant Foods**
Lacustrine Plains (cont.)	East Lake Olduvai (cont.)	***Mid-Upper Lacustrine Plain*** *(Intermittently flooded to intermittently dry zones) (cont.):* ***Spring-oasis model- Small springs*** *–* *Small fresh H_2O streams flow from spring heads a short distance to the lower lake shore*	Dead Hippo Spring (=Mti Moja), (Ngorongoro Crater)	*Prime scavenging opportunities.* Hazards include carnivores, crocs & exposure	**Small Springs** Wetlands	**Ngorongoro**: Engitati Kidogo Spring Mystery Spring Mti Moja Seneto Vernonia	Generally support a marsh with a variety of sedges, some like *Cyperus immensus* and *Cyperus laevigatus* have edible underground parts, and in less alkaline areas one finds *Typha latifolia* with edible rootstocks and seasonally available edible pollen (a high quality food).
				Surrounding grassland = non-habitat	Adjacent Dry Lands		Dry lands adjacent to small springs are mainly grassy, with a few edible grass species. Some edible shrubs like *Vangueria madagascariensis*, and edible trees like *Acacia xanthophloea* and *Euphorbia candelabrum*.
		Large springs*-* *Large hippo pools and fresh H_2O influenced vegetation covering a few km^2*	*Ngoitokitok Springs (Ngorongoro Crater)*	*Game: migrating birds in the sedge marshes.* *Edible rootstocks from* Typha. *Arboreal sleeping sites in* Acacia xanthophloea *groves.*	**Large Springs** Wetlands	**Ngorongoro**: Ngoitokitok North Ngoitokitok South	A large marsh with *Typha latifolia* which has edible rootstocks and seasonally available edible pollen (a high quality food), and *Cyperus papyrus* and *Phragmites mauritianus* with edible pith. Along the edges of the pool are edible forbs and grasses.
				Surrounding thicket-bushland and grassland = non-habitat. *Prime scavenging opportunities.* *Hazards include carnivores, crocs & exposure.*	Adjacent Dry Lands		Associated with an *Acacia xanthophloea* woodland, and, if higher ground is present, other trees and shrubs that provide edible fruits (*Croton machrostachyus*, *Cordia* sp., *Vangueria* sp.). Also grassy areas with 2-3 edible grass and sedge spp.

Table 6-2 (cont.)

Landscape Units, as shown in Figure 2-7.		**PETERS & BLUMENSCHINE 1995, 1996**			**THIS STUDY**		
Land-scape assoc-iation	**Landscape locale (P&B, 1995)**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances-Plant Foods**
Lacustrine Plains (cont.)	East Lake Olduvai (cont.)	Uppermost lacustrine plain ***Interfluvial areas -*** *Between fresh H_2O sites, very rarely flooded by lake; strongly alkaline, slightly to moderately saline clayey soils*	*Lake Manyara* *Lake Nakuru (Kenya)*	Acacia xanthophloea *woodland* *Arboreal sleeping sites* *Vantages over the east lake margin* *No major plant foods* *Hazards include carnivores*	Interfluves on Uppermost Lacustrine Plain	**Manyara:** Ndala Lake Flat Msasa Lake Flat	Sparse scattered trees: *Acacia tortilis* with edible pods, lvs, & flowers, *Acacia xanthophloea* with edible gum, *Hyphaene petersiana* palms with edible fruits/seeds. Some shrubs with edible fruits/seeds/leaves. A great variety of edible forbs and grasses, particularly in the wet season.
					Rivers on Uppermost Lacustrine Plain	**Manyara:** Mkindu River on Lacus Plain Msasa River on Lacus Plain	Along upper lacustrine plain rivers may be *Acacia tortilis* trees with edible pods, leaves, and flowers, and a variety of shrubs with edible fruits and roots, and edible forbs and grasses. Closer to the lake, *Acacia xanthophloea* trees with edible gum line rivers to form linear patches surrounded by grassland. Under the trees are very sparse edible shrub, forb, and grass species.

Table 6-2 (cont.)

Landscape Units, as shown in Figure 2-7.		**PETERS & BLUMENSCHINE 1995, 1996**			**THIS STUDY**		
Land-scape assoc-iation	**Landscape locale (P&B, 1995)**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances-Plant Foods**
Lacustrine Terraces	East Lake Olduvai	*Interfluvial areas: narrow transition zones between the lake-margin and the piedmont alluvial plain, corresponding to the old high lacustrine plain; soils somewhat alkaline and non-saline clays, sandy clays and loams; moisture depends mainly on local rainfall; moisture availability marginal during the dry season*	*Olbalbal Depression* *Lake Manyara*	*Fruit/seed and gum trees:* Balanites, Acacia tortilis *Arboreal sleeping sites*	Interfluves, Lacustrine Terrace	**Manyara:** Ndilana-Msasa Interfluve Ndala-Chemchem Interfluve	Scattered mature *Acacia tortilis* trees with edible pods, leaves, and flowers. Many shrubs with edible fruits, such as *Salvadora persica*, *Cordia monoica*, and *Acalypha fruticosa*. Many edible forbs and grasses present during the wet season, including *Hibiscus ovalifolius* (woody forb/shrub) and *Monechma debile*, and *Commelina africana*.
Lacustrine Terraces (cont.)	East Lake Olduvai	*Drainage lines*	*Lake Manyara*	*Fruit bushes?*	Rivers, Lacustrine Terrace	**Manyara:** Msasa R. on Lacus Terr. Ndilana R. on Lacus. Terr. Endabash R. on Fluv. Terr.?	Trees are mainly mature *Acacia tortilis* with edible pods, leaves, and flowers. Occasional trees are *Balanites aegyptiaca* with edible fruit pulp and seeds. Rivers with greater flow volume and deeper, more alluvial soils (Endabash) have a greater variety of trees, such as *Ziziphus pubescens* with edible fruits & leaves and *Kigelia africana* with edible fruits, seeds, flowers, and bark/cambium. There are numerous and varied edible shrub species, especially shrubs with edible fruits (*Salvadora persica*, *Cordia monoica*, *Cordia sinensis*). Also many edible forbs and grasses present during the wet season, including *Hibiscus ovalifolius* (woody forb/shrub) and *Monechma debile*.

Table 6-2 (cont.)

Landscape Units, as shown in Figure 2-7.		**PETERS & BLUMENSCHINE 1995, 1996**			**THIS STUDY**		
Land-scape assoc-iation	**Landscape locale (P&B, 1995)**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances-Plant Foods**
Lacustrine Terraces (cont.)	West Lake Olduvai	*General*	*Lake Magadi (West Serengeti)*	*Non-habitat? (shrublands?)*	Interfluve and Rivers	No analogs.	
Piedmont Alluvial Plain	Olmoti Alluvial Plain (coalescing alluvial fans)	*Upper fan-zone: deep loams, sandy soils and gravelly apices; regularly flooded and partially waterlogged during wet season; groundwater within tree rooting depth throughout the year*	*Ngorongoro Crater (southwest lower inside rim and upper crater floor)* *Lake Manyara*	*Riverine and groundwater forest-fruit trees and bushes:* Ficus, Vangueria, Cordia, Grewia, Tabernae-montana (?), Tamarindus, *and* Ziziphus *Prime opportunities for scavenging along wooded drainage lines* *Lava cobbles* *Arboreal escape and sleeping sites*	Upper Alluvial Fans	No analogs.	

Table 6-2 (cont.)

Landscape Units, as shown in Figure 2-7.		**PETERS & BLUMENSCHINE 1995, 1996**			**THIS STUDY**		
Land-scape assoc-iation	**Landscape locale (P&B, 1995)**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances**	**Landscape Facet descriptions**	**Modern Analogs**	**Affordances-Plant Foods**
Piedmont Alluvial Plain (cont.)	Olmoti Alluvial Plain (coalescing alluvial fans) (cont.)	*Lower fan-zone: relatively shallow loams and clayey soils, somewhat alkaline, locally slightly saline?; depressions (with salt bush?) and dead stream channels with higher salinity; floodplains of major streams inundated during wet season (?)*	*Lake Manyara (in part)* *OlBalbal Depression (in part)*	***Riparian model*** *Riverine woodlands: fruit trees and bushes.* *Plains: fruit/seed and gum trees.* ***Spring-oasis model*** *Shrubland, thicket-bushland and grassland = non-habitat.* *Hazards include carnivores and exposure.*	Lower Alluvial Fans	**Manyara:** Mkindu R. on alluvial fan Mkindu Interfluve	Lower alluvial fans support a young forest dominated by *Trichilia emetica* trees with edible fruits (seed arils), and fig trees (*Ficus* sp.) with edible fig fruits. Very few edible shrubs and no edible grasses. Forbs such as *Achyranthes aspera* and *Hypoestes forskalei* provide edible leaves.
Piedmont Alluvial Plain (cont.)	Ngorongoro/ Lemagrut Alluvial Plain (coalescing alluvial fans, adjoining the Olmoti alluvial plain)	*Alluvial fans with shallow soils in comparison with the Olmoti fans*	*Unknown*	*Riverine woodlands-fruit bushes:* Cordia *and ??*		**Manyara:** Mkindu R. on alluvial fan Mkindu Interfluve Endabash R. on Fluv. Terr.?	As above. Areas with less forest canopy cover (e.g., Endabash R.) have a greater variety of shrubs that provide edible fruits, as in the lacustrine terrace, particularly along streams.

Below I reconstruct the plant foods across the Olduvai paleolandscape facets by using the modern analogs in a direct or formal analogy for the past. At the end of the section I summarize the differences between my reconstructions and those of Peters and Blumenschine.

Serengeti Peneplain

My modern analog studies of the interfluves of the Serengeti Plain reveal some plant foods in the form of edible forbs and grass seeds, particularly in the wet season, in contrast to Peters and Blumenschine, who considered this area a non-habitat. My model shows the riverine corridors to provide edible fruit/pod and gum from trees of *Acacia xanthophloea* and *Acacia tortilis*. My model corresponds to Peters and Blumenschine's in that I found the riverine corridors to be richer in edible shrubs, forbs, and grasses than the surrounding interfluves.

In the modern Serengeti Woodland (not shown in Table 6-2, and not modeled by Peters and Blumenschine), which are west of the Serengeti Plain, rivers were lined with a higher diversity of edible tree species than those of the Serengeti Plain. High-quality edible shrub fruits from species such as *Cordia* and *Grewia* also were relatively numerous.

Lacustrine Plain

Due to my limited number of study areas, I have used some of the same modern analogs to represent both the Western and Eastern Lacustrine Plains. Therefore this analysis is not useful for assessing potential differences between the Western and Eastern Lacustrine Plain at Olduvai's paleolandscape.

Peters and Blumenschine considered the Western Lacustrine Plain a "non-habitat" in terms of plant foods, but I assume that there was some fresh water input into that side of the basin, as indicated during Middle Bed I times (Blumenschine *et al.*, 2003). If Manyara analogs are relevant to the western portion of the basin, then the western uppermost Lacustrine Plain may have supported scattered edible fruit- and seed/pod-bearing trees and shrubs, and abundant edible forbs and grasses in the wet season. Along streams there would have been a higher concentration of edible fruit- and seed- bearing trees at increasing density with increasing amounts of water carried by ephemeral streams.

For the streams and interfluves of the middle to upper Eastern Lacustrine Plain, Peters and Blumenschine predicted minor deltas and some marshy areas surrounded by shrublands. The only plant foods they note are the edible rootstocks in the *Typha* marshes. In my modern analog sites in Ngorongoro Crater, stream-fed wetlands support marsh plants like *Typha latifolia*, *Cyperus immensus*, and *Cyperus laevigatus*, which provide edible rootstocks, rhizomes, and stem bases, respectfully. Dry lands adjacent to stream-fed wetlands are usually grassland with few or no shrubs, and provide a few edible grass species and sparse, small edible sedges.

In the spring-oasis model, Peters and Blumenschine (1996) predicted small springs to provide prime scavenging opportunities, but to be hazardous due to mammalian carnivores, crocodiles, and exposure, and to be surrounded by grasslands that are "non-habitat". My survey of six small springs within Ngorongoro Crater suggests that the wetland area typically supports a small marsh with a variety of sedge species, many of which have edible rhizomes, bulbs, and/or rootstocks. The dry lands adjacent to small springs are mainly grassland, containing a few edible grass species, but in some instances a very small, localized shrubland or woodland is associated with a small spring. At small springs whose adjacent dry land has no trees or shrubs, there are only a few edible grass and small sedge species.

Large springs in the spring-oasis model discussed by Peters and Blumenschine (1996) were predicted to provide edible rootstocks from *Typha* and sleeping groves composed of *Acacia xanthophloea* trees, while surrounding thicket-bushland and grassland was described as “non-habitat”. My study found spring-fed marshes to have many edible rootstocks and rhizomes, including those from *Cyperus immensus* and *Typha latifolia*. The dry lands adjacent to the large springs harbor more potential plant food and refuge resources than small springs within their wooded areas. There are also some areas adjacent to the large spring Ngoitokitok (in Ngorongoro Crater) that are grass-covered, with no woody plants, and those areas provide about the same edible grasses and sedges as the grasslands near small springs.

Peters and Blumenschine (1996) predicted the Eastern uppermost Lacustrine Plain to be composed of an *Acacia xanthophloea* woodland that provided arboreal sleeping sites and vistas over the lake margin, but no major plant foods. I found in my study that the interfluves in the uppermost lacustrine plain at Manyara consist of sparse scattered *Acacia tortilis* trees with edible pods, leaves and flowers, occasional *Acacia xanthophloea* trees with edible gum, and a few palm trees, *Hyphaene petersiana*, with edible fruits and seeds. The interfluves also supported some shrubs with edible fruits, seeds, and leaves. An unexpected find in my study was the flourishing of large amounts of edible forbs and grasses on the upper lacustrine plain after the rains.

Lacustrine Terrace and Fluvial Terrace

The lacustrine terrace is a narrow, relatively flat transition zone between the lake-margin and the piedmont alluvial plain that corresponds to an old high lacustrine plain (Loth and Prins, 1986). If a lacustrine terrace existed in the paleo-Olduvai basin, it probably occurred only on the eastern/southern side of the lake where the slope gradient was higher than in the west, as shown in the reconstruction in Figure 2-7.

The modern analog lacustrine terrace at Lake Manyara is dominated by evenly spaced mature *Acacia tortilis* trees, which provide edible pods, flowers, and leaves. An important characteristic that was not noted by Peters and Blumenschine (1995) is the high diversity and abundance of edible fruit-, leaf-, and flower-producing shrubs, such as *Salvadora persica*, *Cordia* spp, and *Acalypha* spp in the lacustrine terrace. Edible forbs and grasses are common in the wet season, but very sparse in the dry season.

The rivers that cross the lacustrine terrace are covered with evenly spaced *Acacia tortilis* trees, similar to those in the adjacent interfluves. Edible shrubs are more diverse and abundant along these rivers than in the adjacent interfluves, and edible forbs and grasses are present in the wet season, but sparse in the dry season.

At Lake Manyara, the larger Endabash River on a fluvial terrace has deeper, less volcanic, alluvial soils, and supports a much larger diversity of tree types, including *Ziziphus* sp. with edible fruits, *Kigelia africana* (the sausage tree) with edible fruits, seeds, flowers, bark, and cambium, and other edible tree species. Like the lacustrine terrace sites, edible (and non-edible) forbs and grasses are rare in the dry season and present in the wet season, though never as abundant as the forbs of the upper Lacustrine Plain interfluves.

Lower Alluvial Fan (Piedmont Alluvial Plain)

In the landscape reconstruction of lowermost Bed II, an evolving fan system dominates the eastern and southern sides of the lake basin (Blumenschine *et al*., 2000). Peters and Blumenschine (1995) originally referred to this area as the piedmont alluvial plain, but it is more appropriately referred to as an upper alluvial fan zone and a lower alluvial fan zone (also used by Peters and Blumenschine, 1995). Since I did not study any analogs for the upper alluvial fans, my results are only applicable to the lower fan zone.

Peters and Blumenschine describe the lower fan zone under their riparian model as supporting riverine woodlands with fruit trees and bushes, while the interfluves were plains with fruit/seed and gum trees (e.g., *Acacia* and *Balanites*). In the modern analog for lower alluvial fans at Manyara, a high groundwater table strongly affects the vegetation, and whether such a high groundwater table existed at Olduvai is not known. If there was a high groundwater table under the lower alluvial fans in the paleo-Olduvai basin, then that area could have supported a groundwater forest with several edible fruit-producing tree species. Such forests have few edible shrubs, no edible grasses, and a few edible forbs.

The fluvial terrace of the Endabash River at Manyara may be a partial analog for the lower alluvial plain/piedmont plain situation in which there was not necessarily a high groundwater table. Compared to a groundwater forest, the fluvial terrace analog suggests that rivers were lined with fewer and shorter trees, and more shrubs, but the tree density and diversity was still much greater than that along the rivers of the Lacustrine Plain and lacustrine terrace. Many of the trees and shrubs in the fluvial terrace have edible fruits and seeds.

Major Rock Outcrops and Mountain Sides

I did not systematically study any analogs for the major rock outcrop or mountain side landscape associations at Olduvai. My own casual observations at rock outcrops near modern Olduvai Gorge and in the Serengeti indicate that these land units have significantly different vegetation than the surrounding plain and riverine habitats. The unique suite of plants that grows on rock outcrops often included *Euphorbia* trees and various succulents. Affordances that hominins might encounter there include plant foods such as *Ximenia americana*, animals foods such as hyraxes, and raw materials for stone tools.

Mountain sides are even more different floristically from surrounding lowland savannas than rock outcrops. Accordingly, montane flora is assigned to a unique phytochoria, the Afromontane zone (White, 1983). It is unclear as yet what unique affordances mountain sides might have provided for hominins, but arboreal refuge at least would seem to be plentiful there because of the abundant forests. On the other hand, cold night-time temperatures and arboreal carnivores such as leopards and sabertooth cats may have posed significant hazards.

Summary of differences between this study and Peters and Blumenschine (1995, 1996)

In sum, my quantitative studies of modern analog vegetation differ from Peters and Blumenschine's (1995; 1996) observations in the following ways. Whereas they considered the interfluves in the Serengeti Peneplain to be non-habitat for hominins, I found that a few edible forbs and grasses were present there.

For the Western Lacustrine Plain, I assumed that there was more fresh water surface flow than was thought by Peters and Blumenschine, who described the area as non-habitat for hominins. I predicted the interfluves to have scattered edible fruit- and seed/pod-bearing trees and shrubs, and the riverine habitats to support a concentration of edible fruit- and seed/pod- bearing trees.

For the Eastern Lacustrine Plain, Ngorongoro analogs suggest that small springs may have a localized shrublands in their vicinity, which provide a small amount of shade and edible shrubs in addition to the edible rootstocks from marsh plants in the wetland. While Peters and Blumenschine predicted the interfluves in the uppermost Lacustrine Plain to provide little more than vantage and arboreal refuge, I predict that there was a diversity of edible plants including palm trees, shrubs, and, unexpectedly, large amounts of edible forbs and grasses during the wet season.

Peters and Blumenschine report that the modern analog lacustrine terrace at Manyara supports *Acacia* trees and arboreal refuge, but they did not recognize that there is also a high diversity and abundance of edible shrubs there. Those shrub resources would have been important to hominins by providing edible fruits and underground parts.

Finally, Peters and Blumenschine predicted alluvial fans to have riverine forests with sparsely treed interfluves, while my modern analog alluvial fans at Manyara have riverine or “groundwater” forest along both the rivers and the interfluves. The question of which, if either, was the situation in the paleo-Olduvai basin will depend on our gaining a better understanding of the groundwater situation of the alluvial fan zone of lowermost Bed II.

Relative Resource Abundance Models

Peters and Blumenschine (1995: Tables 3a and b; 1996: Tables 3a and b) made an initial attempt to show the *relative* rankings of hominin affordances among landscape facets across the lowermost Bed II paleolandscape based upon casual or qualitative field observations. In an effort to test and improve their models, I used quantitative analyses of modern analogs to create a comparable table and a series of maps that model the distribution of various types of plant foods and refuge trees across lowermost Bed II.

In Tables 6-3 and 6-4, I incorporate the results of the relative rankings of modern analog plant resource abundance from Figures 5-12 and 5-19, correlating specific modern analog landscape facets to paleo-Olduvai landscape facets as shown in Table 6-2. As described in Chapter Five, the scale of increasing abundance is 0, +, ++, +++, and ++++. For the plant food rankings, the results of each plant food part are independent of other affordances in the table. Thus the rankings of edible fruits, for example, are relative only within their own category, and cannot be used to compare its abundance to that of USOs or any other plant part. For arboreal refuge, the rankings *are* comparable between the >3m, >10m, and >20m height categories, as described in Chapter Five.

The columns in Tables 6-3 and 6-4 are roughly arranged to show a transect from west to east across the Olduvai paleolandscape. Comparable landscape units described by

Table 6-3. Relative plant food abundance for lowermost Bed II, Olduvai as predicted by Peters & Blumenschine for a wet season, wet climate (1995&1996: Table 3a) and a dry season dry climate (1995&1996: Table 3b) versus the results of this study.

PETERS & BLUMENSCHINE		**Serengeti Peneplain**		**W. Lacus. Plain**	**Eastern Lacustrine Plain**					**Lacus. Terrace**		**Major rock oucrops**	**Piedmont alluvial plain**		**Mountain sides**	
		Rivers	Open plains (inter.)	Inter-fluves	Lower	Mid-to-Upper	Mid or Upper with stream mouth	Upper	Upper w/ springs	NA	NA		Drainage Lines	Plains (Inter-fluves)	Slopes	Drainage lines (rivers)
Wet Season-Wet Climate	Fruit	+	0	0	0	0	0	0	0			0	++++	+++	+?	+++
	Root-stocks	+	0	0	0	0	+++	0	+++			0	+	?	0	0
Dry Season-Dry Climate	Fruit	+	0	0	0	0	0	0	0			+	+++	+	0	+
	Root-stocks	0	0	0	0	0	+++	0	0 (if springs are dried up)			0	0	0	0	0

THIS STUDY	**Ser. Wood lands**	**Serengeti Peneplain**		**W. Lacus. Plain**	**Eastern Lacustrine Plain**								**Lacus Terrace**		**Major rock oucrops**	**Lower Alluvial Fans**		**Mountain sides**	
	rivers	rivers	Open plains (inter.)	Inter-fluves	Low-Mid-Upper		Upper		Low-Mid-Upper with springs				river	inter-fluve	NA	river	inter-fluve	NA	NA
					Stream-Fed		river	interfluve	Large Springs		Small Springs								
					dry land	wetland			wetland	dry land	wetland	dry land							
Fruit	+	+	+	+	0	0	++	+	0	+	0	+	++	+		++++	++		
USO	+	++	+	++	+	+++	++++	+++	++++	+	+++	+	++++	+++		++	+		
Seed/ pod	++	+++	++	++	+	+	++++	++++	+	+++	+	++	++++	++++		+	+		
Flowers	+	+++	++	+	+	+	++	++	+	+	+	++	++++	++++		++	+		
Leaf/ Shoot	+	+	+	+	+	0	+	++	+	+	+	+	+++	++		+++	+		
Stem	++	+++	++	+++	+	+	++	+++	+	+	+	++++	+++	+++		++	+		
Bark/ gum	+	++	+	++	0	0	++++	+++	0	++	0	0	++++	+++		+	++		

Table 6-4. Relative refuge tree abundance for lowermost Bed II, Olduvai as predicted by Peters & Blumenschine for a wet season, wet climate (1995&1996: Table 3a) and a dry season dry climate (1995&1996: Table 3b) versus the results of this study.

PETERS & BLUMENSCHINE		**Serengeti Peneplain**		**W. Lacus. Plain**	**Eastern Lacustrine Plain**					**Lacus. Terrace**		**Major rock oucrops**	**Piedmont alluvial plain**		**Mountain sides**	
		Rivers	Open plains (inter.)	Inter-fluves	Lower	Mid-to-Upper	Mid or Upper with stream mouth	Upper	Upper w/ springs	NA	NA		Drainage Lines	Plains (Inter-fluves)	Slopes	Drainage lines (rivers)
Wet Season-Wet Climate	Refuge travel	+	0	0	0	0	+	++	+?			0	+++	++	++	+++
	Refuge sleep	+	0	0	0	0	0	++	+?			0	+++	+	+?	+++
Dry Season-Dry Climate	Refuge travel	+	0	0	0	0	0	+++	+			+	+++	+	++	+++
	Refuge sleep	+	0	0	0	0	0	+++	+			0	+++	+	++	+++

THIS STUDY	**Ser. Wood lands**	**Serengeti Peneplain**		**W. Lacus. Plain**	**Eastern Lacustrine Plain**								**Lacus Terrace**		**Major rock oucrops**	**Lower Alluvial Fans**		**Mountain sides**	
	rivers	rivers	Open plains (inter.)	Inter-fluves	Low-Mid-Upper		Upper		Low-Mid-Upper with springs				river	inter-fluve	NA	river	inter-fluve	NA	NA
					Stream-Fed		river	interfluve	Large Springs		Small Springs								
					dry land	wetland			wetland	dry land	wetland	dry land							
Shade >3m	++++	++	+	+	NA	0	++++	++	0	NA	0	NA	++++	++++		++++	++++		
Sleep >10m	+	+	0	0	0	0	++++	+	0	+++	0	+	+	+		+++	+++		
Sleep >20m	+	+	0	0	0	0	+++	0	0	0	0	0	+	0		++	++		

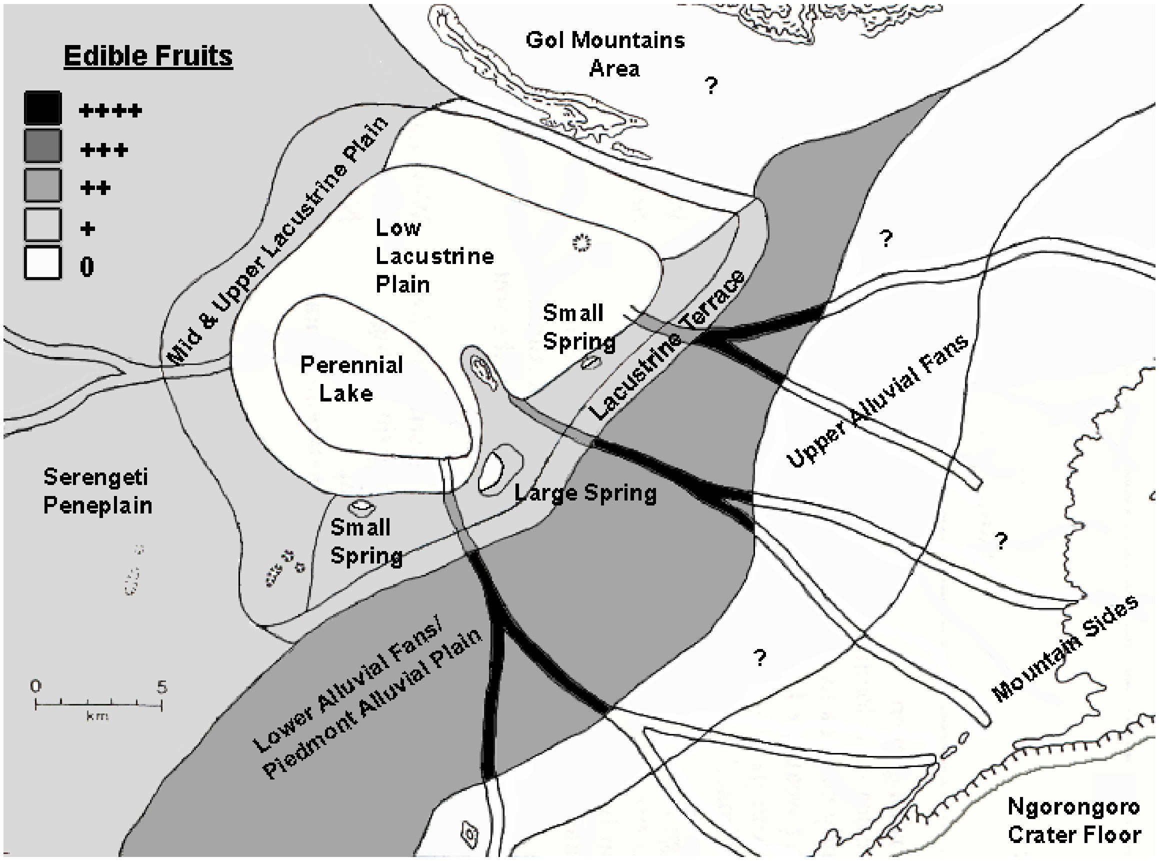
Peters and Blumenschine and myself are aligned vertically. In my study there are more landscape facets defined within the Eastern Lacustrine Plain zone because I divided large springs, small springs, and stream-fed wetland areas into “wetlands” and “dry lands” for sampling (see Chapter Three). I also have data on seven different edible plant parts, while Peters and Blumenschine modeled only fruits, rootstocks, traveling refuge, and sleeping refuge.

Plant Foods

The main features in Peters and Blumenschine’s plant food resource distribution models (1995: Table 3; 1996: Table 3; the top of Table 6-3) are abundant edible fruits in the piedmont alluvial plain and, for the wet season, wet climate, on the mountainsides. They also predict abundant edible rootstocks in the mid- and upper Lacustrine Plain wetlands (Table 6-3).

Whereas Peters and Blumenschine predicted that fruits were concentrated mainly in the piedmont alluvial plain and mountain sides, my model suggests the presence of edible fruits in low to moderate abundance within at least one landscape facet of each landscape association across the basin (Table 6-3 and Figure 6-1). In concordance with Peters and Blumenschine’s (1995) predictions, my model shows the highest concentration of fruits along the drainage lines of the lower alluvial fan, with moderately high abundance across the lower alluvial fan interfluves. Edible fruits of the lacustrine terrace and upper Lacustrine Plains are more concentrated along streams, and those fruits derive mostly from shrubs. I predict a low overall abundance of edible fruits in the

Figure 6-1. Hypothetical distribution of edible fruits for hominins across the lowermost Bed II, Olduvai paleolandscape, from least abundant (0) to most abundant (++++). Based on the modern analog results from Manyara, Serengeti, and Ngorongoro (Figure 5-12).



Serengeti peneplain from sparsely scattered shrubs and forbs, and rare fruit-bearing trees near the rivers.

The general pattern of edible underground parts is quite different from that of edible fruits. My analysis includes all edible underground parts such as tubers, rootstocks, bulbs, and roots, while Peters and Blumenschine's model only referred to rootstocks. In agreement with Peters and Blumenschine, my model predicts a high abundance of edible underground parts from marsh plants within the spring- or stream-fed wetlands of the

Lacustrine Plain (Table 6-3). As shown in the map of edible underground part distribution (Figure 6-2), I also predict a high abundance of edible underground parts in the form of roots from shrubs across the upper Lacustrine Plain and lacustrine terrace, and low but persistent abundance of edible roots across the lower alluvial fans. The species from the modern analog sites with edible underground parts are listed in Table 6-5.

Figure 6-2. Hypothetical distribution of edible underground storage organs (USOs) for hominins across the lowermost Bed II, Olduvai paleolandscape, from least abundant (0) to most abundant (++++). Based on the modern analog results from Manyara, Serengeti, and Ngorongoro (Figure 5-12).

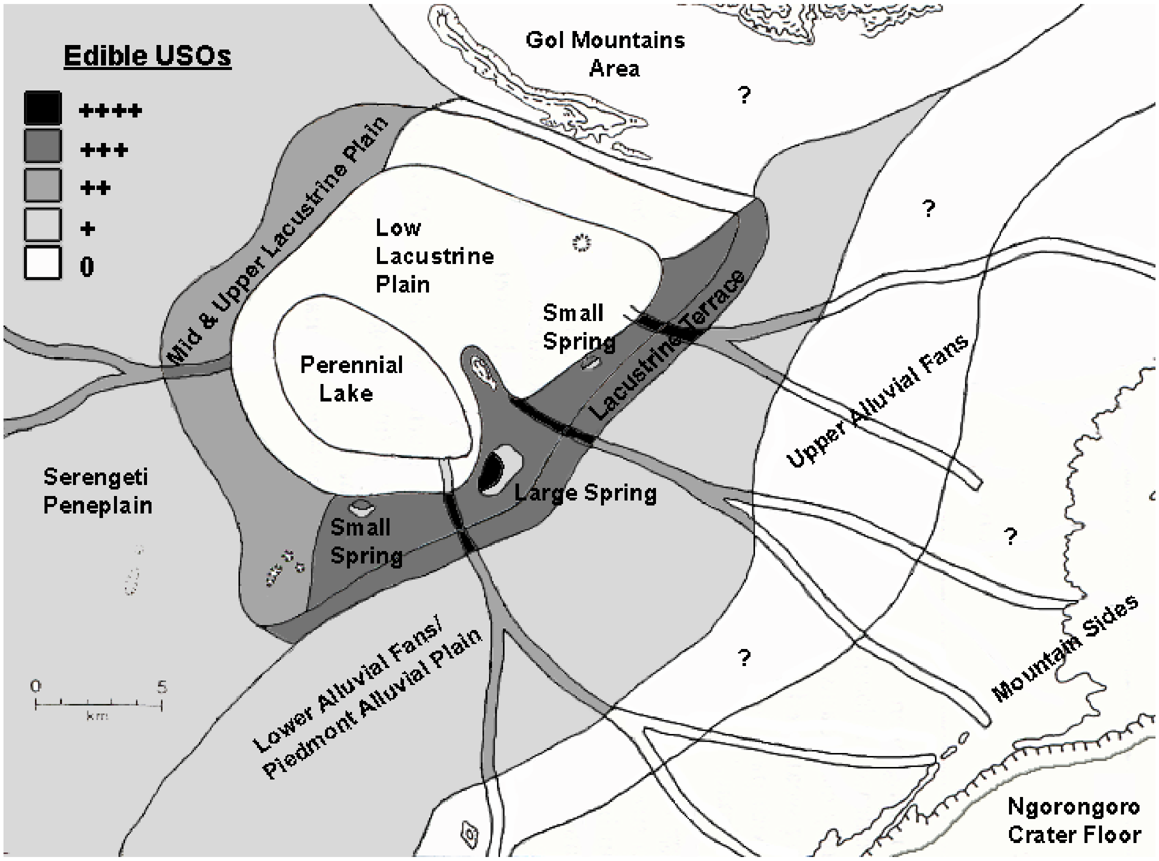
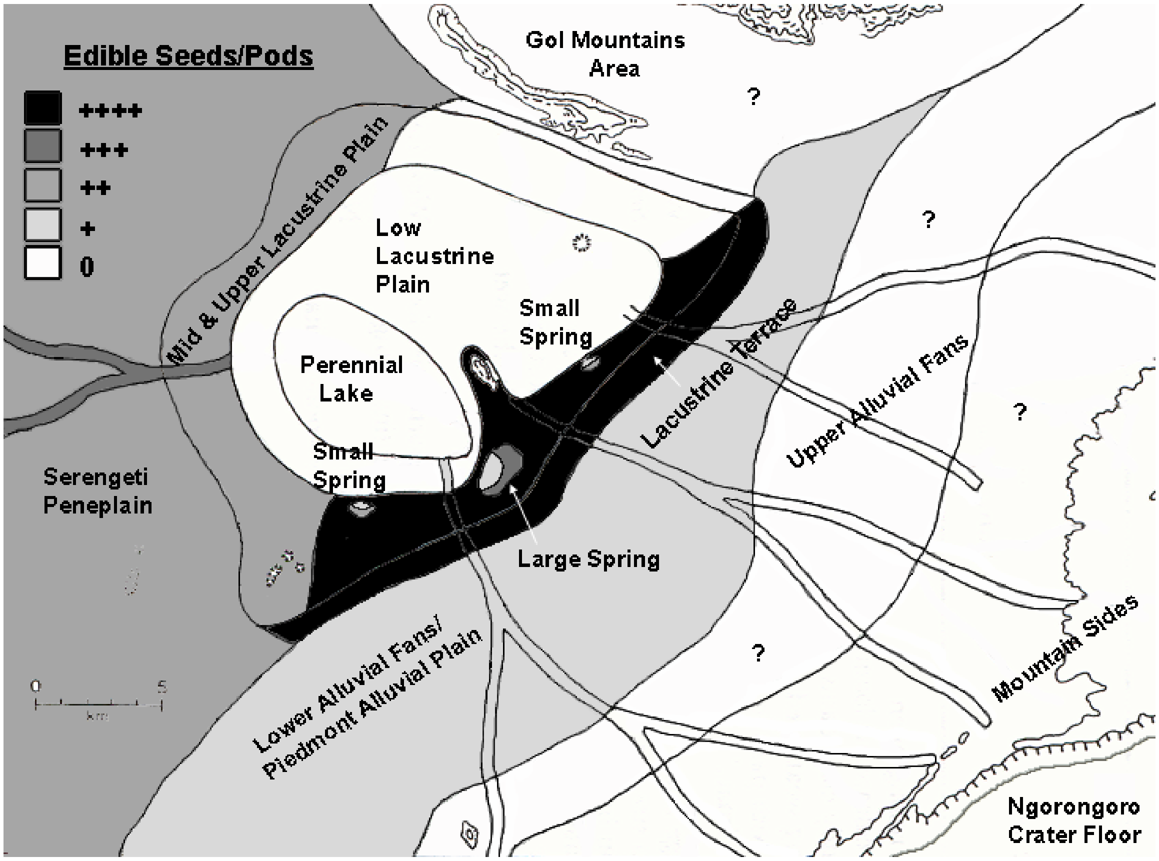


Table 6-5. All species from the modern study areas with edible underground parts. References for Notes on Edibility are in Peters *et al*. (1992).

Family	**Species**	**Notes on Edibility**
Anacardiaceae	*Lannea triphylla*	Humans eat root raw.
Apocynaceae	*Carissa edulis*	Humans eat fruit raw and root boiled.
Asclepiadaceae	*Stathmostelma pedunculatum*	Humans eat tap root (eaten by children).
Asparagaceae	*Protasparagus africanus*	Humans eat young shoot and root.
Boraginaceae	*Cordia sinensis*	Humans eat fruit and root raw. Baboons eat fruit.
Burseraceae	*Commiphora africana*	Humans eat root pith raw; long tuberous roots chewed for sweet juicy sap; sapling roots.
Capparaceae	*Boscia salicifolia*	Humans eat leaf, bark, and root.
	Maerua triphylla	Humans eat fruit "(may be poisonous)" and root "(may be poisonous)".
	Thilachium africanum	Humans eat tuberous root "(toxic; famine food)". Baboons eat flower and flower bud.
Convolvulaceae	*Ipomoea sinensis*	Humans eat leaf, shoot, and root. Baboons eat fruit capsule and flower bud.
Cyperaceae	*Cyperus immensus*	Baboons eat rhizome (bulb).
	Cyperus laevigatus	Baboons eat stem base (bulb).
	Cyperus rotundus	Humans eat rhizome (bulb) raw. Baboons eat root.
	Cyperus usitatus	Humans eat bulbs raw. Baboons eat bulbs raw.
	Kyllinga alba (Cyperus alatus?)	Baboons eat stem base (bulb).
Gramineae	*Brachiaria deflexa*	Baboons eat grain, young leaf, and tiller.
	Cynodon dactylon	Baboons eat whole plant.
	Cynodon plectostachyus	Baboons eat whole plant.
	Dactyloctenium aegyptium	Humans eat grain and rhizome raw.
	Digitaria velutina	Humans eat whole plant.
	Heteropogon contortus	Baboons eat tiller.
	Sporobolus consimilis	Baboons eat grain, leaf, and rhizome.
	Urochloa mosambicensis	Baboons eat grain and tiller.
Leguminosae (Papilionoideae)	*Indigofera arrecta*	Humans: root is edible.
	Tephrosia purpurea	Humans eat root (flavoring).
	Vigna vexillata	Humans eat pod, leaf, and tuber (water source). Baboons eat pod, seed, flower, flower bud, tuber.
Nyctaginaceae	*Boerhavia diffusa*	Humans eat seed, leaf (potherb), and root.
Polygonaceae	*Persicaria senegalensis*	Humans eat leaf and onion-like tuber.
Typhaceae	*Typha latifolia*	Humans eat flower and rhizome.

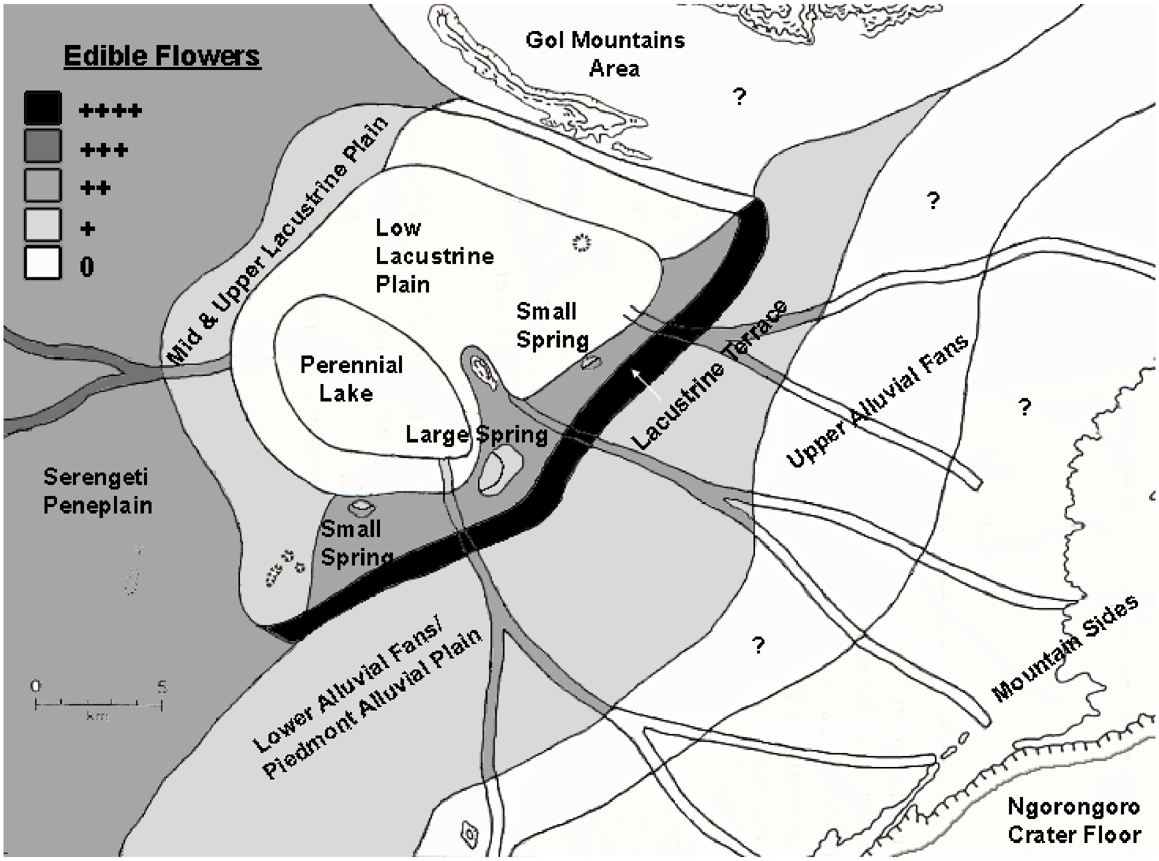
Edible seeds/pods show another unique pattern of abundance across the paleo-Olduvai basin (Table 6-3, Figure 6-3). Edible seeds/pods occur in very high abundance across the lacustrine terrace and upper Lacustrine Plain. They are also abundant at dry lands adjacent to small and large springs and along rivers of the Serengeti peneplain. They occur in moderate abundance across the large interfluvial areas of the Serengeti peneplain.

Figure 6-3. Hypothetical distribution of edible seeds and pods for hominins across the lowermost Bed II, Olduvai paleolandscape, from least abundant (0) to most abundant (++++). Based on the modern analog results from Manyara, Serengeti, and Ngorongoro (Figure 5-12).



The seeds/pods in the modern analog sites come mainly from two distinct sources: *Acacia* trees and grass species. In the map shown in Figure 6-3, most of the edible seeds/pods in the lacustrine terrace, upper Lacustrine Plain, and Serengeti peneplain rivers would derive from *Acacia* trees. On the other hand, grass seeds are predicted to provide the main source of edible seeds/pods for the Serengeti peneplain interfluves and the dry lands near springs and the upper Lacustrine Plain.

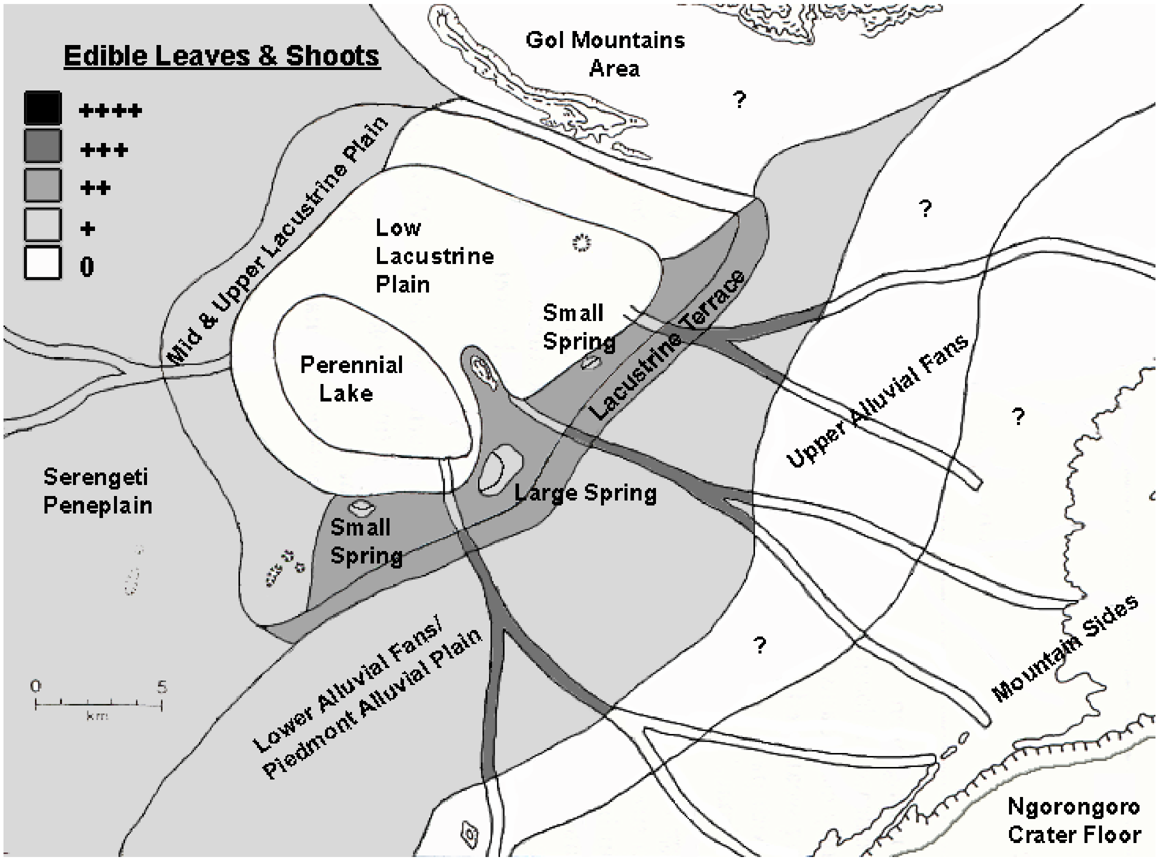
Figure 6-4. Hypothetical distribution of edible flowers for hominins across the lowermost Bed II, Olduvai paleolandscape, from least abundant (0) to most abundant (++++). Based on the modern analog results from Manyara, Serengeti, and Ngorongoro (Figure 5-12).



Modern people consider *Acacia tortilis* pods “famine foods”, and even baboons will only rarely eat *Acacia xanthophloea* seeds/pods. Grass seeds are nutritious but can be energetically expensive to process. These factors must be taken into consideration when modeling hominin land use.

The remaining edible parts in Table 6-3, flowers, leaves/shoots, stems, and bark/gum/cambium, show a general pattern of low abundance in the low-mid Lacustrine

Figure 6-5. Hypothetical distribution of edible leaves and shoots for hominins across the lowermost Bed II, Olduvai paleolandscape, from least abundant (0) to most abundant (++++). Based on the modern analog results from Manyara, Serengeti, and Ngorongoro (Figure 5-12).



Plain wetlands, and higher abundance in both western and eastern portions of the basin away from the lake. The lacustrine terrace has particularly high concentrations of those edible parts in both riverine and interfluvial landscape facets. The distribution of edible flowers is depicted in the map in Figure 6-4, showing moderate contrast between landscape facets with the exception of the lacustrine terrace which has very high abundance compared to the surrounding landscape units. Edible leaves, mapped in Figure 6-5, in general are more evenly distributed across the paleo-Olduvai basin landscape facets, but do occur in high abundance along rivers of the lower alluvial fan.

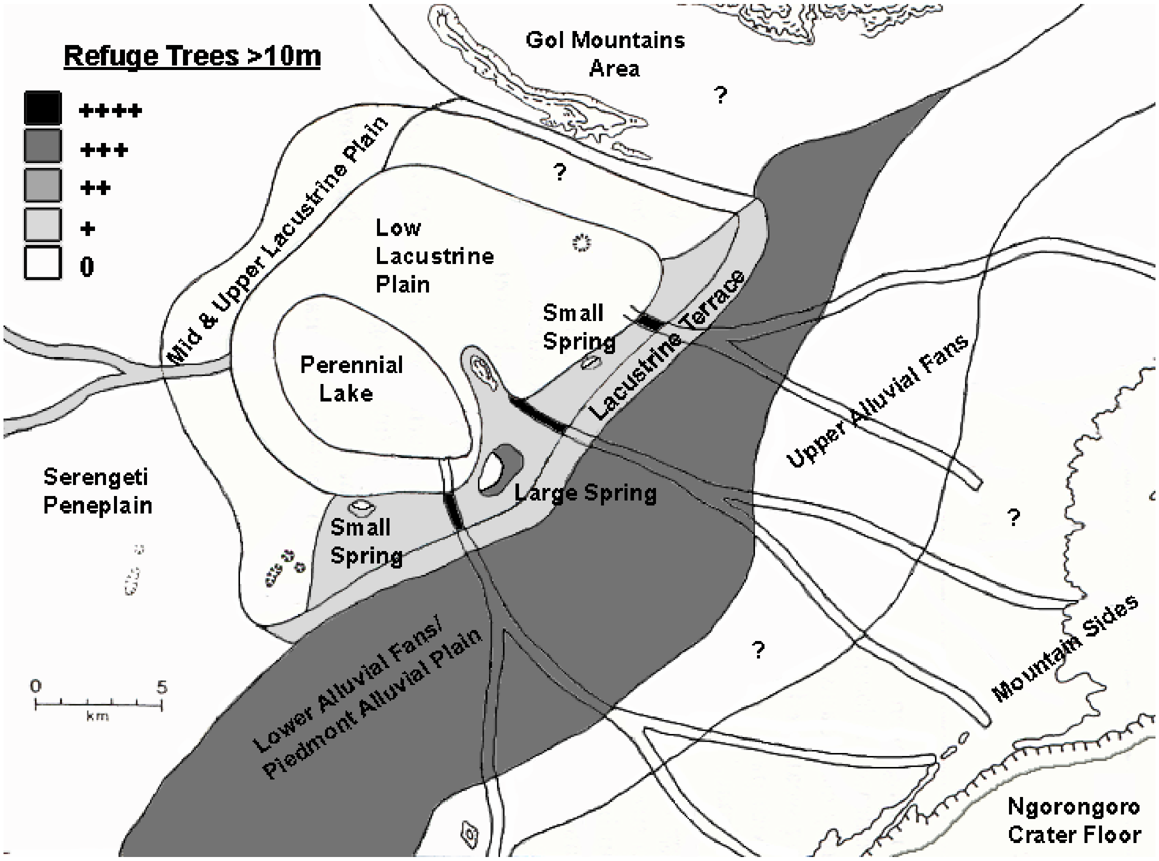
Arboreal Refuge

My model of relative refuge tree abundance includes three types of "refuge" as described in Chapter Five: shade (shrubs or trees > 3m tall), trees for sleeping (> 10m tall), and very tall trees for sleeping (> 20m tall). Peters and Blumenschine (1995; 1996) predicted arboreal refuge availability in two categories, "for sleeping" and "while traveling" (Table 6-4). Their model shows both types of refuge to be highest in the mountains and piedmont alluvial plain, particularly along drainages, and in the upper Eastern Lacustrine Plain. They predicted a low availability of sleeping and travel refuge along rivers of the Serengeti Peneplain.

In my model, shade in the western basin can be found in sparse patches interspersed with open plains away from the lake, and in abundance as far west as the Serengeti Woodland (Table 6-4). In the eastern basin, there is much shade to be found in the upper Lacustrine Plain and in other landscape facets further east and south, away from the lake.

The distribution of sleeping trees greater than ten meters tall are modeled on the map in Figure 6-6. High densities of sleeping trees occur along rivers in the upper Lacustrine Plain, near the eastern lake shore at large springs, and in the lower alluvial fans. There is no sleeping refuge in the low Lacustrine Plain, and in the Serengeti peneplain sleeping trees occur only along rivers. High concentrations of sleeping refuge trees in the upper alluvial fans and mountain sides is likely, but since I did not study any

Figure 6-6. Hypothetical distribution of refuge trees greater than 10 meters tall for hominins across the lowermost Bed II, Olduvai paleolandscape, from least abundant (0) to most abundant (++++). Based on the modern analog results from Manyara, Serengeti, and Ngorongoro (Figure 5-19).



modern analogs of these landscape associations, they are not modeled in the figure. Potential sleeping trees taller than 20 meters show a similar pattern to the >10 meter trees, with reduced overall density (Table 6-4).

The sleeping refuge at a large spring on the Lacustrine Plain such as that depicted in Figure 6-6 would likely occur as an isolated patch, possibly surrounded on all sides by open, nearly treeless habitat. On the upper Lacustrine Plain, perennial rivers might be densely lined with trees like the modern Mkindu at Manyara, but in that modern analog the landscape facet is linear, very narrow, and composed of thorn trees that might not make good sleeping places. In addition, the upper Lacustrine Plain rivers are surrounded by grassland with only scattered bushes and trees. The population density of elephants and other large animals can affect the character of *Acacia xanthophloea* forests or woodlands (Pellew, 1983). In general, more large animals mean that the underbrush is cleared, and the knobby tree trunks that form from repeated bark stripping are easier to climb. In this and other ways, the herbivore population can affect the nature of the vegetation and should ultimately be incorporated into models of vegetation reconstruction.

According to the Lake Manyara model, the lacustrine terrace does have sleeping trees, but they are well spaced across the landscape facets with minimal overlapping canopy. Hominins there would be more visible to and vulnerable to nocturnal predators than in more densely forested areas. The lower alluvial fans would probably offer the best sleeping refuge option for hominins given the choices in this model (Figure 6-6). The trees are dense throughout that landscape facet, both along rivers and away from rivers, and often trees have overlapping canopies that would provide arboreal escape routes for hominins. The diversity of tree types there is also greater, and the trees tend to be non-thorny with large, perhaps more easily climbable trunks and limbs.

Summary of plant resource distribution

My modern analog results, as applied to the paleo-Olduvai basin, lend themselves to a grouping of the basin into three major areas, each of which has a characteristic and unique suite of plant resources. First is the lower alluvial fans, where along the rivers are the highest concentrations of edible fruits and leaves/shoots, two very important plant food types for primates in general. The alluvial fans also provide the largest area of a continuous concentration of sleeping refuge trees in the parts of the basin that were modeled. Second is the lacustrine terrace and upper Lacustrine Plain on the southeastern side of the lake, including stream-fed and spring wetlands and adjacent dry lands, interfluves, and rivers. Those land facets support the highest concentrations of edible underground parts, seeds/pods, and flowers, in addition to localized patches of sleeping refuge near large springs and along some rivers. The third major area is the western basin, including the (poorly understood) Western Lacustrine Plains and the vast Serengeti peneplain. Modern analogs suggest that there was a moderate, widespread availability of edible grass seeds and edible flowers in this area, particularly along the rivers. Sleeping refuge trees were few in the western basin, unless the rivers were more well-watered than suggested by modern analogs, and in that case would provide sleeping refuge trees.

At a scale that is slightly broader than that of landscape associations, there is an interesting juxtaposition of vegetation resources for hominins across the paleo-Olduvai basin. Edible fruits, leaves/shoots, and sleeping refuge trees are concentrated mainly in the lower alluvial fans to the east and south of the lake, while edible seeds/pods and edible USO's are concentrated in the lacustrine terrace and upper Lacustrine Plains adjacent to the eastern lake shore. The western basin is characterized by relatively low abundances of all plant resources in general, with the exception of widespread grass seeds and edible flowers.

Longer-term variations in climate, landscape facets, and plant resources

The distribution of some landscape facets would have changed across the lowermost Bed II paleolandscape over thousands of years with climatic changes, such as cyclical variations due to the earth's orbit, or Milankovitch cycles. The stratigraphy within lowermost Bed II records multiple expansions and contractions of the lake, generally reflecting periods of wetter and drier climate. The lake level fluctuations are represented in the Eastern lake margin by alternating strata of waxy and earthy claystones (Hay, 1996; Deocampo *et al*., 2002), in the lowest alluvial fans by the presence of clay lake deposits near the base and near the top of two sections (Ashley and Driese, 2000), and in the central basin of paleo-lake Olduvai by changes in ultrafine clay chemistry as represented by the octahedral cation index (Deocampo, 2004a). At a regional scale, the faulting that occurred with the rifting in East Africa also may have caused shifts in lake levels during the deposition of lowermost Bed II (Hay, 1996).

How would the landscape facets have changed from times of lowest lake level to times of highest? The distribution of paleolandscape facets as shown in Figure 2-7 represents the landscape during a dry period in which the lower Lacustrine Plain is flooded in some years, but the upper Lacustrine Plain is rarely flooded. This drier climate is the situation that I have modeled for most of this thesis. During wet phases, the lake extended to its maximum size (shown as the upper boundary of the upper Lacustrine Plain in Figure 2-7) for several hundred years at a time or more (Hay, 1976). Deocampo (2004a) estimated based on sedimentation rates (following Hay and Kyser, 2001) that at Locality 49, which is near the center of the lake, the two meters of deposits above Tuff IF and below a disconformity represent about 18,000 years. The first 10,000 years were a period of very high lake stand, followed by 4,000 years of lower lake stand when the Eastern Lake Margin would have been exposed. The final 4,000 years were also a period of high lake stand. Thus, during the deposition of lowermost Bed II, the Eastern Lake Margin may have only been exposed for use by hominins and accumulation of artifacts for a small portion of time.

During a wetter climate, the lake would have become larger, but I argue that the catena of landscape facets would not have simply shifted together to higher elevations. The lithology differs across the basin and vegetation that prefers one type of soil may not be able to grow in a soil derived from a different type of lithology. Lake deposits from lowermost Bed II, Olduvai are about 90% claystone, 5% sandstone, and 5% tuff (Hay, 1976: 67). Eastern lake margin deposits are fairly similar with 82% claystone and 15% tuff. The alluvial fan deposits in the east, however, are 89% tephra deposits such as reworked tuffs and lapilli tuffs, only 6% claystone, and 4% conglomerate (Hay, 1976: 73). The types of vegetation that grew in the clayey lake margin zone likely would not have fared well on the tuffaceous soils of the lower alluvial fans. Therefore, the Lacustrine Plain and its vegetation probably shrank to a very narrow zone during periods of lake expansion. Within the alluvial fans, only the vegetation of the lowermost fans would have been affected directly by the periodic inundation of saline-alkaline lake waters. Otherwise, alluvial fan vegetation probably did not shift to higher elevations during periods of lake expansion. Higher groundwater tables during wet periods may have altered the vegetation composition of the alluvial fans by favoring the growth of vegetation that prefers moister habitats, such as the trees of Manyara's groundwater forest. The rivers crossing the alluvial fans may have become larger and/or more perennial in a wet climate due to higher rainfall in the highlands, with subsequent expansion of riverine forest extent and density.

How would plant resources for hominins have changed from times of dry climate to times of wetter climate? The Eastern Lake Margin is the most well-studied and archaeologically rich area of lowermost Bed II. Clay geochemistry suggests that when this area was exposed at times of low lake level, there was a concentration of freshwater in the vicinity of HWK-E, grading to more saline-alkaline conditions both east toward Long K and west toward FLK-NN (Deocampo *et al*., 2002). Deocampo (2004b) has found that in modern Ngorongoro Crater, wetland areas with marsh vegetation maintain freshwater conditions while surrounded by saline-alkaline soils. It is likely that within the exposed Eastern Lake Margin zone, a marshy wetland existed in the area of HWK-E and freshwater conditions persisted long enough to alter the clay chemistry from its original saline/alkaline signature when the clays were deposited under a high lake stand (Deocampo *et al*., 2002). This area may have been maintained by a freshwater spring or by a concentration of surface water runoff from the eastern highlands (a stream-fed wetland).

In previous sections I have discussed how the Lacustrine Plain and lacustrine terrace facets provide the highest concentrations of edible underground parts from shrub roots and the rootstocks of marsh plants. These areas also provide the most edible seeds from *Acacia* trees and from grasses. Spring woodlands have also been modeled as likely places for scavenging opportunities for hominins (Peters and Blumenschine, 1996). During wet climate phases, the Eastern Lake Margin area was inundated with saline-alkaline lake waters and the Lacustrine Plain zone was probably reduced to a very narrow band, while the lacustrine terrace at times disappeared altogether. This would have substantially reduced the availability of edible underground parts and seeds for hominins, at least in the eastern and southeastern portions of the Olduvai basin. Tree fruits and refuge would still be available in the alluvial fans during wet climates, perhaps in greater abundance than during dry climates due to higher groundwater tables and denser riverine forests. In sum, the availability of edible underground parts, seeds, and possibly scavenging opportunities for hominins would have been much reduced during wet climate phases, although fruits may have been more abundant at those times.

Modeling Hominin Land Use

The models of plant food parts and arboreal refuge distribution can be used to partially reconstruct potential hominin land use patterns across the lowermost Bed II Olduvai basin for hominins with specific ecological characteristics. Peters and Blumenschine (1995; 1996) modeled hominin land use for a fruit- and root-eating hominin versus a scavenging, fruit and root eating hominin. They defined major corridors and patches of hominin affordances across the paleo-Olduvai basin, and differentiated resource availability between wet and dry seasons and between wet and dry climate periods.

Since my study deals only with plant foods and refuge trees, and not explicitly with the distribution of animal foods or hazards, here I focus on potential differences between land-use for hominins with different plant food diets, such as a mainly fruit-eating hominins versus those that might have focused on seeds/pods or underground parts. I also consider a more generalized, omnivorous hominin that ate all available plant foods, and considerable amounts of animal foods. The main reconstructions represent a phase of relatively dry climate during which all of the landscape facets as shown in Figure 2-7 were exposed, but I also discuss some aspects how wet climate phases might have differed.

I will consider first a hominin with a chimpanzee-like diet that focused mainly on fruits, and was mainly vegetarian. Such an animal would spend most of its time on the eastern and southern sides of the basin foraging along the rivers of the lower alluvial fan for fruits (Figure 6-1). It would also find fruits in the lower alluvial fan interfluves, along the rivers of the upper Lacustrine Plain, and in the lacustrine terrace. Edible leaves/shoots are also most abundant along the lower alluvial fan rivers, and these would supplement the fruits. In times of dry climate and low lake levels, forays to the spring wetlands of the upper Lacustrine Plain might be made during the dry season to exploit rhizomes and bulbs of marsh plants. During periods of wetter climate, a mainly frugivorous hominin would still find abundant foods in the alluvial fans, especially along the rivers and during the rainy season. This scenario is similar to that of Peters and Blumenschine's (1995; 1996) fruit- and root-eating hominin, or frugi-rootivore.

In contrast, a hominin that focused particularly on edible underground parts would need to spend the majority of its time in the upper Lacustrine Plain and lacustrine terrace. The highest abundance of these foods was in the eastern and southern portions of the basin. During periods of dry climate and low lake levels, nutritious edible rootstocks would be almost a guaranteed source of food at the marshes associated with springs or stream-fed wetlands in the Eastern Lake Margin. Underground roots from shrubs would also have been available in the upper Lacustrine Plain and lacustrine terrace. The edible roots of shrubs and herbs might have become more accessible with the use of digging implements, such as digging sticks.

It is possible that some hominin species depended largely on edible seeds/pods for their nutrients, including grass seeds (e.g., Jolly, 1970). As seen in Figure 6-3, seed and pod foods are concentrated in the lacustrine terrace and Eastern Lacustrine Plain, while lower, widespread abundance occurs in the western upper Lacustrine Plain and Serengeti peneplain. This hypothetical hominin might be thought of as having a baboon-like diet. For example, the baboons at Amboseli National Park in Kenya live in a near-lake habitat similar to that being reconstructed here for lowermost Bed II Olduvai (Altmann and Altmann, 1970). Those baboons subsist mainly on grasses and *Acacia* trees (*Acacia xanthophloea* and *Acacia tortilis*) for their sustenance. Hominins that focused on eating actual grass seeds might have found densities of nutritious grass seeds in the upper and lower Lacustrine Plains of the lake, such as the nutritious grasses that occur near modern lakes Nakuru, Makat (in Ngorongoro Crater), and Manyara (Marean and Ehrhardt, 1995). More plentiful grasses were available in the vast Serengeti Peneplains in the western side of the basin. Of course, the lack of refuge trees in the Serengeti Peneplains, and the probable abundance of large predators, might discourage grass-eating hominins from spending too much time there, at least very far from tree-lined rivers. During wet climate phases, a hominin specializing in a seed/pod diet would have little to attract it to the Olduvai basin because the Lacustrine Plains and lacustrine terrace would be inundated with the lake, and the main foods of the alluvial fans are fruits and leaves.

Perhaps a more credible type of hominin is one that was very generalized in terms of the types of plant foods it exploited. In that case, the hominin would probably spend the wet season in the alluvial fan areas feeding on fruits and leaves. The seeds/pods available in the lacustrine terrace and upper Lacustrine Plain were probably low on the list of favored foods, since the seeds/pods of *Acacia* trees tend to be high in tannins and phenolics as opposed to most easily digestible ripe fruits (Wrangham and Waterman, 1981; Hausfater and Bearce, 1976). On the other hand, edible marsh rootstocks and bulbs tend to be easily acquired and digestible (Conklin-Brittain *et al*., 2002), so during times of low lake level, trips to the spring woodlands and marshes of the upper Lacustrine Plain would have provided almost guaranteed food even during sparse dry seasons. Animal foods might have included termites, tortoises, and eggs at a minimum. Hominins with stone tools, which we know existed at Olduvai, also may have had significant contributions to their diets from larger mammals, perhaps through scavenging. This food source could have been particularly important during the dry season, when many plant foods are scarce.

Peters and Blumenschine's scavenging/plant food-eating hominin (carno-frugi-rootivore) also focuses on the rivers of the piedmont alluvial plain, but in general uses more of the basin than the vegetarian hominin, visiting sites not otherwise visited in order to look for scavenging opportunities. It traverses interfluves more often, and ventures into the upper Olmoti alluvial fan, the western side of the basin (for raw material), and forages in the upper Lacustrine Plain for rootstocks and carcasses during the dry season.

The main difference I would predict between a large mammal-consuming (scavenging) and mostly vegetarian (non-scavenging) hominin during periods of dry climate and low lake levels is the scavenging hominin's more frequent use of the Serengeti peneplain and Western Lacustrine Plain, and perhaps more extended or frequent forays into the Eastern Lacustrine Plain. Scavenging opportunities are more likely to occur in wooded areas adjacent to open grasslands where grazing animals dominate (Blumenschine, 1986), and open grasslands were probably most abundant in the Serengeti peneplain, Western Lacustrine Plain, and Eastern Lacustrine Plain. If there were a perennial river entering the basin from the western side, then that river might be lined with a taller, thicker, and more diverse riverine forest that could provide substantial plant foods and drinking water. In the Eastern Lacustrine Plain, the large spring wooded "islands" might be ideal focal points for scavenging hominins; from there they could have vantage points of the nearby grasslands and its carnivores, plus plant foods from the trees and shrubs and plenty of edible USO's from the marsh plants. During periods of wet climate and very high lake levels, dry season foods such as the marsh USO's, *Acacia* seeds/pods, and possibly scavenging opportunities on the Eastern Lacustrine Plain would not have been available because of the high lake levels. Grasslands may have existed in the western portion of the basin, perhaps making it a better place for scavenging opportunities during periods of wet climate.

In sum, hominins living at least part of the time in the Olduvai basin would probably have had to take advantage of any feeding opportunities they could, because the modern analogs suggest that compared to forests or miombo woodlands (e.g., Suzuki, 1969; Wrangham, 1977), only limited plant foods are available for large-bodied primates in semiarid savannas. Perhaps only a hominin with a specialized gut morphology and/or masticatory system, such as a robust australopithecine, would have been able to subsist on the seeds/pods that were abundant on the lacustrine terrace and upper Lacustrine Plain during dry climate phases. Many *Acacia* seeds/pods are considered inedible by modern humans, especially when uncooked. If a hominin could subsist on *Acacia* seeds/pods, then it might not need to venture much further from the wooded ring (or partial ring) of upper Lacustrine Plain and lacustrine terrace around the lake. A hominin with a more human-like gut, unable to process the harsh leaves and other foods eaten by baboons, for example, would have had to focus on fruits and underground parts, and probably a significant contribution from animal foods. This might cause it to have a larger ranging area in order to collect both fruits from the alluvial fans, roots and scavengeable carcasses from the upper Lacustrine Plain and lacustrine terrace, and raw materials from the western side of the basin.

During phases of wetter climate when the Olduvai lake was at its maximum expansion, the Lacustrine Plains with their marshes and *Acacia xanthophloea*-lined streams were substantially reduced, if they did not disappear altogether. In some cases the lake may also have inundated the *Acacia tortilis*-dominated lacustrine terrace. Overall this situation would substantially reduce the variety of edible plant foods available to hominins. A hominin specializing in *Acacia* pods, grass seeds, or rootstocks would not find much food available at Olduvai during wet climate phases. A hominin focusing on fruits would still find the tree fruits of the alluvial fans during the wet seasons of wet climates, and perhaps a small amount of marsh exposed during dry seasons. For a generalist hominin, however, drier climatic phases would have made the Olduvai basin more appealing due to the more diverse and abundant plant food types.

Archaeological Predictions

Blumenschine and Peters (1998) outline a methodology by which the archaeological record can be used to test hominin land use models. The approach depends on hominin behaviors being "linked predictively to their material traces by causal ecological mechanisms related to the ecostructure of specified landscape facets" (Blumenschine and Peters, 1998: 570). The key components to this methodology are: (1) The affordances in a landscape facet ultimately determine the behavioral residues produced there. (2) The contrast in affordances among adjacent landscape facets determines our ability to discriminate the nature of hominin-affordance interactions via stone artifact and bone traces. (3) The causal mechanisms between hominin behaviors and the stone and bone traces of those behaviors must be known. This refers not to the simple physical or mechanical linkages that connect marks on bones with the stroke of a tooth or a stone tool, but to the broader and less clearly defined ecologically based linkages that connect landscape ecostructure to hominin behavioral residues.

Blumenschine and Peters (1998) use the cover abundance of trees and shrubs, representative of ecostructure, and the effect of that on levels of competition for larger mammal carcasses, or scavenging affordances, as the major conceptual linkage that connects landscapes to trace fossils of hominin behavior. They focus on larger mammal scavenging and predation risk to hominins as the most important factors immediately affecting hominin archaeological residues. Most bone and stone tool artifact residues are the result of hominins consuming larger mammal carcasses. There are a few potential archaeological residues that are predicted to relate to wood chopping and nut pounding, but other behaviors of hominins, such as consuming plant foods without tools, no matter how important, are unfortunately invisible in the archaeological record.

Blumenschine and Peters (1998:571) predicted bone and stone archaeological signatures for 11 out of 17 of their proposed landscape facets of the lowermost Bed II paleo-landscape, based mainly on the degree of tree and shrub cover and proximity of refuge trees in those landscape facets. Since their ideas of the ecostructure in those landscape facets were hypothetical, idealized, and based only on their own casual, qualitative (as opposed to quantitative) experiences in modern habitats, here I present my quantitative data from modern analog landscape facets analogous with those hypothetical ones at Olduvai, and compare my tree and shrub cover values with those predicted by Blumenschine and Peters. Throughout this exercise I am modeling the paleo-Olduvai basin during times of relatively dry climate, when the facets of the Eastern Lake Margin are not inundated year-round with lake waters. Finally, I discuss how my results change Blumenschine and Peters' predicted archaeological signatures for bones and stones in specific landscape facets.

Physiognomy and Refuge Trees in the Lowermost Bed II Olduvai Paleolandscape

In my quantitative study of modern habitats, I collected information on physiognomic structure, including tree cover, shrub cover, and tree density, as presented in Chapters Four and Five. These results are directly comparable to Blumenschine and Peters' (1998) models of tree and shrub cover for various paleo-landscape facets at Olduvai, which they base on their earlier characterizations of the basin within a landscape classification system (Peters and Blumenschine 1995, 1996). In Table 6-6, I compare my analog results with those of Blumenschine and Peters (1998). Table 6-7 shows the key categories of cover abundance and density/spacing of refuge trees used in Table 6-6.

For the Western Lacustrine Plain, my results differ somewhat from Blumenschine and Peters' (1998). These differences stem in part from new field evidence for the presence of streams crossing the western lake margin during Bed I times (Blumenschine *et al*., 2003), and the possibility of similar streams being present during lowermost Bed II times. This suggests more fresh water available in general in the western basin in a groundwater table and/or on the surface. Rather than having lowest and very low tree and shrub cover, I predicted that the Western Lacustrine Plain interfluves would range from lowest to moderate tree and shrub cover. I predicted that streams of the Serengeti peneplain probably ranged all the way from low to high tree and shrub cover, depending on whether they were perennial, their size, and the amount of water they carried both on the surface and underground.

For the Eastern Lacustrine Plain my results differ from Blumenschine and Peters regarding canopy cover near springs. Modern analogs for small springs show that some support high or very high tree and shrub cover, while others have no trees and shrubs.

Table 6-6. Tree cover, shrub cover, and arboreal refuge density for lowermost Bed II paleo-Olduvai basin based on Blumenschine & Peter's (1998) Table 1 (B&P) versus the findings of this study (C).

Landscape Association	**Facet**	**Item**	**Blumenschine & Peters, 1998**	**This Study** % cover and climbable density/ha trees	**Modern Analogs**
Serengeti Peneplain	B&P: Interfluve (wet season) C: Interfluve	Tree cover	Very low (0/1/r>+)	Lowest (0)	E. & W. Serengeti Plain Interfluves: Barafu Plain Nyamara Interfluve Seronera-Wandamu Interfluve
		Shrub cover	Very low (0/r)	Lowest-Low (0/1)	
		Climbable tree density	100s of meters apart	0,0,0 Nil	
Serengeti Peneplain	B&P: Stream C: Rivers	Tree cover	Low (1/+/r>0)	Moderate,High (2,3)	E., W. Serengeti Plain Rivers: Barafu R. Seronera R. Nyamara R. Serengeti Woodland Rivers: Mbalageti R. Sangare R.
		Shrub cover	Low (1/+/r>0)	Moderate (2)	
		Climbable tree density	10s of meters apart	10s of meters apart	
Western Lacustrine Plain	B&P: Interfluve (wet season) C: Interfluve	Tree cover	Lowest (0)	Lowest,Low,Moderate (0,1,2)	Manyara lacustrine plain interfluves: Ndala Lake Flat Msasa Lake Flat Ngorongoro lacustrine plain stream-fed dry land Gorigor Midwest Gorigor North Munge Marsh Munge River
		Shrub cover	Very low (0/r)	Lowest,Low,Moderate (0,1,2)	
		Climbable tree density	Nil	Nil to 20-30 m apart	
Eastern Lacustrine Plain	B&P: Uppermost lacustrine plain, lake flat/Interfluves. C: upper lacustrine plain interfluves	Tree cover	Moderate (2-4)	Low,Moderate (1,2)	Manyara upper lacustrine plain interfluves: Ndala Lake Flat Msasa Lake Flat
		Shrub cover	Lowest-Low (0/r/1)	Low,Moderate (1,2)	
		Climbable tree density	? (Nil except in uppermost plain woodland)	20-30 m apart	

Landscape Association	**Facet**	**Item**	**Blumenschine & Peters, 1998**	**This Study** % cover and climbable density/ha trees	**Modern Analogs**
Eastern Lacustrine Plain	B&P: Small Stream (lowermost Msasa-like) C: stream-fed wetland	Tree cover	Lowest (0)	Lowest (0)	Ngorongoro Stream-fed wetlands: Munge Marsh Munge River Gorigor Midwest Gorigor North Gorigor West
		Shrub cover	Very low (r/0)	Lowest (0)	
		Climbable tree density	Nil	Nil	
Eastern Lacustrine Plain	B&P: Marsh (stream/river mouth; Simba-like) C: Stream-fed wetland	Tree cover	Lowest (0)	Lowest (0)	Ngorongoro Stream-fed wetlands: Munge Marsh Munge River Gorigor Midwest Gorigor North Gorigor West
		Shrub cover	Lowest (0)	Lowest (0)	
		Climbable tree density	Nil	Nil	
Eastern Lacustrine Plain	B&P: Small spring (Dead Hippo-like) C: small spring dry land	Tree cover	Lowest (0)	Lowest, Low, High (0,1,4)	Ngorongoro Small Spring dry lands: Kidogo Spring Mti Moja Mystery Spring Seneto (woodland & grassland) Vernonia
		Shrub cover	Lowest (0)	Lowest, Moderate, High, Very High (0,2,4)	
		Climbable tree density	Nil	Nil to 20-30 m apart	
Eastern Lacustrine Plain	B&P: Large Spring (Ngoitokitok-like) C: Large spring dry land	Tree cover	Moderate (2-3/+)	Lowest, Highest (0,5)	Ngorongoro Large Spring dry lands: Ngoitokitok North (woodland & grassland) Ngoitokitok South
		Shrub cover	Low (1/+)	Low, Moderate, Highest (1,2,5)	
		Climbable tree density	<20-30m apart	Nil to 10’s m apart	

Landscape Association	**Facet**	**Item**	**Blumenschine & Peters, 1998**	**This Study** % cover and climbable density/ha trees	**Modern Analogs**
Piedmont Alluvial Plain	B&P: Interfluve C: Interfluves on lacustrine terrace and alluvial fan	Tree cover	Moderate to high (2-4)	Moderate, High, Highest (2,3,5)	Manyara lacustrine terrace interfluves: Ndilana-Msasa Interfluve, Ndala-Chemchem Interfluve Manyara alluvial fan interfluves: Mkindu Interfluve
		Shrub cover	Moderate to high (2-4)	Moderate (2)	
		Climbable tree density	High	10, 20, or 30 m apart	
Lower Piedmont Alluvial Plain	B&P: Stream C: Rivers on lacustrine terrace, fluvial terrace, and alluvial fan	Tree cover	High (3-4)	Moderate, High, Highest (2,3,5)	Manyara lacus. terrace rivers: Msasa R. on Lacus. Terrace Ndilana R. on Lacus. Terrace Manyara fluvial terrace rivers: Endabash R. on Fluvial Terrace Manyara alluvial fan rivers: Mkindu R. on alluvial fan
		Shrub cover	High (3-4)	Moderate, High (2,3)	
		Climbable tree density	High	10, 20, or 30 m apart	
Upper Piedmont Alluvial Plain	B&P: Stream: upper channel bed	Tree cover	None (0)		No analogs
		Shrub cover	Lowest (0/r)		
		Climbable tree density	Nil (but very close to a densely wooded facet)		
Upper Piedmont Alluvial Plain	B&P: Stream: Levee	Tree cover	Highest (4-5)		No analogs
		Shrub cover	Highest (3-5; in patches)		
		Climbable tree density	Highest		
Upper Piedmont Alluvial Plain	B&P: Stream: floodplain grassland	Tree cover	Lowest (0/r) (r=termite mound)		No analogs
		Shrub cover	Lowest (0)		
		Climbable tree density	Nil		

Table 6-7. Categories used in Blumenschine & Peters (1998: Table 1) and Table 6-6.

Cover Abundance Scale	
5	>75%, Highest
4	50-75%, High, Very high
3	25-50%, High
2	5-25%, Moderate
1	1-5%, Low
+	a few individuals together providing only small cover, Very low
r	solitary individuals providing only small cover, Very low
0	0%, Lowest

Categories for Density/Spacing of climbable trees for hominins	
Meters apart	Density of trees/ha
Nil	0
100’s m apart	1-4
<20-30 m apart	12-30
10’s m apart	<100
high	?
very high	?
highest	500?

Physiognomic Categories	
Dense woodland/Forest	trees + shrubs > 75%, trees dominant
Thicket	trees + shrubs > 75%, shrubs dominant
Woodland	trees + shrubs 25-75%, trees dominant
Bushland	trees + shrubs 25-75%, shrubs dominant
Shrubland	shrubs >20%, trees <1/10th woody cover
Bush Grassland	trees + shrubs 2-20%
Grassland, Marsh	trees + shrubs < 25%

Definition of Tree and Shrub	
Tree	height >5 m for single-stem growth forms
Shrub	height 1-5 m for single-stem growth forms; height 1-10 m for multi-stem growth forms

I also found areas adjacent to large springs to show a great deal of variability in woody cover, from lowest to highest. My model of the Eastern Lacustrine Plain provides more overall tree cover and refuge opportunities than Blumenschine and Peters’ (1998) at small springs (though minimal) and large springs.

Tree and shrub cover on the piedmont alluvial plain should be moderate to high, with refuge trees consistently available. This is fairly consistent with Blumenschine and Peters (1998) predictions of high tree density there.

Changes in Predictions of Bone and Stone Tool Assemblages

My modern analog studies resulted in different tree and shrub cover abundance estimates compared to Blumenschine and Peters in four landscape facets for dry climate/low lake level times, shown in Table 6-8. Of those, I did not see that my changes in increased estimates of shrub and tree cover along either the Serengeti peneplain streams or in the Western Lacustrine Plain of the wet season would have affected the predicted bone and stone assemblages for those landscape facets (Blumenschine and Peters, 1998: Tables 2, 3). Large proportions of scavengeable carcasses should have been available there, especially along the Serengeti Peneplain streams. Wood might have been a raw material that was processed (chopped) in the western upper Lacustrine Plain if it indeed supported trees.

Table 6-8. Major differences in Vegetation Structure estimates between this study and Blumenschine and Peters (1998: Table 1) that affect archaeological predictions for the Lowermost Bed II facets.

	Tree Cover		**Shrub Cover**	
Landscape Association/Facet	**Blumenschine & Peters**	**This Study**	**Blumenschine & Peters**	**This Study**
Serengeti Peneplain stream	Low (1/+/r>0)	Moderate, High (2,3)	Low (1/+/r>0)	Moderate (2)
Western Lacustrine Plain wet season	Lowest (0)	Lowest, Low, Moderate (0,1,2)	Very low (0/r)	Lowest, Low, Moderate (0,1,2)
Eastern Lacustrine Plain Small Spring (Dead Hippo-like)	Lowest (0)	Lowest, Low, High (0,1,4)	Lowest (0)	Lowest, Moderate, High, Very High (0,2,4)
Eastern Lacustrine Plain Large Spring (Ngoitokitok-like)	Moderate (2-3/+)	Lowest, Highest (0,5)	Low (1/+)	Low, Moderate, Highest (1,2,5)

I agree with Blumenschine and Peters' carnivore competition and bone and lithic archaeological predictions regarding small springs and large springs, if they are modeling the wooded portions of spring dry lands during dry climate phases in which the lake level was low enough to expose the Eastern Lake Margin area. Large spring woodlands should have less carnivore competition from hyaenids and vultures, and both arboreal and terrestrial scavengeable carcasses would have been available, as well as large refuge trees. Small springs, if wooded, would have only a very localized woodland or shrubland, probably without good sleeping or even escape refuge, hence they would be perhaps short-lived feeding areas. Due to the shade in an otherwise open landscape, one would expect scavenging opportunities occasionally, and the stone tools associated with processing those carcasses.

There are also areas of "dry land" adjacent to large and small springs that are open grassland. Those areas would offer resources similar to the large patch of Lacustrine Plain grassland that provides some herbaceous plant foods during the wet season, but lacks any refuge except for possible nearby spring or riverine woodlands. The only way to distinguish these open versus wooded areas archaeologically might be with carbon isotope analysis, but that would assume either long-term persistence of the woodland/grassland border, or a very fine degree of time resolution that is not yet possible for lowermost Bed II.

Discussion and Conclusion

In this chapter I applied the results of my modern analog vegetation studies to a paleo-case study of the lowermost Bed II Olduvai Basin using five inter-dependent methods. They are 1) comparing my list of modern plant species with those identified in fossil pollen for lowermost Bed II, 2) creating a model of the general picture of landscape units and vegetation across the Olduvai basin in Table 6-2, which compared my vegetation reconstructions to those of Peters and Blumenschine (1995; 1996), 3) creating a table and maps for relative abundance of various plant resources across the paleo-Olduvai basin, 4) creating models of hominin land use for hominins with different diets, and 5) commenting on changes that my study implies for archaeological predictions of hominin land use (Blumeschine and Peters, 1998).

Examination of the fossil pollen taxa confirms that although similarities exist between the vegetation of modern versus Plio-Pleistocene northern Tanzania, there are also differences. For example, after subtracting Afromontane elements from the fossil pollen list, only 68% of the families attributed to the fossil pollen are present in my modern study areas. This is expected, because paleobotanical studies have found that particular plant communities, or species associations, that exist today did not necessarily exist as similar ecological units in the past. This fact presents a unique challenge to reconstructing the vegetation of paleo-landscape units (discussed further in Chapter Seven), and, for example, casts doubt on the validity of the species-level reconstructions of vegetation presented in the last column of Table 6-2. Despite these caveats, the fossil pollen does suggest that Olduvai's Plio-Pleistocene setting was partially wooded savanna, with more apparent affinities to the arid savanna as Olduvai is today, than the moist miombo savannas that occur further south in Africa.

It has been pointed out before that a table such as Table 6-2 is really a simple place-for-time substitution of the sort that one would ideally strive to avoid as a final methodology for applying modern analog information to the past (Peters and Blumenschine, 1996:201). In the terms of Gifford-Gonzalez's (1991) inferential model, the overall goal of the modern vegetation studies conducted in this thesis was to develop relational analogies by understanding the causal linkages between a particular suite of environmental conditions (e.g., climate, geomorphology, landscape units, hydrology) and modern characteristics of the vegetation in those circumstances (e.g., the presence of particular plant food types or physiognomic structures). The causal relationships between vegetation and multiply defined landscape units are very complex, and cannot be expected to be fully understood from the few studies that have been conducted thus far. To complicate matters, situations of historical circumspect, including some unexpected climate changes, introduce non-predictable variables into the picture (Watts, 1988).

In Table 6-2 the analogies that link the modern habitats to those of Olduvai in some cases tend to be more formal than relational simply because the causal linkages are only just beginning to be understood. It will require multiple field studies in a wide array of modern analog settings in order to increase our confidence that we are applying relational as opposed to formal analogies in vegetation reconstructions of particular landscape units. It will also require a more detailed reconstruction of the paleoenvironmental setting for the Olduvai basin, such as a better picture of the hydrology, the location of rivers and/or springs, and how plant-available water was distributed.

The third approach hopes to overcome the insurmountable difficulties involved in the reconstruction of *precise* elements or species in an ancient vegetative setting. In this case I used the *relative* abundance of particular plant food types in landscape units to predict the relative abundances of those plant foods across the paleo-landscape units. The maps are a visual presentation of the results. Ultimately this technique may prove more useful than a table such as Table 6-2 because it avoids the aforementioned inherent and unpredictable differences in species associations and plant communities in the past versus the present. This relative approach argues that the general characteristics of plants living in particular environmental conditions or landscape units could be expected to produce predictable types of edible products such as fruits, flowers, and leaves.

The creation of hominin land use models of the paleo-Olduvai basin is the fourth way of applying the modern analog results to the past. Hominin land use predictions rely on previously created models of resource distribution, and therefore, in Gifford-Gonzalez's (1991) terms, require even higher levels of inference than the vegetation model alone. I chose to focus on potential different land uses for hominins with different plant food specialties since that is an important question regarding niche differentiation of hominins, and because my data particularly lent themselves to such a technique. I concluded that a generalized hominin with gut tolerances approximately equivalent to that of a chimpanzee would probably forage for fruits in the alluvial fans, roots in the upper Lacustrine Plain and lacustrine terrace when those Eastern Lake Margin facets were exposed during times of low lake levels, and perhaps acquire animal foods throughout the basin. On the other hand, a hominin that was capable of masticating and digesting large amounts of *Acacia* seeds/pods might find enough to eat by staying in the area of the upper Lacustrine Plain and lacustrine terrace during dry climate/low lake level periods. These different feeding strategies could represent *Homo habilis* the generalist versus *Australopithecus boisei*, the seed/pod specialist.

The final application of my modern analog results to the Olduvai case study was to examine whether the archaeological predictions of Blumenschine and Peters (1998) should change based on my results. If scavenging opportunities are indeed a function of vegetation structure, then predicting and interpreting the nature of archaeological assemblages requires a very spatially refined paleo-vegetation reconstruction. The only changes I suggest are those that incorporate the high degree of variation in tree and shrub cover in areas of land adjacent to spring sites of the upper Lacustrine Plain. Since archaeological traces mainly reflect animal carcass processing, they cannot be used to test some of the models of plant food use that I proposed in this chapter. We will have to rely on other techniques such as dental microwear and stable isotopic analysis to test hypotheses about the plant food component of early hominin diets. In order to be more confident about making archaeological predictions, future detailed investigations should focus on documenting more precisely the relationships between vegetation structure, carnivore competition, bone taphonomy, and scavenging opportunities.

CHAPTER 7. CONCLUSIONS

Introduction

In this thesis I have examined some of the relationships between plants and early hominins. In the first chapter, I gave a general background about why vegetation-related issues have been difficult to address in paleoanthropology. I then outlined a methodology by which I would use modern vegetation to model plant resources for hominins across the Olduvai lowermost Bed II paleolandscape. In Chapter Two I provided a background of vegetation in Africa and descriptions of the modern study areas at Lake Manyara, Serengeti, and Ngorongoro Crater. Chapter Three outlined the methods I used for collecting and analyzing the modern vegetation data. In Chapters Four and Five I presented the results of the modern vegetation studies, including some findings on the relationships between physiognomic structure, floristic composition, land units, and plant resources for hominins. Finally, in Chapter Six I applied the findings from the modern analog studies toward reconstructing vegetation, plant foods, and refuge trees for the lowermost Bed II paleolandscape.

In this final chapter I summarize some of the most important findings of the previous chapters and discuss their implications for paleoanthropology. The chapter is divided into three main sections reflecting conclusions drawn at three different levels. The first section concerns the methodology for modern analog vegetation studies that I developed in this thesis. It discusses some of the inherent challenges involved when using modern vegetation to model ancient habitats, and suggests how the methodology might be improved in future studies.

In the second section I summarize the conclusions from this thesis that are directly relevant to the Olduvai Gorge case study. This includes findings on the relationships between physiognomy and other aspects of vegetation in the modern habitats, and a discussion on the relevance to Olduvai of the particular modern analogs chosen for this study.

The third section of this chapter explores other issues in paleoanthropology that are related to hominins and plant foods. I discuss the relative importance of plant versus animal foods in early hominin diets, C_3 versus C_4 foods, and the role of technology in subsistence changes. These are some of the important current issues in the discipline of paleoanthropology to which the findings of this thesis are relevant.

Conclusions and Future Directions for the Methodology of Modern Analog Vegetation Studies

The first goal of this thesis was to develop and implement a methodology for characterizing the relationships in modern habitats between vegetation structure, species composition, and resources for hominins in quantitative terms, at a landscape scale. That required first locating modern analog study areas that fit within the parameters defined by a particular fossil case study, identifying landscape units, creating an appropriate sampling strategy, and conducting field work in the modern habitats. My study areas at Manyara, Serengeti, and Ngorongoro Crater all had portions of their landscapes that fell within the environmental parameters reconstructed for portions of the lowermost Bed II Olduvai paleolandscape, for example in geomorphology, landscape unit type, hydrology, and climate. I defined the modern landscape units – regions, landscape associations, landscape facets, and landscape elements –with the help of previously published landscape unit divisions for Serengeti and Manyara, and through my own observations at Ngorongoro Crater. I then devised a sampling strategy for the vegetation of those modern landscape units using the methods developed in plant ecology, and conducted the field work over a total of about one year's time.

Overall my vegetation data collection methods worked well, but there are some improvements that I would suggest for future modern vegetation studies. First, a larger number of study areas need to be sampled for all of the plant growth forms in order to enable statistically valid comparisons between landscape facets, associations, and regions. Within each study area I often had at least ten plots, but I had only one or two study areas to sample each facet type (e.g., riverine lacustrine terrace). At least five study areas of each facet type need to be sampled in order to statistically compare them. Since time is the limiting factor, in future studies this might be accomplished by streamlining the amount of quantitative data collected so as to have time to sample a larger number of plots.

Second, it would be beneficial to have more information about the seasonal changes in modern vegetation. In the East African savanna sites that I sampled, the herbaceous component of the vegetation was typically more well-represented in wet season samples. Ideally one would sample each study area during both the dry and wet seasons so that separate wet and dry season models of vegetation resource availability could be generated. Ultimately, the affordances of the paleo-Olduvai basin should be considered with respect to surrounding areas such as the Crater Highlands and other nearby lake basins, particularly in terms of potential seasonal usages of these different areas. This idea is discussed further in the next major section of this chapter.

Identifying patterns and ultimately causal factors in the vegetation distribution of modern habitats is crucial, but it is the most difficult aspect of this methodology. The technique of multivariate analysis is particularly well-suited for elucidating which environmental elements are most important in determining the vegetation community of an area, and should be used to a greater extent in future modern analog vegetation studies. In this thesis, I used the multivariate technique of detrended correspondence analysis (DCA) to graphically illustrate which sites were similar in species composition. In Figures 4-17, 4-18, 4-20, 4-21, 4-24, and 4-25, the graph axes represent the theoretical environmental variables that are most important in determining community composition, but the identity of those environmental variables in this case had to be determined, or best-guessed, based on published ecological characteristics of the plant species.

In future modern analog vegetation studies, it would be useful to collect measures of environmental data in each of the vegetation plots so that the identity of the most important environmental variables could be tested. For example, if measures of pH, soil salinity, soil conductivity, and ion concentrations were collected from each vegetation plot, then one could graphically plot the site scores of each DCA axis against the environmental measures taken at those sites. A correlation would indicate that the environmental variable is potentially important in plant community composition (Jongman *et al*., 1995).

Applying Modern Analog Results to a Fossil Setting

According to the methodology developed here, once the characteristics of the modern vegetation in particular land units are described, then similar characteristics can be tentatively assigned to the analogous paleo-landscape units. The links between present and past are the landscape units themselves, whose ecologically-, geomorphologically-, and hydrologically-defined characteristics control the vegetation to a large degree.

In the first stages of implementing this methodology, we assume that the multitude of similar circumstances in the modern and ancient settings will result in the same general types of vegetation. However, the degree of confidence with which one can ascribe specific vegetation characteristics to a paleo-landscape will increase as the environmental factors controlling certain aspects of the vegetation become known. As mentioned above, this could be accomplished through studies of environmental variables (soil pH, salinity, etc.) in the modern analog study areas. The next step is to identify those environmental variables themselves in the fossil/geological record either directly or through proxies. In this sense, researchers that are working with the geological record need guidance from modern analog studies as to which environmental variables are the most important to identify for the ancient settings.

Some of the most important controlling factors of vegetation that I identified in Chapter Four were the availability of moisture, well- versus poorly-drained soils, salinity, and alkalinity. Deocampo (2004a; Deocampo *et al*., 2002) has successfully used the chemical composition of fine clays to identify saline/alkaline conditions in modern habitats and in the geological record of the Eastern Lake Margin of lowermost Bed II, Olduvai. We now need similar information from other landscape associations in order to fine-tune paleo-vegetation reconstructions in those parts of the paleolandscape.

A start has been made in the lower alluvial fans, where Ashley and Driese (2000) analyzed a red paleosol from two trenches in that landscape association. They describe pedogenic features sensitive to soil moisture conditions, such as vadose siliciclastic and zeolite crystal silt, which records episodic water-table fluctuations. From this they claim that the upslope site (Trench 86) had a lower water table and better-drained conditions than the downslope site (Trench 46), which had a higher water table and poorly drained conditions. Since plant-available water via the groundwater table and soil drainage conditions have central roles in determining the physiognomy and species composition of semi-arid woodland, bushland, and forest habitats, these types of micromorphological studies might be useful if expanded to more of the trenches in lowermost Bed II. Then at least relative comparisons of groundwater table fluctuations and soil drainage conditions could be made across the lower alluvial fans, for example, and in the western basin.

Armed with the information that both the general circumstances of landscape units and the most important environmental controlling factors are similar in the modern analog and ancient settings, we can increase the confidence with which the modern analog is applied to the ancient setting.

Implications of long-term vegetation change

The observation from late Pleistocene and Holocene temperate environments that plant associations change over time calls into question the relevance of modern analog vegetation studies to the distant past. Is it possible that even relative contrasts between adjacent landscape units in terms of hominin plant affordances, as emphasized in this study, might have been different in ancient settings? Relative contrasts are linked to the overall ecology of each landscape unit, and not just to plant species composition. Therefore, relative contrasts might only have changed in cases in which only one or very few plant species provide the bulk of hominin resources. For example, Manyara's lacustrine terrace provides some of the most important hominin plant foods in fruits from shrubs belonging to many different species. Even if different species associations existed in a similar environmental setting in the past, it is likely that a variety of edible fruit-bearing shrubs would still be present. The same applies to wetlands, where there are a large variety of marsh plants. Many of those plants provide edible rootstocks, corms, or bulbs, and a difference in actual species composition would not mean much difference in the types of plant foods available there for hominins. In Manyara's alluvial fan groundwater forest, and probably in most East African large riverine forests, a wide variety of fleshy fruit-bearing trees exist, a situation which again may not change even if the actual species composition of the trees changed over time.

Changes in species composition over the long term might be important in settings in which a single plant species dominates a modern landscape unit. Its absence in an otherwise similar past environment could mean differences in hominin resource availability. An example of this from my modern analog sites is the *Acacia xanthophloea* riverine forests from Manyara's Lacustrine Plain. The tree canopy in those forests is composed of virtually a single species, *Acacia xanthophloea*, and would obviously be different if that particular species were not present. At a minimum, its absence could change the arboreal refuge aspect of that landscape unit, and the likelihood of finding other resources there such as scavengeable carcasses.

Given the broad scope of landscape units analyzed here, the majority have a wide variety of hominin resource plants. In those cases the relative contrasts in hominin affordances between landscape units should persist despite some changes in actual species composition.

Conclusions for Improving Modern Analog Vegetation Studies

Modern analog vegetation studies can become more relevant and useful to fossil vegetation reconstructions in three ways. The first is to understand modern communities better in terms of which environmental variables control particular aspects of the vegetation. This has been a major goal of ecology in general, but for paleoanthropology the units of interest may be unique. For example, paleoanthropologists would like to know how certain classes of hominin-edible plant foods, like edible fleshy fruits versus edible hard seeds, vary with particular land forms, soil characteristics, and hydrological features. These relationships were explored in Chapters Four and Five for the Olduvai case study. Addressing these issues for other hominin localities will also require studies of both plants and environmental variables in modern habitats.

The second means by which to get the most out of modern analog vegetation studies is to have highly refined paleoenvironmental reconstructions, thereby strengthening the links between modern and fossil landscape units. Paleoenvironmental reconstruction has been a goal of paleoanthropology in general, but too often we seem satisfied with broad descriptions of the geomorphology, and especially the vegetation structure. For example, the paleoenvironment is often discussed in terms of the degree to which it was “closed” or “open” (e.g., Kappelman, 1984; Plummer and Bishop, 1994). Such broad reconstructions are of little use to the landscape scales being addressed in this thesis, and it is at these landscape scales that we hope to be able to decipher patterns of hominin social behavior, ecology, and seasonal movements. Of course, it is difficult to get refined paleoenvironmental data, but knowledge of the factors that are most important in modern habitats can give us clues as to what to look for in fossil settings.

Thirdly, we can increase the confidence in paleobotanical reconstructions based on modern analog vegetation studies by obtaining fossil evidence for particular plant taxa in the past. Since experience has shown us that past plant associations are likely to be different than those of today, then the only way to know for sure whether potentially key plant food species existed in certain areas in the past is to find direct evidence of their fossils. The approach taken in this study is one which de-emphasizes plant species in favor of comparing broader categories of plant resources between landscape units, and I would argue that that is the best strategy for reconstructing overall vegetation resources for various fossil settings. However, the identification of particular plant taxa can only improve upon those reconstructions of plant resources, and may bring to light plant resources not predicted by other methods. An attempt to improve the direct evidence for fossil plant taxa at Olduvai is currently being undertaken by efforts to look for and identify plant macrofossils, studies of rhizoliths, new work on fossil pollen, and phytolith analysis (Blumenschine *et al*., 2000).

Conclusions from the Olduvai Gorge Lowermost Bed II Case Study

Figure 1-1 represents the overall methodology being followed by OLAPP for reconstructing the landscape paleoecology of lowermost Bed II, Olduvai. As described in Chapter One, an important focus for this thesis work regards the relationships between the geomorphologically-defined landscape units with floristic composition and physiognomic structure, and also the relationships between those aspects and plant foods and arboreal refuge. This study of modern environments has begun to recognize the nature of those relationships for semi-arid East African savannas, and has found that the relationships are complicated, as would be expected for ecological processes.

Physiognomic structure is necessarily central to the model because it is the aspect of vegetation that is mostly likely to be reconstructed at fossil localities. My results show that indirect relationships often exist between physiognomic structure, floristic composition, and plant foods. For example, the modern forested habitats sampled in this study are similar structurally (in that they have a nearly continuous tree canopy), but are of two very different floristic types with different edible parts. Manyara’s groundwater forest on the alluvial fan was dominated by tall, broad-leaved, fleshy-fruit bearing trees that are typical of riverine forests in East Africa (Hughes, 1988). In contrast, Manyara’s forest along the small but perennial lower Mkindu River on the upper lacustrine plain had an almost mono-specific tree species composition of *Acacia xanthophloea*, whose main edible component is gum, though the pods and seeds are potentially edible as well (Peters *et al*., 1992; Wrangham and Waterman, 1981). The most likely type of forest to have occurred in a particular paleo-landscape unit is predictable beyond structure if one is armed with additional information regarding the geomorphological and hydrological settings. *Acacia xanthophloea* forests occur in frequently flooded, low-lying areas near the water's edge, while riverine forests and groundwater forests occur on well-drained soils where the roots can tap a source of fresh groundwater.

Many variations in the species compositions of woodland and bushland habitats exist as well, as exemplified by Herlocker's (1975) landscape classification map of the Serengeti, showing numerous landscape facets with different dominant tree species (most are *Acacia* spp.). Yet within the semiarid savannas sampled here, the plant food composition (in terms of plant food parts available) of grassland, bush grassland, or bushland landscape facets were quite similar within each of those physiognomic categories, unlike the differences in forests just mentioned. Bushland landscape facets are characterized by a high density of edible fruit-bearing shrubs, many of the species of which overlap between landscape facets, especially landscape facets within a single region. In a study of edible plants along the Semliki River, eastern Congo (then Zaire), Sept (1994) also found that the highest density of edible fruits from shrubs was consistently in bushland habitats. In my study, bush grassland and grassland landscape facets varied in species composition between regions, but nonetheless each of those habitat types provided predictable types of plant foods for hominins. Grasses tended to have edible seeds and underground parts, while the forbs often provided edible leaves and other herbaceous parts. Marsh landscape facets, despite some differences in species composition, consistently provided edible underground parts from sedges (Cyperaceae), cattails (Typhaceae), and grasses (Gramineae).

Not surprisingly, physiognomic structure is strongly correlated to arboreal refuge availability, and physiognomy is a good predictor of tall tree density. The different forest types mentioned above vary in the quality of refuge available, where groundwater forest trees are probably preferable for sleeping over the *Acacia* thorn trees of the low lacustrine plain or lake edge forests. The groundwater forest trees have larger, smoother trunks and soft leafy branches, whereas the *Acacia* forests have thinner trunks, very thorny branches, and tend to be adjacent to open grassland areas. In bushland, bush grassland, and grassland, refuge trees are isolated or in small clusters.

The patterns found in this study in the dichotomy of forest composition and in the consistency of edible parts provided within grassland, bush grassland, bushland and marsh habitats may be restricted to semi-arid and arid savannas, and these results should not be extrapolated to other vegetative settings such as “moist savannas” or miombo woodlands.

As suggested by the DCA ordinations and general observations of the modern study areas, the ratio of herbaceous to woody plant biomass, or physiognomic structure, in semiarid savanna landscapes depends largely on the amount and spatial distribution of soil moisture that is available to plants. Soil moisture is not necessarily directly related to local annual rainfall, nor even to surface features such as rivers, although it often correlates with those features. Groundwater, or the redistribution of regional rainfall, is more important than surface water distribution because surface water tends to be very ephemeral in semiarid savannas. Other studies have found groundwater distribution to be one of the most important environmental factors controlling woody vegetation in semiarid savanna habitats as well (Coughener and Ellis, 1993; Belsky, 1990; Greenway and Vesey-Fitzgerald, 1969). In riverine study areas, the size, volume of discharge carried, and the degree to which a river is perennial are also important factors controlling the vegetation because they influence the amount of water available to plants (Hughes, 1990; Coughener and Ellis, 1993).

Some work has been conducted towards identifying the nature of groundwater and riverine characteristics for lowermost Bed II, such as geological studies (Hay, 1996; 1976), isotopic studies of paleosol carbonates (Cerling and Hay; 1986; Sikes, 1994; 1995), geochemical studies (Deocampo, 2004a,b; Deocampo *et al*., 2002; Deocampo and Ashley, 1999; Hay and Kyser, 2001; Hay, 1996), and recent work by Stanistreet that could potentially define successive channel-unconfined (braided) and channel-confined (low sinuosity) river systems in the Eastern Lake Margin (Blumenschine *et al*., 2000). Future studies should continue to pursue these goals, particularly with regard to groundwater distribution, since it is such an important control of vegetation structural types across the paleolandscape.

At the modern analog study areas in Lake Manyara, groundwater distribution is one of the most important factors controlling vegetation structure. The particularly high groundwater table in the northern area of the park supports the unique groundwater forest in the alluvial fan area, and a moderately high groundwater table may support the *Acacia tortilis*-dominated bushland in the lacustrine terrace (Greenway and Vesey-Fitzgerald, 1969), although Loth and Prins (1986) claim that the *Acacia tortilis* trees depend on rainfall. The groundwater situation at Manyara relates to recent tectonic activity and the particular geological setting of that area, with its adjacent rift escarpment (Loth and Prins, 1986). The geological and tectonic setting of the paleo-Olduvai basin was different, for one, in the absence of a rift escarpment so close to the lakeshore. The hydrological setting at Manyara is questionable as an appropriate modern analog in that sense, because the paleo-Olduvai situation could have differed in its distribution of groundwater from that of Manyara. Whether the alluvial fans at Olduvai were overlying a high groundwater table is not known at this time. Sikes' (1994) stable isotope results on pedogenic carbonates from OLAPP's trenches indicate that a grassy woodland to wooded grassland existed in the areas of the Eastern Lacustrine Plains and near-lake shore, but they have yet to be related to the landscape structure of the lower alluvial fan (Blumenschine *et al*., 2000). The paleoenvironmental evidence from Olduvai gives little indication of extensive forested habitats, which suggests that perhaps there was not a groundwater forest in Olduvai's alluvial fans. The most likely alternative is that there was a dense woodland or forest along the river channels, and away from the river the vegetation graded into bushland, bush grassland, or even grassland habitats in a relatively sharp green/brown transition that is typical of semi-arid savannas (e.g., Belsky, 1989; Sept, 1990).

Therefore the vegetation reconstructions for the alluvial fans based on these modern analog studies are in my opinion the most tenuous of the landscape units. Unfortunately, very few modern alluvial fan settings in East Africa exist that are undisturbed (in National Parks or Reserves) because alluvial fans are typically the richer soils that are the first to be farmed. The nature of the alluvial fan vegetation is clearly central to models of hominin land use at Olduvai, so future studies should attempt to refine the paleoenvironmental reconstruction of that area, ideally by broadening the study of modern analogs to include modern alluvial fans other than those at Manyara. To further complicate matters, much of the area that was the alluvial fan in the Olduvai paleolandscape is now subsided under the Olbalbal Depression, the current drainage sump, and therefore is not amenable to direct paleoenvironmental testing. Nonetheless, geological work concerning the evolution of the paleo-Olduvai basin may be able to shed more light on the likely soil characteristics and groundwater/surface water situation of the alluvial fans area.

The theoretical foundation for OLAPP's landscape approach is evolving from a somewhat static earlier version in which a key element was the persistence of paleo-landscape units, or landscape facets, throughout the entire duration of lowermost Bed II. Recent geological work by Stanistreet focuses on the Eastern Lake Margin as an alluvial fan-dominated landscape succession in which successive stages of fan development and lake-level fluctuations structure the eastern basin landscape. The evolutionary succession that created lowermost Bed II began with a surge of volcanic materials and mudflows from Mount Olmoti that formed Tuff IF. This was followed by channel formation in the alluvial fans consisting initially of braided, dynamic river systems which eventually developed into more stable, channel-confined systems along which riverine forests might develop. In the mature phase, which is also the phase of longest duration in lowermost Bed II, wetlands and a Lacustrine Plain developed on the Eastern Lake Margin.

In Chapter Four I speculated on the long-term vegetation dynamics of the paleo-Olduvai basin. Accepting the more dynamic fan-dominated landscape succession framework, it still holds that some landscape facets likely persisted for thousands of years, while others changed in physiognomy and plant species composition over tens to hundreds of years (Figure 4-26). In the modern Serengeti, grasslands, evergreen forest, and inselberg vegetation can be considered climax because they are stable in time and replace themselves after disturbance (Belsky, 1987). Geomorphologically controlled wetland areas also can persist for thousands of years. Periods of lake expansion and contraction during lowermost Bed II lasted for thousands of years (Deocampo, 2004a), so that during a 4000-year period of dry climate, wetland facets would have been able to persist within the exposed Eastern Lake Margin area. On the other hand, the physiognomic structure of the “dry lands” adjacent to a lake edge (lower Lacustrine Plain) and some wetlands probably varied over short time periods depending upon water table fluctuations (e.g., Western and Van Praet, 1973; Vesey-Fitzgerald, 1974).

In areas such as paleo-Olduvai’s lacustrine terrace and alluvial fans during the mature succession phase, time of duration of vegetation physiognomy might depend on the frequency of disturbance factors such as fire and large herbivore population fluctuations. When disturbed, some interfluves would have varied from bushland or woodland to wooded grassland, as has been observed in parts of the Serengeti National Park during the past century (Belsky, 1987; Sinclair, 1979a). Isolated refuge trees could have persisted over decades and even centuries as localized “safe places.”

One question that remains to be solved concerns the nature of the vegetation along the rivers flowing into the Olduvai basin. On the eastern side of the basin, rivers during the mature phase of alluvial fan development may have been more typical “lowland” riverine forests with tree species like *Ficus* and *Trichilia* (Hughes, 1988). On the other hand, the rivers of the upper and possibly even the lower alluvial fans may have emerged as fingers of Afromontane floral elements extending down from the highlands. Perhaps future fossil wood studies will give us a firmer basis for understanding the species composition and/or floristic types of any riverine forests that existed in the vicinity of Olduvai, as that information could be important regarding the types of plant foods that were available there.

Peters and Blumenschine (1995) pointed out that in a regional perspective, we must consider whether the Olduvai Basin was an area of only peripheral significance for early hominins (Figure 2-6). The Olduvai Basin exists in a rain shadow, but the southeastern side of the Crater Highlands, including the area north of Manyara, receives greater rainfall. Thus those areas were probably richer in certain types of plants and possibly plant foods like fruits and leaves, and certainly would have provided plenty of arboreal refuge. As I will discuss in the next section, however, at least some species of hominins appear to have survived in, and perhaps preferred, a combination of open grassy habitats and denser wooded habitats, in which they occupied ecological niches not seen in any living modern primates. The paleo-Olduvai basin itself might have had advantages for early hominins such as the proximity of open grasslands for scavenging and/or hunting opportunities, or the richness of edible underground parts from its marshes. If hominins were interested in eating marsh plants, then the Olduvai Basin would have been more attractive during periods of drier climate in which low lake levels made way for rich wetlands and marshes in the Lacustrine Plains.

It is impossible to judge the relative importance of resources from the paleo-Olduvai basin compared to nearby areas such as the Eyasi, Manyara, and Ndutu Basins, or nearby montane areas, until the paleoenvironments and affordances in those nearby areas are modeled in a manner similar to that which has been done at Olduvai. Such an exercise would be informative regarding the broader issues of hominin habitat preferences, and the ecological preferences of sympatric hominin species, but it would remain difficult to test hypotheses regarding regional hominin land use patterns without a regional landscape archaeological record. Stable isotopic analyses of hominin fossils, such as that of strontium, could potentially answer some questions about hominin ranging patterns without having to rely on the physical distribution of archaeological materials (e.g., Sillen *et al*., 1995; Müller *et al*., 2003).

Conclusions for Paleoanthropology

Plants and plant-food consumption are far less conspicuous in the archaeological record than animal food processing with the use of stone tools. That makes modern analogs one of the only ways to get a sense of what plant-hominin interactions might have been like. In this section I explore some of the broader issues in paleoanthropology related to hominin use of plant resources, and discuss what light this study of modern vegetation might shine on important questions in human evolutionary studies. For example, how were plant foods distributed across savanna habitats? How does the morphological and stable isotopic evidence for early hominin diets compare to those of chimpanzees, savanna baboons, or modern human foragers? Are recent theories proposing that plant foods were central to the change to the larger bodied *Homo ergaster* feasible? Did certain types of plant foods lend themselves to a home base or central place foraging arrangement, or were they more likely to be feed-as-you-go items? What might we say about hominin niches, given that there were often two or more hominin species living sympatrically at various localities throughout the past several million years?

Plant Resource Distribution

My studies of plant resources in East African habitats confirm that plant foods and arboreal refuge for hominins are distributed non-randomly across landscapes. In semiarid savanna environments, plant-available water is not ubiquitous, but is patchily distributed along rivers, springs, wetlands, or underground. Physiognomic types in part reflect this water distribution, such as the typical tree-lined rivers adjacent to grassland interfluves. Plant foods and refuge tree patches also reflect the uneven distribution of plant-available water and other environmental variables like soil salinity, porosity, and alkalinity. For example, most trees that produce edible fleshy fruits were found in this study in groundwater forest, where plants have access to a high, fresh groundwater table. Many of those same plant species and edible tree fruits are also found in large East African riverine forests that were not specifically sampled in this study (Hughes, 1988). Another example is the edible seeds and pods from *Acacia tortilis.* They occur in relatively localized groves of trees such as along the ecotone of the Serengeti grassland/woodland landscape associations or along a lacustrine terrace. Isolated patches of marshy wetlands would be predictable places for hominins to find edible sedge and cattail rootstocks and bulbs.

In sum, different types of plant foods can be predicted to have occurred in particular places on the landscape, which is highly beneficial to the pursuit of landscape paleoanthropology. It allows for the testing of models of hominin land use across space. This modern analog study has improved our ability to predict the localities of plant foods across the paleo-Olduvai basin in particular, but these finding could potentially be useful for other early hominin sites in similar, semi-arid settings.

Isotopic analyses and plant foods for hominins

As discussed in Chapter One, all early hominins whose tooth enamel has been tested isotopically to determine their $^{13}C/^{12}C$ ratios consumed a substantial proportion of C_4 foods (ultimately derived from tropical grasses or sedges) in their diets, ranging from 20% to greater than 50% (van der Merwe *et al*., 2003; Lee-Thorp *et al*., 2000; Sponheimer and Lee-Thorp, 1999). These include *Australopithecus africanus* dating back to approximately three million years ago, *Australopithecus robustus*, and early *Homo*.

There are three main candidates for the types of foods that could be responsible for the C_4 component of hominin diets. They are C_4 grasses, C_4 sedges, and animal foods (Sponheimer and Lee-Thorp, 2003). Grasses are relatively low-quality foods in that they are high in fiber and low in protein and long chain polyunsaturated fatty acids (Sponheimer and Lee-Thorp, 2003), and therefore it seems unlikely that hominins would have subsisted on grasses as the mainstay of their diet. Furthermore, a diet specializing in grasses would be expected to leave a dental microwear pattern similar to that of modern grass specialists like gelada baboons, which is dominated by scratches with little evidence of pitting (Teaford, 1992). Early hominins have frequently pitted molars (Grine, 1986; Grine and Kay, 1988). On the other hand, the isotopic evidence shows that C_4 foods composed only a portion of early hominin diets, so that perhaps hominins ate some grass seeds, grass stems, and grass underground parts, but ate even more hard fruits and other C_3 plant parts. Further comparative studies of hominin dental microwear patterns to those of modern baboons who eat partial grass diets could shed light on this possibility (e.g., Daegling and Grine, 1999).

Another possibility is that hominins ate C_4 sedges. In the modern analog studies conducted for this thesis, sedges were common at wetlands and were a predictable food resource for which few animals competed. Unfortunately, information on which of the sedges in my study were C_4 and which were C_3 is not available, but in a study of sedges in Kruger National Park, South Africa, Sponheimer and Lee-Thorp (2003) found that 45% of the sedges they encountered were C_4, while the rest were C_3. In order to account for a 33% C_4 signature in its diet, a hominin would have had to consume 90% sedges, assuming that 45% of sedges were C_4, that sedges were the only C_4 foods consumed, and that C_4 sedge species were not preferentially taken over C_3 sedges (Sponheimer and Lee-Thorp, 2003). Such an extreme does not seem likely, particularly given the frequent pitting in the microwear analysis of hominin tooth molars (Grine, 1986; Grine and Kay, 1988), but studies have not yet been published that describe the microwear pattern that results from sedge consumption. *Typha*, or cattails, are common, non-sedge, edible marsh plants in this modern analog study. Presumably a hominin that ate sedges would also eat the pleasant-tasting rootstocks and other parts of *Typha*, but since *Typha* are C_3 plants, then they would only contribute further to a C_3 signature for the hominin.

A third possibility is that the C_4 component of hominin diets derived from animal foods. There are many different types of animal foods that carry a C_4 or mixed C_3 and C_4 signal, including insects like termites and grasshoppers, small animals like rodents, hyraxes, and hares, the vulnerable young of antelopes that are left hidden in tall grass, and of course larger adult grazers and mixed feeders that constitute the major animal biomass of the savannas, such as antelopes, hippos, and equids. Insects and small animals could have been exploited without necessarily requiring any tool use. Chimpanzees and baboons occasionally catch hares and small monkeys with their bare hands, for example. The exploitation of termites might require the use of some sort of tool, such as a termite fishing twig or a digging implement. Since chimpanzees use a variety of tools, then it is reasonable to assume that the common ancestors of chimpanzees and humans were capable of simple tool use. Therefore, even the most primitive australopithecines were likely to have been capable of simple tool use and small animal exploitation. The fact that bone tools recovered from Swartkrans show evidence of having been used to extract termites from mounds strengthens the case for termite exploitation by early hominins (Backwell and D'Errico, 2001).

We know that at least some hominins were exploiting large mammals by 2.5-2.6 mya with stone tools (Semaw *et al*., 1997; 2003; de Heinzelin *et al*., 1999), but we do not know which hominin species were involved, whether they had access to entire carcasses or merely the left-over scraps from another carnivore's kill, or how important this foraging strategy was to their overall diets. In any case, the evidence for large mammal exploitation post-dates the evidence for C_4 food consumption by hominins by at least half a million years (Sponheimer and Lee-Thorp, 1999). Therefore carcass processing with stone tools was a strategy that evolved after semi-arid or arid savannas were already being utilized by hominins.

It is also possible, perhaps even likely, that hominins ate some combination of animal foods, C_4 grasses, and C_4 sedges. According to archaeological evidence and the findings of the modern vegetation studies conducted in this thesis, all of those items would have been readily available to hominins living in semi-arid East African savanna settings.

Were Changes in Plant Food Consumption a Driving Force in Hominin Evolution?

The many significant changes in the body form, life history, and ranging behaviors of *Homo ergaster* have often been associated with an increase in meat eating, which was thought to correspond to increased nutrient quality and ultimately increased brain size (Aiello and Wheeler, 1995; Milton, 1999). However, several recently proposed theories argue that it was new ways of using plant foods that caused, or allowed for, important changes in the morphology and life history aspects of some hominins by increasing the quality of their diet.

Conklin-Brittain *et al*. (2002) point out that one of the factors that distinguishes modern humans' diets from those of apes is the reduction of fiber. All human populations consume diets with much less fiber than the diets of wild apes. Whereas chimpanzees at Kibale National Forest in Uganda had 34% annual average fiber content, modern human foragers of the Obo tribe of the Democratic Republic of the Congo, for example, had only 9% fiber intake (Conklin-Brittain *et al*., 2002). One way to increase the quality of a diet is by decreasing the amount of indigestible fiber, and Conklin-Brittain *et al*. (2002) argue that australopithecines did this when they began exploiting the shallow underground corms, bulbs, and rhizomes of wetland plants like sedges as a food source. This strategy paved the way for the exploitation of other, deeper underground roots and tubers of dry land plants, which tend to be much lower in fiber than foods like wild fruits or herbaceous piths (Conklin-Brittain *et al*., 2002). Thereby, they argue, the stage was set for early *Homo* to incorporate additional improvements to the quality of their diets.

O’Connell *et al*. (1999) and Wrangham *et al*. (1999) both argue that it was the exploitation of underground storage organs and, especially in the case of Wrangham *et al*. (1999), the invention of cooking that were key to the emergence of the more highly mobile, larger-bodied *Homo ergaster*. O’Connell, Hawkes, and colleagues focus on the fact that deeply buried USOs cannot be acquired by children on their own, which means that mothers had to acquire and process foods for their children. Grandmothers could then increase their fitness in a novel way, by digging more USOs to help provide for their grandchildren. That in turn allowed daughters to have the next baby sooner, ultimately leading to a more human-like life history pattern with increased longevity (Hawkes *et al*., 1997; O’Connell *et al*., 1999). In this “grandmother hypothesis”, increasing aridity between 2.5 and 1.7 mya is purported to have changed the habitat types and plant foods that were available to early hominins, thereby causing them to exploit novel plant food resources that required adult acquisition and possibly pre-oral processing like cooking.

Wrangham *et al*. (1999) argue that cooking was invented around 1.9 mya, and that the reduced oral processing and digestive effort necessary for cooked foods is reflected in the smaller teeth and gut size of *Homo ergaster*. Again, USOs are argued to be the key plant food that lent itself to exploitation and cooking, and digging sticks like those of the Hadza would have been required to exploit the USOs. Wrangham *et al*. (1999) also argue that cooking of both plant and animal foods involved central place foraging and delayed consumption of food.

The timing of the invention of cooking is of undoubted importance in human evolution, but evidence for control of fire during the early Pleistocene is equivocal. Most anthropologists agree that the earliest evidence for rock-lined or rock-filled hearths dates to the Middle Pleistocene, about 250-400 thousand years ago (Clark and Harris, 1985; James, 1989). However, the types of fires used to cook plant tubers such as those made by modern Hadza foragers are large fires kindled on unprepared ground surfaces, and may be ephemeral archaeologically (O'Connell *et al*., 1999). The best evidence for hominin use of fire in the early Pleistocene is the patches of reddened earth associated with archaeological remains at Chesowanja and East Turkana (Rowlett, 1999; Bellomo, 1994; Gowlett *et al*., 1981; Isaac and Harris, 1978).

Rather than pinpointing either key plant food changes or increased meat eating as a prime-mover for certain aspects of human evolution, some emerging theories suggest that changes in plant food foraging strategies went hand in hand with changes in animal food foraging strategies. Hawkes and colleagues point out that, paradoxically, plant foraging strategies may explain the increased archaeological evidence for carnivory in the early Pleistocene (Hawkes, 1991; Hawkes *et al*., 1999). They argue that hominins could only adopt the high-risk, high-gain foraging strategy of hunting (or scavenging) if there were gains in efficiency in other areas of foraging, i.e. plants. The increased energy that became available by either cooking plant materials or choosing higher quality plant foods allowed for the intensification of hunting. This is analogous to periods of fruit abundance in chimpanzees that allow for intensification of chimpanzee hunting during those time periods (Wrangham *et al*., 1999; Stanford, 1996).

Early Hominin Diets and Niche Differentiation

The stable isotopic evidence from enamel tells us that from very early on, at least as early as the oldest hominin fossils that have been tested, or 3 million years ago, hominins had a feeding strategy that was unique compared to modern apes in that it incorporated C_4 foods (van der Merwe *et al*., 2003; Lee-Thorp *et al*., 2000; Sponheimer and Lee-Thorp, 1999). In other words, from some of the earlier stages of human evolution hominins were ecologically adapted to living in savanna environments, as seen by the fact that they managed to exploit the "grass-bound" C_4 nutrients of semiarid or arid savannas. Since archaeological evidence for stone tool manufacture and butchery of large savanna mammals does not occur until 2.5 mya (Semaw *et al*., 1997; 2003; deHeinzelin *et al*., 1999), then it must have been resources in savanna habitats other than large mammals to which hominins were adapted initially.

Clearly, though, there was not a single hominin feeding strategy, because there were often two or more sympatric hominin species living in a given environment. The competitive exclusion principle would argue against different hominin species exploiting their habitats in exactly the same way. We may begin to understand actual hominin diets when the morphological and isotopic evidence discussed above are complemented with a discussion of the foods available to hominins.

The C_4 signature averaging 20-40% in all of the early hominins tested so far indicates that those individuals obtained that proportion of their foods from either grasses, sedges, animal foods, or some combination thereof, while the remaining portion of the diet derived from C_3 sources. Table 7-1 presents a simplified summary of the major types of foods available to hominins and their isotopic signatures.

The increasingly robust morphology of the australopithecines over time was probably geared toward processing large quantities of hard objects, and not C_4 foods like grass seeds, sedges, or soft animal foods. Therefore, it is most likely that the

Table 7-1. A summary of foods for African hominins grouped according to whether their isotopic signatures reflect a C_3 or C_4 photosynthetic pathway.

	C_3 Foods	**C_4 Foods**	**Mixed C_4/C_3 Foods**
Animal Foods	Large animals: Browsing large mammals (antelopes, giraffes, etc.)	Large Animals: Grazing large mammals (suids, equids, hippos, antelopes, etc.)	Large animals: Mixed feeder large mammals (antelopes, elephants, etc.)
	Small animals (monkeys, rodents, etc.)	Small animals: (hyraxes, etc.)	Small animals: (rodents, birds, etc.)
	Insects	Insects (grasshoppers, etc.)	Insects (termites, etc.)
Plant foods available in the Manyara, Serengeti, Ngorongoro study areas	C_3 marsh plants (bulbs, corms, & rhizomes of C_3 sedges and *Typha*)	C_4 marsh plants (bulbs, corms, & rhizomes of C_4 sedges)	
	C_3 grasses	C_4 grasses	
	Large Tree Fruits (figs, *Trichilia*, etc.)		
	Shrub/Small tree fruits (*Cordia*, *Grewia*, etc.)		
	Acacia seeds/pods, gum		
	Edible roots (USOs) from forbs, shrubs		
	Leaves		
	Palm tree fruits & seeds		
Plant foods available elsewhere in Africa	Nut-like oil seeds (mongongo, marula, etc.)		
	Baobab		
	Tubers (e.g., *Vigna* sp.)		
	Brachystegia seeds/pods		
	Terrestrial herbaceous vegetation (THV)		

australopithecine trend in megadontia was an adaptation to C_3 foods such as berries, seeds and pods, or hard fruits. Those foods may or may not have been the dietary staples of robust australopithecines, because their large masticatory apparatus should be seen as an adaptation that was required during times of resource stress, and was not necessarily needed all of the time. There remains a possibility that the robust masticatory system was an adaptation to eating C_4 sedge underground parts, but that possibility can only be tested when studies of the dental microwear left by sedge eating have been conducted and compared to the patterns on australopithecine molars. Perhaps the most likely way to account for the 20-40% C_4 component of australopithecine diets is that they were consuming small C_4 animal foods like termites, other insects, hyraxes, or rodents (Table 7-1). It is also plausible that australopithecines ate a good deal of marsh plants and grasses, some of which would have contributed to the C_4 signal.

Since early *Homo* had smaller teeth than the robust australopithecines, then it must not have required the same degree of mastication, even in times of resource scarcity when it potentially had to rely on less desirable food items. Therefore, at a minimum, a dietary difference between australopithecines and early *Homo* must have been in their fallback food items. If *Homo* evolved from an earlier hominin species with larger cheek teeth, as is likely, then the diet-related selection pressures acting on the cheek teeth of the *Homo* line must have been quite different than those acting on the robust australopithecines. Since the robust morphology is most likely an adaptation to C_3 foods, then the most parsimonious explanation is that some of the C_3 foods eaten by the robust australopithecines differed from the foods consumed by *Homo*.

From Table 7-1, the small, hard C_3 plant foods that were fallback foods for the robust australopithecines might have been *Acacia* seeds/pods, *Brachystegia* seeds/pods, shrub/small tree fruits, leaves, or large tree fruits. Perhaps early *Homo* lessened the need for extensive mastication by manually processing or even cooking plant foods, as suggested by O'Connell *et al*. (1999) and Wrangham *et al*. (1999). For example, they may have learned how to exploit the high quality, protein- and fat-rich nut-like oil seeds, such as the mongongo (*Ricinodendron rautanenii*) and marula (*Sclerocarya birrea*) (Peters, 1987) using pounding or crushing tools. It is also possible that early *Homo* began to dig up USO species such as those exploited by the Hadza today. Neither the nut-like oil seeds nor the favorite Hadza tuber species occurred in the Serengeti, Manyara, or Ngorongoro study areas, but this does not necessarily mean that those key plant foods were not present in the Olduvai Basin or other areas in which hominins lived. As discussed in the previous section, plant species can migrate independently over time, so evidence for their presence in the past could require the identifications of macro- or microbotanical fossils.

The few specimens of *Homo ergaster* that have been tested isotopically show no statistical difference in the proportions of C_4 foods in their diets compared to contemporaneous *Australopithecus robustus* specimens from Swartkrans (Lee-Thorp *et al*., 2000). Therefore, if the C_4 foods of australopithecines and *Homo* are assumed to derive from animal foods, then the isotopic evidence does not support the claim for increased animal food consumption (whether collected, hunted, or scavenged) by *Homo ergaster*. Instead, it supports theories such as the cooking hypothesis or the grandmother hypothesis, in which a change in the plant food component of the diet is key to a higher quality diet in early *Homo* (O'Connell *et al*., 1999; Wrangham *et al*., 1999).

On the other hand, it is possible that consumption of sedges and/or grasses is responsible for the C_4 component of some early hominin diets. It seems likely that at least some hominins would have exploited the readily available marsh plants in places like paleo-lake Olduvai, particularly given the fact that they can be considered relatively high quality foods due to their low amounts of fiber (Conklin-Brittain *et al*., 2002). It also is possible that sympatric hominin species such as australopithecines versus early *Homo* had different sources contributing to the C_4 components of their diets. Archaeological evidence of butchered remains of large grazing animals is unequivocal for the late Pliocene and early Pleistocene, so we know that at least some hominins were consuming large mammals that would have contributed to a C_4 signal. It is possible that only one hominin species, or only one group of early hominins (e.g., *Homo*) began to acquire animal foods from larger savanna mammals.

Implications for the Socioeconomic Function of Archaeological Sites

According to the home base or central place foraging hypothesis, animal and plant resources were brought by hominins to a particular safe location, such as a grove of tall trees, where they were shared between individual hominins belonging to a social group. The purpose of bringing items back to a single place would be to process the items further, such as by cooking, removing pods, or grinding, or simply to share with other individuals. If the main purpose for a central place was sharing, then that implies some sort of division of labor in which not all individuals participated in the plant food gathering expedition. For example, males might have spent time hunting or scavenging while females and children gathered plant foods and small animal foods. In any case, one would expect an energetic or social benefit in return for expending the time and energy to carry plant and animal foods to a central place.

The plant foods that I encountered in my modern analog studies for Olduvai would be amenable with a central place foraging lifestyle, for example, seeds and pods, fruits, and rootstocks could be gathered and brought to a central place for sharing. On the other hand, the nature of these wild plant foods does not require a central place foraging strategy. The plant foods that I encountered in the modern study areas could just as easily be eaten on the spot, without much processing. Thus they would be consistent with a routed foraging or “feed-as-you-go” scenario. Given that “feed-as-you-go” is the general behavior pattern of other apes, then it should be considered the most parsimonious explanation unless it can be proven otherwise.

Cooking would make a good reason to return to a central place, and would probably improve the digestibility of many plant foods such as *Acacia* pods and seeds, herbaceous leaves, and roots from shrubs (Stahl, 1984). However, cooking was not necessary for any of the major plant foods I encountered (at least it was not necessary for chimpanzees or baboons to consume those items), and the archaeological evidence for cooking is as yet too sparse for it to be considered a part of the daily food processing activities of hominins around 1.9-1.7 mya.

In favor of a central place foraging strategy, the rootstocks and bulbs of sedges and cattails might be brought to a central place not for cooking, but in order to husk or peel them in a relatively safe setting. The marsh sites in the modern analogs that were not adjacent to woodlands were typically surrounded by open grassland and high densities of carnivores, making them dangerous localities at which hominins might want to minimize their time. Sharing would also provide an impetus for central place foraging if a division of labor caused certain members of the hominin social group to forage in different parts of the landscape. In sum, at this point the actualistic evidence for plant foods is not strong enough by itself to either refute or support a central place foraging hypothesis for early hominins.

Conclusion

This was the first systematic and quantitative attempt to conduct a modern analog vegetation study specifically aimed toward addressing the nature of plant foods, refuge trees, and vegetation structure across the landscape during Olduvai's lowermost Bed II times (see Peters and Blumenschine, 1995, 1996 for earlier but less quantitative approaches to the same problem). The exercise has resulted in a better understanding of the types of plant foods available in modern East African semi-arid savannas, and quantitative data on the relationships between vegetation structure, species composition, and plant food availability. This study has also resulted in a working model of relative plant food and arboreal refuge distribution across the paleo-Olduvai basin and some ideas about the possible niche differentiation of various hominin species. In this thesis I developed a methodology by which paleoanthropology and plant ecology can be combined, and provided some lessons learned upon which future studies will benefit.

Since the relationships between plants and early hominins tend to be elusive, this study also has value to paleoanthropology in general due to its focus on this poorly understood topic. My data in combination with other findings suggest that there were substantial differences in the diets of early hominins compared to modern chimpanzees, because hominins were able to survive in arid savannas of the type that no chimpanzees inhabit today. Plant foods in the semi-arid habitats that I studied are different from those in moist savannas such as the area near Lake Tanganyika which is occupied by chimpanzees (e.g., Goodall, 1986). The fact that at least some hominins were eating animal foods is a certainty, but the use of stone tools for processing carcasses appears at least half a million years later than hominin exploitation of and presence in arid savannas, according to the isotopic evidence for a C_4 component in hominin diets by three million year ago (Sponheimer and Lee-Thorp, 1999).

My modern analog studies suggest a potential importance for sedges as early hominin plant foods, which is consistent with isotopic data for a significant C_4 contribution to early hominin diets. Evidence that sedges are a relatively high quality food because of their low fiber content also supports the idea that hominins would have exploited marsh plants (Conklin-Brittain *et al*., 2002). More actualistic work on sedge distribution and ecological tolerances, the identification of which sedges use the C_3 versus the C_4 photosynthetic pathway, dental microwear traces left by sedge consumption, and the mechanical forces required for sedge chewing will help to resolve questions about the importance of sedges to actual early hominin diets.

The nature of the plant foods found in my modern analog sites does not particularly support nor refute the idea of a central place foraging strategy among early hominins. A feed-as-you-go foraging strategy would be equally plausible for the plant foods encountered in my modern analog study areas.

The results of my actualistic vegetation studies, in combination with isotopic evidence, also support the idea that changes in the plant food components of hominin diets might have contributed significantly to the differences between *Homo habilis* and the australopithecines, and enabled the increased body size and brain size in *Homo ergaster*. Increasing archaeological evidence for large mammal exploitation during the Plio-Pleistocene and later time periods also suggests that animal food exploitation became increasingly important over time to at least some species of hominins.

As I have emphasized throughout this thesis, the nature of the relationships between land units, vegetation structure, plant community composition, and plant resources for hominins is inherently complex due to the multitude of controlling factors involved. Due to this we will never be able to reconstruct the precise vegetation of the past, but we can reconstruct important aspects of past vegetation with relative certainty, and greatly improve upon the simplistic vegetation reconstructions that exist for most early hominin sites currently. This study has brought us one step closer toward realizing that goal by taking a multidisciplinary approach that combines archaeology, landscape ecology, paleobotany, and plant ecology to address issues in paleoanthropology.

APPENDIX 1

APPENDIX 1. All Plant species encountered in the modern study areas, showing locations, edible parts, and fruit types for trees.

Family	**Species**	**Abbreviation**	**fruit type**	Flower/Inflorescence	Fruit	Seed/Pod	Leaf/Shoot	Stems	Bark/Cambium	Underground Storage	Unspecified	Endabash R.	Ndilana R.	Msasa R.	Msasa R Lac Plain	Mkindu R Lac Plain	Ndil-Msasa Interfl.	Ndala-Chem. Interfl.	Ndala Lake Flat	Msasa Lake Flat	Mkindu All Fan	Mkindu Interfl. Al.Fan	Seronera R.	Nyamara R.	Barafu R.	Mbalageti R.	Sangare R.	Ser-Wandamu Interfl	Nyamara Interfl.	Barafu Plain	Engitati	Gorigor Midwest	Gorigor North	Gorigor West	Munge Marsh	Kidogo	Mti Moja	Munge River	Mystery Spring	Ngoitokitok N & S	Seneto	Vernonia
Acanthaceae	Asystasia schimperi	Assc					x																	x	x					x												
Acanthaceae	Asystasia sp.	Assp																								x																
Acanthaceae	Barleria eranthemoides	Baer											x	x	x		x																									
Acanthaceae	Barleria micrantha	Bami																								x																
Acanthaceae	Barleria submollis	Basu													x										x																x		
Acanthaceae	Blepharis maderaspatensis	Blma										x	x				x																										
Acanthaceae	Blepharis panduriformis	Blpa																						x																			
Acanthaceae	Dicliptera sp.	Dics																		x																							
Acanthaceae	Dicliptera verticillata	Dive										x	x	x	x		x																										
Acanthaceae	Dyschoriste sp.	Disp																										x															
Acanthaceae	Hypoestes forskalei	Hyfo					x					x	x	x							x	x	x			x	x																
Acanthaceae	Hypoestes sp.	Hysp															x																										
Acanthaceae	Justicia betonica	Jube																						x		x	x														x	x	
Acanthaceae	Justicia caerulea	Juca		x											x		x																										
Acanthaceae	Justicia cordata	Juco											x					x	x																								
Acanthaceae	Justicia diclipteroides	Judi																		x																							
Acanthaceae	Justicia exigua	Juex																x		x																							
Acanthaceae	Justicia flava	Jufl					x						x	x			x	x	x	x																							
Acanthaceae	Justicia glabra	Jugl										x	x		x	x		x		x	x	x																					
Acanthaceae	Justicia matammensis	Juma		x	x		x	x															x				x																
Acanthaceae	Justicia palustois	Jupa																								x																	

Family	Species	Abbreviation	fruit type	Flower/Inflorescence	Fruit	Seed/Pod	Leaf/Shoot	Stems	Bark/Cambium	Underground Storage	Unspecified	Endabash R.	Ndilana R.	Msasa R.	Msasa R Lac Plain	Mkindu R Lac Plain	Ndil-Msasa Interfl.	Ndala-Chem. Interfl.	Ndala Lake Flat	Msasa Lake Flat	Mkindu All Fan	Mkindu Interfl. Al.Fan	Seronera R.	Nyamara R.	Barafu R.	Mbalageti R.	Sangare R.	Ser-Wandamu Interfl	Nyamara Interfl.	Barafu Plain	Engitati	Gorigor Midwest	Gorigor North	Gorigor West	Munge Marsh	Kidogo	Mti Moja	Munge River	Mystery Spring	Ngoitokitok N & S	Seneto	Vernonia
Acanthaceae	Justicia sp.	Jusp																							x	x			x	x												
Acanthaceae	Justicia stachytarpheta	Just											x	x			x	x	x																							
Acanthaceae	Justicia striata	Jusr		x			x										x										x															
Acanthaceae	Lepidagathis scabra	Lesc															x																									
Acanthaceae	Monechma debile	Mode		x			x					x	x	x	x		x	x	x	x			x																			
Acanthaceae	Peristrophe bicalyculata	Pebi											x	x	x		x	x	x	x																						
Acanthaceae	Phaulopsis imbricata	Phim					x														x	x																				
Acanthaceae	Ruellia megachlamys	Rume											x	x			x																									
Acanthaceae	Ruellia patula	Rupa					x												x	x																						
Aizoaceae	Gisekia pharnaceoides	Giph					x												x																							
Aizoaceae	Sesuvium portulacastrum	Sepo					x													x																						
Aizoaceae	Zaleya pentandra	Zape					x										x																									
Aloaceae	Aloe volkensii	Alvk																							x																	
Amaranthaceae	Achyranthes aspera	Acas					x					x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x													x	x	x	
Amaranthaceae	Aerva lanata	Aela					x																	x	x	x																
Amaranthaceae	Cyathula orthacantha	Cyor												x			x	x																								
Amaranthaceae	Digera muricata	Dimu					x						x																													
Amaranthaceae	Pupalia lappacea	Pula											x	x			x									x																
Anacardiaceae	Lannea schweinfurthii	Lasc	fleshy		x			x																		x																
Anacardiaceae	Lannea triphylla	Latp								x																x																
Anacardiaceae	Rhus natalensis	Rhna			x																																					
Anacardiaceae	Rhus quartiniana	Rhqu																						x																		
Apocynaceae	Carissa edulis	Caed			x					x														x																		

Family	Species	Abbreviation	fruit type	Flower/Inflorescence	Fruit	Seed/Pod	Leaf/Shoot	Stems	Bark/Cambium	Underground Storage	Unspecified	Endabash R.	Ndilana R.	Msasa R.	Msasa R Lac Plain	Mkindu R Lac Plain	Ndil-Msasa Interfl.	Ndala-Chem. Interfl.	Ndala Lake Flat	Msasa Lake Flat	Mkindu All Fan	Mkindu Interfl. Al.Fan	Seronera R.	Nyamara R.	Barafu R.	Mbalageti R.	Sangare R.	Ser-Wandamu Interfl	Nyamara Interfl.	Barafu Plain	Engitati	Gorigor Midwest	Gorigor North	Gorigor West	Munge Marsh	Kidogo	Mti Moja	Munge River	Mystery Spring	Ngoitokitok N & S	Seneto	Vernonia
Apocynaceae	Jasminum fluminense	Jafl										x												x	x																	
Apocynaceae	Landolphia buchananii	Labu			x							x																														
Apocynaceae	Rauvolfia caffra	Raca	fleshy													x					x																					
Apocynaceae	Tabernaemontana ventricosa	Tave	fleshy													x				x	x	x																				
Asclepiadaceae	Calotropis procera	Capr		x															x																							
Asclepiadaceae	Cynanchum hastifolium	Cyha			x																						x															
Asclepiadaceae	Gomphocarpus integer	Goin																					x																			
Asclepiadaceae	Gomphocarpus physocarpus	Goph																							x																	
Asclepiadaceae	Gomphocarpus semilunatus	Gose																								x																
Asclepiadaceae	Pentarrhinum insipidum	Pein			x		x						x																													
Asclepiadaceae	Stathmostelma pedunculatum	Stpe								x																			x													
Asparagaceae	Protasparagus africanus	Praf					x			x															x																	
Balanitaceae	Balanites aegyptiaca	Baae	fleshy		x				x				x				x							x	x				x													
Balanitaceae	Balanites glabra	Bagl	fleshy																						x	x																
Bignoniaceae	Kigelia africana	Kiaf	dry	x	x	x			x			x																														
Boraginaceae	Buglossoides arvensis	Buar																							x																	
Boraginaceae	Cordia goetzei	Cogo	fleshy													x					x	x																				
Boraginaceae	Cordia monoica	Como	fleshy		x							x	x	x	x	x	x	x					x	x		x	x		x											x		
Boraginaceae	Cordia sinensis	Cosi	fleshy		x					x		x	x	x	x		x		x	x																						
Boraginaceae	Heliotropium steudneri	Hest																						x	x				x													
Boraginaceae	Heliotropium zeylanicum	Heze																	x																							

Family	**Species**	**Abbreviation**	**fruit type**	Flower/Inflorescence	Fruit	Seed/Pod	Leaf/Shoot	Stems	Bark/Cambium	Underground Storage	Unspecified	Endabash R.	Ndilana R.	Msasa R.	Msasa R Lac Plain	Mkindu R Lac Plain	Ndil-Msasa Interfl.	Ndala-Chem. Interfl.	Ndala Lake Flat	Msasa Lake Flat	Mkindu All Fan	Mkindu Interfl. Al.Fan	Seronera R.	Nyamara R.	Barafu R.	Mbalageti R.	Sangare R.	Ser-Wandamu Interfl	Nyamara Interfl.	Barafu Plain	Engitati	Gorigor Midwest	Gorigor North	Gorigor West	Munge Marsh	Kidogo	Mti Moja	Munge River	Mystery Spring	Ngoitokitok N & S	Seneto	Vernonia
Boraginaceae	Trichodesma zeylanicum	Trze		x		x	x						x						x																							
Burseraceae	Commiphora africana	Coaf			x		x	x	x	x															x																	
Burseraceae	Commiphora eminii	Coem																								x																
Burseraceae	Commiphora merkeri	Come																							x																	
Burseraceae	Commiphora schimperi	Cosc																						x	x	x			x													
Burseraceae	Commiphora sp.	Coms																									x															
Capparaceae	Boscia angustifolia	Boan																																								
Capparaceae	Boscia mossambicensis	Bomo			x																					x																
Capparaceae	Boscia salicifolia	Bosa					x		x	x																x																
Capparaceae	Cadaba farinosa	Cafa					x	x				x	x	x	x		x	x						x		x																
Capparaceae	Capparis fascicularis	Cafs			x							x		x										x																		
Capparaceae	Capparis sepiaria	Case																								x																
Capparaceae	Capparis sp.	Casp																						x																		
Capparaceae	Capparis tomentosa	Cato			x							x		x	x			x		x				x		x			x											x		
Capparaceae	Cleome gynandra	Clgy		x			x	x					x																													
Capparaceae	Maerua sp.	Maer																																								
Capparaceae	Maerua triphylla	Matr			x					x		x	x	x	x		x	x		x						x																
Capparaceae	Thilachium africanum	Thaf		x						x		x		x	x		x					x																				
Celastraceae	Hippocratea africana	Hiaf																								x																
Celastraceae	Hippocratea paniculata	Hipa																			x																					
Celastraceae	Maytenus heterophylla	Mahe			x																			x	x																	
Combretaceae	Combretum sp.	Comb																						x																		

Family	**Species**	**Abbreviation**	**fruit type**	Flower/Inflorescence	Fruit	Seed/Pod	Leaf/Shoot	Stems	Bark/Cambium	Underground Storage	Unspecified	Endabash R.	Ndilana R.	Msasa R.	Msasa R Lac Plain	Mkindu R Lac Plain	Ndil-Msasa Interfl.	Ndala-Chem. Interfl.	Ndala Lake Flat	Msasa Lake Flat	Mkindu All Fan	Mkindu Interfl. Al.Fan	Seronera R.	Nyamara R.	Barafu R.	Mbalageti R.	Sangare R.	Ser-Wandamu Interfl	Nyamara Interfl.	Barafu Plain	Engitati	Gorigor Midwest	Gorigor North	Gorigor West	Munge Marsh	Kidogo	Mti Moja	Munge River	Mystery Spring	Ngoitokitok N & S	Seneto	Vernonia
Commelinaceae	Aneilima petersii	Anpe														x																										
Commelinaceae	Commelina africana	Coma		x	x		x	x					x	x			x	x	x	x																						
Commelinaceae	Commelina benghalensis	Cobe		x	x		x	x				x		x											x		x		x													
Commelinaceae	Commelina erecta	Coer		x				x																	x																	
Commelinaceae	Commelina foliacea	Cofo											x																													
Commelinaceae	Commelina imberbis	Coim										x																														
Commelinaceae	Commelina sp.	Cosp										x					x																									
Compositae	Acanthospermum hispidum	Achi										x	x	x	x		x	x	x	x																						
Compositae	Acanthospermum sp.	Acts																x																								
Compositae	Ageratum conyzoides	Agco		x			x												x																							
Compositae	Aspilia mossambicensis	Asmo					x																x	x		x	x															
Compositae	Bidens pilosa	Bipi					x						x	x			x	x	x	x		x																		x		
Compositae	Bidens schimperi	Bisc					x					x	x	x	x								x																			
Compositae	Blumea mollis	Blmo												x																												
Compositae	Conyza bonariensis	Cobo												x																												
Compositae	Conyza newii	Cone																																						x		
Compositae	Conyza stricta	Cost																												x												
Compositae	Crassocephalum picridifolium	Crpi																																						x		
Compositae	Crassocephalum rubens	Crru					x																																			
Compositae	Crassocephalum vitellinum	Crvi					x																																	x		
Compositae	Eclipta prostrata	Ecpr		x	x		x	x								x		x	x																							
Compositae	Emilia coccinea	Emco					x																					x														

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Compositae	Galinsoga parviflora	Gapa												x				x																								
Compositae	Gutenbergia cordifolia	Guco										x	x	x			x						x				x	x												x		
Compositae	Gutenbergia petersii	Gupe																							x		x	x														
Compositae	Gutenbergia polycephala	Gupc																								x																
Compositae	Gutenbergia polytrichotoma	Gupo											x	x			x	x	x	x				x																		
Compositae	Helichrysum forskahlii	Hefo																												x												
Compositae	Helichrysum glumaceum	Hegl																							x					x												
Compositae	Hirpicium diffusum	Hidi																							x					x												
Compositae	Launaea cornuta	Laco					x													x																	x					
Compositae	Microglossa pyrrhopappa	Mipy																											x													
Compositae	Osteospermum vaillantii	Osva																							x																	
Compositae	Pluchea dioscoridis	Pldi																								x																
Compositae	Pluchea sordida	Plso																								x																
Compositae	Sphaeranthus cyathuloides	Spcy																	x																							
Compositae	Sphaeranthus napierae	Spna																															x									
Compositae	Sphaeranthus steetzii	Spst																									x															
Compositae	Sphaeranthus suaveolens	Spsu																																			x			x		x
Compositae	Sphaeranthus ukambensis	Spuk												x						x																						
Compositae	Tagetes minuta	Tami												x				x		x						x														x		
Compositae	Vernonia	Vega																																						x		

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	galamensis																																									
Compositae	Vernonia myriantha	Vemy		x			x	x																																		x
Compositae	Vernonia sp.	Vesp																							x	x																
Compositae	Vernonia sp. 1	Ves1																							x																	
Compositae	Vernonia sp. 2	Ves2																							x																	
Compositae	Xanthium pungens	Xapu																		x																						
Convolvulaceae	Ipomoea arachnosperma	Ipar											x														x															
Convolvulaceae	Ipomoea cairica	Ipca					x									x										x																
Convolvulaceae	Ipomoea coptica	Ipco		x	x														x																							
Convolvulaceae	Ipomoea hochstetteri	Ipho																	x																							
Convolvulaceae	Ipomoea jaegeri	Ipja																							x																	
Convolvulaceae	Ipomoea mombassana	Ipmo			x																						x															
Convolvulaceae	Ipomoea obscura	Ipob			x		x						x	x			x	x	x																							
Convolvulaceae	Ipomoea purpurea	Ippu										x																														
Convolvulaceae	Ipomoea sinensis	Ipsi		x	x		x			x													x				x	x														
Convolvulaceae	Ipomoea sp.	Ipsp											x											x																		
Crassulaceae	Kalanchoe densiflora	Kade																							x	x	x															
Cruciferae (nom alt. Brassicaceae)	Rorripa nasturtium-aquaticum	Rona																																							x		
Cucurbitaceae	Coccinia grandis	Cogr			x		x						x	x			x	x	x	x																						
Cucurbitaceae	Corallocarpus epigaeus	Coep																							x																	
Cucurbitaceae	Ctenolepis ceraciformis	Ctce											x				x		x																							
Cucurbitaceae	Cucumis aculeatus	Cuac											x																													
Cucurbitaceae	Cucumis dipsaceus	Cudi				x							x				x		x	x																						

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Cucurbitaceae	Cucumis figarei	Cufi																						x		x																
Cucurbitaceae	Cucumis grandis	Cugr											x																													
Cucurbitaceae	Kedrostis foetidissima	Kefo					x						x	x			x	x	x																							
Cucurbitaceae	Kedrostis hirtella	Kehi			x								x																													
Cucurbitaceae	Lagenaria siceraria	Lasi			x		x							x			x	x		x																						
Cyperaceae	Cyperus immensus	Cyim								x																					x	x	x	x	x		x	x	x	x	x	x
Cyperaceae	Cyperus involucrates	Cyin														x					x					x																
Cyperaceae	Cyperus laevigatus	Cylv						x		x																					x	x	x	x		x	x	x		x	x	
Cyperaceae	Cyperus laxus	Cylx																													x			x			x				x	x
Cyperaceae	Cyperus oblongus subsp. flavus	Cyob																	x																							
Cyperaceae	Cyperus pulchellus	Cypu																	x																							
Cyperaceae	Cyperus rotundus	Cyro								x													x						x						x					x		
Cyperaceae	Cyperus sesquiflorus	Cysq																																			x			x	x	x
Cyperaceae	Cyperus sp.	Cysp																		x																						
Cyperaceae	Cyperus usitatus	Cyus								x									x																							
Cyperaceae	Kyllinga alba	Kyal								x																																
Cyperaceae	Mariscus mollifes	Mamo																											x													
Cyperaceae	Scirpus inclinatus	Scin																													x				x		x		x	x	x	x
Ebenaceae	Euclea divinorum	Eudi			x		x																	x																		
Ebenaceae	Euclea racemosa	Eura			x																						x															
Ebenaceae	Euclea sp.	Eusp																						x																		
Euphorbiaceae	Acalypha crenata	Accr																									x															
Euphorbiaceae	Acalypha fruticosa	Acfr			x			x				x	x	x	x	x	x	x	x	x	x	x				x	x															
Euphorbiaceae	Acalypha indica	Acin					x						x	x			x		x	x		x																				
Euphorbiaceae	Acalypha ornata	Acor			x		x					x	x								x	x		x			x															

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Euphorbiaceae	Acalypha sp.	Aca2																								x																
Euphorbiaceae	Acalypha volkensii	Acvo																						x		x	x															
Euphorbiaceae	Croton macrostachyus	Crma	dry		x																x	x																		x		
Euphorbiaceae	Croton megalocarpus	Crme	dry									x																														
Euphorbiaceae	Dalechampia adherensis	Doad										x																														
Euphorbiaceae	Dalechampia parvifolia	Dopa										x																														
Euphorbiaceae	Euphorbia candelabrum	Euca	dry	x			x																																		x	
Euphorbiaceae	Euphorbia heterophylla	Euhe												x																												
Euphorbiaceae	Euphorbia mossambicensis	Eumo																							x					x												
Euphorbiaceae	Euphorbia systyloides	Eusy			x																				x																	
Euphorbiaceae	Flueggea virosa	Flvi			x								x											x		x	x															
Euphorbiaceae	Phyllanthus amarus	Pham																							x					x												
Euphorbiaceae	Phyllanthus fischeri	Phfi										x							x				x	x	x	x	x															
Euphorbiaceae	Phyllanthus nummulariifolius	Phnu																	x																							
Euphorbiaceae	Phyllanthus odontadenius	Phod											x																													
Euphorbiaceae	Phyllanthus sepialis	Phse										x	x	x																												
Euphorbiaceae	Tragia benthamii	Trbe																				x																				
Fern	Stegnogramma pozoi	Stpo																																						x		
Flacourtiaceae	Dovyalis centrocarpa	Doce										x																														
Flacourtiaceae	Dovyalis sp.	Dosp																			x	x																				

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Flacourtiaceae	Dovyalis xanthocarpa	Doxa			x									x							x																					
Gentianaceae	Enicostema axillare	Ecax																												x												
Geraniaceae	Monsonia angustifolia	Moan																							x					x												
Gramineae	Andropogon greenwayi	Angr																																						x		
Gramineae	Aristida adscensionis	Arad				x								x			x		x				x		x					x							x					
Gramineae	Brachiaria deflexa	Brde				x	x			x		x	x	x			x		x	x																						
Gramineae	Brachiaria nubica	Brnu																	x																							
Gramineae	Brachiaria scalaris	Brsc																	x																							
Gramineae	Brachiaria serrifolia	Brse				x											x																									
Gramineae	Brachyachne patentiflora	Brpa																							x																	
Gramineae	Cenchrus ciliaris	Ceci												x											x																	
Gramineae	Cenchrus sp.	Cesp																						x					x													
Gramineae	Chloris gayana	Chga																					x	x	x		x	x	x			x	x				x			x		
Gramineae	Chloris pycnothrix	Chpy																					x		x					x							x					
Gramineae	Chloris virgata	Chvi											x	x			x	x	x	x					x					x												
Gramineae	Chloris sp.	Chsp																							x																	
Gramineae	Cymbopogon caesius	Cyca																																								
Gramineae	Cynodon dactylon	Cyda				x	x	x		x						x			x	x			x		x					x	x	x	x			x	x	x		x	x	
Gramineae	Cynodon nlemfuensis	Cynl												x																										x		
Gramineae	Cynodon plectostachyus	Cypl				x	x	x		x		x	x	x	x		x																									
Gramineae	Dactyloctenium aegyptium	Daae				x				x			x	x			x	x	x	x					x																	
Gramineae	Digitaria ciliaris	Digc				x																					x															
Gramineae	Digitaria	Dima																											x	x	x											

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	macroblephara																																									
Gramineae	Digitaria milanjiana	Dimi				x																			x				x												x	
Gramineae	Digitaria velutina	Digv				x	x	x		x		x	x	x	x		x	x	x	x					x					x												
Gramineae	Diplachne fusca	Difu																																x			x			x	x	x
Gramineae	Echinochloa colona	Ecco				x								x																												
Gramineae	Echinochloa haploclada	Echa				x												x	x	x			x																			
Gramineae	Echinochloa sp.	Ecsp											x																													
Gramineae	Eleusine indica	Elin				x														x																						
Gramineae	Enneapogon cenchroides	Ence											x	x			x		x						x																	
Gramineae	Enteropogon machrostachyus	Enma															x																									
Gramineae	Eragrostis arenicota	Erar																																			x					
Gramineae	Eragrostis aspera	Eras															x								x																	
Gramineae	Eragrostis cilianensis	Erci				x																								x												
Gramineae	Eragrostis cylindriflora	Ercy																					x																			
Gramineae	Eragrostis heteromera	Erhe																							x					x												
Gramineae	Eragrostis racemosa	Erra																							x																	
Gramineae	Eragrostis superba	Ersu												x																												
Gramineae	Eragrostis tenuifolia	Erte																																						x		
Gramineae	Eriochloa fatmensis	Erfa																		x																						
Gramineae	Eriochloa meyerana	Erme												x						x																						
Gramineae	Gramineae	Gram																																								
Gramineae	green river edge	grri																								x																

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	grass																																									
Gramineae	Harpachne schimperi	Hasc																							x					x												
Gramineae	Heteropogon contortus	Heco								x				x											x																	
Gramineae	Hyparrhenia filipendula	Hyfi				x	x	x																	x			x														
Gramineae	Hyparrhenia hirta	Hyhi						x																																x		
Gramineae	Oplismenus hirtellus	Ophi														x						x																				
Gramineae	Oplismenus undulatifolius	Opun																				x																				
Gramineae	Panicum atrosanguineum	Paat																					x							x												
Gramineae	Panicum cf. repens	Pare																														x		x								
Gramineae	Panicum cf. subalbidum	Pasb				x																																x				
Gramineae	Panicum deustum	Pade				x								x		x																										
Gramineae	Panicum maximum	Pama				x	x	x										x	x	x	x			x			x	x														
Gramineae	Pennisetum clandestinum	Pecl																																		x		x	x		x	x	
Gramineae	Pennisetum mezianum	Peme																						x	x	x	x	x	x	x	x												
Gramineae	Pennisetum spinaculatum	Pesn																								x																
Gramineae	Pennisetum sp.	Pesp																							x																	
Gramineae	Pennisetum subanguatum	Pesu																					x	x	x	x		x		x												
Gramineae	Phragmites mauritianus	Phma					x	x																																x		
Gramineae	Psilolemma jaegeri	Dija																																			x					
Gramineae	Rhynchelytrum repens	Rhre													x																											

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Gramineae	Setaria homonyma	Seho										x	x	x				x									x													x		
Gramineae	Setaria incrassata	Sein				x																						x														
Gramineae	Setaria sagittifolia	Sesa											x	x	x		x	x	x																							
Gramineae	Setaria sp.	Sesp												x																												
Gramineae	Setaria verticillata	Seve											x	x			x	x	x	x			x		x	x	x													x		
Gramineae	Sporobolus africanus	Spaf					x																																	x		
Gramineae	Sporobolus consimilis	Spcn				x	x			x									x	x			x	x	x	x																
Gramineae	Sporobolus cordofanus	Spco											x	x			x		x	x			x																			
Gramineae	Sporobolus fimbriatus	Spfi				x																	x		x			x	x	x												
Gramineae	Sporobolus ioclados	Spio				x												x	x	x			x	x	x		x			x												
Gramineae	Sporobolus spicatus	Spsp				x													x				x		x								x				x					
Gramineae	Sporobolus tenuissimus	Spte											x																													
Gramineae	Tetrapogon cenchriformis	Tece												x			x																									
Gramineae	Themeda triandra	Thtr		x		x	x	x															x	x	x			x	x	x	x		x							x		
Gramineae	Tragus berteroniarus	Trgb											x	x					x																							
Gramineae	unid. tall grass	unta																								x																
Gramineae	Urochloa mosambicensis	Urmo				x				x		x	x	x	x		x	x																								
Gramineae	Urochloa panicoides	Urpa											x	x			x																									
Hypoxidaceae	Hypoxis sp.	Hyxs																											x													
Illecebraceae	Pollichia campestris	Poca		x	x		x	x																	x																	
Labiatae	Becium capitatum	Beca																							x					x												
Labiatae	Becium filamentosum	Befi																												x												

Family	**Species**	**Abbreviation**	**fruit type**	Flower/Inflorescence	Fruit	Seed/Pod	Leaf/Shoot	Stems	Bark/Cambium	Underground Storage	Unspecified	Endabash R.	Ndilana R.	Msasa R.	Msasa R Lac Plain	Mkindu R Lac Plain	Ndil-Msasa Interfl.	Ndala-Chem. Interfl.	Ndala Lake Flat	Msasa Lake Flat	Mkindu All Fan	Mkindu Interfl. Al.Fan	Seronera R.	Nyamara R.	Barafu R.	Mbalageti R.	Sangare R.	Ser-Wandamu Interfl	Nyamara Interfl.	Barafu Plain	Engitati	Gorigor Midwest	Gorigor North	Gorigor West	Munge Marsh	Kidogo	Mti Moja	Munge River	Mystery Spring	Ngoitokitok N & S	Seneto	Vernonia
Labiatae	Becium sp.	Besp																											x	x												
Labiatae	Hoslundia opposita	Hoop			x							x		x																												
Labiatae	Hoslundia sp.	Hosp																						x																		
Labiatae	Leonitis nepetifolia	Lenp		x			x						x	x				x	x				x													x					
Labiatae	Leonitis sp.	Lesp											x																												
Labiatae	Leucas glabrata	Legl														x												x													
Labiatae	Leucas martinicensis	Lema											x												x		x														
Labiatae	Leucas neuflizeana	Lene																		x					x			x		x											
Labiatae	Leucas sp.	Leus																		x																					
Labiatae	Ocimum basilicum	Ocba					x						x	x			x	x	x	x																					
Labiatae	Ocimum sp.	Ocsp																								x															
Labiatae	Ocimum suave	Ocsu										x		x							x			x		x													x		x
Labiatae	Orthosiphon pallidus	Orpa												x																											
Labiatae	Orthosiphon parvifolius	Orpv															x													x											
Labiatae	Plectranthus flaccidus	Plfl																		x																					
Labiatae/Verbenaceae	Labiatae/Verbenaceae	Lave																								x															
Leguminosae (Caesalpinioideae)	Caesalpinia trothae	Catr																								x															
Leguminosae (Caesalpinioideae)	Cassia angustifolia	Caan																																						x	
Leguminosae (Caesalpinioideae)	Chamaecrista mimosoides	Chmi				x	x																					x													
Leguminosae (Caesalpinioideae)	Senna bicapsularis	Sebi														x					x	x																			

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Leguminosae (Caesalpinioideae)	Senna didymobotrya	Sedi																				x																	x		x	
Leguminosae (Caesalpinioideae)	Senna obtusifolia	Seob				x																																		x		
Leguminosae (Caesalpinioideae)	Senna occidentalis	Seoc				x							x						x	x		x																				
Leguminosae (Caesalpinioideae)	Senna sp.	Senn																																						x		
Leguminosae (Caesalpinioideae)	Sesbania bispinosa	Sebs																									x															
Leguminosae (Mimosoideae)	Acacia albida	Acal	dry			x			x											x																						
Leguminosae (Mimosoideae)	Acacia brevispica	Acbr	dry								x																x															
Leguminosae (Mimosoideae)	Acacia drepanolobium	Acdr	dry			x																			x																	
Leguminosae (Mimosoideae)	Acacia kirkii	Acki	dry						x															x		x																
Leguminosae (Mimosoideae)	Acacia lahai	Acla	dry																	x																						
Leguminosae (Mimosoideae)	Acacia mellifera	Acme				x	x		x																																	
Leguminosae (Mimosoideae)	Acacia robusta	Acro	dry	x		x	x		x													x				x	x															
Leguminosae (Mimosoideae)	Acacia robusta subs. usambarensis	Acru	dry	x		x	x		x					x	x																											
Leguminosae (Mimosoideae)	Acacia schweinfurthii	Acsc	dry									x	x																													

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Leguminosae (Mimosoideae)	Acacia seedlings	Acsd	dry																										x													
Leguminosae (Mimosoideae)	Acacia senegal	Acse	dry	x		x	x		x																				x													
Leguminosae (Mimosoideae)	Acacia sieberiana	Acsi	dry	x		x			x			x																														
Leguminosae (Mimosoideae)	Acacia sp. 1	Acsp	dry																					x																		
Leguminosae (Mimosoideae)	Acacia sp. 2	Acs2	dry																					x																		
Leguminosae (Mimosoideae)	Acacia sp. 3	Acs3	dry																								x															
Leguminosae (Mimosoideae)	Acacia tortilis	Acto	dry	x		x	x		x			x	x	x	x		x	x	x	x				x	x	x			x													
Leguminosae (Mimosoideae)	Acacia xanthophloea	Acxa	dry			x			x							x				x			x	x	x	x	x												x	x	x	
Leguminosae (Mimosoideae)	Albizia gummifera	Algu	dry																							x	x													x		
Leguminosae (Mimosoideae)	Albizia harveyi	Alha	dry	x		x																		x		x	x															
Leguminosae (Mimosoideae)	Dichrostachys cinerea	Dici					x		x															x			x		x													
Leguminosae (Papilionoideae)	Aeschynomene indica	Aein																	x																							
Leguminosae (Papilionoideae)	Aeschynomene schimperi	Aesc																																				x				
Leguminosae (Papilionoideae)	Calpurnia aurea	Caau																																						x		

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Leguminosae (Papilionoideae)	Crotalaria deflersii	Crde																							x																	
Leguminosae (Papilionoideae)	Crotalaria incana	Crin															x			x			x																			
Leguminosae (Papilionoideae)	Crotalaria kirkii	Crki																										x														
Leguminosae (Papilionoideae)	Crotalaria polysperma	Crpo					x												x											x												
Leguminosae (Papilionoideae)	Crotalaria spinosa	Crsp																					x		x			x														
Leguminosae (Papilionoideae)	Crotalaria sp.	Crot																																								x	
Leguminosae (Papilionoideae)	Glycine sp.	Glsp																						x																		
Leguminosae (Papilionoideae)	Indigofera arrecta	Inar								x			x	x			x	x	x	x					x	x																
Leguminosae (Papilionoideae)	Indigofera basiflora	Inba																						x					x													
Leguminosae (Papilionoideae)	Indigofera colutea	Inco				x													x						x					x												
Leguminosae (Papilionoideae)	Indigofera hochstetteri	Inho																							x					x												
Leguminosae (Papilionoideae)	Indigofera spicata	Insp											x																	x												
Leguminosae (Papilionoideae)	Indigofera sp.	Inds											x				x							x	x																	
Leguminosae (Papilionoideae)	Indigofera tenuis	Inte																	x																							

Family	**Species**	**Abbreviation**	**fruit type**	Flower/Inflorescence	Fruit	Seed/Pod	Leaf/Shoot	Stems	Bark/Cambium	Underground Storage	Unspecified	Endabash R.	Ndilana R.	Msasa R.	Msasa R Lac Plain	Mkindu R Lac Plain	Ndil-Msasa Interfl.	Ndala-Chem. Interfl.	Ndala Lake Flat	Msasa Lake Flat	Mkindu All Fan	Mkindu Interfl. Al.Fan	Seronera R.	Nyamara R.	Barafu R.	Mbalageti R.	Sangare R.	Ser-Wandamu Interfl	Nyamara Interfl.	Barafu Plain	Engitati	Gorigor Midwest	Gorigor North	Gorigor West	Munge Marsh	Kidogo	Mti Moja	Munge River	Mystery Spring	Ngoitokitok N & S	Seneto	Vernonia
Leguminosae (Papilionoideae)	Indigofera volkensii	Invo																							x					x												
Leguminosae (Papilionoideae)	Lotus arabicus	Loar																																						x		
Leguminosae (Papilionoideae)	Lotus goetzei	Logo																																			x					
Leguminosae (Papilionoideae)	Medicago laciniata	Mela																							x					x												
Leguminosae (Papilionoideae)	Ormocarpum kirkii	Orki					x																	x																		
Leguminosae (Papilionoideae)	Rhynchosia minima	Rhmi				x																		x	x		x			x												
Leguminosae (Papilionoideae)	Tephrosia pumila	Tepu				x																						x														
Leguminosae (Papilionoideae)	Tephrosia purpurea	Tepr								x													x																			
Leguminosae (Papilionoideae)	Tephrosia rhodesica	Terh											x																													
Leguminosae (Papilionoideae)	Tephrosia villosa	Tevi												x					x																							
Leguminosae (Papilionoideae)	Vigna schimperi	Visc																																						x		
Leguminosae (Papilionoideae)	Vigna vexillata	Vive		x		x	x			x																														x		
Lemnaceae	Lemna gibba	Legi														x																										
Lemnaceae	Lemna sp.?	Utla																													x						x					
Loranthaceae	Plicosepalus curviflorus	Plcu												x																												

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Malvaceae	Abutilon angulatum	Aban																								x																
Malvaceae	Abutilon bidentatum	Abbi											x		x	x	x			x																						
Malvaceae	Abutilon grandiflorum	Abgr											x																													
Malvaceae	Abutilon hirtum	Abhi				x							x				x																									
Malvaceae	Abutilon longicuspe	Ablo											x														x															
Malvaceae	Abutilon mauritianum	Abma		x		x							x	x			x	x							x	x	x														x		
Malvaceae	Abutilon ridentatum	Abri												x																												
Malvaceae	Abutilon sp.	Absp										x					x			x		x				x																
Malvaceae	Azanza sp.	Azsp												x																												
Malvaceae	Hibiscus aponeurus	Hiap					x																				x															
Malvaceae	Hibiscus cannabinus	Hica		x	x	x	x		x											x			x																			
Malvaceae	Hibiscus flavifolius	Hifl																							x																	
Malvaceae	Hibiscus micranthus	Himi			x							x		x					x					x	x		x		x													
Malvaceae	Hibiscus ovalifolius	Hiov		x		x	x					x	x	x	x		x	x	x	x	x	x		x		x	x															
Malvaceae	Hibiscus sp.	Hisp															x							x																		
Malvaceae	Malvastrum coromandelianum	Maco												x	x	x					x	x																				
Malvaceae	Malvastrum sp.	Masp																			x																					
Malvaceae	Pavonia patens	Papa											x	x			x	x	x	x		x																				
Malvaceae	Pavonia urens (Car.)	Paur										x																														
Malvaceae	Sida acuta	Siac		x		x						x		x																												
Malvaceae	Sida alba	Sial		x		x	x								x		x			x																						
Malvaceae	Sida ovata	Siov					x						x	x			x	x	x	x					x			x		x												

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Malvaceae	Wissadula paplosidifolia	Wipa										x																														
Meliaceae	Ekebergia capensis	Ekca	fleshy		x											x					x																					
Meliaceae	Trichilia emetica	Trem	dry		x							x	x	x	x	x					x	x																				
Menispermaceae	Cissampelos mucronata	Cimu														x																										
Moraceae	Antiaris toxicaria	Anto			x																	x																				
Moraceae	Ficus sp.	Fisp	fleshy		x																						x															
Moraceae	Ficus sycomorus	Fisy	fleshy		x		x							x		x					x	x		x																		
Moraceae	Maclura africana	Maaf										x																														
Nyctaginaceae	Boerhavia diffusa	Bodi				x	x			x			x	x			x	x																								
Nyctaginaceae	Boerhavia erecta	Boer												x			x		x	x																						
Onagraceae	Ludwigia sp.	Lusp																																					x				
Onagraceae	Ludwigia stolonifera	Lust																																							x		
Opiliaceae	Opilia amentacea	Opam										x		x	x																											
Orchidaceae	Ansellia sp.	Ansp																								x																
Orobanchaceae	Cistanche tubulosa	Citu													x																											
Palmae	Hyphaene petersiana	Hype	fleshy		x	x														x																						
Palmae	Phoenix reclinata	Phre			x		x		x							x					x	x																				
Passifloraceae	Commicarpus pedunculosis	Cope																							x																	
Passifloraceae	Commicarpus plumbagineus	Copl																x								x																
Phytolaccaceae	Phytolacca dodecandra	Phdo					x																	x																	x		
Plumbaginaceae	Plumbago dawei	Plda																						x																			
Plumbaginaceae	Plumbago zeylanica	Plze																								x																
Polygalaceae	Polygala sphenoptera	Posp																												x												

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Polygonaceae	Oxygonum sinuatum	Oxsi			x		x											x	x																							
Polygonaceae	Persicaria decipiens	Pede					x																												x							
Polygonaceae	Persicaria senegalensis	Pese					x			x																														x		
Portulacaceae	Portulaca foliosa	Pofo																	x																							
Portulacaceae	Portulaca oleracea	Pool					x	x											x																							
Rhamnaceae	Helinus mystacinus	Hemy																																						x		
Rhamnaceae	Ziziphus mucronata	Zimu			x		x																	x		x																
Rhamnaceae	Ziziphus pubescens	Zipu	fleshy		x		x					x										x																				
Rhamnaceae	Ziziphus sp.	Zisp																				x																				
Rubiaceae	Canthium pseudosetiflorum	Caps										x																														
Rubiaceae	Gardenia ternifolia	Gate	fleshy		x							x	x	x			x	x				x																				
Rubiaceae	Kohautia caespitosa	Koca																	x						x																	
Rubiaceae	Oldenlandia fastigiata	Olfa																	x																							
Rubiaceae	Pavetta dolichantha	Pado											x												x																	
Rubiaceae	Pavetta sepium	Pase										x	x	x	x		x	x				x																				
Rubiaceae	Pavetta sp.	Pasp																						x		x																
Rubiaceae	Pavetta subcana	Pasu										x																														
Rubiaceae	Vangueria madagascariensis	Vama			x							x										x																		x		x
Rubiaceae	Vangueria sp.	Vasp																						x		x																
Rutaceae	Clausena anisata	Clan			x																			x		x																
Rutaceae	Vepris lanceolata	Vela	fleshy																					x																		
Rutaceae	Vepris madagascarensis	Vema										x																														

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Rutaceae	Vepris uguenensis	Veug											x	x	x		x	x																								
Salvadoraceae	Salvadora persica	Sape			x		x		x			x	x	x	x		x	x	x	x																						
Sapindaceae	Cardiospermum halicacabum	Caha					x												x																							
Sapindaceae	Pappea capensis	Paca			x		x																		x																	
Scrophulariaceae	Alectra vogelii	Alvo																							x																	
Scrophulariaceae	Craterostigma plantagineum	Crpl																											x													
Scrophulariaceae	Striga gesnerioides	Stge																	x																							
Simaroubaceae	Harrisonia abyssinica (Oliv.)	Haab			x							x																														
Solanaceae	Datura stramonium	Dast											x						x	x																				x		
Solanaceae	Lycium europaeum	Lyeu											x				x								x				x													
Solanaceae	Nicandra physalodes	Niph												x																												
Solanaceae	Solanum incanum	Soin			x		x	x				x	x	x			x	x	x	x			x	x	x	x	x	x	x	x									x		x	
Solanaceae	Solanum nigrum	Soni											x	x		x									x																	
Solanaceae	Solanum setaceum	Sose												x			x	x	x						x			x														
Solanaceae	Solanum sp.	Sosp																											x									x				
Sterculiaceae	Dombeya cincinnata	Doci																						x																		
Sterculiaceae	Dombeya malacoxylon	Doma																								x																
Sterculiaceae	Mansonia sp.	Mans																																						x		
Sterculiaceae	Melhania ovata	Meov									x														x				x	x												
Sterculiaceae	Melhania velutina	Meve												x					x																							
Tiliaceae	Corchorus tridens	Cotr					x												x	x																						
Tiliaceae	Corchorus trilocularis	Coti					x							x									x																			
Tiliaceae	Grewia bicolor	Grbi			x																			x		x	x															
Tiliaceae	Grewia forbesii	Grfo		x	x		x																				x															

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Tiliaceae	Grewia sp.	Grsp			x																																					
Tiliaceae	Grewia stolzii	Grst			x																						x															
Tiliaceae	Grewia tembensis	Grte			x																					x	x															
Tiliaceae	Triumfetta flavescens	Trfl																		x																						
Typhaceae	Typha latifolia	Tyla		x						x																							x		x					x	x	
Ulmaceae	Celtis africana	Ceaf	fleshy				x								x																											
Ulmaceae	Celtis zenkeri	Ceze																			x	x																				
Umbelliferae	Centella asiatica	Ceas														x																										
Umbelliferae	Hydrocotyle ranunculoides	Hyra														x																										
Umbelliferae (nom. alt. Apiaceae)	Hydrocotyle mannii	Hyma																														x										
Umbelliferae (nom. alt. Apiaceae)	Hydrocotyle sibthorpioides	Hysi																																x		x			x	x		
Verbenaceae	Lantana rhodesiensis	Larh			x														x																							
Verbenaceae	Lantana sp.	Lasp																																								
Verbenaceae	Lantana trifolia	Latr			x																				x																	
Verbenaceae	Lippia javanica	Lija					x																	x	x														x	x		
Verbenaceae	Lippia ukambensis	Liuk				x																		x	x	x														x		x
Verbenaceae	Priva adhaerens	Prad										x			x		x																									
Verbenaceae	Priva curtisiae	Prcu										x													x																	
Verbenaceae	Priva parvifolia	Prpa															x																									
Vitaceae	Cyphostemma kerkrooderi	Cyke																											x													
Vitaceae	Cyphostemma kilimandscharicum	Cyki																							x																	
Vitaceae	Cyphostemma serpens	Cyse																											x													

Family	**Species**	**Abbreviation**	**fruit type**	Flower/Inflorescence	Fruit	Seed/Pod	Leaf/Shoot	Stems	Bark/Cambium	Underground Storage	Unspecified	Endabash R.	Ndilana R.	Msasa R.	Msasa R Lac Plain	Mkindu R Lac Plain	Ndil-Msasa Interfl.	Ndala-Chem. Interfl.	Ndala Lake Flat	Msasa Lake Flat	Mkindu All Fan	Mkindu Interfl. Al.Fan	Seronera R.	Nyamara R.	Barafu R.	Mbalageti R.	Sangare R.	Ser-Wandamu Interfl	Nyamara Interfl.	Barafu Plain	Engitati	Gorigor Midwest	Gorigor North	Gorigor West	Munge Marsh	Kidogo	Mti Moja	Munge River	Mystery Spring	Ngoitokitok N & S	Seneto	Vernonia
Zygophyllaceae	Tribulus terrestris	Trte		x			x										x		x																							

APPENDIX 2

Summary description of edible plants (Peters *et al*., 1992) in each of the modern study areas. For regions, M=Manyara, S=Serengeti, and N=Ngorongoro.

Reg-ion	**Land-scape Assoc-iation**	**Facet**	**Study Area**	**Description of Edibles**
M	Lacus-trine Plain	riverine	Mkindu River on lacustrine plain (M-MKILF)	*Acacia xanthophloea* trees with edible gum (and marginally edible seeds and pods); a few *Acacia tortilis* trees and shrubs have more nutritious edible pods and also edible leaves and flowers. Very small amounts of edible shrub fruits: *Acalypha fruticosa* and *Cordia monoica*. Small amount of edible herbaceous greens, *Achyranthes aspera*, and one edible grass (*Cynodon dactylon*) is present.
M	Lacus-trine Plain	riverine	Msasa River on lacustrine plain (M-MSALF)	Trees dominantly *Acacia tortilis* with edible pods, leaves, and flowers, and *Trichilia emetica* with edible seed arils (fruits). Several shrubs with edible fruits: *Acalypha fruticosa*, *Salvadora persica*, *Capparis tomentosa*, *Maerua triphylla*, and *Cordia sinensis*, the latter two of which also have edible roots. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Monechma debile* with edible flowers and leaves, and *Hibiscus ovalifolius* with edible leaves, seeds, and flower buds. Four edible grasses are present.
M	Lacus-trine Plain	non-riverine	Msasa Lake Flat (M-MLF)	The few trees that are present are *A. tortilis* with edible pods, leaves, and flowers, *A. xanthophloea* with edible sap (and marginally edible seeds/pods), and *Hyphaene petersiana* palms which have edible fruits and seeds. Edible shrub fruits include *Acalypha fruticosa*, *Salvadora persica*, *Capparis tomentosa*, *Maerua triphylla*, and *Cordia sinensis*, the latter two of which also have edible roots. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Monechma debile* with edible flowers and leaves, *Solanum incanum* with edible leaves and possibly fruit, *Sida ovata* with edible leaves, *Hibiscus ovalifolius* with edible leaves, seeds, and flower buds, *Commelina africana* with edible whole plant, *Indigofera arrecta* with edible root, *Ocimum basilicum* with edible leaves/shoots, and *Bidens pilosa* with edible leaves/shoots. Nine edible grasses are present.

Reg-ion	**Land-scape Assoc-iation**	**Facet**	**Study Area**	**Description of Edibles**
M	Lacus-trine Plain	non-riverine	Ndala Lake Flat (M-NLF)	The only trees are scattered *A. tortilis* (some are shrubs) with edible pods, leaves, and flowers. Edible shrub fruits and leaves come from *Salvadora persica* and *Acalypha fruticosa*, while *Hibiscus ovalifolius* provides edible shrub seeds, leaves, and flowers. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Monechma debile* with edible flowers and leaves, *Solanum incanum* with edible leaves and possibly fruit, *Sida ovata* with edible leaves, *Commelina africana* with edible whole plant, *Indigofera arrecta* with edible root, *Ocimum basilicum* with edible leaves/shoots, and *Bidens pilosa* with edible leaves/shoots. Ten edible grasses are present.
M	Lacus-trine Terrace	riverine	Msasa River on Lacustrine Terrace (M-MSA)	Edible trees are many *Acacia tortilis* with edible pods, leaves, and flowers, and the occasional *Ficus sycomorus* with high quality edible fig fruits and edible leaves. Edible shrubs include *Acacia tortilis* leaves, edible shrub fruits from *Acalypha fruticosa*, *Salvadora persica*, *Capparis tomentosa*, *Cordia monoica*, *Maerua triphylla*, and *Cordia sinensis*, the latter two of which also have edible roots, and *Hibiscus ovalifolius* provides edible shrub seeds, leaves, and flowers. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Monechma debile* with edible flowers and leaves, *Solanum incanum* with edible leaves and possibly fruit, *Sida ovata* with edible leaves, *Hibiscus ovalifolius* with edible leaves, seeds, and flower buds, *Commelina africana* with edible whole plant, *Indigofera arrecta* with edible root, *Ocimum basilicum* with edible leaves/shoots, *Bidens pilosa* with edible leaves/shoots, and *Hypoestes forskalei* with edible leaves. Eight edible grass species are present.

Reg-ion	**Land-scape Assoc-iation**	**Facet**	**Study Area**	**Description of Edibles**
M	Lacus-trine Terrace	riverine	Ndilana River (M-NDI)	Edible trees are mainly *Acacia tortilis* with edible pods, leaves, and flowers, and the occasional *Balanites aegyptiaca* with edible fruit pulp, seed kernel, exudates, and bark. Edible shrubs (same as M-MSA) include *Acacia tortilis* leaves, edible shrub fruits from *Acalypha fruticosa*, *Salvadora persica*, *Capparis tomentosa*, *Cordia monoica*, *Maerua triphylla*, and *Cordia sinensis*, the latter two of which also have edible roots, and *Hibiscus ovalifolius* provides edible shrub seeds, leaves, and flowers. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Monechma debile* with edible flowers and leaves, *Solanum incanum* with edible leaves and possibly fruit, *Sida ovata* with edible leaves, *Hibiscus ovalifolius* with edible leaves, seeds, and flower buds, *Commelina africana* with edible whole plant, *Indigofera arrecta* with edible root, *Ocimum basilicum* with edible leaves/shoots, *Bidens pilosa* with edible leaves/shoots, and *Hypoestes forskalei* with edible leaves. Six edible grass species are present.
M	Lacus-trine Terrace	non-riverine	Ndala-Chemchem Interfluve (M-NCI)	The only trees present are *Acacia tortilis*, which have edible pods, leaves, and flowers. Edible shrubs include the leaves of *Acacia tortilis*, and edible shrub fruits from *Acalypha fruticosa*, *Salvadora persica*, *Capparis tomentosa*, *Cordia monoica*, and *Maerua triphylla*, the latter of which also has edible roots. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Monechma debile* with edible flowers and leaves, *Solanum incanum* with edible leaves and possibly fruit, *Sida ovata* with edible leaves, *Hibiscus ovalifolius* with edible leaves, seeds, and flower buds, *Commelina africana* with edible whole plant, *Indigofera arrecta* with edible root, *Ocimum basilicum* with edible leaves/shoots, and *Bidens pilosa* with edible leaves/shoots. Six edible grass species are present.

Reg-ion	**Land-scape Assoc-iation**	**Facet**	**Study Area**	**Description of Edibles**
M	Lacus-trine Terrace	non-riverine	Ndilana-Msasa Interfluve (M-NMS)	The only trees present are *Acacia tortilis*, which have edible pods, leaves, and flowers. Edible shrubs include the leaves of *Acacia tortilis*, edible shrub fruits from *Acalypha fruticosa*, *Salvadora persica*, *Capparis tomentosa*, *Cordia monoica*, and *Maerua triphylla*, the latter of which also has edible roots, and *Hibiscus ovalifolius* provides edible shrub seeds, leaves, and flowers. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Monechma debile* with edible flowers and leaves, *Solanum incanum* with edible leaves and possibly fruit, *Sida ovata* with edible leaves, *Commelina africana* with edible whole plant, *Indigofera arrecta* with edible root, *Ocimum basilicum* with edible leaves/shoots, and *Bidens pilosa* with edible leaves/shoots. Eight edible grass species are present.
M	Fluvial Terrace	riverine	Endabash River (M-END)	Edible trees here are diverse: *Acacia tortilis* is present with edible pods, leaves, and flowers, *Trichilia emetica* has edible fruit (red seed arils), *Ziziphus pubescens* has edible fruits and leaves, *Kigelia africana* (the sausage tree) has edible fruits, seeds, flowers, and bark/cambium, and *Acacia sieberiana* trees have edible seeds, flowers, and gum. Edible shrubs include the typical Manyara mix: *Acacia tortilis* leaves, edible shrub fruits from *Acalypha fruticosa*, *Capparis tomentosa*, *Cordia monoica*, *Maerua triphylla*, and *Cordia sinensis*, the latter two of which also have edible roots. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Monechma debile* with edible flowers and leaves, *Hibiscus ovalifolius* with edible leaves, seeds, and flower buds, and *Hypoestes forskalei* with edible leaves. Four edible grass species are present.
M	Alluvial Fan	riverine	Mkindu River on Alluvial Fan (M-MKIR)	Edible trees parts include the fruits (red seed arils) of *Trichilia emetica*, the high quality edible fruits and edible leaves of *Ficus sycomorus*, and edible fruits of *Ekebergia capensis*. Edible shrubs are sparse: *Acalypha fruticosa* provides edible fruits, leaves, and stems, and *Hibiscus ovalifolius* provides edible shrub seeds, leaves, and flowers. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Hibiscus ovalifolius* with edible leaves, seeds, and flower buds, and *Hypoestes forskalei* with edible leaves. No edible grass species are present.

Region	**Landscape Association**	**Facet**	**Study Area**	**Description of Edibles**
M	Alluvial Fan	non-riverine	Mkindu Interfluve (M-MKII)	The dominant trees here are *Trichilia emetica* which provide edible fruits (red seed arils), and there are occasional *Ficus sycomorus* trees which provide high quality edible fruits and edible leaves. Edible shrubs are sparse: *Acalypha fruticosa* provides edible fruits, leaves, and stems, and *Hibiscus ovalifolius* provides edible shrub seeds, leaves, and flowers. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Hibiscus ovalifolius* with edible leaves, seeds, and flower buds, *Bidens pilosa* with edible leaves/shoots, and *Hypoestes forskalei* with edible leaves. No edible grass species are present.
S	E. Serengeti Plain	riverine	Barafu River (S-BAR)	The main trees are scattered, mature *Acacia tortilis*, which provide edible pods, leaves, and flowers. There are very few *Acacia xanthophloea* trees, but these have edible gum (and marginally edible seeds/pods). Shrubs are also sparse here: *Acacia tortilis* shrubs provide edible leaves, and *Commiphora africana* provides edible fruits, leaves, roots, bark, and gum. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Solanum incanum* with edible leaves and possibly fruit, *Sida ovata* with edible leaves, and *Indigofera arrecta* with edible root. Twelve edible grass species are present.
S	E. Serengeti Plain	non-riverine	Barafu Plain (S-BPL)	No trees or shrubs. Forbs that are edible include *Solanum incanum* with edible leaves and possibly fruit, and *Sida ovata* with edible leaves. Seven edible grass species are present.

Reg -ion	**Land-scape Assoc-iation**	**Facet**	**Study Area**	**Description of Edibles**
S	W. Ser-engeti Plain	riverine	Nyamara River (S-NYA)	The main trees present are *Acacia xanthophloea* with edible gum (and marginally edible seeds/pods), and there are a few *Ficus sycomorus* trees with high quality edible fruits and edible leaves. Edible shrub parts include *Acacia xanthophloea* gum, *Acacia tortilis* leaves, small amounts of *Capparis tomentosa* and *Cordia monoica* which both provide edible fruits, *Hibiscus ovalifolius* with edible shrub seeds, leaves, and flowers, *Aspilia mossambicensis* with edible leaves/shoots. Forbs that are edible include *Achyranthes aspera* with edible leaves and *Solanum incanum* with edible leaves and possibly fruit. Three edible grass species are present.
S	W. Ser-engeti Plain	riverine	Seronera River (S-SER)	The trees along this portion are all *Acacia xanthophloea* with edible gum (and marginally edible seeds/pods). Edible shrubs are *Acacia xanthophloea* with edible gum, and small amounts of *Cordia monoica* with edible fruits and *Aspilia mossambicensis* with edible leaves/shoots. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Monechma debile* with edible flowers and leaves, *Solanum incanum* with edible leaves and possibly fruit, and *Hypoestes forskalei* with edible leaves. Nine edible grass species are present.
S	W. Ser-engeti Plain	non-riverine	Nyamara Interfluve (S-NIN)	The very sparse trees here include *Balanites aegyptiaca* with edible fruit pulp, seed kernel, exudates, and bark. The sparse shrubs include *Acacia tortilis* with edible leaves, and *Capparis tomentosa* and *Cordia monoica* which both have edible shrub fruits. Forbs that are edible include *Solanum incanum* with edible leaves and possibly fruit. Three edible grass species are present.
S	W. Ser-engeti Plain	non-riverine	Seronera-Wandamu Interfluve (S-SWI)	No trees or shrubs. Forbs that are edible include *Solanum incanum* with edible leaves and possibly fruit and *Sida ovata* with edible leaves. Four edible grass species are present.

Reg-ion	**Land-scape Assoc-iation**	**Facet**	**Study Area**	**Description of Edibles**
S	Seren-geti Wood-lands	riverine	Mbalageti River (S-MBA)	The main trees are *Acacia xanthophloea* with edible gum (and marginally edible seeds/pods), and a rare *Acacia tortilis* with edible pods, leaves, and flowers. *Acacia kirkii* trees are present, but their only "edible" part is bark used today by people to make a tea. Edible shrub parts include *Acacia xanthophloea* gum, rare *Acacia tortilis* shrub leaves, *Cordia monoica* which provides edible fruits, *Hibiscus ovalifolius* with edible shrub seeds, leaves, and flowers, *Aspilia mossambicensis* with edible leaves/shoots, and *Maerua triphylla* with edible fruits and roots. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Solanum incanum* with edible leaves and possibly fruit, and *Hypoestes forskalei* with edible leaves. Two edible grass species are present.
S	Seren-geti Wood-lands	riverine	Sangare River (S-SAN)	The main trees are *Acacia xanthophloea* with edible gum (and marginally edible seeds/pods), but there is also a *Ficus* sp., which likely has high quality edible fig fruits. Edible shrubs include *Acacia xanthophloea* gum, *Acalypha fruticosa* fruits and leaves/pith, *Hibiscus ovalifolius* with edible shrub seeds, leaves, and flowers, *Aspilia mossambicensis* with edible leaves/shoots, and *Cordia monoica* with edible fruits, and several species of *Grewia*, all likely to have edible fruits. Forbs that are edible include *Achyranthes aspera* with edible leaves, *Solanum incanum* with edible leaves and possibly fruit, and *Hypoestes forskalei* with edible leaves. Three edible grass species are present.
N	Crater Floor	small spring wetland	Engitati (N-ENG)	The sedge *Cyperus immensus* has edible rhizome/underground bulb, and sedge *Cyperus laevigatus* has edible stem base/underground bulb. There are 2 edible grasses: *Themeda triandra* and *Cynodon dactylon*.
N	Crater Floor	stream-fed dry land	Gorigor Midwest (N-GMG)	The sedge *Cyperus laevigatus* has edible stem base/underground bulb. There is 1 edible grass: *Cynodon dactylon*.
N	Crater Floor	stream-fed wetland	Gorigor Midwest (N-GMM)	The sedge *Cyperus immensus* has edible rhizome/underground bulb, and sedge *Cyperus laevigatus* has edible stem base/underground bulb.

Reg-ion	**Land-scape Assoc-iation**	**Facet**	**Study Area**	**Description of Edibles**
N	Crater Floor	stream-fed dry land	Gorigor North (N-GNG)	There are 3 edible grasses: *Themeda triandra, Cynodon dactylon*, and *Sporobolus spicatus*.
N	Crater Floor	stream-fed wetland	Gorigor North (N-GNM)	*Typha latifolia* has edible rhizomes and pollen. The sedge *Cyperus immensus* has edible rhizome/underground bulb, and sedge *Cyperus laevigatus* has edible stem base/underground bulb.
N	Crater Floor	stream-fed wetland	Gorigor West (N-GWE)	The sedge *Cyperus immensus* has edible rhizome/underground bulb, and sedge *Cyperus laevigatus* has edible stem base/underground bulb.
N	Crater Floor	stream-fed dry land	Munge Marsh (N-HPG)	The forb *Persicaria decipiens* has edible leaves. The sedge *Cyperus rotundus* has an edible root/rhizome.
N	Crater Floor	stream-fed wetland	Munge Marsh (N-HPM)	*Typha latifolia* has edible rhizomes and pollen. The sedge *Cyperus immensus* has edible rhizome/underground bulb.
N	Crater Floor	small spring dry land	Kidogo Spring (N-KSG)	There is 1 edible grass: *Cynodon dactylon*.
N	Crater Floor	small spring wetland	Kidogo Spring (N-KSM)	The sedge *Cyperus laevigatus* has edible stem base/underground bulb.
N	Crater Floor	stream-fed dry land	Munge River (N-MRG)	The sedge *Cyperus laevigatus* has edible stem base/underground bulb. There is 1 edible grass: *Cynodon dactylon*.
N	Crater Floor	stream-fed wetland	Munge River (N-MRM)	The sedge *Cyperus immensus* has edible rhizome/underground bulb, and sedge *Cyperus laevigatus* has edible stem base/underground bulb. There is 1 edible grass: *Panicum* cf. *subalbidum*.
N	Crater Floor	sm spr dry land	Mystery Spring (N-MSS)	*Acacia xanthophloea* small trees and shrubs have edible gum and marginally edible seeds/pods. The shrub *Lippia javanica* has edible leaves. Forbs include *Achyranthes aspera* with edible leaves and *Solanum incanum* with edible leaves and possibly edible fruit.

Reg -ion	**Land-scape Assoc-iation**	**Facet**	**Study Area**	**Description of Edibles**
N	Crater Floor	small spring wetland	Mystery Spring (N-MSM)	The sedge *Cyperus immensus* has edible rhizome/underground bulb.
N	Crater Floor	small spring dry land	Mti Moja (N-MTG)	The forb *Leonitis nepetifolia* has edible leaves and flower nectar, and the forb *Launaea cornuta* has edible leaves and the whole plant can be eaten young. There are 3 edible grasses: *Cynodon dactylon*, *Sporobolus spicatus*, and *Aristida adscensionis*.
N	Crater Floor	small spring wetland	Mti Moja (N-MTM)	The sedge *Cyperus immensus* has edible rhizome/underground bulb, and sedge *Cyperus laevigatus* has edible stem base/underground bulb.
N	Crater Floor	large spring dry land (wood-land)	Ngoitokitok North (N-NGW)	An edible tree is *Acacia xanthophloea* with edible gum and marginally edible pods and seeds. The sedge *Cyperus laevigatus* has edible stem base/underground bulb. There is one edible grass: *Cynodon dactylon*.
N	Crater Floor	large spring dry land (grass-land)	Ngoitokitok North (N-NGG)	The shrub *Lippia javanica* has edible leaves. There are 3 edible grasses: *Cynodon dactylon*, *Sporobolus africanus*, and *Hyparrhenia hirta*.
N	Crater Floor	large spring wetland	Ngoitokitok North (N-NGP)	*Typha latifolia* has edible rhizomes and pollen. The sedge *Cyperus immensus* has edible rhizome/underground bulb, sedge *Cyperus laevigatus* has edible stem base/underground bulb, and the sedge *Cyperus rotundus* has an edible root/rhizome. The forb *Crassocephalum vitellinum* has edible leaf/shoot and the forb *Vigna vexillata* has edible pod and seed, leaf, flower, and tuber. There are 2 edible grasses: *Cynodon dactylon*.and the marsh-inhabiting *Phragmites mauritianus*.

Reg-ion	**Land-scape Assoc-iation**	**Facet**	**Study Area**	**Description of Edibles**
N	Crater Floor	lg spr dry land	Ngoitokitok South (N-NGS)	Edible trees include *Acacia xanthophloea* with edible gum and marginally edible pods and seeds, and *Croton machrostachyus* with edible fruits. Edible shrubs are *Lippia javanica*, *Lippia ukambensis*, *Phytolacca dodecandra*, and *Senna obtusifolia* with edible leaves, *Cordia monoica* and *Vangueria madagascariensis* with edible fruit, and *Capparis tomentosa* with marginally edible fruit. Edible forbs include *Achranthes aspera* with edible leaves, *Bidens pilosa* with edible leaves/shoots, and *Abutilon mauritianum* with edible seeds and flower buds. 2 edible grasses: *Cynodon dactylon* and *Themeda triandra*.
N	Crater Floor	large spring wetland	Ngoitokitok South (N-NSM)	The sedge *Cyperus immensus* has edible rhizome/underground bulb. The forb *Persicaria senegalensis* has edible leaf and tuber.
N	Crater Floor	small spring dry land (wood-land)	Seneto (N-SEW)	Edible trees are *Acacia xanthophloea* with edible gum and marginally edible pods and seeds, and *Euphorbia candelabrum* with edible shoots and flower buds.
N	Crater Floor	small spring dry land (grass-land)	Seneto (N-SEG)	There are 2 edible grasses: *Cynodon dactylon* and *Digitaria milanjiana*.
N	Crater Floor	small spring wetland	Seneto (N-SEM)	*Typha latifolia* has edible rhizomes and pollen. The sedge *Cyperus immensus* has edible rhizome/underground bulb and the sedge *Cyperus laevigatus* has edible stem base/underground bulb.
N	Crater Floor	small spring dry land	Vernonia (N-VSW)	Edible plants present are the shrubs: *Lippia ukambensis* with edible leaves, *Vangueria madagascariensis* with edible fruit, and *Vernonia myriantha* with edible flowers, leaves, and pith.
N	Crater Floor	small spring wetland	Vernonia (N-VSM)	The sedge *Cyperus immensus* has edible rhizome/underground bulb.

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Academic and Employment Positions

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Publications

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