

# Primate Communities: Past, Present, and Possible Future

Kaye E. Reed<sup>1,2\*</sup> and Laura R. Bidner<sup>1</sup>

<sup>1</sup>*Department of Anthropology, Arizona State University, Tempe, Arizona 85287*

<sup>2</sup>*Institute of Human Origins, Arizona State University, Tempe, Arizona 85287*

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**ABSTRACT** An understanding of the fundamental causes of the structure of primate communities is important for studies of primate evolutionary history, primate behavioral ecology, and development of conservation strategies. Research into these structuring factors has benefited from new perspectives such as consideration of primate phylogenetic history, metacommunities, and interactions with predators and nonprimate competitors. This review presents the underlying factors of primate community structure within the biogeographic regions of Madagascar, the Neotropics, Africa, and Asia. One of the major differences among these locations likely resulted from the initial primate taxa that colonized each region (a single colonization event in the case of Madagascar and South America, and multiple radiations of higher-level taxa in Africa and Asia). As most primates live in forests, the differences among the forests in these locations, caused by various climatic influences, further influenced

speciation and the development of primate communities. Within these habitats, species interactions with different groups of organisms were also instrumental in developing community dynamics. Through an investigation of these fundamental factors, we identify some of the most important effects on primate communities in each region. These findings suggest that low primate richness in Asia may be caused by either the abundance of dipterocarp trees or high levels of monsoon rains. High numbers of frugivores and a lack of folivores in neotropical communities may be associated with competition with sloths that were already present at the time of initial radiation. Climatic patterns which affect forest structure and productivity in Madagascar may be responsible for high numbers of folivorous lemurs. The identification of these factors are important for the conservation of existing primate communities, and indicate directions for future studies. *Yrbk Phys Anthropol* 47:2–39, 2004. © 2004 Wiley-Liss, Inc.

A primate community can be loosely defined as all primate species that live together and utilize resources at one geographic location. Each community can also be viewed as the end result of one or more adaptive radiations. That is, ancestral primates have colonized each continent and undergone subsequent species diversification with regard to resource partitioning. As such, comparisons of extant primate communities offer insights into how different evolutionary histories, habitats, and species interactions shaped primate evolution in particular regions. The understanding of how primates migrated, evolved, and currently exist together is also important for planning conservation strategies for their diminishing habitats. Prior studies led researchers to hypotheses about why there are major differences among primate communities on different continents. Our goal is to review the causes associated with these questions and outline possible answers: What are the major causes of differences among primate communities? Why is Asia characterized by low primate species richness? What is the reason for the species density and low adaptive diversity of primates in neotropical communities? Why is there a bias toward folivorous primates in

Madagascar? Is there a trade-off between frugivore richness and population densities in Africa and the Neotropics?

In this paper, we begin by summarizing some of the proposed reasons for the development and maintenance of community structure. We refer to structure as the different patterns with which communities can be identified, such as taxonomic composition, species diversity, ecological diversity and adaptations, and species interactions (Morin, 1999). For example, the pattern of ecological diversity in a primate community may consist of contrasting diets, activity patterns, substrate use, and body size of member species, while a species diversity pattern may indicate population dynamics of the resident primates defining dominant vs. rare species. Either of these patterns is representative of the structure of

\*Correspondence to: Kaye Reed, Institute of Human Origins, Arizona State University, Box 874101, Tempe, AZ 85287-4101.  
E-mail: kaye.reed@asu.edu

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the community. Since early in the 20th century there have been hypotheses regarding how community structure is maintained. These ideas include concepts wherein the underlying causes of communities are contrasted as extrinsic or intrinsic. Newer theoretical viewpoints of phylogeny and metacommunities advocate the inclusion of speciation patterns and regional dynamics when considering community constructs. We discuss these concepts and relate them to primate community studies whenever possible.

Abiotic and biotic factors that have influenced or are currently shaping community structures include historical circumstances, climate and habitats, productivity and food resources, and species interactions. We consider colonization, speciation, migration patterns, and areas of land mass, as well as climatic and environmental factors, to be some of the underlying external causes for community development. These extrinsic causes are referred to as such because they do not directly interact with primate species. These factors for the development and maintenance of community structure have mostly occurred in the past, but also have ramifications for the present and future of communities. Prior primate studies in this area examined species-area relationships (e.g., Reed and Fleagle, 1995; Eeley and Foley, 1999; Cowlshaw and Dunbar, 2000), isolation and refugia issues (e.g., Struhsaker, 1981; Ayres and Clutton-Brock, 1992; Harcourt, 1999; Abeg and Thierry, 1992), primary productivity and species numbers (Hladik, 1978; Terborgh and Van Shaik, 1987; Chapman et al., 1994; Reed and Fleagle, 1995; Kay et al., 1997; Cowlshaw and Dunbar, 2000; Stevenson, 2001), primary productivity and biomass (Oates et al., 1990; Reed, 1999), and other extrinsic underlying factors of primate community composition (Oates et al., 1990; van Schaik et al., 1993; Kappler and Heymann, 1996; Peres, 1997).

Other fundamental reasons for community structure include species interactions such as resource utilization, interspecific competition, and predation. These are intrinsic to the primate species represented in the community because these factors directly involve primate behavioral ecology. The total interaction of each primate species with the environment creates its ecological niche. Therefore, each primate species occupies a unique niche, and all niches in a community represent the ecological space or pattern of ecological diversity of that community (Fleagle and Reed, 1996). Primate studies of an intrinsic nature have included comparing ecological space in various primate communities (Bourliere, 1985; Fleagle and Reed, 1996, 1999a; Reed, 1999; Shultz, 2003; Chapman et al., 1999a; Gupta and Chivers, 1999; Ganzhorn et al., 1999b), competition and polyspecific associations among primate species (Gautier-Hion et al., 1983; Tutin et al., 1997), and interactions of primates and predators (Bshary and Noë, 1997a,b; Zuberbühler and Jenny,

2003; Shultz et al., 2003). Both extrinsic and intrinsic influences affect the ultimate niche space of individual primates within the community, thus affecting community structure.

We will present the ideas in general and then discuss current primate community composition and structure through comparisons of differences and similarities within and among continental and island regions. We begin with the island of Madagascar as the strepsirrhine radiation that occurred there began in the most distant past. We then describe various attributes of neotropical and Old World (both Africa and Asia) primate communities. Finally, we discuss proposed hypotheses for the differences seen among communities on different continents, and propose future directions for community studies.

## COMMUNITY DYNAMICS

Species that exist in the same place are more than random species associations; they are ordered in particular patterns (Elton, 1927; Shelford, 1929; Clements, 1936; Gleason, 1939; Roughgarden, 1989; Brooks and McLennan, 1991; Morin, 1999; Rosenzweig, 1999; Mouquet and Loreau, 2002; Kneitel and Chase, 2004). Historically, two major views were espoused regarding how processes controlled the structure of communities: closed and open concepts. The closed concept derives from the extrinsic viewpoint and suggests that communities consist of special sets of species that interact not only with each other but with their environment such that, for secondary consumers, habitats provide sharp boundaries that delineate the area encompassed (Clements, 1936), i.e., the habitat and environment constrain the animal members of the community. In contrast, the open community concept originates from the intrinsic view and advocates that the structure and function of a community are a result of species interactions, such that immigration of new species, variability of the environment, and the adaptations of each species are what control the structure (Gleason, 1939), i.e., the habitat and environment do not directly constrain the animal members of the community. Additional theories of community organization and maintenance involve species interactions such that a community is maintained due to resource availability (bottom-up) or predator modification (top-down) factors.

However, most studies seem to have utilized the closed concept of community, i.e., one defined by a particular habitat, e.g., the várzea, or flooded forests, of Amazonia. In fact, in the last 25 years, community ecology has often focused on species existing in homogeneous habitats, and research on the interactions of component species was basically extended examination of the competitive exclusion principle (the elimination of one species by another due to resource competition; Kneitel and Chase, 2004). Newer ideas on the organization of communities incorporate both phylogenetic (Brooks and McLennan,

nan, 1991; Webb et al., 2002) and metacommunity (Mouquet and Loreau, 2002) perspectives.

Brooks and McLennan (1991) advocated that, irrespective of either the open or closed concept, the structure of any community is the result of resident and colonizing species. Phenotypic differences among closely related species, such as primates, are either ancestral or derived, and as such reflect the resident and colonizing species of the community. Thus, phylogeny is extremely important in community structure, as the underlying causes lie in historical circumstances. Isolating particular lineages can be fruitful for understanding underlying adaptive patterns in niche structure (Brooks and McLennan, 1991; Losos, 1996; Eeley and Foley, 1999; Webb et al., 2002), as greater competitive interaction is expected among closely related species. Root (1967) suggests that species sharing the same functional role can be studied to the exclusion of other such organisms, and methodologically this identification of a subgroup is beneficial as a building block of further study (Schoener, 1986). Primate community studies are important to this phylogenetic perspective because primates share morphological adaptations that are unique within many communities, and as such their functional role in communities can be compared across time and space. The acquisition of convergent ecological traits in closely related primates with respect to other mammalian community members can be contrasted, and the role of the primate community can be integrated into wider-ranging community studies. In fact, some of the differences among primate communities on different continents must be understood in relation to other types of species that existed in the region prior to primate arrival (Fleagle and Reed, 1999b).

Metacommunities, a complex of communities with links through corridors of habitat or other networked connections for some species, were also recently advocated as necessary for understanding community dynamics (Wilson, 1992; Mouquet and Loreau, 2002). Mouquet and Loreau (2002) discovered that patterns of species diversity in particular communities are better explained if both stenotopic species (those that only exist in narrow habitats) and eurytopic species (those that can cross barriers and are habitat generalists) are analyzed with respect to their spatial distributions and interactions. Primate communities have sometimes been studied within such a broader, regional framework (Thomas, 1991; Eeley and Foley, 1999; Chapman et al., 2000; Brugiére et al., 2002). Eeley and Foley (1999) considered species diversity in primates, but, in contrast to Mouquet and Loreau (2002), looked at the distributions of stenotrophic (dietary specialist) and eurytrophic (dietary generalist) species and latitudinal variation. Eeley and Foley (1999) also suggested that studying regional patterns is important for understanding the structures of individual communities. Adding spatial dynamics allows theories that test trade-offs of species performing similar func-

tions to be analyzed beyond the local to include the regional scale (Kneitel and Chase, 2004). For example, most primates live in tropical forests, and corridors of dispersal for some species exist between fairly large forest patches. Forest characteristics shift along gradients from primary to secondary forest and other habitats, making the region physiognomically heterogeneous. Within this framework, river systems limit some primate species dispersal. Consequently, the structure of each perceived primate community is also a part of changing regional dynamics, i.e., part of a metacommunity. Cowlshaw and Dunbar (2000) noted that primate species diversity increases across regions with more habitat variation, and others (Ganzhorn, 1994; Schwartzkopf and Rylands, 1989) suggested that increase in habitat diversity creates more niches.

The interrelationship of localized communities within the metacommunity and subsequently broader spatial areas is important for understanding historical circumstances and for planning conservation measures. As primates are among the most well-studied mammals, exist on almost all continents, and are the result of a number of unique adaptive radiations, they are useful for testing hypotheses regarding community structure. Studies of primate communities are therefore extremely important for examining theoretical constructs of open and closed communities and those theoretical concepts advocating the use of phylogeny and regional dynamics.

## UNDERLYING FACTORS OF PRIMATE COMMUNITIES

Primate species that exist together occupy niches based on a variety of past and current conditions. The primary extrinsic factors contributing to the structure of primate communities are abiotic parameters such as climate and soils. These abiotic features organize the plants into a particular physiognomy, e.g., primary forest with three canopy levels and emergent trees or woodlands with less rainfall, grass ground cover, and no interlaced canopies. Thus, amount of rainfall, temperature, latitude, and type of soil dictate the physiognomy of forests, control plant distribution, and influence primary productivity. The climate and other environmental factors have changed throughout the history of the earth, and are important for understanding past colonization by primates in particular regions, as well as current aspects of primate life. Plants, in turn, are actually secondary factors in structuring primate communities. Seasonal variations affect resource production, which influences primate interactions with the habitat, other primates (competition), and predators. Below, we discuss these important factors.

### Historical factors

History plays an extremely important role in understanding primate community dynamics. Migra-

tion and speciation, land mass limitations, isolation and refugia, and recent extinctions all contribute to the underlying causes of community structure. Starting with the common ancestor to all primates, speciation events have affected primate adaptive radiations in all biogeographic regions. Subsequent migrations and speciations are responsible for the current placement of particular primate groups. After the arrival of a common ancestor, other factors such as changing climate and habitat influenced adaptation, and thus future speciation and extinction events in an area. The bottom line is that the structure of any primate community is contingent upon the ancestral community and any subsequent migratory primate species.

Historical circumstances also influenced changes in vegetation structure, i.e., physiognomy, which may consequently have impacted extinction and speciation events. Thus, patterns of isolation, past refugia, and changing habitats of a particular region are often identified as ultimate causes of the structure of an extant community.

**Migration and speciation.** Migration of primates to a region for the first time figures prominently in the outcome of the community structure. Subsequent migrations alter the interactions of the resident species to each other and to the newcomers. Thus, modifications to a common primate ancestor result in similar anatomical designs, or bauplans, for various phylogenetic lineages, but different trajectories depending on the timing of the arrival of particular descendents to a new area. For example, in Madagascar, historical circumstances deposited ancestral primates approximately 50 million years ago with no subsequent colonization by higher primate taxa. The ultimate outcome of this event is that primate communities in Madagascar consist only of strepsirrhines. In contrast, only members of the Platyrrhini exist in the New World. The ancestral primates in South America were members of the Haplorrhini clade, and arrived in the Neotropics about 30 million years ago (Takai et al., 2000). A more complex situation exists in primate communities of Africa and Asia because various radiations throughout the Cenozoic resulted in several primate migrations between and among these continents. These adaptive radiations (speciation events) and migrations (colonizing events) across time resulted in contrasting primate communities among continental regions. The basal phylogeny and migration of more distantly related primates to an area are important to understanding why communities developed the way they did. Ensuing factors then affected various speciation and extinction events, resource partitioning, and other niche differences (i.e., adaptations), to result in the extant communities we study today.

Brooks and McLennan (1991) suggested that although interest may focus on the current adaptations of primates (e.g., brachiation), the origination

of an adaptation is obviously most important in understanding the cause of its appearance. This idea can be expanded to community structure such that unless the phylogenetic history of a particular site, region, or continent is understood, the underlying reason for the structure may not be evident. Speciation events are both a cause and result of changes in community dynamics. Habitat change and other vicariance events cause some primate species to be isolated from those that were previous community members. Isolation can promote speciation, and if barriers change again, these new primate species become colonizers as they migrate back into the community.

**Area, isolation, and refugia.** The relationship between land area, isolation, and primate species richness was reviewed by Cowlshaw and Dunbar (2000). In general, the greater the forested area on islands and continents, the greater the number of primate species (Reed and Fleagle, 1995; Cowlshaw, 1999). The major cause for this may be that larger areas of forest likely support higher carrying capacities than smaller forested areas (Cowlshaw and Dunbar, 2000).

The more distant a region from the geographic area in which source species likely originated, the lower the total number of species there may be in a community, i.e., the region is more isolated and therefore there are fewer species. For example, Struhsaker (1981) showed that the number of primate species supported in East African forests declines as a factor of increased distance from Pleistocene forest refugia. According to Cowlshaw and Dunbar (2000), primate species that colonized islands relatively recently, e.g., Borneo and Sumatra, are limited not by the ability of the primates to get to the island over a land bridge, but by the ultimate extinction rate after the island colonization. That is, can colonizing species actually survive long-term in a new island area? On the other hand, islands that were colonized millions of years ago have undergone multiple speciation, extinction, and radiation events, and have more primate species than might be expected, e.g., Madagascar.

### Climatic and habitat influences

Abiotic components of environmental control include sunlight, soil type, rainfall, seasonality, and other parameters that affect the growth of plant species. While primates are directly influenced by a few of these physical parameters (e.g., solar intensity), their interactions with the environment for resource acquisition are mostly with the plant species. Thus, abiotic factors determine the physiognomy of the habitat, as well as seasonal differences in fruiting cycles, leaf growth, etc. Primates then respond at a secondary level to these cycles by utilizing primary resources, and finding alternative resources during the lean seasons.

Theories of the origin of the order Primates suggest habitats in which the vegetation was vertically stratified, at least to small-bodied ancestors, thus providing access to insects and/or fruits on smaller branches (Cartmill, 1972; Sussman, 1991; Rasmussen, 1990). Since the majority of extant primates live within the tropical belt and within forest habitats, it appears as if this original adaptation has remained of primary importance in the radiation of various primate lineages. For the most part, we will discuss these abiotic factors with regard to forested environments, although there are a few primate communities in nonforested environs.

**Climate.** The climate of tropical regions is generally warm and moist, while the higher the latitude is from the equator, the more arid and cold the climate. Tropical rainforests are broadly classified as having climates with fairly high, constant temperatures and plentiful rainfall (Archibold, 1995). The plants in these forests receive nutrients and water to maintain growth from the soil. Soils can change due to climate and vegetation differences that accumulate over time, resulting in different vegetation and obvious changes in the other biota that the plants support.

Rainfall was proposed to be important in structuring the richness of primate communities (Reed and Fleagle, 1995). The amount of mean annual rainfall is related to the origination and maintenance of forest plant communities (Reed, 1998). However, rainfall patterns are also extremely important in resource production, as changes in seasonality can profoundly affect the vegetation production cycle. Climate, as influenced by latitude, also partially dictates seasonal differences, which in turn affect habitat type. Low-latitude forest habitats usually experience long wet and short dry seasons, while woodlands at the same latitudes have shorter wet and longer dry seasons. Local and regional factors, as well as monsoon patterns, also contribute to differences in the lengths of wet and dry months. These variations shape the production of leaves and fruits in tropical forests, and as such also influence the resource use of component primate species.

As most primate species are forest dwellers, they are greatly influenced by vertical stratification patterns and differences. Substrate use in forests is one of the ways in which primate species alter their niche occupation. Accordingly, primates utilize the ground, intermediate canopy levels, and emergent tree crowns. Even if there are a number of species focusing on similar fruits, the stratification in substrate use will allow more resource use (Gautier-Hion et al., 1983).

The horizontal distribution of plants across the landscape is also important, dependent on both abiotic factors and unfortunately more recently anthropogenic habitat destruction. Physical changes in topography, soils, etc., account for the density of trees intraregionally, e.g., across the African continent, as

well as interregionally, e.g., between Africa and Madagascar. As forests expand and contract, open patches result in the limiting of some primate species migrations. The end result is that primate communities can shift intraregionally due to forest spacing differences across the landscape over time.

Abiotic effects also control plant productivity and variation through time, whether daily, seasonally, or over eons. It was noted that protein concentration in leaves can increase at dawn and dusk, possibly affecting primate activity patterns (Ganzhorn and Wright, 1994). Seasonal differences among plants often include variations in fruiting, leafing, and flowering. Long-term seasonal changes caused by glacial advances and retreats result in trade-wind changes that bring more or less rain across time, affecting plant growth and production.

**Forest structure.** Forest structure as exemplified by plant physiognomy is of utmost importance when examining primate communities that live within forests. Tropical evergreen forests in which primates live can be found in lowlands or on mountains, can be flooded or nonflooded, may be found only along rivers within other habitats, or can be cloud forests (Archibold, 1995). The stratification of the canopy and other vegetative structures of these forests are important for determining primate niche space. Lowland forests tend to have at least some trees greater than 30 m in height and multiple canopy levels. The canopies are intertwined, thus providing horizontal travel highways for primate and other species. There is little ground cover, and few palm trees or epiphytes. Tree height and crown volume are thus seen as important characteristics for primate behavioral ecology. Montane forests tend to have shorter trees and more lianas, tree ferns, palm species, mosses, and epiphytes. Swamp forests usually have less tree species diversity, but have more abundant ferns than lowland forests. Each of these forest types alters the possibilities of component primate species within them. More generalist species may be found intracontinentally, in many forest types, e.g., *Cebus apella*, while more habitat-specific species would be found in only one type of forest (e.g., Eeley and Foley, 1999). Depending on the position of forests during radiations, smaller species may also be limited to particular tracks of forests due to historical circumstances, river barriers, etc.

Dominance by particular plant species in forests was also proposed as a limiting element in primate distribution (Caldecott, 1986; Thomas, 1991). These tree species sometimes support no primate species (Thomas, 1991), limit the number of frugivorous primate species (Caldecott, 1986), or contribute to low density and biomass through productivity patterns (Terborgh and van Schaik, 1997).

Finally, human actions such as deforestation and selective logging have had major effects on tropical forests in the last 100 years, such that all primate species have probably been affected. It is therefore

TABLE 1. Families and genera of woody plants which are dominant, abundant, conspicuous, or subendemic to rainforests in each biogeographic region inhabited by primates<sup>1</sup>

Region	Family	Genera	Common names
Madagascar	Leguminosae	<i>Albizia, Dalgergia, Tamarindus</i>	Mimosa, Indian rosewood, tamarind tree
	Sapotaceae	<i>Sideroxylon, Gambeya/Chrysophyllum</i>	Bully tree, longui
	Euphorbiaceae	<i>Bridelia, Macaranga, Uapaca</i>	Bridelia, macaranga, sugar plum
Neotropics	Moraceae	<i>Bosqueia, Ficus</i> (24)	Bread fruit, fig
	Bombacaceae	<i>Adansonia</i>	Baobab/monkey bread tree
	Leguminosae	<i>Andira, Apuleia, Dalbergia, Dinizia, Hymenolobium, Mora</i>	Cabbage tree, grapia, Brazilian rosewood, angelim vermelho, angelim, mora
	Sapotaceae	<i>Manilkara, Pradosa</i>	Brazilian redwood
	Meliaceae	<i>Cedrela, Swietenia</i>	Spanish cedar, mahogany
	Euphorbiaceae	<i>Hevea</i>	Rubber tree
	Myristicaceae	<i>Virola</i>	Banak or virola
Africa	Moraceae	<i>Ficus</i> (145), <i>Cecropia</i>	Fig, cecropia/embauba
	Lecythidaceae	<i>Bertholletia</i>	Brazil nut
	Leguminosae	<i>Albizia, Brachystegia, Cynometra, Gilbertiodendron</i>	Mimosa, miombo/bean-pod tree, namnam, limbali
	Sapotaceae	<i>Afroseralisia, Chrysophyllum</i>	Giant miracle fruit, longui
	Meliaceae	<i>Entandrophragma, Khaya</i>	Cedar mahogany, mahogany
	Euphorbiaceae	<i>Macaranga, Uapaca</i>	Macaranga, sugar plum
	Moraceae	<i>Chlorophora, Ficus</i> (105), <i>Musanga</i>	Fustic tree, fig, African corkwood
Asia	Sterculiaceae	<i>Cola, Triplochiton</i>	Kola nut, obeche
	Ulmaceae	<i>Celtis</i>	Sugarberry/hackberry/stinkwood
	Dipterocarpaceae	<i>Dryobalanops, Hopea, Shorea</i>	Kapur/Borneo camphorwood, thingan, meranti
	Leguminosae	<i>Koompassia</i>	Kempas uses
	Meliaceae	<i>Aglaia, Dysoxylum</i>	Langsat/kanehira, mahogany
	Moraceae	<i>Artocarpus, Ficus</i> (176)	Jack fruit, fig
	Anacardiaceae	<i>Mangifera</i>	Mango
	Dilleniaceae	<i>Dilena</i>	Red beech
	Thymelaeaceae	<i>Gonystylus</i>	Ramin

<sup>1</sup> Number of species provided in parentheses for *Ficus* within each region; number of *Ficus* species listed for Asia includes those reported from Borneo and India (Shanahan et al., 2001).

sometimes difficult to know if some of the community patterns are the result of natural abiotic factors, or the effects of logging many kilometers away.

**Summary of abiotic factors.** In general, abiotic features such as temperature and rainfall, and broad physiognomy, determine geographic dispersal of primate species. Vertical stratification, elevation, or geographic barriers such as rivers often determine where a primate species lives within its geographic range. Ultimately, because many primate species occupy similar geographic ranges and habitats, each species has its own specialized activity pattern and occupation at a particular location in space, i.e., has a niche. Observations of populations of the same primate species at different localities may show that species' populations have slightly different niches because of replacements of other community members, changes in forest structure, or alterations in resource availability. These differences can also occur in the same community, wherein the same species alter their occupied niche space depending on differences in abiotic factors through time (Onderdonk and Chapman, 1999). Onderdonk and Chapman argue that simple analyses of primate species at one locality, i.e., Kibale, are useless unless the long-term plasticity of each species is observed at various locales and incorporated

into community studies. Nevertheless, both short- and long-term studies will contribute valuable knowledge to the study of primate communities.

Varying abiotic features on different land masses have provided the background for primate evolution. These factors are similar on all continents in which primates are found. However, forests diverged in both plant species representation and physiognomy on different continents. Table 1 provides a listing of the most common tree species on each continent. All share *Ficus* species, but a perusal of this list shows that the majority of genera differ among continents. These differences in turn affected the adaptations of primates and primate community structure in each region (Fleagle and Reed, 1996).

### Productivity and food resources

Access to sufficient food resources to meet metabolic requirements has undoubtedly been an important ecological factor in the daily life of primates past and present. Thus, key to the effect of habitat on the structure of primate communities is the production of food resources available to community members. Many of the abiotic factors discussed above such as rainfall and temperature directly influence primary productivity of plant species within primate habitats. In turn, this productivity directly

influences food resources available to primates in communities. These food resources include not only plant parts, but also insects and other animals that are attracted to the vegetation. The connection between primary productivity and primate communities is certainly complicated by the foraging ecology and behavior of primate species as well as the anti-herbivore strategies of plants. However, the production and availability of limiting food resources have the potential to influence the number and type of species that can coexist at any particular site.

**Resource productivity.** As primates tend to live within relatively complex habitats, measuring plant productivity in these habitats can be difficult, demanding, and time-consuming. The most common direct measure for productivity is litterfall, in which catchments are set up to retrieve all plant matter that falls to the forest floor over a certain area in a certain amount of time which is then dried, weighed, counted, and often classified (e.g., Hladik, 1978; Kay et al., 1997; Stevenson et al., 1998). Unfortunately, litterfall data are not available for all primate community sites. However, rainfall, the most common proxy measure for productivity, is often available for most sites. Rainfall and productivity are tightly correlated, at least up to mean annual rainfall levels around 2,500 mm (Kay et al., 1997), signifying that relationships between rainfall and primate communities at many sites with rainfall below 2,500 mm may indeed be related to the effects of productivity. However, for neotropical sites, both primate species richness and productivity show similar patterns of decline at rainfall levels above 2,500 mm, suggesting that primate community structure is actually more directly affected by productivity than by rainfall (Kay et al., 1997).

While rainfall can be useful when other measures of productivity are not available, in some cases, very specific data on productivity of particular plant parts within a habitat are available. For example, Stevenson (2001) investigated the relationship between neotropical primate biomass and diversity, and fruit productivity specifically. The primary measure of fruit productivity used in his study was fruit collected in litterfall traps. It was pointed out that these traps provide only an indirect measure of actual fruit abundance, as they catch only the fruits not eaten by frugivores (Terborgh, 1983). However, Stevenson (2001) also investigated the effects of additional indexes of fruit abundance, including basal area of fruiting trees, incorporating separate measures for possible keystone species, which had been found to correlate with the weight of fruit caught in fruit traps, as well as overall tree density and tree species richness (Terborgh, 1983; Symington, 1988; Stevenson et al., 1998; but see Chapman et al., 1994). A positive correlation was found between primate biomass and all indices of fruit abundance but not with measures of overall productivity such as litterfall excluding fruit, and total tree species rich-

ness. This not only underscores the importance of productivity as a probable underlying factor of primate communities, but also suggests strongly that finer-scale investigations of productivity of particular plant parts may be able to pinpoint key resources influencing communities.

The productivity of other plant parts such as leaves, often measured through leaf fall (e.g., Hladik, 1978), might be of more significance to primate communities in biogeographical areas outside the Neotropics, as paleotropical communities tend to have higher densities and diversity of folivorous primates (Fleagle and Reed, 1996). Further studies incorporating measurements that capture information on the seasonal patterns of productivity, such as were used by Gupta and Chivers (1999), who compared the number of months of peak availability of young leaves, fruit, and flowers at Asian sites, may also provide interesting information on the effects of resource seasonality on primate communities.

**Resource seasonality.** While it seems clear that the production of food resources within a habitat is an important underlying factor of primate community structure, the fact that many of these resources are not produced uniformly on a temporal scale may more directly affect community dynamics than does overall production. This seasonality in resource availability is generally tied to climatic seasonality. For instance, evidence from forests in West and East Africa suggests that minimum temperatures during the season prior to the main fruiting season may trigger flowering and fruiting, although both seasonality in rainfall and sunlight likely play roles as well (Lopé, Gabon: Tutin and Fernandez, 1993; Tutin and White, 1998; Kibale, Uganda: Chapman et al., 1999b).

A critical aspect of seasonality in resource production is that it results in periods of food scarcity, particularly in terms of fruit resources, which can potentially limit many members of primate communities. Terborgh (1986) suggested that the availability of a few "keystone" resources such as figs and palm nuts during periods of scarcity sets the carrying capacity of frugivores in neotropical communities. The extent to which this is true for most communities is largely untested, although Stevenson (2001) found positive correlations between primate biomass and the density of both palms and members of the family Moraceae, which includes figs (*Ficus*), in neotropical sites.

Although the availability of leaf resources is not marked by seasonal peaks to the same extent as that of fruit resources, slight seasonal patterns do exist. For example, a seasonal pattern was detected in leaf-fall in Makakou, Gabon, with peaks occurring during the rainy seasons and a clear low occurring during the major dry season (Hladik, 1978). However, new leaves, which are often preferred to mature leaves by primates as they can contain a higher protein to fiber ratio, made up only a small propor-

tion of this measured leaf-fall. Terborgh and van Schaik (1987) noted that the availability of young or new leaves and fruit is actually negatively correlated in Makakou. This pattern may influence the number of frugivores-folivores that can exist within the primate community at the site. Thus, it seems likely that seasonal patterns of availability of fruit and leaves work together to influence the structure of primate communities, as both generally constitute important, often complementary parts of primate diets.

**Resource quality.** For primates who depend primarily on leaf resources, it is possible that resource quality may be an equally or more important factor than resource seasonality. Leaf quality for folivores varies based on both the ratio of protein to fiber, as mentioned above regarding young vs. mature leaves, as well as the amount of secondary compounds, particularly phenolics. Both aspects of leaf quality vary among trees within sites as well as between sites (Chapman et al., 1999b). Some evidence suggests that differences in leaf quality between sites are related to soil quality. For example, Janzen (1974) proposed that the cost of replacing foliage in poor-quality sandy soils would make it advantageous to deter herbivory through high levels of phenolics. This proposal held up in an investigation of two sites in Africa which revealed that the extremely sandy soils of Douala-Edeá Reserve in Cameroon supported trees that produced significantly higher amounts of phenolics than those supported by the dark gray to red sandy loams of the Kanyawara study site in Kibale Forest, Uganda (McKey et al., 1978).

These findings connecting soil type and leaf quality have implications for primate community studies, particularly in regard to folivorous primate densities. McKey et al. (1978) discovered that the population density of black colobus monkeys, *Colobus satanas*, at Douala-Edeá was much lower than that of the red colobus, *Procolobus badius*, or black and white colobus, *Colobus guereza*, at Kibale. *C. satanas* at Douala-Edeá was also found to consume fewer leaves in its diet than did either colobine species at Kibale, suggesting that leaf phenolics may indeed limit colobine monkey population density and possibly species numbers at African sites. However, Oates et al. (1990) argued that sandy or poor-quality soils may not negatively affect the resources available to folivorous primates such as colobines. They noted a high colobine biomass on Tiwai Island in Sierra Leone, which has relatively sandy poor-quality soils and high levels of condensed tannins in mature leaves. However, the leaves were found to have a higher protein-to-fiber ratio than at any other site aside from Kibale, suggesting that soil quality may have less of an effect on nutrient content than on secondary compounds. Chapman et al. (2002) found a positive correlation between protein/fiber ratio in leaves and colobine density at various sites

within Kibale. Ganzhorn (1992) suggested a similar relationship between this aspect of nutrient quality and folivore biomass in Madagascar. Thus, it seems that leaf quality does have an effect on folivorous members of primate communities, such that further investigation into leaf quality in terms of protein/fiber content and secondary compounds, as well as how this relates to soil type at more primate community sites, may further our understanding of how it affects community dynamics. Furthermore, it was suggested that the low species diversity of primate communities in the Guianan shield region relative to other regions of South America is directly related to the poor nutrient quality of the Precambrian soils found in this region (Terborgh and Andresen, 1998; Lehman, 2000). Thus, studies investigating the effect of soil quality on all food types may provide a better understanding of differences in communities at local scales.

### Species interactions

The habitats in which primate communities are found are commonly considered in terms of vegetation structure and productivity, which are influenced by a number of abiotic factors. However, these habitats are also affected by the animal species that reside in them. It is often claimed that the interactions between these animal species, particularly competitive interactions, strongly influence the structure of the animal community that exists within the habitat (e.g., Hutchinson, 1959; Hairston et al., 1960; MacArthur and Wilson, 1967; Connell, 1980). Although other species interactions have not received as much attention in this realm, it is likely that predation (along with competition) plays a role as an underlying factor of primate community structure, as suggested below.

**Competition.** Competition between species has often been the mechanism-of-choice used to explain patterns of diversity observed in nature (e.g., Hutchinson, 1959; Roughgarden, 1983). Much of the supporting evidence for competition is based on descriptive data or anecdotal evidence that remains consistent with predicted patterns of diversity induced by competition. This has been strongly criticized by many researchers, especially those who feel that experimental data are necessary to test the significance of interspecific competition on community structure (e.g., MacNally, 1983). Competition has undoubtedly contributed to community structure, along with many other factors, by influencing the niche space occupied by community members.

Unfortunately, it is difficult if not nearly impossible to detect the extent to which past competition has shaped the communities we see today. It has been pointed out that lack of competition between species in communities today does not necessarily indicate that competition was not an important factor in the past, but rather that competition in the past may have resulted in divergent adaptations

which release species from competition today (Connell, 1980). Connell (1980) suggested that the support necessary to indicate past competition includes 1) evidence of evolutionary divergence in the fossil record, 2) experimental evidence for present-day competition based on observed niche changes in transplant or removal experiments, and 3) evidence of genetic bases for species differences, also based on transplant or removal experiments. Evidence such as this is virtually impossible to gather for any primate community. However, the presence of congeneric species, as closely related but divergent forms, may provide a clue indicating that past competition influenced these communities to some extent. Congeneric species in primate communities address the first and possibly third of the necessary lines of evidence of Connell (1980). The presence of congeneric species is a simple measure that can easily be compared among communities, but should be considered a clue rather than clear evidence of competition. It should also be cautioned that a lack of congeneric species cannot be interpreted as a lack of competition, as such an absence may be a result of a number of factors, including competitive exclusion.

It is also difficult to detect current competition between species within communities. Unfortunately, mere overlap in resource use does not necessarily evince competition. Anecdotal evidence of aggression between species at food resources may clearly indicate the presence of food competition. However, the importance of such evidence is minimal due to its qualitative rather than quantitative nature, which makes it difficult to compare between and within communities. Although it is impractical to attempt transplant or removal experiments to collect quantitative data on interspecific competition in primate communities, a natural experiment involving polyspecific associations among forest monkeys seems to have produced such data. Diana monkey (*Cercopithecus diana*) troops, which often form polyspecific associations with other monkey species, show an increase in group movement when they are associated with other species. This likely indicates interspecific competition over resources between members of these polyspecific groups (Shultz et al., 2003). As polyspecific associations are commonly formed by forest monkeys in Africa and South America, they provide an interesting potential measure for interspecific competition within primate communities in these areas.

It was suggested (Terborgh, 1990) that these particular polyspecific associations evolved in response to the risk of predation by large, monkey-eating eagles which are only common in Africa (*Stephanoaetus coronatus*, crowned eagle) and South America (*Harpia harpyja*, harpy eagle). In this way, past predation may influence primate communities by increasing competitive interactions among community members during polyspecific associations.

It is also possible that predation has had an opposite effect on competition in primate communities. It

was shown experimentally in intertidal communities where prey species are in competition that predators can influence the densities of these competitors. Predators that preferentially devour the top competitor species actually allow inferior competitors to coexist in the same community by keeping numbers of top competitors low (Paine, 1969). Although likely impossible to test experimentally in primate communities, predation may support diversity among primate competitors in similar ways. For instance, of the three colobus monkey species which coexist at Taï National Park, Côte d'Ivoire, *Colobus polykomos*, *Piliocolobus badius*, and *Procolobus verus*, red colobus monkeys (*P. badius*) are preyed upon in the highest proportion by both chimpanzees (*Pan troglodytes*) and leopards (*Panthera pardus*) (Hoppe-Dominik, 1984; Boesch, 1994; Boesch and Boesch-Achermann, 2000; Zuberbühler and Jenny, 2002). Although red colobus are found at the highest density of the three colobine species, it is *hypothetically* possible that high predation rates keep their population density at a level low enough for the olive (*P. verus*) and black and white (*C. polykomos*) colobus to coexist due to a release from high competition.

However, recent studies showed that the black and white colobus population actually has a higher proportional predation rate (i.e., the number of individuals that are predated each year divided by total population) than the red colobus population at Taï. This total, however, includes data on crowned eagle as well as leopard and chimpanzee predation (Shultz, 2003; Shultz et al., 2004). This underscores the need for further investigations into differential rates of predation by all predatory species on primate community members in order to fully understand the extent to which predation influences such patterns of competition in communities.

Both intraspecific as well as interspecific competition with nonprimates may also influence community structure (e.g., Ganzhorn, 1999). For instance, in many communities, primates may compete with frugivorous birds and other mammals (Terborgh, 1986). Additionally, Shultz (2003) suggested that intragroup competition in combination with predation risk directly influences the biomass of primates in communities, as these factors most unequivocally affect resource use and mortality.

**Predation.** The effect that major predators may have on animal communities in which they live has been emphasized as critically important by researchers who advocate top-down control (Hairston et al., 1960; Terborgh, 1988; Terborgh et al., 2001). Conversely, predation is deemphasized by those who advocate bottom-up control (Polis and Strong, 1996). Members of primate communities are likely constrained to some extent by both predation and resources. It is clear that even with quite sophisticated antipredatory behaviors, primate populations can be decimated by peaks in predation. For example, Isbell (1990) reported that leopard predation on

vervet monkeys, *Chlorocebus aethiops*, in Amboseli National Park, Kenya, virtually decimated this population. Severe drops in resource availability also hold the potential to significantly reduce primate populations (e.g., severe drought influencing howler monkey (*Alouatta palliata*) resources on Barro Colorado Island, Panama; Milton, 1982). However, while such instances emphasize the potentially limiting influences of each, the importance of factors such as predation on community structure is probably much less dramatic.

In ecosystems with large numbers of predator species, members of the prey community often experience uneven predation pressure from each of the different predators (Sinclair et al., 2003). This seems to be a key aspect to the effect of predation on community structure as described in the above hypothetical example regarding three sympatric colobines. Shultz (2003) and Shultz et al. (2004) were the first to give a detailed picture of current rates of predation by multiple predators on all members of a primate community.

In a unique intraregional investigation of predation on primates, Shultz (2003) used estimates of predation risk for eight primate communities, based on aspects of both the potential predators present and the primates, to compare overall risk at each site. In her comparison, those sites with fewer predator species, such as the Asian sites of Kuala Lompat and Ketambe, or reported low predator densities, such as for leopards at Kibale, had lower average predation risk (Shultz, 2003). Broad-scale patterns of predation attempts by such predator groups as felids, raptors, canids, and reptiles show that raptor attacks are rare in comparison to felid attacks in Asia, while raptors perpetrate most attacks in Madagascar and the Neotropics, and both felid and raptor attacks are prevalent in Africa (Hart, 2000). This suggests that information on the number and types of predatory species at primate study sites may be useful for interpreting key differences between primate communities such as body size ranges, population densities, and even locomotor adaptations.

Although the studies mentioned above are only a first step in comparing the effects of predation between continents and communities, they indicate the potential for future studies that might be able to include more detail on the presence of predator groups, predation rates, and their effects on community structure. Zuberbühler and Jenny (2002) suggested that predation has selected for increased behavioral flexibility in primates. In the same vein, it is possible that predation has influenced diversity within primate communities as well. Investigation into the variation in predation pressures among primate communities may well provide interesting insights into the underlying factors of community structure.

Finally, some striking differences can be seen between the structures of primate communities that

experience human hunting and those that do not (e.g., Peres, 1999; Peres and Dolman, 2000). The extent to which human hunting can be considered along with nonhuman predation is questionable, as the former often causes much higher mortality rates in prey species than does the latter (Fleagle et al., 1999). Regardless, human hunting causes structural changes in certain primate communities. Thus, investigations into these effects on communities have implications for conservation. For instance, Peres (1999) pointed out that while density compensation by medium-bodied primates may occur in areas where large-bodied primates have been heavily hunted or extirpated by hunting, most if not all of the medium-bodied species are far less effective than large-bodied species at seed dispersal. Thus, the effects of hunting and predation on primate communities past and present not only stand to provide clues on how the communities have been and are being shaped by these forces, but also on the potential fate of many communities and habitats in the future.

## CONTINENTAL SUMMARY OF PRIMATE COMMUNITIES

Primate community structure varies on different continents. One of the most obvious factors affecting the outcome of primate communities among individual land areas is the date of probable original primate colonization. Asia may possess the longest-lived lineage of primates, with tarsiers possibly being related to some of the earliest primate taxa recovered there (Gebo et al., 2001). In this case, tarsiers would be the resident species, and lorisooids, apes, and cercopithecoids would be colonizing taxa. Madagascar and the New World each have unique colonization histories, with primates arriving very early on Madagascar, and possibly late Eocene/early Oligocene in South America. Africa possesses primate clades that also extend back to the Eocene, in addition to primates from several other adaptive radiations (Table 2). Adaptive radiations in this case refer to speciation events among colonizing primates that result in the ecological diversity that is seen among extant communities.

The structure of primate communities has also been affected by unique climates, different plant species, and forest physiognomy, providing differences in types and distribution of resources. Other animals that resided on continental land masses before the arrival of primates also contributed by providing a backdrop for differences in competition and predation.

### Madagascar

**Adaptive radiations.** The primate communities on Madagascar represent endpoints of an extraordinary adaptive radiation that began at least 50 million years ago with colonization of the island by ancestral lemur species (Yoder et al., 1996, 2003). Certainly, historical circumstances, particularly ex-

TABLE 2. Adaptive radiation events of primate taxa in different biogeographic regions<sup>1</sup>

Biogeographic region	Primate taxa	Date	Epoch	References
Madagascar	Lemuriformes	~55–50 mya	Eocene	Yoder et al., 1999, 2003
Neotropics	Platyrrhini	~30 mya	Oligocene	Takai et al., 2000
Africa	Lorisiformes	?55–50 mya	Eocene	
	Hominoidea	~25–15 mya	Miocene	Fleagle, 1999
Asia	Cercopithecoidea	~5 mya	Pliocene	Fleagle, 1999
	Tarsiformes	~45 mya	Eocene	Gebo et al., 2001
	Lorisiformes	?50 mya	Eocene	
	Hominoidea	~17 mya	Miocene	Fleagle, 1999
	Cercopithecoidea	~5.0 mya	Mio-Pliocene	Fleagle, 1999

<sup>1</sup> Various primate families had different colonization and subsequent radiation dates on various land masses. Most dates (mya = millions of years ago) refer to initial radiations and not first appearance dates and therefore subsequent radiations are also possible. The date for the radiation of Malagasy strepsirrhines is based on molecular data and refers to colonization, not necessarily a large radiation at ~50 mya. Assuming colonization of Madagascar at that time, other strepsirrhines must have existed and subsequently radiated in Africa and Asia.

tended isolation (geologic evidence shows that the island split from India around 88 million years ago with few later migrations; Storey et al., 1995; Yoder et al., 2003), and recent megafaunal extinctions (e.g., Godfrey et al., 1997; Goodman and Rakotozafy, 1997), as well as aspects of the island's endemic flora and fauna and stochastic climatic events, contributed in structuring current primate communities. Not only are Malagasy communities unique due to these factors, but the communities also stand out as flagships for biodiversity conservation and warning signs due to drastically high levels of habitat destruction, which has left nearly all lemur species endangered (Smith, 1997).

**Community structure.** Studies of Malagasy primate communities have only flourished relatively recently, as most early studies focused on only one or two primate species (Sussman, 1974; Hladik et al., 1980; Ganzhorn, 1988, 1989; Godfrey et al., 1997; Ganzhorn et al., 1997, 1999a,b). Comparative studies of primate communities used data from such studies and others to reveal that Malagasy communities, while arguably unique, seem to largely fit ecological patterns observed in primate communities from other biogeographic regions (Bourliere, 1985; Terborgh and van Schaik, 1997; Fleagle and Reed, 1996).

The current species diversity of lemur communities is actually greater than expected, given the estimated area of forest in Madagascar before human colonization (Reed and Fleagle, 1995). Lemur communities today are characterized by particularly high numbers of folivores as well as frugivores and insectivores, and include many nocturnal and cathemeral species, all of which range in body size from very small (30 g: *Microcebus berthae*/M. *myoxinus*) to medium-bodied (7 kg: *Indri indri*). Further, the locomotor repertoire of members of lemur communities tends heavily toward vertical clinging and leaping. In addition to comparisons with primate communities in other biogeographic regions, the unique aspects of lemur communities led Smith and Ganzhorn (1996) to compare them to Australian possums and gliders.

Extant Malagasy primate communities are characterized by large numbers of folivorous species relative to primate communities of other biogeographic regions (Fleagle and Reed, 1996). Most of the extinct subfossil species were also folivorous, further shifting the ratio of folivores to frugivores and insectivores in Malagasy subfossil communities (Godfrey et al., 1999). The subfossil lemurs greatly expanded the upper range of body sizes in communities to 200 kg. The addition of subfossil lemurs also expanded the locomotor repertoire of lemur communities by adding suspensory locomotor forms (Symons, 1997). These recently extinct lemurs, found in the fossil record with living species, also increase species richness, which is striking considering that extant Malagasy communities contain more primate species than expected. Godfrey et al. (1997) estimated that the ecospace occupied by past communities, including the extinct subfossil species, was considerably larger than that occupied by modern Malagasy communities. Ecospace or ecological space refers to the area held by primates in multivariate analyses of ecological adaptations, e.g., diet, substrate use, or locomotor pattern (Fleagle and Reed, 1996). As the ecospace occupied by extant Malagasy primate communities is similar in size to primate communities elsewhere, the much larger ecospace occupied by past Malagasy communities indicates that primates filled many niches in Madagascar which are likely occupied by other animal groups in different biogeographic regions. The fact that there are only four clades of land mammals (including lemurs) on Madagascar likely increased available niches in the past within Malagasy habitats relative to other regions, especially if lemurs were some of the earliest colonizers (Yoder et al., 2003).

**Climate and habitats.** The differences among Malagasy habitats are quite dramatic, ranging from the dry spiny desert in the south to the eastern tropical rain forest belt and the western tropical deciduous forests, all of which are inhabited by lemurs (Wright, 1999). Unfortunately, the entire island of Madagascar is now marked by extreme habitat destruction, such that each of these habitats

exists in only small strips and patches along the coasts, a fraction of their past size (Tattersall and Sussman, 1975). Western deciduous forests have been most heavily impacted by deforestation and now encompass only 2.8% of their original extent (Smith, 1997). Eighty percent of the island is now dominated by grasslands and savannas, primarily located in the central plateau due to human activities such as slash-and-burn agriculture (Richard and Sussman, 1975).

The fact that many sites containing subfossil lemurs (e.g., Ampasambazimba, Antsirabe, Masinadraina, and Tsirave) are located in the center of the island suggests that the current habitats utilized by lemurs extended into the central plateau in the recent past (Godfrey et al., 1999; Godfrey and Jungers, 2003). Indeed, the central subfossil sites (Ankarana with 16 and Ampasambazimba with 15 subfossil lemur species) had some of the highest species numbers found in primate communities (Godfrey et al., 1997). The geographic expanse of past Malagasy habitats obviously extended the range of ancient lemur communities. The destruction of these habitats in the recent past and today continues to influence the biogeographical ranges of lemur communities. Ganzhorn et al. (1999a,b) contrasted the regional pools of genera and species found in eastern wet and western/southern dry forests, showing relatively equal numbers of genera in each, although eastern rainforests are more species-rich. Some genera are today confined to only one of the two primary regions, including *Lemur* and *Mirza*, which are found only in dry forests, and *Varecia*, *Indri*, *Hapalemur*, and *Allocebus*, which are only found in eastern wet forests. However, these distributions do not necessarily reflect the distribution of genera and species in the recent past. For example, Godfrey et al. (1999) indicated that remains of the greater bamboo lemur, *Hapalemur simus*, are found at subfossil sites in the northwest and center of the island, well outside of their current, extremely restricted range on the eastern coast. However, they also noted that the composition of extant species in ancient lemur communities resembles nearby modern lemur communities. This suggests that the biogeographic patterns of lemur distribution that exist today are similar to those in the past, although ranges of many extant species are contracted today.

Certainly in the past, the central plateau added area as well as complexity to the habitats available to lemurs on the island. However, the extent to which it preserved the distinct differences currently seen between eastern and western forests is somewhat contentious. Goodman and Ganzhorn (2004) suggested that the past vegetation of the central highlands represented an intermediate zone which may have effectively damped the stark differences between eastern and western habitats seen today. In contrast, Godfrey et al. (1999) suggested that the central highlands served as a dispersal corridor with oases of forests or gallery forests extending into the

center, but maintained that the stark habitat differences between east and west also existed in the past. They also contended that the dry forest habitats of the west and northwest may not have been quite as dry in the past. The presence of lemur species, which are currently found only in eastern wet forests, at subfossil sites in western and northwestern Madagascar bears out this contention. Past forest extent likely played a part in influencing species richness based on species-area relationships. In fact, Smith and Ganzhorn (1996) attributed the higher species richness of Malagasy lemur communities today as compared with Australian arboreal mammal communities of possums and gliders to the larger forested area in Madagascar (~112,00 km<sup>2</sup>) prior to anthropogenic clearing. Also, given the steep elevation gradient particularly in eastern Madagascar, members of lemur communities occupy a broader and higher elevation gradient than do neotropical and Asian primates (Goodman and Ganzhorn, 2004).

Finally, rivers have been emphasized as an important biogeographic factor affecting primate dispersal and possibly even species richness in the Neotropics (e.g., Ayres and Clutton-Brock, 1992; but see Lehman, 2004a). A recent investigation into the effect of rivers on the geographic distribution of lemurs revealed that while rivers may act as dispersal barriers at low elevations, dispersal often occurs at the headwaters at higher elevations (Goodman and Ganzhorn, 2004).

Current climatic influences on lemur habitats in Madagascar include extreme fluctuations in rainfall including cyclical patterns of drought and cyclones, as well as periodic severe drops in temperature (Ganzhorn et al., 1999b; Wright, 1999). Seasonal variation in rainfall occurs in all habitats in Madagascar. Hladik (1980) emphasized the quite lengthy dry seasons lasting 7–8 months in a western deciduous Malagasy forest, where mean annual rainfall reaches 800 mm. By contrast, eastern Malagasy rainforests have slightly shorter dry seasons lasting 6 months, but annual rainfall is greater. Here rainfall averages about 2,000 mm per annum, although maximums of 5,000 mm have been recorded (Tattersall and Sussman, 1975; Overdorff, 1993a; Tan, 1999). Severe droughts have affected many habitats, particularly in the west and southwestern areas of the island, but also in eastern rainforests (reviewed in Wright, 1999). These lengthy dry seasons and frequent droughts may account for the plethora of strepsirrhine folivores on Madagascar.

Cyclones, that originate in the Indian Ocean, specifically threaten the eastern rainforest belt of the island each year, with the potential to blow down canopy trees, defoliate remaining trees, and cause landslides and flooding (Ganzhorn, 1995b). Such stochastic events not only directly affect the lemur populations by drastically decreasing food availability, but also may indirectly affect food availability. Tree crown volume is decreased in forests vulnerable to

cyclones in order to decrease the likelihood of the trees being blown down in the next storm (Ganzhorn et al., 1999a,b). This effect on tree physiognomy by past cyclones may also have influenced the evolution of locomotor strategies of lemurs by causing vertical clinging and leaping between relatively small crowns to be advantageous. Sites in Madagascar also occasionally experience drops of temperature, during which times frost has affected or killed vegetation (Wright, 1999). Such dramatic temperature changes directly affect the availability of lemur food resources. Indeed, as all the climatic patterns mentioned above affect the availability of food resources, they have also been suggested to be related to such unique lemur traits as the strict seasonal patterns of birth and weaning, which have evolved to maximize scarce resources (Wright, 1999).

**Resources.** Patterns of seasonal peaks in food abundance in Malagasy habitats are often unpredictable from year to year, likely due to droughts, frost, or cyclone damage. Wright (1997) compared the fruiting seasonality in Ranomafana National Park, Madagascar to that in Cocha Cashu in Manu National Park, Peru, revealing an overall longer period of scarcity in Ranomafana. However, the seasonal availability of fruit and young or new leaves is reported to be complementary in Malagasy rainforests (Smith and Ganzhorn, 1996). The tree crowns of eastern Malagasy rainforest trees are smaller than those of other tropical forests, likely as a response to frequent cyclone disturbance. A decrease in tree crown volume also decreases food resources in the form of both fruit and leaves for lemurs in these forests. The height of trees in the eastern rainforests is also much lower than those of tropical rainforests in other biogeographic areas (e.g., Ranomafana mean height is 9.6 m; "tall trees" are >25 m; Dagosto and Yamashita, 1998; in Cocha Cashu, Peru, mean height is 30–35 m; emergent trees are 50–60 m; Terborgh, 1983; in Tai National Park, Côte d'Ivoire, emergent trees are up to 60 m; Shultz, 2003; in Kuala Lompat, Malaysia, emergent trees are over 60 m; Raemaekers et al., 1980). However, low-level disturbances due to selective logging may actually slightly increase fruit production, as most logged trees do not produce fruit eaten by lemurs and their absence reduces competition with trees that do produce fruit resources utilized by lemurs (Ganzhorn, 1995a). While Ganzhorn et al. (1997) did find that overall lemur species diversity is positively correlated with tree species diversity, within sites, lemurs appear to prefer slightly disturbed areas to pristine areas.

Close relationships between lemur and tree species may reflect the importance of lemurs as primary seed dispersers for many plants. Experimental data from Ranomafana by Dew and Wright (1998) indicated that *Eulemur rubriventer*, *E. fulvus*, and *Varecia varecia* are particularly important seed dispersers, as seeds which passed through the guts of these

species were more likely to germinate than those that did not. Smith and Ganzhorn (1996) suggested that the fact that there are few frugivorous birds in Madagascar encouraged the coevolution of fruiting plants and lemurs, in contrast to Australian forests in which most tree seeds are dispersed by birds and no truly frugivorous mammals are present. For example, mistletoe seeds are dispersed in western Madagascar by *Cheirogaleus*, which smear their feces on branches rather than letting them drop to the forest floor like most primates, whereas the seeds of mistletoes in Australia are dispersed by the specialized Mistletoe bird, *Diaceum hirundinaceum*. Furthermore, Ganzhorn et al. (1999a) suggested that regeneration of all primary forest trees in the western deciduous forests is dependent entirely on seed dispersal by the brown lemur, *Eulemur fulvus*. This relationship between lemurs and seed dispersal/germination also has important conservation implications for maintaining lemur populations in these forests.

While coevolution between trees and lemurs may help explain the maintenance of frugivorous lemur populations, folivorous lemurs seem to have become abundant and diverse by avoiding efforts by tree species to deter herbivory. Ganzhorn (1992) found that the overall biomass of folivorous lemurs is positively correlated with average leaf quality, based on protein-to-fiber ratio. In Madagascar, there is a significant negative correlation between rainfall and leaf quality which may be related to the positive correlation that is present between folivorous lemur biomass and seasonality. The relationships between the biomass of folivorous lemurs and patterns of rainfall, leaf quality, and seasonality have interesting implications for past environments which supported a far higher biomass of folivorous lemurs. Interestingly, Ganzhorn (1995a) also noted that low levels of selective logging in Malagasy forests positively affect leaf quality in standing trees by providing more available sunlight, which increases the protein content in sun-exposed leaves. Thus, the biomass of folivorous lemurs in a community is influenced by the protein content in leaves rather than by secondary compounds for which some species have developed amazing tolerances. For example, *Lepilemur* species can consume leaves with very high levels of alkaloids, and *Hapalemur* species can consume bamboo containing high levels of cyanide (Ganzhorn, 1992).

**Species interactions.** As suggested previously, the presence of sympatric congeneric species may indicate some level of past competition. In the case of Malagasy communities, many contain congeneric folivorous (e.g., *Hapalemur*), frugivorous (*Eulemur*), or insectivorous/frugivorous (*Microcebus*) species. Overdorff (1993a,b) studied the ecology of sympatric rufous lemurs (*Eulemur fulvus rufus*) and red-bellied lemurs (*E. rubriventer*) in the eastern rainforest of Ranomafana National Park. The two species ex-

perience much dietary overlap in fruit, but rufous lemurs were found to eat more unripe fruit and mature leaves than did red-bellied lemurs. During periods of fruit scarcity, rufous lemurs increased their range by migrating out of the study area. This suggests that these species currently compete for limited resources. Therefore, competition between frugivorous lemur species may be most affected by seasonal periods of scarcity in fruit production.

Although interspecific competition is not typically high between folivorous species, evidence also suggests that the nocturnal folivorous lemurs, *Lepilemur mustelinus* and *Avahi laniger*, may compete for high-quality leaves (Ganzhorn, 1993). When sympatric with *A. laniger*, *L. mustelinus* has been found to eat leaves with lower protein-to-fiber ratios than it consumes at sites where *A. laniger* is absent (Ganzhorn, 1993). All extant *Lepilemur* species are allopatric, but subfossil communities reveal the existence of two *Lepilemur* species at one site that deviate considerably in body size. Differences in body size may have helped release them from competition with one another (Godfrey et al., 1997). Ganzhorn (1989) suggested that differences in microhabitat preferences within both frugivorous and folivorous lemur guilds may help reduce competition in lemur species today.

It is impossible to completely understand the species interactions between extinct subfossil species and those still living today. It seems likely, however, that the extinction of at least 16 relatively large-bodied lemur species in the past 2,000 years released the largest extant lemurs from competition. These extinct lemur species appear to have made up a significant proportion of lemur communities in the past and probably consumed great quantities of resources, particularly leaves (Godfrey et al., 1997). The communities in the center of the highlands have been drastically changed since the loss of the subfossil lemurs (e.g., only three lemur species occur in the forest of Ambohitantely today, although at least 15 lemur species were present at the nearby subfossil site of Ampasambazinba in the past), likely due to isolation through habitat destruction. Also, isolation on an island with only three other mammal lineages may have released members of lemur communities from past competition with nonprimate mammals, unlike primates in other biogeographic regions (Yoder et al., 2003). However, it is becoming clear that Malagasy lemurs have not been released from the pressures of predation in either the past or the present.

It was suggested that current predation risks for Malagasy primates are low, such that current risks perceived by lemurs are based largely on recently extinct large predators (Goodman et al., 1993; Goodman, 1994; but see Csermely, 1996). Shultz (2003) estimated relatively high predation risk at Ranomafana and Morondava based on the risk posed by each extant potential predator on each primate prey species in accordance with the abundance of both

predators and prey. Predation by both mammalian (fossa, *Cryptoprocta ferox*; ringtailed mongoose, *Galidia elegans*: Goodman et al., 1993; Wright et al., 1997; Wright, 1998) and avian (Madagascar harrier hawks, *Polyboroides radiatus*; Henst's goshawks, *Accipiter henstii*; barn owls, *Tyto alba*; long-eared owl, *Asio madagascariensis*; Madagascar buzzard, *Buteo brachypterus*: Goodman et al., 1993; Karpanty and Goodman, 1999; Karpanty and Grella, 2001; Karpanty, 2003) predators was shown to impact various members of lemur communities. It seems that certain avian Malagasy predators such as the Madagascar harrier hawk preferentially prey on lemurs, at least seasonally (Karpanty and Goodman, 1999; Brockman, 2003). Recent research indicates that seasonal peaks in harrier hawk predation on lemurs occur during both the hawk courtship season (August), which coincides with lemur birth seasons, and the hawk nestling season (November–February) (Brockman, 2003; Karpanty, 2003). Wright et al. (1997) estimated that predation by the fossa may significantly affect lemur population densities, especially due to their tendency to prey on adult individuals from the largest lemurs in extant communities (e.g., *Propithecus* spp. at both Ranomafana and Morondava). Thus, predatory cycles of both mammalian and avian predators may cause drastic changes in the density of members of lemur communities that reproduce more slowly.

Alarm-calling behavior from playback experiments (Fitchel and Kappeler, 2002) indicates that lemurs may generally perceive a higher risk from avian than terrestrial predators. This is interesting, given new evidence that the lineage of terrestrial predators, including the fossa, *C. ferox*, did not arrive on Madagascar until at least 14 million years after strepsirrhines arrived (Yoder et al., 2003). Although it is clear that a much larger suite of avian predators existed on the island in the recent past (Goodman and Rakotozafy, 1997), further information on the tenure of this lineage on Madagascar is not available. Consequently, the coevolution between both avian and terrestrial predators and lemur prey cannot be compared at this point.

Currently, human hunting may be more influential on many lemur communities than is nonhuman predation (Richard and Sussman, 1975). It is likely that human hunting also played a part in the extinction of at least some of the large-bodied subfossil lemur species, based on cut-mark evidence on remains of *Paleopropithecus* bones from Taolambiby (Godfrey et al., 1997; Godfrey and Jungers, 2003). Hunting by Malagasy tribes still occurs today, although local taboos exclude some lemurs such as *Propithecus verreauxi*, *Avahi laniger*, *Indri indri*, and *Daubentonia madagascariensis*, causing differential hunting pressures on different species (Richard and Sussman, 1975). However, current sport hunting of lemur species has the potential to affect populations more rapidly than traditional hunting. For instance, Richard and Sussman (1975) reported

the killing of 12 individual *Propithecus* in one day by a single hunter using firearms.

Thus, humans not only influence lemur communities indirectly through massive deforestation, but also through both traditional and nontraditional hunting practices. It is likely that this has been the case since humans first colonized Madagascar (Godfrey et al., 1997; Godfrey and Jungers, 2003). The underlying factors of the lemur communities that remain include such important natural factors as abiotic disturbances, and food quality and production, but human influences, which have driven species to extinction and extirpated others, stand out as the most rapid and influential factors providing an unfortunate warning to all primate communities.

### Neotropics

**Adaptive radiations.** Although a more recent radiation than the Malagasy lemurs, neotropical primates, the Platyrrhini, have also been isolated from other primate radiations since their arrival on South America from Africa approximately 30 million years ago (Takai et al., 2000). As the early fossil platyrrhines of Argentina and Chile are markedly different from later fossil platyrrhines and extant lineages (Fleagle et al., 1997; Takai et al., 2001), one might consider multiple adaptive radiations, or even multiple dispersal events, to have occurred within the Platyrrhini in the past 30 million years. Today, neotropical primate communities inhabit the largest expanses of tropical rainforests on earth (Mittermeier, 1988). These areas of rainforest have provided a plethora of niches for primate diversification through macro- and microhabitat differences. These differences are driven to a great extent by rivers, which 1) limit small primate dispersal, 2) seasonally flood forests, 3) affect soil quality, and 4) may have even represented the boundaries of forest refuges in the Pleistocene (Ayres and Clutton-Brock, 1992; Peres et al., 1996; Haffer, 1997; Peres, 1997). These factors, along with species interactions, including human impacts, have worked together to influence the structure of neotropical primate communities, which are some of the most species-rich of all primate-inhabited biogeographic regions (Reed and Fleagle, 1995).

**Community structure.** The first studies of primate communities in the Neotropics were undertaken in the late 1970s and early 1980s (Fleagle and Mittermeier, 1980; Mittermeier and van Rossmalen, 1981; Freese et al., 1982; Terborgh, 1983). These studies, and those comparing communities from different biogeographic regions (Bourliere, 1985; Terborgh and van Schaik, 1997; Reed and Fleagle, 1995; Fleagle and Reed, 1996; Fa and Purvis, 1997; Reed, 1999), highlighted the fact that neotropical primate communities tend to be biased toward small-bodied frugivore-insectivores, with very low numbers of nocturnal or folivorous species, and completely lacking in terrestrial species. Al-

though many neotropical primate communities exhibit high species diversity, the biomass of these communities is much lower than that of communities in other regions (Reed, 1999). The low biomass may be due in part to the dearth of folivorous primates, which contribute heavily to the biomass of paleotropical communities. The small-bodied callitrichine radiation may also influence the low overall biomass, as multiple callitrichine species are found in most neotropical communities, adding much to the species diversity but very little to the community biomass. Indeed, large-bodied primates are conspicuously missing in the Neotropics, where no living primate exceeds 12 kg. However, at cave sites near Brazil's Atlantic forest region, recently discovered fossil species, which existed around 10,000 years ago, were estimated to weigh around 25 kg (Cartelle and Hartwig, 1996; Hartwig and Cartelle, 1996). This not only adds to the body-size range of neotropical primates, but also likely increased the biomass of at least Brazilian primate communities in the geographic vicinity of those that include the largest-bodied neotropical primate today, *Brachyteles arachnoides*. As all neotropical primates are arboreal, the upper limits on body size may be related to the physiognomy of neotropical forests, such that the slender branches of trees and lianas cannot support arboreal mammals above a particular body mass. However, these same factors also likely stimulated unique adaptations to arboreality, such as the semibrachiating locomotion of many larger-bodied atelines and the prehensile tails present in the ateline and cebine lineages.

**Climate and habitats.** The historical biogeography of Central and South America, particularly during the Pleistocene, may have been quite influential, given the necessity of forested habitats for the strictly arboreal radiation of neotropical primates. Haffer (1969) proposed that forested areas contracted to form small forest refugia during dry periods in the Pleistocene in South America which isolated forest fauna, promoting allopatric speciation. The refugia in this hypothesis (Haffer, 1969) may correlate with areas of higher primate species diversity in the Neotropics today. Struhsaker (1981) found this to be the case with areas of high species diversity in East Africa, which corresponded with proposed Pleistocene refugia. Although da Silva and Oren (1996) found that current centers of endemism for neotropical primates correspond relatively well with the refugia of Haffer (1969), more recently the existence of forest refugia during the Pleistocene was seriously questioned, primarily on the basis of Pleistocene geology (e.g., Colinvaux et al., 2000). At this time it seems that the mere existence of these refugia is tenuous, making it difficult to know to what extent the historical distribution of forests served as a mechanism of current community structure. Figure 1 shows the positions of refugia in Amazonia

during the Pleistocene, 18,000 years ago. We compared this to a cluster analysis of primate species living in extant communities to test for relationships between closely related species and hypothetical Pleistocene refugia. To arrive at the cluster analyses of related sites, we calculated similarity indices between the localities based on the presence and absence of primate species in each community. We used the dice similarity index (Magurran, 1988) to calculate similarity using the presence and absence of species in pairs of localities. The equation is

$$D = 2j / (2j + a + b)$$

where  $j$  is the number of species in common at both sites,  $a$  is the number of species at site A, and  $b$  is the number of species at site B. Unweighted pair group means analysis (UPGMA) was used to calculate the dendrogram. Figure 1 identifies living primate species from communities that correspond with proposed refugia, and those in boldface exist only in these hypothesized areas of previous isolation. These species tend to be congeneric, lending credence to the idea that the radiation of these species occurred in the relatively recent past. In addition, Espírito Santo of the remnant Atlantic forest is most distinct from the other communities, likely having been isolated from the other sites for a longer period of time.

The expansive (although rapidly dwindling) areas of forest present in the Neotropics today are by no means homogeneous. Microhabitat differences present within forests as well as more broad-scale differences, e.g., between flooded várzea and nonflooded terra firme forests, are both important factors for primate community structure. While Peres and Janson (1999) found an overall trend for decreasing primate species richness with increased distance from the equator in the Neotropics, they suggested that finer-scale variations in forested habitat may better explain the variation in species richness throughout the Neotropics. Many studies of spatial heterogeneity of primate habitats in the Neotropics in the past two decades arose from conservation-focused studies of forest fragmentation (e.g., Mittermeier et al., 1989; Rylands et al., 1997; Chiarello, 2000). Some approaches concerning the effect of forest fragmentation on primate communities stem from the island biogeography theory of MacArthur and Wilson (1967), as each forest fragment may be considered a pseudo-island (Cowlshaw and Dunbar, 2000). Habitat destruction through clear-cutting, for example, can create forest fragments which are highly isolated from other forested areas, resulting in fewer species per unit area due to the limitations of dispersal into or out of the forest fragment. Less isolated forests (i.e., those with intact corridors to other forested areas) may be able to maintain higher population levels and greater numbers of species through increased levels of immigration, even in the face of habitat alteration. In their comparison of 185

neotropical primate communities, Peres and Janson (1999) pointed out that communities are most diverse where the forested habitat is most extensive. Dispersal ability may be primarily responsible for the trend for larger biogeographic areas to have greater primate species richness. Indeed, primate communities existing in forest fragments, especially those in the Atlantic forest region of Brazil, have much lower species richness than communities elsewhere (Pinto et al., 1993; Rylands et al., 1996; Chiarello, 2000), undoubtedly due in large part to isolation. The prevalence of isolated forest fragments within the Neotropics today may help explain why Reed and Fleagle (1995) found that neotropical primate communities had fewer species than expected, given the total area of rainforest in the Neotropics.

Within forests, rivers can act as barriers to dispersal for primates that cannot cross them. The importance of rivers as dispersal and range barriers to Amazonian primates was strongly emphasized by Ayres and Clutton-Brock (1992). Genetic and morphological evidence indicates that rivers act as barriers to gene flow in small-bodied primate species (e.g., saddleback tamarins, *Saguinus fuscicollis*, Peres et al., 1996). As an alternative to his Pleistocene refuge hypothesis, Haffer (1997) reviewed suggestions that the Amazon and its larger tributaries may have acted as barriers between forest tracts, therefore increasing speciation of Amazonian fauna. Cowlshaw and Dunbar (2000) suggested that the crosscutting of rivers through areas of tropical forest may in part account for the greater species richness found within larger geographical areas, as different species may be found on either side of each of these rivers. Thus, the presence and number of rivers may influence the current species richness of forested areas. However, Lehman (2004a) recently found a strong negative correlation between primate species diversity and the number of rivers in Guyana. Although many rivers do act as dispersal barriers to primates in this region, it is likely that other factors such as the low incidence of keystone resources like palms in certain areas of Guyana, as mentioned by Lehman (2004a), are equally or more influential than rivers on primate diversity at this scale.

Another way in which rivers can affect neotropical primate habitats is through flooding patterns, which leave many forests seasonally inundated. Flooded várzea often support different animal communities than unflooded, or terra firme, forests. Peres (1997) found significant differences in primate species richness and density between the communities in 20 flooded and unflooded forests along the Jurua River in western Amazonian Brazil. The number of primate species in communities inhabiting terra firme forest sites ranged from 10–14, whereas the number of species inhabiting várzea forests ranged from only 3–7. The density and total primate biomass, on the other hand, were much higher in várzea forest sites than in terra firme forests.

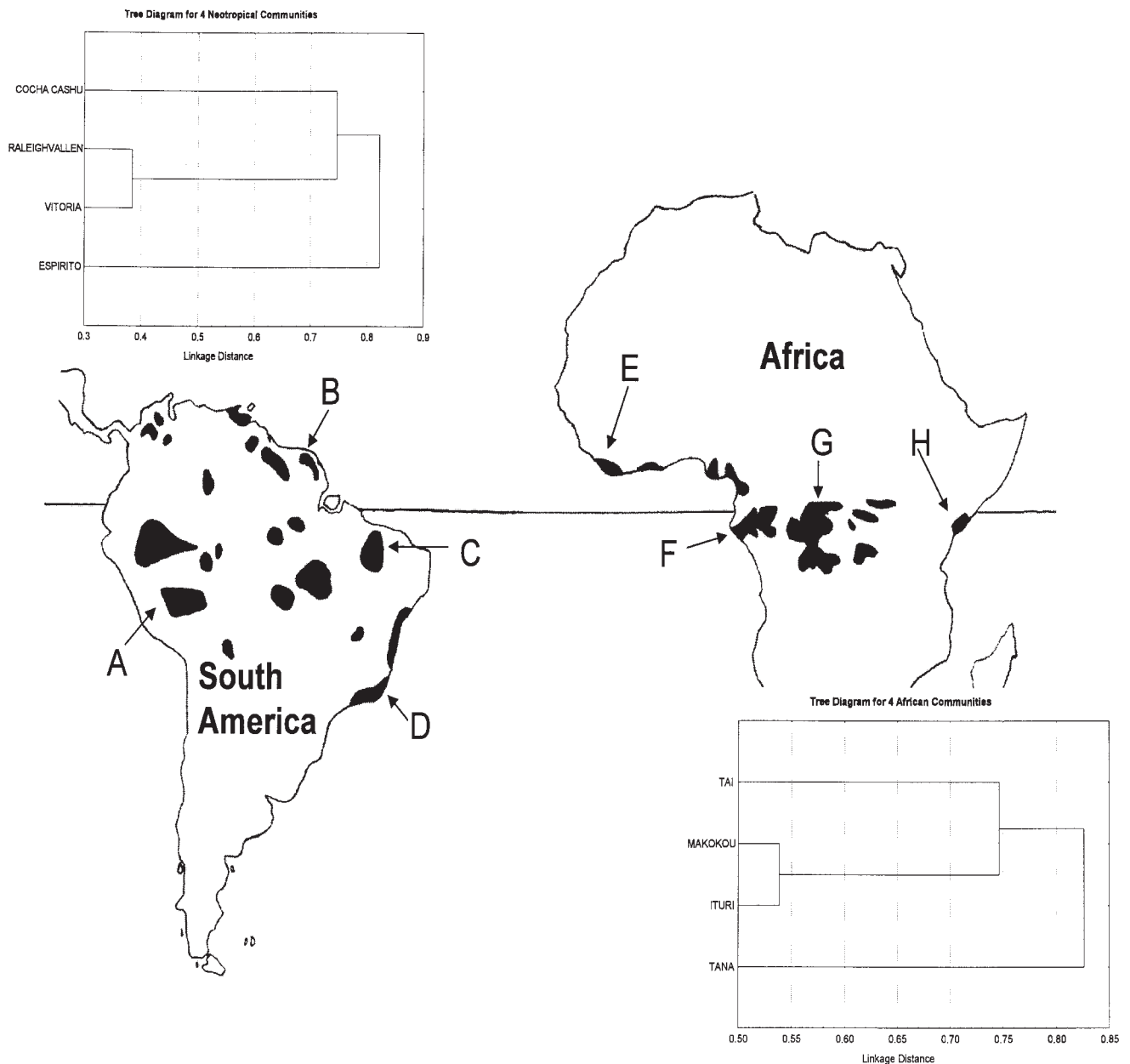


Fig. 1. (See legend Page 19.)

The lower species numbers in flooded forests are primarily due to the lack of smaller (120–600 g) callitrichid species, which primarily inhabit the lower levels of the canopy and understory, relying partially on insect prey found in this area. When the forests are flooded, sometimes for up to half the year or more, neither the understory/lower canopy levels nor the insects found there are available. Densities of *Alouatta*, *Saimiri*, and *Cebus albifrons* were found to be significantly higher in várzea forests than in terra firme forests. The largest proportion of primate biomass in these communities is made up by the more folivorous *Alouatta seniculus*, which may benefit from possibly more nutrient-rich and less toxic resources in várzea forests compared to terra

firme forests. Peres (1997) suggested that soil quality may facilitate the high-density and large community biomass of primates in várzea forests. The whitewater flooding the várzea forests carries nutrient-rich debris, which Peres (1997) suggested has had a direct effect on the quality of the forest foliage. However, as mentioned previously, Oates et al. (1990) failed to find a significant relationship between soil quality and primate species biomass in communities in both afrotropical and neotropical primate habitats, suggesting that tree communities can adapt to poor soil conditions and manage to provide sufficient nutrients for primates. An increase in density of folivorous primates also exists in neotropical forests that were selectively logged,

<u>A.Cocha Cashu, Peru</u> <i>Alouatta seniculus</i> <b><i>Aotus trivirgatus</i></b> <i>Ateles paniscus</i> <b><i>Callicebus moloch</i></b> <i>Cebus albifrons</i> <i>Cebus apella</i> <b><i>Saguinus fuscicollis</i></b> <b><i>Saguinus imperator</i></b> <b><i>Saimiri boliviensis</i></b>	<u>B.Raleighvallen, Surinam</u> <i>Alouatta seniculus</i> <i>Ateles paniscus</i> <i>Cebus apella</i> <i>Chiropotes satanas</i> <b><i>Pithecia pithecia</i></b> <b><i>Saguinus midas</i></b> <i>Saimiri sciureus</i>	<u>C.Fazenda Vitória, Brazil</u> <b><i>Alouatta belzebul</i></b> <b><i>Aotus infulatus</i></b> <i>Cebus apella</i> <i>Chiropotes satanas</i> <i>Saguinus midas</i> <i>Saimiri sciureus</i>	<u>D.Espírito Santo, Brazil</u> <b><i>Alouatta fusca</i></b> <b><i>Callicebus personatus</i></b> <b><i>Callithrix geoffroyi</i></b> <i>Cebus apella</i>
<u>E.Taï, Côte d'Ivoire:</u> <b><i>Cercocebus atys</i></b> <b><i>Cercopithecus campbelli</i></b> <b><i>C. diana</i></b> <i>C. nictitans</i> <b><i>C. petauristi</i></b> <b><i>Colobus polykomos</i></b> <i>Galagoides demidoff</i> <i>Pan troglodytes</i> <i>Perodicticus potto</i> <i>Ptilocolobus badius</i> <b><i>Procolobus verus</i></b>	<u>F.Makokou, Gabon:</u> <b><i>Arctocebus calabarensis</i></b> <i>Cercocebus galeritus</i> <b><i>Cercopithecus cephus</i></b> <i>C. neglectus</i> <i>C. nictitans</i> <i>C. pogonias</i> <i>Colobus guereza</i> <b><i>Euoticus elegantulus</i></b> <i>Galago alleni</i> <i>Galagoides demidoff</i> <b><i>Galagoides thomasi</i></b> <i>Gorilla gorilla</i> <i>Lophocebus albigena</i> <b><i>Mandrillus sphinx</i></b>	<u>G.Ituri, D.R.Congo:</u> <i>Cercocebus galeritus</i> <b><i>Cercopithecus ascanius</i></b> <i>C. mitis</i> <i>C. neglectus</i> <i>C. pogonias</i> <i>Colobus angolensis</i> <i>Colobus guereza</i> <i>Galagoides demidoff</i> <i>Lophocebus albigena</i> <i>Pan troglodytes</i> <i>Perodicticus potto</i> <i>Ptilocolobus badius</i>	<u>H.Tana River, Kenya:</u> <i>Cercocebus galeritus</i> <i>C. mitis</i> <i>Chlorocebus aethiops</i> <b><i>Galago senegalensis</i></b> <b><i>Otolemur crassicaudatus</i></b> <b><i>Papio cynocephalus</i></b> <i>Ptilocolobus badius</i>

**Fig. 1.** Locations of proposed forest refugia in South America and Africa in late Pleistocene, adapted from Archibold (1995). Selected extant primates within forest communities that correspond with forest refugia are also identified. Species found only in refugial regions are in bold face. Cluster analyses of regions show linkages among migratory species. Cluster analyses are based on dice similarity indices and UPGMA cluster algorithm.

which indicates that factors other than soil quality influence folivore populations, although both factors mentioned may result in higher leaf nutrient quality (Peres, 1988).

The extent to which mean annual rainfall is related to species diversity was addressed previously in this article. Reed and Fleagle (1995) found a high positive correlation between mean annual rainfall and the number of primate species at sites in the Neotropics as well as sites in Africa and Madagascar. Kay et al. (1997) found a similar correlation based on data from a larger sample of neotropical primate communities; however, they reported a decline in primate diversity at sites receiving over 2,500 mm of rain per year. This decline is paralleled by a decline in primary productivity at sites with high rainfall. Although it appears from this that patterns of primate diversity respond more closely to plant productivity than to rainfall, placing too much emphasis on this pattern of decline was criticized, as the data are derived from very few sites with rainfall over 2,500 mm (Cowlshaw and Dunbar, 2000).

**Resources.** The primary productivity of neotropical forests sustains large communities of animals. The lowland wet forests of the Neotropics hold the world's highest total diversity of frugivorous birds, primates, and bats (Fleming et al., 1987). Indeed, fruit makes up the primary component of most neotropical primate diets (Rosenberger, 1992). Even

members of the most folivorous neotropical primate genus, *Alouatta*, devote as much as 50% or more of their feeding time to fruit (Estrada and Coates-Estrada, 1986). Given this reliance on fruit resources, it is not surprising that Stevenson (2001) found fruit productivity to be positively correlated with both neotropical primate biomass and primate species richness.

The production of fruit, however, is highly seasonal, resulting in a relatively long period of superabundance and a shorter but critical period of fruit scarcity (Terborgh, 1983, 1986; van Schaik et al., 1993; Terborgh and van Schaik, 1997). Although neotropical primate richness and biomass may be related to overall fruit productivity, it was suggested that the availability of a few keystone resources during periods of scarcity sets the carrying capacity of frugivores in a community (Terborgh, 1986). Rosenberger (1992) suggested that responses to seasonal dietary requirements, which may be biomechanically challenging, can have a great influence on morphological adaptations, particularly in the dentition, although they may only constitute a small proportion of the annual diet which further influences community structure.

Certain morphological adaptations of the primates at Cosha Cashu, in Peru, were equated with the use of keystone resources identified by Terborgh (1983, 1986; see also Terborgh and van Schaik,

1997). For example, the brown capuchin (*Cebus apella*) is the only member of the primate community able to access the mature nuts of relatively abundant *Astrocaryum* palms during periods of fruit scarcity, due to their especially strong jaws, which possess the 140 kg of bite force necessary to break the protective hard shell of the nut. These palm nuts constitute the majority of the diet of *C. apella* during periods of scarcity. In support of the importance of keystone resources on primate communities, Stevenson (2001) found a positive correlation between frugivorous primate biomass and the density of palms, and a significant positive correlation between total primate biomass and the density of tree species of the family Moraceae. Figs (*Ficus*), members of the family Moraceae, are considered keystone species for neotropical frugivores, largely because entire fig tree crowns come into fruit during periods of scarcity, providing prized patches of abundant food resources.

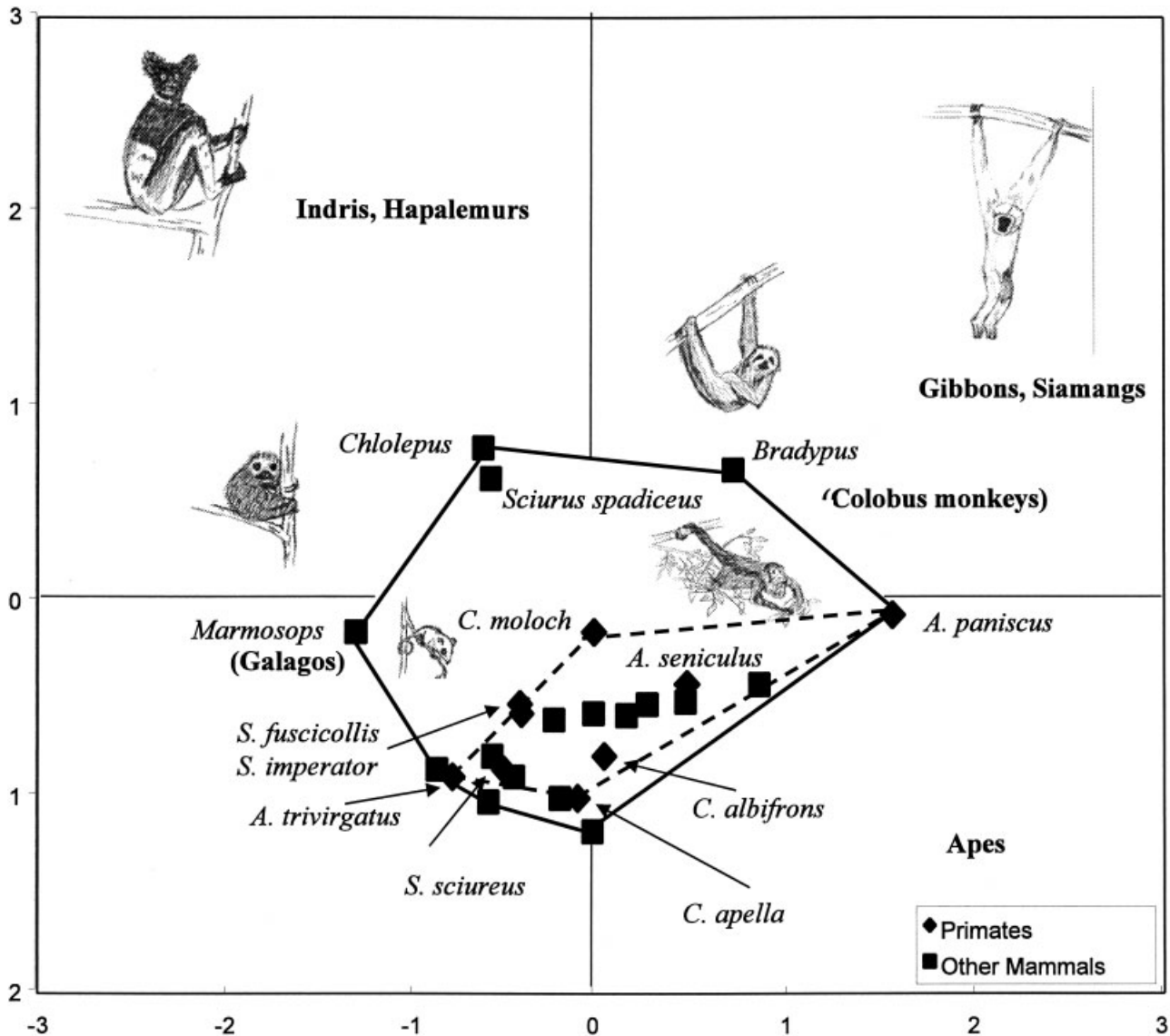
**Species interactions.** Although measures of fruit productivity at Cocha Cashu indicate that fruit abundance usually far exceeds the amounts which could possibly be consumed by all frugivores at the site (Terborgh, 1986), the fact that the fruit availability during brief periods of scarcity is lower than that required by resident frugivores suggests that fruit may be a limiting resource inducing competition between community members at these times. Anecdotal evidence indicates that interference as well as exploitive interspecific competition occurs within the primate community. For example, while members of brown capuchin groups normally tolerate the proximity of large groups of squirrel monkeys (*Samiri sciureus*) while feeding, capuchins were observed to chase the smaller-bodied squirrel monkeys out of feeding trees (Terborgh, 1983). Similarly, Wright (1996) reported that similarly small-bodied titi monkeys (*Callicebus moloch*) were frequently chased out of fruiting trees by larger monkeys. Terborgh (1986) also suggested that the even smaller-bodied tamarins avoid eating figs even in their defended territories during periods of fruit scarcity when larger monkeys are feeding in the tree. However, Fleming et al. (1987) noted that there is less dietary overlap among neotropical frugivores (primarily primates, bats, and birds), than among paleotropical frugivores.

We pointed out previously that the existence of dietary overlap does not necessarily indicate the occurrence of competition. However, the low levels of dietary overlap among neotropical frugivores, especially considering the abundance of frugivores particularly within primate communities, may indicate that current levels of interspecific competition among frugivores are low. However, this may indicate the existence of past interspecific competition. Congeneric primate species exist sympatrically at many neotropical sites, including *Cebus apella* and either *C. abifrons* or *C. olivaceus*, in addition to *Saguinus fuscicollis* and either *S. imperator* or *S.*

*mystax*. This may give some indication of past competition among frugivore-insectivores in these communities.

Although folivory is uncommon among neotropical primates, the question of whether or not primarily folivorous howler monkeys (*Alouatta* spp.) compete with other neotropical folivores, particularly the very successful and prominent lineage of folivorous sloths, over food resources is of some importance (Moynihan, 1976; Bourliere, 1985, but see Terborgh and van Schaik, 1997). Sloths are apparently quite difficult to detect in censuses, as exemplified by an investigation of harpy eagle predation (Galetti and de Carvalho, 2000), which discovered large numbers of sloth remains in an area where no sloths had been detected in transect censuses. Further, in contrast with the assertion of Terborgh and van Schaik (1997) that primates are the preeminent arboreal consumers in the world's rainforests, Eisenberg and Thorington (1973) pronounced sloths (*Bradypus* and *Choloepus*) to be the most important consumers in the canopy in the Neotropics. No direct data exist on the effect of sloths on howler monkey populations. While it seems that howler monkeys live in relatively high densities where sloths are prevalent, it is difficult to compare densities of howlers where sloths are not prevalent, considering the possibly low detectability of sloths in many areas leading to unreliable estimates of density. It is interesting, however, that when sloths and possums (*Marmosops*) are included in a multivariate analysis of neotropical community ecological space, the two-dimensional space more closely resembles paleotropical primate communities (Fig. 2; Fleagle and Reed, 1999a). Fleagle and Reed (1996) used primate characteristics to define ecological spaces of primates worldwide, and then plotted results for individual communities on various continents. Figure 2 adds sloths and possums to that principal coordinates analysis to understand the ecological space that is held by these nonprimates in the Neotropics. *Bradypus* is positioned in the ecospace occupied by colobus monkeys in Africa and Asia, while *Marmosops* occupies the area filled by galagos in Africa (Fleagle and Reed, 1999a).

Another factor, synchrony in neotropical fruiting and leafing cycles, which may preclude young leaves from serving as a significant alternative to fruit during periods of scarcity, was employed as an alternative causal factor of the low diversity of neotropical primate folivores (Terborgh and van Schaik, 1997). However, Heymann (2001) found that this pattern of synchronization of fruiting and leafing, detected by Terborgh and van Schaik (1997) at only one site (Barro Colorado Island, Panama), was not found at most neotropical sites. Thus it seems that exploitive competition by arboreal sloths, which were present in South America prior to or concurrent with colonization by primates in the late Oligo-



**Fig. 2.** Principal coordinates analysis of mammals from Cocha Cashu, Peru. Ecological space is defined from Fleagle and Reed (1996) for all primates from eight communities (Cocha Cashu, Peru; Raliaghvallen, Suriname; Ranamafana, Madagascar; Mornodava, Madagascar; Tai Forest, Côte d'Ivoire; Kibale National Park, Uganda; Ketambe; Kalimantan; and Kuala Lompat, Malaysia). Adding sloths, possums, and squirrels to analysis expands ecological space for neotropical community to approximate sizes of African and Asian communities. This indicates that sloths may be filling arboreal folivore niche of primates in other communities.

cene/early Miocene, might be a more likely limiting factor for folivorous neotropical primates (Carroll, 1988).

Neotropical primate community members face an impressive suite of sympatric predatory species, including large raptors such as harpy eagles (*Harpia harpyja*), and large felids such as jaguars (*Panthera onca*) and pumas (*Felis concolor*). Attacks from such large predators ensure that even the largest-bodied neotropical primates are not released from predation risk (Izor, 1985; Peres, 1990; Sherman, 1991; Peetz et al., 1992; Julliot, 1994). A study of harpy eagles in Guyana (Izor, 1985) revealed that adult members of *Alouatta*, *Ateles*, and *Cebus* comprised one third of prey re-

main, which constituted a higher proportion of primates than that reflected in the habitat. Smaller neotropical primates fit into the prey size range of a larger number of predatory species, particularly smaller raptors which occur within the diverse raptor communities of the Neotropics (e.g., 35 diurnal raptor species regularly inhabit 800 ha of Manu National Park, Peru; Robinson, 1994). The frequency of raptor attacks on squirrel monkeys (*Saimiri boliviensis*) and capuchins (*Cebus* spp.) is particularly high in some areas (Boinski, 1987; Terborgh, 1983; Boinski et al., 2003). Indeed, raptor attacks make up 78% of the total reported predatory events on primates in the Neotropics (Hart, 2000).

Shultz (2003) calculated the average predation risk for primates in two neotropical communities, Cocha Cashu, Peru, and Raleighvallen, Surinam, to be the highest among the eight communities she investigated from each biogeographical region. Shultz et al. (2004) suggested that the fact that there are no terrestrial neotropical primates may be related to the abundance of terrestrial predators in the Neotropics. As mentioned previously, it was proposed that the formation of polyspecific groups among neotropical primates may have evolved in response to predation by large monkey-eating eagles (Terborgh, 1990). It was also suggested that the predation risk posed by raptors may influence activity pattern in the only nocturnal neotropical primate, the owl monkey (*Aotus* spp.) (Wright, 1996). In contrast to their typical nocturnal pattern, *Aotus* was observed to spend a few hours active during daylight hours in addition to the active period at night at one site in Paraguay where large hawks and eagles were absent. This indicates that a nocturnal activity pattern may reflect an effort to avoid predation by diurnal raptors. However, nocturnality may not completely preclude a primate from predation by diurnal raptors, as diurnal raptors are reported to prey on nocturnal lemurs in Madagascar (Goodman et al., 1993; Wright, 1999).

Humans have also proven to be proficient and influential predators of neotropical primates (Mittermeier, 1991; Peres, 1999; Peres and Dolman, 2000). Hunting by humans often targets the largest-bodied primate species, thus influencing communities by either decreasing the density of large-bodied species or extirpating the species from sites with intensive hunting (Peres and Dolman, 2000). In this way, human hunting can affect overall community biomass, density of species within the community, or even the species richness of the community. There is currently no evidence that hunting played a part in the recent extinction of the two large-bodied primate species found in Brazilian caves (Hartwig and Cartelle, 1996; Cartelle and Hartwig, 1996). However, the timing of those extinctions, which coincide with human migrations into South America, and recent evidence indicating that hunting may have influenced the extinction of large-bodied subfossil lemurs in Madagascar suggest that this possibility should not be ruled out (Godfrey and Jungers, 2003). Regardless, it is clear that humans have the potential to substantially affect primate community structure through hunting, while nonhuman predators may have more subtle effects on the adaptations of community members, due likely to longer periods of coevolution between the two groups.

Freese et al. (1982) suggested that the impact of increasing human activity had so affected neotropical primate communities that it may mask all other ecological mechanisms important to community structure. While current human activities such as habitat destruction, fragmentation, and hunting rapidly impact neotropical communities, it is possible to detect the effects of other factors such as fruit

productivity, soil quality, and even dispersal barriers on community structure. A more complete understanding of these factors (as well as their relation to human impact) is of utmost importance for future conservation decisions, in order to maintain the primate communities of the Neotropics into the future.

## Africa

**Adaptive radiations.** African primate communities are the product of at least three major radiations: strepsirrhines, cercopithecoids, and hominoids. Each radiation occurred at a different time in the past. Strepsirrhines were recovered from the Fayum in Egypt from the late Eocene and early Oligocene. Early haplorrhines were also recovered from the same site and time period. Whether early haplorrhines evolved in Africa or migrated into the continent from Asia remains controversial. However, as strepsirrhine primates likely had a prior radiation in Africa, early haplorrhines must be considered one of the secondary radiations on this continent.

During the Miocene, apes evolved and spread throughout eastern Africa, reaching southern Africa (Namibia) by 13 million years ago. Apes also migrated out of the continent into Eurasia during the middle of this epoch, and possibly back again toward the end of the Miocene. Their initial radiation is suggested to have occurred in forest habitats (Andrews and Humphreys, 1999). Cercopithecoids were also present in the early Miocene, but are relatively uncommon at many fossil sites. The Victoriapithecidae exist with various ape species, but appear to have inhabited drier environments than many of the ape species (Fleagle, 1999). The Pliocene environment from which cercopithecoid species are recovered is not tropical forest but woodlands and grasslands (Reed, 1997). The fossil record is thus depauperate in evidence for forest-dwelling cercopithecine and colobine radiations. The African Pliocene fossil record reveals the earliest members of the Colobinae subfamily and the Papionini tribe. Both groups have a preponderance of species that were reconstructed as terrestrial, woodland dwellers (Frost and Delson, 2002). While the presence of the Papionini indicates that members of Cercopithecini existed, they were likely concentrated in forested areas apart from Plio-Pleistocene hominin localities. New *Cercopithecus* fossils were recovered recently, however, in the Busidima area of Ethiopia, dating to about 500 kya (Orr and Alemseged, 2002).

According to Archibold (1995), expansive African tropical rainforests were reduced to isolated refugia during the last glaciation of the Pleistocene, approximately 18 kya (Fig. 1). These refugia likely influenced current primate community species composition within extant African forests. As seen in Figure 1, the refugial forests hugged the equatorial region in both western and eastern Africa. Figure 1 identifies living primate species from communities that correspond to the area of each refuge, and notes

those that today exist only in these hypothesized areas of previous isolation. Some of these species are congeners, lending credence to the idea that the radiation of these species occurred in the relatively recent past. The dissimilarity of the Tai and Tana River forests with Makakou and Ituri also reflects their isolation from one another in deep time, i.e., perhaps 1–2 million years. Primate species diversity in Africa as a whole appears somewhat dependent on at least three major prior radiations at the family level or above, and the contraction and expansion of forest areas.

Irrespective of the different species in these refugial areas, the primate communities in the rain forests of Africa share ecological equivalents, and thus the community structure for these communities is similar. Fleagle and Reed (1996) showed that communities from Tai and Kibale, although separated by thousands of miles, hold a similar ecological space in comparison with communities on other continents. Interestingly, these ecological vicars (different species that occupy relatively similar ecological niches in two different areas) also happen to be phylogenetically related (Fleagle and Reed, 1999b). In the case of apes and some prosimians, the species are often identical, but cercopithecoids within various communities are usually different species (Chapman et al., 1999a). Both apes and prosimians have fairly ancient radiations, while the cercopithecoid radiation is likely more recent. It is possible that *Perodicticus potto* and *Galago demidovii* are present in most of the communities discussed by Chapman et al. (1999a) because they radiated long ago across an African forest that may have been intact. Other primate species, including *Colobus guereza*, *Cercocebus galeritis*, *Cercopithecus neglectus*, and *Miopithecus talapoin*, are associated with riverine forests (Chapman et al., 1999a), and as such, possibly have corridors within and between communities and are thus more widespread. Most studied communities also include one *Pan* species, and in some areas, *Gorilla* species add to the diversity.

**Community structure.** African primate communities have been studied for several decades (Charles-Dominique, 1977; Gautier-Hion, 1978, 1983; Hladik, 1978; Bourliere, 1985; Galat and Galat-Luong, 1985; Gautier-Hion et al., 1988; Terborgh and van Schaik, 1997; Oates et al., 1990; McGraw, 1998; Chapman et al., 1994, 1999a; Fleagle and Reed, 1996; Mitani et al., 2000; Shultz et al., 2004), and importantly several sites have been studied long-term, e.g., Kibale in Uganda, Makakou and the Lopé Reserve in Gabon, and the Tai Forest Reserve in Côte d'Ivoire. Chapman et al. (1999a) provided an excellent review of the causes for the structure of African primate communities, and highlighted the need for renewed conservation efforts. African primate communities located in tropical forests share fairly high numbers of arboreal frugivores, 2–3 arboreal folivores, terrestrial cryptic

foragers of the Papionin tribe, and 2–5 nocturnal gummivore/insectivores. While each forest community is dominated by medium to large-sized, frugivorous, arboreal, diurnal species, high biomasses, where they occur, are the result of the presence of arboreal folivores (Fleagle and Reed, 1996).

African tropical forests are distributed mainly throughout western and central (consisting of countries associated with the Congo River Basin) parts of the continent. As primate diversity has at least somewhat been regulated historically by the area of tropical forests, it is worth noting that primate species diversity in Africa is greater than expected based on this parameter (Reed and Fleagle, 1995). Calculated primate species diversity in localized African communities is also quite high and is exceeded only by some communities on Madagascar (Reed, 1999). Considering the limited extent of forested areas during the late Pleistocene, high primate species diversity within Africa may have been propagated by the expansions and contractions of forests. Patterns of species diversity are also associated with the arrangement of rivers across the continent. Smaller species would be restricted to areas surrounded by rivers, as they likely would have trouble dispersing across them. For example, primate communities in forests on the east and west sides of the Niger River share medium to large-sized species, but differ in the smaller strepsirrhines (Happold, 1987). Large terrestrial primates are also often isolated due to larger rivers, e.g., mandrills on either side of the Ogooué River (Telfer et al., 2003). On the other hand, larger arboreal primate species, e.g., *Colobus guereza*, may have used riverine forests as refugia during the Pleistocene, and then followed the river courses as dispersal mechanisms when forests re-expanded.

Diversity in Africa is also a product of the numbers of primate species within a particular community vs. their population densities. Only the few colobine species exist in great numbers, while Cercopithecini, great apes, and strepsirrhines have fairly to extremely small population densities. In addition, many of these species also have small range sizes (Eeley and Foley, 1999). Perhaps greater species diversity in African communities is at the cost of reduced population sizes due to the carrying capacity of these tropical forests.

**Climate and habitats.** Although having the second largest expanse of tropical ancient forest on the planet, African climate is drier overall than that on other primate-inhabited continents (Chapman et al., 1999a). Mean annual rainfall in the tropical forests of Africa is greater than 1,400 mm per year, and as rainfall increases, primate species numbers increase (Reed and Fleagle, 1995). As Kay et al. (1997) suggested that this relationship falls off after about 2,500 mm for neotropical primate communities, a closer look at African communities may be enlightening. Chapman et al. (1999a) noted that Douala-

Edéa, Cameroon, receives about 4,000 mm of rainfall per year, and contains 13–14 primate species. In contrast, Makokou, Gabon, receives 1,755 mm of rain per annum with 17 primate species. Chapman et al. (1999a) documented that the difference occurs in the number of dry-season months at Douala-Edéa, when precipitation falls below 50 mm for 3–4 months of the year, whereas there are only 2 dry months at Makokou. Seasonal differences in rainfall pattern are also evident at the Taï Forest primate community, where rainfall is ~1,800 mm per year. At Taï, there are 11 primate species, and 3–4 dry-season months. These data suggest that primate species richness is more controlled by seasonal differences than by total amount of rainfall received each year. Chapman et al. (1999a) also suggested that cloud cover during the dry season in these forests reduces evapotranspiration levels, such that primate species diversity may not be reduced as much as expected with low-level rainfall in extended dry seasons.

The forests of Africa have complex heterogeneity despite reduced rainfall and increased seasonal differences compared with other continents. In the Ituri Forest, for example, there are regions dominated by one particular tree species, areas of seasonally flooded forests, riverine forests, and secondary forests (Thomas, 1991). Despite the dry climate, Africa possesses thousands of acres of permanent swamp forests in addition to those that are seasonally flooded. This may account in part for the high numbers of arboreal primate species.

Africa is one of the few places where primate communities exist in more open, xeric habitats. These woodland communities have lower species diversity, experiencing from 2–6 primate species. In some areas, these primate species actually survive within the more open habitats, e.g., *Galago crassicaudatus*, *G. moholi*, *Papio ursinus*, and *Chlorocebus aethiops* exist together in the Makapan Valley in South Africa. In other more open or arid habitats, primate species are located in the riverine forests that course through them, e.g., *Colobus guereza*, *Chlorocebus aethiops*, and *Papio* spp. at Awash National Park, Ethiopia (but see Dunbar and Dunbar, 1974). While individual species in these regions have been well-studied, few studies of the interactions of primates in these open communities have been undertaken. Cowlshaw and Hacker (1999) suggested, however, that while primate species that live in arid woodland habitats extend the range of primates away from the equator in Africa, they possibly increase the richness of species in core forested areas. That is, generalists such as *Papio anubis* live within forests, albeit in low densities, and also in woodlands.

**Resources.** Primary productivity is often represented by mean annual rainfall, and average African yearly rainfall is less than that found on other continents (Chapman et al., 1999a). As primate species numbers are greater than expected for the amount

of rainforest (Reed and Fleagle, 1996), this presents an interesting conundrum. Given that there is lower primary productivity, as evinced by rainfall, why are there more primates relative to forest area? A consideration of species diversity based on both number of species and population densities also supports high diversity for African communities (Reed, 1999). African sites exhibit higher diversity indices than neotropical or southeast Asian communities. Primate diversity in African communities could represent an artifact of historical circumstances. The number and population densities of primates in neotropical communities may have been influenced by the animals in residence before the arrival of primates, e.g., sloths in the Neotropics may have influenced the lack of folivorous species. African forests may be able to support high numbers of primate species because primates experience less competition with other arboreal species. In addition, there are more semiterrestrial and terrestrial species in African primate communities (e.g., *Cercocebus*, *Mandrillus*, *Papio*, *Gorilla*, and *Pan*) than in primate communities elsewhere, which could also account for the richness differences.

Fruit and flower phenology is important to resource partitioning and carrying capacity among primates. Chapman et al. (1999b) showed that the phenologies in two different regions of Kibale National Park were independent from one another, despite similar abiotic factors. This leads to the conclusion that phenology patterns may be site-dependent and caused by factors inherent at sites. Comparisons of communities across Africa show that those with higher rainfall and less seasonality tend to have more frugivorous primate species, and central African sites in general have more fruiting tree species (Gautier-Hion, 1983). In fact, the community of Makokou, Gabon, more resembles the community structure and species diversity of neotropical forests rather than the communities of Kibale and Taï because of the greater number of frugivorous primates at Makokou (Reed, 1999). Thus, although African primate communities share many similarities, there also appear to be differences based on resource supply in which the availability of fruit limits species numbers, density, and biomass (Chapman et al., 1999a). Variation in the protein-to-fiber ratio of leaves across Africa also affects the population densities of red colobus monkeys (*Piliocolobus badius*), while having little influence on the biomass of other colobines, e.g., *Colobus guereza* (Chapman et al., 1999b).

At the community level, many primate species in African forests prefer fleshy fruits, but supplement them with other resources in lean seasons. Primates in African communities have greater body size ranges than primate species in the Neotropics. Small-bodied lorisoidea are size vicars of callitrichids, and guenons encompass much of the size range in other platyrrhines. However, the presence of colobines, papionins, and apes extends the size range

into much larger categories. The body sizes of these primates are important, as this allows the expansion of dietary niches within these communities. Smaller primates often supplement their intake of fruits with insects or gums, while larger frugivores ingest leaves (Kay, 1984). Keystone resources in Africa, where there are varying lengths of dry seasons, vary as well. Tutin et al. (1997) examined keystone resources for the eight primate species of the Lopé Reserve, Gabon, for over 10 years. These resources include the bast, leaves, pith, fruits, seeds, and flowers of approximately 20 herbaceous species, with varying exploitation depending on which of the eight primates were considered. In flush times, 7 of the 8 species rely on fruit, and the last, *Colobus satanus*, relies on seeds. Fruit there is limited for at least 2–3 months of the year, and only *Pan* and *Cercopithecus* species have predominantly fruit diets during the times of fruit scarcity, which occurs both in the dry season and during fruit production stoppage. The other species focused on seeds, leaves, and animal matter in the lean season. Brugiére et al. (2000) reported that frugivorous primates in Makandé, south of Lopé in Gabon, utilized dry seeds from Caesalpiniaceae trees when necessary. Although relatively close to Lopé, Makandé is dominated by these tree species, and thus plants producing fleshy fruits are few. In both localities there is very low primate biomass supported.

**Species interactions.** When examined mathematically, African communities have the largest ecological distances among species (i.e., the adaptations are farther apart in two-dimensional space), such that the ecospace is pulled away from the center of the polygon defining that space (Fleagle and Reed, 1996). The presence in Africa of suspensory great apes, leaping, folivorous colobines, and nocturnal prosimians all contribute to widely spaced ecological adaptations. Part of the reason for this may be in the number of past radiations. However, the species that cluster toward the center of this ecological space are predominantly frugivores. Thus the ecological distance among the *Cercopithecus* species is among the closest and therefore reflects not only close phylogeny, but possibly greater competition among them. It was mentioned previously that polyspecific associations of primates are important for increasing group size for antipredator behavior (van Schaik, 1983; Dunbar, 1988). Guenons have been noted for forming these mixed-species groups with both colobine and *Cercocebus* species (e.g., Wachter et al., 1997; McGraw and Bshary, 2002), possibly because most guenons occur in low population densities within communities. McGraw and Bshary (2002) recorded the behavior of *Piliocolobus badius* and *Cercopithecus diana* with *Cercocebus atys*, and showed that the mangabeys functioned as lookouts against ground predators. This allowed both the red colobus and the Diana monkey to extend their foraging efforts into lower levels of the

forest. Stanford (2002), however, found that red colobus monkeys acted as sentinels for guenon species at Gombe. Wolter and Zuberbühler (2003) also studied the Diana monkey in terms of its association with a congener, *C. campbelli*. They concluded that benefits of long-term mixed-species associations to both *C. diana* and *C. campbelli* occurred. For example, when *C. campbelli* was present, *C. diana* was more likely to broaden its foraging strategy to include lower forest strata, thus exhibiting less vigilant behavior overall. In contrast, the more cryptic *C. campbelli* increased its foraging efforts into higher strata with more group spread, and included more vocalization when in the company of *C. diana*. Both species added additional resources by foraging in areas where they normally would not. Thus within the primate community at Tai, polyspecific associations went beyond the expected antipredator benefit of a large group to maximizing foraging potential. Of course, exploiting resources in an expanded area, due to antipredator strategy, is also probably necessary due to resource competition.

There are various terrestrial and avian predators throughout Africa, with varied evidence of their predation on primates (e.g., Brain, 1981; Kitchener, 1991; Cowlshaw, 1997a–c). Recently, several studies examined the effects of leopards, birds of prey, and chimpanzees on primate groups within a primate community (Zuberbühler and Jenny, 2002; Shultz et al., 2004; Shultz, 2003). Leopard predation on primates in the Tai forest appeared to be associated with higher abundance of individual primate species. The predation rate showed positive correlations with group size, body size, and primate males per group. These researchers had hypothesized that these factors would be a deterrent to leopard predation, but found results opposite these expectations. The upshot is that it was unlikely that predation, at least by leopards, had a constraining influence on these factors in primate evolution. Zuberbühler and Jenny (2002) suggested that leopard predation may have actually increased behavioral flexibility in primates. For example, many guenons in the Tai forest have specific alarm calls in response to leopards, with other predators eliciting different behavioral responses. Recent reevaluation of the predation data at the community level included all major predators in the Tai community: raptors, leopards, and chimpanzees (Shultz et al., 2004). These researchers found no relationship between prey abundance (i.e., primate abundance) and predation rates for individual predators. These authors concluded that primate individuals in large groups do not receive the benefit of large-group antipredator strategy until all potential predators are considered.

In African communities, *Pan troglodytes* is also a predator of primates. Various researchers reported on male hunting bands (Stanford et al., 1994; Stanford, 1995; Mitani and Watts, 1999). This is an important community interaction, as chimpanzees often successfully hunt other primate species. Chimpanzee preda-

tion was observed at Gombe, Tai, Mahale, and Kibale (Busse, 1977; Boesch and Boesch, 1989; Boesch, 1994; Stanford et al., 1994; Stanford, 1995, 1998; Mitani and Watts, 1999; Bshary and Noë, 1997a,b; Boesch and Boesch-Achermann, 2000; Watts and Mitani, 2002). Mitani and Watts (1999) observed predation on *Ptilocolobus badius* (91%), *Cercopithecus ascanius* (2%), *C. mitis* (1%), and *Colobus guereza* (3%) at the Ngogo site within Kibale National Park. Chimpanzee hunting appears to have a serious effect on red colobus populations in most sites where the two species overlap. Unlike carnivore species that cannot decimate populations without harming themselves, chimpanzees are ultimately frugivores and therefore could hunt populations of red colobus to extinction without any detrimental effects to themselves (Teelen, 2004). Treves (1999) suggested that *P. badius* social organization may have evolved as protection against chimpanzees. He observed in Kibale that only the red colobus increased vigilance and intergroup cohesion when they came in contact with chimpanzees, in contrast to red-tailed monkeys (*C. ascanius*).

Finally, as with bushmeat trade in other parts of the world, human hunting is a serious problem for all tropical African primates. The continuation of pursuit and trap hunting will likely lead to extirpation of several if not most primate species (Rowcliffe et al., 2003). These researchers also reported that human hunting in Africa targets many primates and other mammals, and models trying to understand the interrelationship of hunting and species extinction have not considered this aspect of hunting. Their model seeks to better estimate the sustainability of primate species within communities by incorporating the impacts of a multiprey model. Wolfe et al. (2004) examined a human population in central Cameroon for retroviruses (simian foamy virus; SFV) that are contracted from hunting and butchering primates. They discovered that 1% of the people were infected from three separate viral lineages: *Cercopithecus neglectus*, *Mandrillus sphinx*, and *Gorilla gorilla*. Thus, the large-bodied primates of the communities of central Cameroon are in danger, as are the humans who hunt and butcher them, as both *C. neglectus* and *M. sphinx* are also naturally infected with simian immunodeficiency virus (SIV).

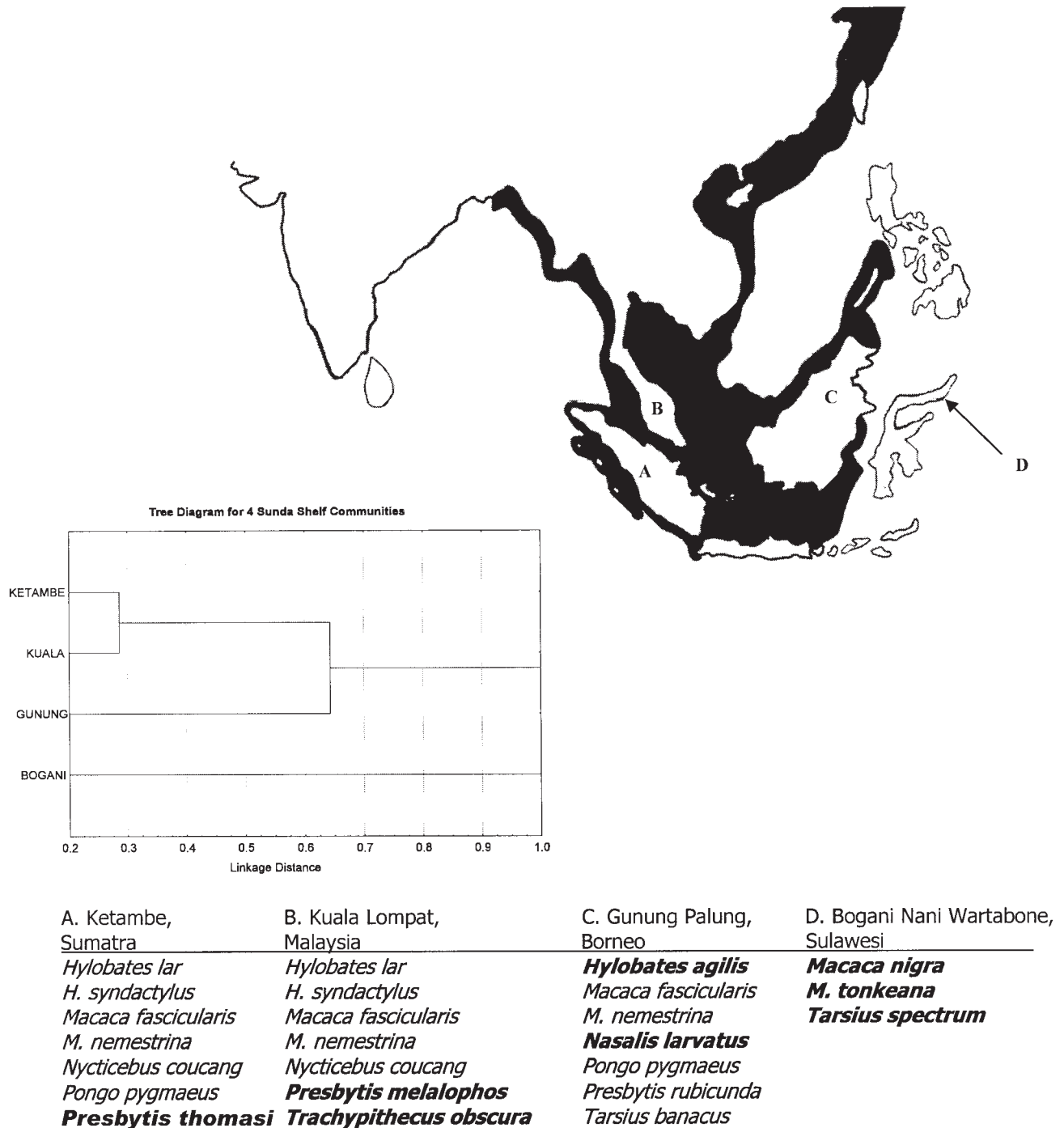
As with many species, especially primates, humans are both hunting species to extinction and destroying primary habitat. Understanding the community and subsequent ecosystem structure of these communities can be used to help conserve primate and other tropical species from extirpation.

### Asia

**Adaptive radiations.** Asian primates currently exist in a broad band across southwestern and southeastern Asia (both peninsular and the Sunda Shelf islands), as well as across parts of China into Japan and the Philippine Islands. Recent analyses reported that Asia is the likely center for the origins of early mammals, including primates (Bowen et al.,

2002). Discovery of one of the earliest euprimate skulls, *Teilhardina asiatica*, from the early Eocene of Hunan Province, China, supports this contention (Xijun et al., 2004). In addition to this early euprimate fossil recovery, Asia also is home to the longest-lived lineage of these early primates, the Sivaladapidae, which existed from the Eocene into the Miocene of China (Fleagle, 1999). Gebo et al. (2001) proposed that Asia is also home to the earliest haplorhines, and as such, tarsiers from the late Eocene and early Oligocene. Much later, apes, colobines, and papionins migrated into the area. Therefore, like African primate communities, the Asian communities are the result of several primate radiations into the area. Fossil species of living primates, including *Pongo*, have been recovered from cave sites in Vietnam outside of their current range (Nisbett and Ciochon, 1993), providing clues about the fossil communities of peninsular Southeast Asia, as living primates are found with extinct species such as *Gigantopithecus*. Due to climate changes caused by serial glaciations throughout the Pleistocene, and the nature of the geomorphology in Southeast Asia, primates in the region appear to have been repeatedly isolated and then reconnected. One of the major questions regarding the primate communities of the region is when and under what conditions various lineages of macaques, leaf monkeys, and apes arrived on various islands (Brandon-Jones, 1996; Harcourt, 1999; Abegg and Thierry, 2002).

The Asian land mass is fairly unique, considering the multiple large islands of the Sunda Shelf and broad continental land masses of India and peninsular Asia. Reed and Fleagle (1996) showed that the Malay Peninsula, Java, Borneo, and Sumatra all hold fewer primate species than expected based on the area of rainforest. Harcourt (1999) discovered no correlation with the number of species on various islands and either the distance to the mainland or the distance to the nearest large island. Harcourt (1999) also reported that primate community structure changes dramatically with island size, such that the largest Asian primates (*Pongo*, *Nasalis*, and *Hylobates syndactylus*) occur only on Borneo and Sumatra, each having an area greater than 400,000 km<sup>2</sup>. In addition, Harcourt (1999) noted that these large primates also occur on these islands at small population densities. Finally, on smaller islands there is usually only one primate species per genus, whereas on larger islands there may be two congeners. Thus, the Pleistocene history of glacial and pluvial alterations may have enabled species distributions, but the survival of various primate species on these islands is likely related to whether the islands can support the influx of migrating species over the long term. As opposed to Pleistocene refugia possibly enabling speciation events through isolation as in Africa and possibly South America, travel among the Asian islands was likely facilitated due to glaciation events lowering sea levels. Figure 3 shows the extent of the Sunda Shelf that likely in-



**Fig. 3.** Locations of selected primate communities in Southeast Asia shown in relation to former extent (in black) of land during Quaternary (adapted from Archibold, 1995). Selected extant primates within communities in forests which correspond with current land mass are identified, with bold-face primates currently restricted to these areas. Cluster analyses of regions show linkages among migratory species. Cluster analyses are based on dice similarity indices and UPGMA cluster algorithm. Sulawesi was not recently connected to Sunda Shelf land mass, and reflects this with three endemic species.

creased primate dispersal during glaciations. It is interesting that Sulawesi does not share any primates with the other sites included in our analysis and, in fact, was not connected to them during maximum glaciation. On the other hand, although primate travel on land bridges and rafting has been

hypothesized, the forest areas during glaciations were also reduced. Areas of savanna type environments are evident on the larger islands and peninsulas of the Sunda Shelf, especially during the last glaciation (Gathorne-Hardy et al., 2002). Harcourt and Schwartz (2001) suggested that despite primate

migration events, when sea levels returned to isolate the islands, smaller islands could likely not support increased species diversity.

Pleistocene environmental changes also affected primate species in China. During the early Pleistocene, hylobatids, pongids, and cercopithecoids lived in southern to northern China, but as climates shifted, ape species are recovered from farther south in China and Southeast Asia (Jablonski et al., 2000). Interestingly, Jablonski et al. (2000) attributed the ape's inability to withstand the more seasonal environments to their slower life-history patterns. Abegg and Thierry (2002) discussed dispersion events within the macaque lineage in the Quaternary with respect to sea level shifts and shifting rainforest presence due to latitude and altitude. They suggested that lion-tailed, Sulawesi, and Mentawai macaques (*Macaca silenus*, *M. tonkeana*, *M. ochreata*, and *M. nigra*) had a common ancestor prior to glaciation events, whereas pig-tailed macaques (*M. nemestrina*) evolved postglaciation.

Brandon-Jones (1996) concluded that major loss of habitat at 190,000 years ago caused the extinction of *Nasalis* on Sumatra, the demise of *Pygathrix* from western Indochina, and the loss of *Presbytis* from Java. He also suggested that after this glaciation event, various species of leaf monkeys rafted first to Sumatra from the Mentawai Islands and then to Borneo, Java, and possibly the Malay Peninsula. Another glaciation at 80,000 years ago altered the distribution of *Presbytis comata* and promoted other speciation events. This implies, as Brandon-Jones (1996) pointed out, rapid speciation rates in leaf monkeys. He also suggested that the morphological differences among leaf monkeys were caused by dispersion into new regions, i.e., adaptive radiation into new niches, rather than by isolation in refugia.

Therefore, not only have primates existed in Asia for millions of years, but they have also undergone radiations within the last 100,000 years. These historical circumstances have caused slight to major differences in primate communities on these islands, e.g., ecological equivalents of various macaque and gibbon species on specific islands and in different regions on the mainland. Nevertheless, Asian sites all have genera in common, and for the most part specific differences result in ecological vicars in communities within and between all islands and the Malay Peninsula. As in Africa, small-bodied nocturnal prosimians are widespread (*Nycticebus* spp., *Tarsius* spp.) and have likely been in residence the longest. Hylobatids occur in nearly all communities, as do one or two species of macaque. For the most part, odd-nosed monkeys have intermittent distributions on the mainland, but are not found in the Sunda Shelf region except for *Nasalis* on Borneo. And as mentioned above, the distribution of *Pongo* is now restricted to two large islands. Unlike similar regions in Africa, drier regions in India and Bangladesh do not have primate communities per se, as at most only two species may co-occur.

**Community structure.** Studies of primate communities in Asia have been done at Kuala Lompat, Malaysia (e.g., Chivers, 1980), Ketembe and the Leuser Ecosystem (e.g., van Schaik and Supriatna, 1996; Buij et al., 2002), and Kuati, Borneo. Primate communities contained by the Asian land mass are exemplified by having low primate species diversity. Various suggestions for this include: 1) low relative areas of forest due to isolated islands and mainland that have been tenuously connected throughout history (Reed and Fleagle, 1996); 2) low species diversity of frugivores in Asia because of variation in fruiting within and between years (Terborgh and van Schaik, 1997); and 3) the abundance of dipterocarp trees that are not seen as particularly edible by most primate species (Caldecott, 1986). These communities are similar to African communities in that the higher-level primate taxa represented are almost all the same (lorisoids, cercopithecoids, and apes), and as such, Asian radiations were similar to those in Africa. In contrast to other primate communities, Asian communities include higher percentages of primate species in the 5–10-kg range (Reed, 1999), and have both fewer numbers of frugivorous species and low population densities of larger species (Terborgh and van Schaik, 1997; Harcourt, 1999).

**Climate and habitats.** There are five different types of forests recognized on the Malay Peninsula alone, and all up to about 1,200 m are dominated by trees of the Dipterocarpaceae family, from lowland through upper montane forests (Gupta and Chivers, 1999). Dipterocarp trees have African relatives (Caesalpiniaceae) in high abundance in the Makandé forest, Gabon. These African species apparently support fewer primates than expected, although they are utilized for dry legumes by all primates in the community during the dry season (Brugiere et al., 2002). This suggests that at least some of the limited diversity of primate species in Asia is caused by the predominance of these dipterocarp trees. There is a shift in tree species from the lower to upper mountain forest zones, with the lower montane losing the dipterocarp dominance to oaks, laurels, myrtles, elms, and birches. The upper montane regions have conifers and Myrtaceae (eucalyptus and guava family). Irrespective of the dominance of dipterocarp trees, there is a great diversity of tree species in Malaysia at ~176 species per ha<sup>2</sup>, which is contrasted with tree species in the same area of Nigeria of 60 species (Archibold, 1995). There are in excess of 2,500 tree species on the Malay Peninsula (Raemakers et al., 1980).

The locality of Kuala Lompat in the Krau Game Reserve in West Malaysia is somewhat unique in that it has relatively few dipterocarp trees and high numbers of tree species in the family Leguminosae (Waterman et al., 1988). This results in an overall higher level of digestibility of leaves in the region due to less fiber and phenolics than in some other

Maylasian sites. In fact, Waterman et al. (1988) showed that the colobine biomass appears to be correlated to higher protein-to-fiber ratios. This is supported by later research in which African colobine mass at various communities was also positively correlated with higher protein-to-fiber ratios (Chapman et al., 2002). Irrespective of the higher-quality leaves at Kuala Lompat, the primate species richness at Kibale is almost twice as much as Kuala Lompat. Forest structure, as represented by the Malay Peninsula, includes emergent trees as tall as 80 m, with fairly small trunks that often do not branch until about 25 m and a myriad of lianas (climbers) including figs (Raemakers et al., 1980).

The climate supporting the forests of Southeast Asia includes two monsoon seasons, one around December–January, and a milder one in late spring. These monsoons increase the annual rainfall in many Asian forests to approximately 5,000 mm, with a low annual rainfall of 2,000 mm in some regions. Chivers (1980) noted that there is rarely a month without rainfall in the Malay Peninsula. This contrasts with the seasonal rainfall at other sites in Asia, e.g., Bangladesh, where there may be no rain from late fall to late winter (Gupta and Chivers, 1999). Western Asian forests are often deciduous, but because leaves are shed by various species in both cold and hot seasons, they appear often to be evergreen. As mentioned earlier, Bangladesh and southern India have only one or two representative primate species in single localities, and thus cannot be counted as having primate communities. This can be contrasted with African savanna and dry woodland sites in which several primate species exist.

In any event, it appears as if low primate species richness is not the result of extended dry months as it might be in Africa. Reed and Fleagle (1995) showed also that there is no relationship between primate species number and rainfall amount in Asia, unlike all other areas. It may be that the monsoon regime and overall high amounts of rainfall actually contribute to low primate species diversity. If, as Kay et al. (1997) reported, primate species are not correlated with rainfall after about 2,500 mm, then it is expected that there would be no relationship between primate species richness and rainfall in Asian communities. Many of the communities have a mean annual rainfall greater than 2,000 mm, and of 33 communities, 13 are  $\geq 2,500$  mm (Gupta and Chivers, 1999). Using mean annual rainfall as a surrogate for primary productivity, however, is problematic in Asian primate communities, because neither increasing rainfall nor overall high rainfall appears to be correlated with primate species richness (Reed and Fleagle, 1995). Species diversity indices, which measure not only primate richness but their diversity with regard to population density, are also low within Asian communities (Reed, 1999). However, species diversity is actual higher than in several communities in the Neotropics (Urucu River, Raleighvallen, and Guatopo), al-

though Cocha Cashu is somewhat higher than the Asian localities (Ketembe, Kutai, and Kuala Lompat).

**Resources.** Raemakers et al. (1980) noted that 67% of all tree species in Malay forests have seeds dispersed by fleshy-fruit eaters. These tree species include those of the *Alphonsea*, *Nephellum*, and *Maranthes* genera. Other tree species have wind-dispersed seeds that have evolved to fruit rarely and/or in synchrony, and as such, provide little fruit for primates. These species include *Shorea*, *Diptocarpus*, and *Koompassia*. Tree species at Kuala Lompat from which gibbons feed appear to be asynchronous in fruit production, and thus supply resources for gibbons throughout the year. This is also beneficial to the tree species, as gibbons are major seed dispersers. McConkey et al. (2002) reported that fruit preference by gibbons on Borneo includes not only larger, yellow, abundant fruits, but those without seeds. However, when seeds are present, they are usually single and protected, but are still dispersed by gibbons at the rate of 81% of the species eaten (McConkey, 2000).

One of the most amazing occurrences in the forests of Southeast Asia is the general flowering (GF) events that occur over thousands of kilometers. The GF events occur irregularly at multiyear intervals when most of the dipterocarps and many other genera flower, and then subsequently mast fruit at the same time (Sakai, 2002). Williamson and Ickles (2002) suggested that this GF occurs at the end of an El Niño Southern Oscillation (ENSO) drought which causes seedling release and high levels of pollination. They also suggest that separating seedling release models from seed predation models may be difficult if both are tied to ENSO droughts. In any case, the lack of regular fruiting cycles in Asian forests was suggested to have caused low species diversity in primate communities (Terborgh and van Schaik, 1997).

Leaf cycles in Asian forests range from species that have continuous leaf production to species that are deciduous and thus synchronous in leaf production (Raemakers et al., 1980). The leguminous trees tend to be deciduous, while the dipterocarps tend to be evergreen. Many trees, however, are intermediate in leaf production, such that trees produce leaves for some parts of the year, stop, and restart with different trees of the same species on a different schedule, e.g., *Sloetia elongata*. These trees are in the majority at Kuala Lompat, as dipterocarp trees there are not as prominent as in other Asian localities (Raemakers et al., 1980). In the larger Asian primate communities, there are often two species of leaf-eating monkeys that utilize leaves as part of their diets. Gibbons also utilize new leaf growth occasionally.

Asian communities, although they have similar numbers of colobines compared with African communities, have fewer species heavily relying on

fruits. For example, in the Tai community, 6 of 10 species are not only frugivorous, but include  $\geq 80\%$  fruit in their diets. At Ketembe and Kuala Lompat, although 6 of 8 and 7 species, respectively, are considered frugivorous, only one (*Macaca nemestrina*) in each community includes  $>80\%$  of fruit in its diet, and one (*Nycticebus couang*) includes 80% (Reed, 1999). There may be several reasons for what is considered the lack of frugivorous primates in Asian communities. It may be the result of the inability to depend on fruit availability due to fruit masting. Lack of frugivores may be partially the result of the patchiness of actual fruit species distribution in Asia (McConkey et al., 2002). Finally, it is possible that primate species classified as frugivorous actually supplement their diets more with leaves than primates in African or the neotropical communities. A greater reliance on leaves may also be related to greater body sizes of primate species in Asian communities. Asian communities are composed of frugivorous primates that are on the whole larger than frugivores in other communities, e.g., gibbons and macaques are larger, in general, than guenons and most neotropical primates. So perhaps the question is not why there are few frugivores, but why the body sizes of Asian primates are predominately in the 5–10-kg range. Another interesting possibility regarding major resource differences between Asian and other primate communities concerns colobines. The so-called Asian leaf monkeys actually eat a very high percentage of seeds. If seeds are considered fruit, then Asian communities might be seen as predominately frugivorous (e.g., *Presbytis melalophus* at Kuala Lompat eats 64% seeds), but with all species constrained somewhat in their choice of fallback foods. MacKinnon and MacKinnon (1980) noted that all of the primate species in the Kuala Lompat community used fruit as a major resource, and the dietary differences among species were not as great as the differences within species on a month-to-month basis.

**Species interactions.** Resource competition in Asian communities appears unique in comparison to African communities. Primates in Asian communities are dependent on patchy distribution of fleshy fruits (McConkey et al., 2002), and all primate species rely predominantly on either fig fruits of a variety of species or *Maranthus corymbosa* (sea beam) (Raemakers et al., 1980; MacKinnon and MacKinnon, 1980). In addition, most of the diurnal species overlap considerably ( $\sim 30\text{--}50\%$ ) in 20 key food items that include figs, fruits of the sea beam, *Sloanea*, *Grewia*, *Xerospermum*, and insects. Despite the overlap in resources, however, there is little range overlap in the Kuala community (Raemakers and Chivers, 1980). Instead, the calls associated with the colobine species effectively keep them separated. The two species of gibbons often call and have conflict if territories are crossed. Polyspecific associations seen in African and neotropical communities

are not utilized in Asian communities, possibly in order to decrease resource competition. Asian primates tend to reduce competition by avoiding each other both intra- and interspecifically. Other possible resource competitors of primates in Asian forests include tree shrews, colugos, mouse deer, and palm civets, all of which eat fruit either arboreally or terrestrially, diurnally or nocturnally.

The lack of polyspecific associations among Asian primates may also be explained by the absence of large raptors at these sites (Terborgh, 1990). However, felid and reptilian predators do pose a risk to members of Asian communities. Predation on primates within some Asian communities by tigers and leopards is apparently dependent on the presence and abundance of other prey animals (Seidensticker, 1983). Seidensticker (1983) suggested that as leopards are subordinate to tigers, leopards tend to avoid overlapping with tigers. However, leopards in India are known to prey more frequently on primate species such as *Macaca mulatta* and *Semnopithecus entellus*. Both leopards and tigers preyed upon primates on Java at the Meru-Betiri Reserve probably because the rusa deer (*Cervus timorensis*), an ungulate prey species of tigers, was not present at the site (Seidensticker, 1983). Reactions to predator experiments on Asian primate species at the Ketambe research area showed that primates could detect predators more easily if they were in larger groups. Thus, van Schaik et al. (1983) concluded that perceived predation risk resulted in group-living for these primate species. There are also a few reports of predation on Asian primates (*Macaca fascicularis* and *Nasalis larvatus*) by crocodiles (Galdikas and Yeager, 1984; Galdikas, 1985). Both of these primate species utilize rivers, and are therefore more vulnerable as crocodile prey than are other primate species in the community of the Tanjung Puting Reserve on Kalimantan. Yeager (1991) reported that *Nasalis larvatus* has increased vigilance against these predators by attempting to swim across rivers at the narrowest points, and having several individuals cross at once. More research on primate predators among Asian communities would assist in understanding if antipredator behavior influences the structure of these primate communities.

In addition to such factors as monsoon rainfall patterns, mast fruiting, and the prevalence of dipterocarps, Asian primate communities are affected and in many cases jeopardized by massive human disturbances, particularly habitat destruction due to logging (e.g., Robertson and van Schaik, 2001; van Schaik et al., 2001; Paciulli, 2004). Asian sites were identified as having higher rates of logging and deforestation than those in Africa or the Neotropics (Laurance, 1999). As Asian primate communities have many unique differences from communities in other regions, it is thus very important for the future of community studies that efforts be made to conserve the remaining Asian forests.

### **DIFFERENCES AMONG CONTINENTS IN PRIMATE COMMUNITIES**

We have discussed several major contrasts regarding primate communities in different biogeographical areas. Table 3 contrasts all of our fundamental factors for the development and formation of communities among continents. Some of the most interesting differences remain elusive as to their causes, but ongoing and new research may be better able to address these questions in the future. The questions that we mentioned in the introduction and that seem most prevalent to us are summarized here.

#### **What is the major cause of differences among primate communities?**

It seems to us that the differences in the phylogenetic groups that constituted the original primate radiations in each biogeographic region discussed above contribute greatly to the differences seen between the primate communities of these regions today. Obviously these initial primate species were then faced with relatively similar climates and habitats in the tropical regions. Changes in the extent of forested areas and the availability of corridors between suitable habitats due to major climatic events throughout primate evolution seem to have affected speciation and thus primate communities in areas such as Africa and South America. The maintenance of the community structure in each region, however, has been dependent on species interactions, including resource competition and predation. As such, the extinction or extirpation of both competitive and predatory species has likely had an effect on present communities, particularly in the case of Madagascar.

#### **What are the causes of low primate species richness in Asia?**

There are several suggestions as to why primate species richness is rather low in Asian communities. Small numbers of species in communities may be a result of the unique forest structure in southeastern Asia. The ENSO fluctuation then causes the GF and fruit masting situation that causes a feast-or-famine situation for frugivorous primates. Low species richness could also be related to overall high mean annual rainfall and monsoon patterns that may limit primary productivity in some way. Asian communities are the only ones in which mean annual rainfall (as a surrogate for primary productivity) does not predict primate species number, suggesting that primary productivity is not coupled with rainfall. Finally, Asia possesses more primate species in the 5–10-kg category, and this may be related to resource acquisition in such a way that species numbers are limited.

### **Is there a trade-off between frugivore richness and population densities in Africa?**

Polyspecific groups of sympatric guenons appear to be conflated with the species richness, population densities, and antipredator strategies of these monkeys. First, the species richness of frugivores, i.e., guenons, is high in African communities. Second, overall frugivore population densities in African communities are low. It is possible that population densities are low because species richness is high. That is, specific differences among guenons were caused by an adaptive radiation resulting in exploitation of various ecological niches. Guenons all share fruit as a resource, but each niche is at least slightly different in order for each species to maximize resource use, e.g., slight differences in body size or substrate use would alter the niche space used. To counterbalance the use of multiple, small frugivorous niches by sympatric species, however, it is possible that each species exists at low densities in order to reduce intraspecific resource competition in areas of finite or limited resources. Low densities or group sizes, however, are apparently not effective antipredator strategies, as the risk to individuals is increased. Therefore, in some communities, guenons form long-term associations with other primate species, including species that are found in high densities such as red colobus monkeys. Terborgh (1990) asserted that these associations are due to the presence of large raptors, both in Africa and South America. The polyspecific associations may be accounted for by antipredator strategies; however, low densities may have more to do with how many frugivorous species in what abundances each forest can support. Much more data must be collected on this aspect of community structure.

#### **What is the reason for the low species and adaptive diversity of primates in neotropical communities?**

Most neotropical species are small, diurnal frugivores. Even atelines that are somewhat larger-bodied and folivorous do not come close to the biomass represented by arboreal primate folivores on other continents. The lack of folivorous species may be due to competition with sloths during an initial (or subsequent) radiation of platyrrhines. The neotropical frugivores, however, if compared to the densities of frugivores in African communities, are actually quite similar. In both sets of communities, frugivores are small-bodied, with low population densities. Perhaps frugivory limits population densities and increases species diversity in both neotropical and African communities. Thus, it seems that the dearth of folivorous primates due to the presence of sloths within the folivorous niche prior to primate colonization (Carroll, 1988) is ultimately responsible for the low species and adaptive diversity in neotropical communities.

TABLE 3. Summary of underlying causes of primate community structure

Biogeographic region	Historical factors		Climate and Habitat		Productivity and food resources			Species interactions	
	Migration and speciation	Area, isolation, and refugia	Climate	Forest structure	Productivity	Seasonality	Resource quality	Competition	Predation
Madagascar	One initial migration ~50 mya, extensive speciation and recent extinctions	Diminishing area of forests, island isolation	Patterns of drought; drops in temperature and stochastic events	Small tree crowns and low canopy height	Smaller crown volume may affect fruit production	Long dry seasons; unpredictable fruiting pattern	Higher quality leaves (more protein) in disturbed forests	Both frugivorous and folivorous lemurs compete; few non primate competitors	Raptors both today and in past; fossa and few other mammal predators
Neotropics	Migration from Africa ~30 mya by ancestor to Platyrrhini	Largest area of rainforest; possible Pleistocene refugia	Relatively high levels of rainfall; short dry season	Flooded (varzea) and unflooded forests with lianas	Abundant fruit production	Long periods of fruit abundance	Leaf quality possibly related to soil in flooded forests	Multiple primate and nonprimate frugivores likely compete; sloths may out compete primate folivores	A large raptor community affects all neotropical primates; risk also from felids
Africa	Lorisoids likely initial colonists, but early anthropoids as well; hominoids originate, migrate, and return (?); cercopithecoid radiation last	Second largest area of rain forest; also Pleistocene refugia	Relatively high levels of rainfall; multiple wet and dry seasons	Rainforests, swamp forests, woodlands and open by habitats inhabited by primates	Relatively low primary productivity	Fruiting and leafing patterns are asynchronous	Leaf protein to fiber ratios vary greatly within and between sites	Polyspecific groupings may increase competition	Multiple predatory species: raptors, felids, and chimpanzees
Asia	Oldest anthropoid primate possible; also radiations by lorids, hominoids, and cercopithecoids	Isolation on Sunda Shelf islands and area of the islands effect extinction and speciation	Extremely high rainfall (monsoons) at many sites	Dipterocarps dominate many forests although species diversity may still be relatively high for Asia	Periodic high productivity	Mast fruiting events	Abundance of dipterocarps may lower food quality in Asia	Primates tend to avoid each other which lowers competition	Some felid and reptile predation; lack of large raptors

### Why is there a bias toward folivorous primates in Madagascar?

The primate communities of Madagascar are well-known for their large numbers of folivorous primates, both extant and recently extinct. This bias toward folivores may be related to the unique climate of Madagascar, which seems to experience far greater seasonal shifts in temperature and rainfall, as well as more stochastic events, than do other biogeographic regions. The low number of mammalian competitors and predators present when strepsirrhines first colonized the island also provided more opportunities to radiate into folivorous niches than were available in other biogeographic regions such as South America, which was inhabited by not only arboreal but also terrestrial sloths when the first primate colonists arrived (Carroll, 1988).

### FUTURE DIRECTIONS AND CONSERVATION

As the extinction of current members of many primate communities seems to be rapidly approaching, it is important to understand the potential effects this will have on both other community members and the habitat in which they live. The fact that many primates are the major mechanisms of seed dispersal for certain tree species within tropical forests suggests that their extinction could have dire consequences for the entire habitat. The loss of natural predators of primates through extinction or extirpation could also have quite detrimental effects on many primate populations within communities, and particularly those that may experience higher levels of competition by those species consequently released from predation. However, further investigations into the effect of predation by all possible predators on each member of primate communities following the example of Shultz et al. (2004) are needed before such conservation issues can be fully understood.

Primate communities are now being studied at different spatial and temporal scales. Mouquet and Loreau (2002) suggested that the ultimate causes of species diversity may be the result of spatial heterogeneity of habitat across space and time. Therefore, studies encompassing either spatial or temporal depth will become increasingly important. Examples of long-term studies of primates within communities, or individual primate communities distributed spatially across a particular site, include Ngogo, Kanyawara, Dura River, Mainaro, and Sebatioli at Kibale National Park, Uganda (Chapman et al., 1999a; Mitani et al., 2000) and Makakou, Lopé, and Makandé in Gabon (Gautier-Hion, 1978, 1988; Tutin et al., 1997; Brugiere et al., 2002). These primate studies began more than 25 years ago in a single area, and research continues both across space and over a short time scale. Both scales are also important for understanding change within and among communities. Broader regional and continental scales are important for understanding adapta-

tions, plasticity, and evolution across habitat gradients and through time. The change in baboon variation from north to south in Africa among baboon species (or subspecies), and their interactions with their habitat and other primate community members, may be one type of possible study (e.g., Kamilar, 2004). Another study already underway is contrasting primate communities from various types of forests, e.g., *terre firme* and *várzea* forests of the Neotropics (Peres, 1999).

Other important areas of future research in primate community ecology which have applications for conservation include investigations into the importance of corridors between habitats in maintaining metacommunity dynamics (e.g., Lehman (2004b) suggested that creating and maintaining corridors between protected areas is as important a conservation concern for the lemurs of Madagascar as is the maintenance, expansion, and creation of protected areas themselves), investigations aimed at understanding the role of rare or understudied primate species within the primate community through seed dispersal or exploitative competition, and investigations of the differential effects of logging on members of primate communities (e.g., Paciulli (2004) found differential effects on population densities of primates on the Pagai, Mentawai Islands based on the time since different forested sites had been logged). Further studies of primate communities in Asia, in addition to the single-species studies which characterize the region, seem to be of the utmost importance due to the catastrophic habitat destruction in this region in particular. Finally, the incorporation of Geographic Information System (GIS) technology into future investigations of primate communities at both small and large scales stands to significantly enhance our ability to tease apart contributing factors of community structure. For example, GIS technology permits the evaluation of rainfall and productivity compared with primate species ranging patterns. That is, GIS has the potential to identify significant factors in various primate patterns over spatial scales. Only through a more thorough understanding of past and present factors affecting primate communities can appropriate plans be laid to maintain these communities into the future.

Research on primate communities is thus important beyond studies of behavioral ecology and the socioecology of individual primate species. Comparing the behavioral ecology of primates within and among communities allows a better understanding of the influence of biotic and abiotic factors among many primate species. The effects of species interactions, polyspecific associations, and predator-prey relationships may influence some primate communities more than others. Understanding these stimuli within historical contexts will enable the formation of further hypotheses regarding adaptive radiations of primate taxa. Perhaps most importantly, focusing on immediate possible extinctions in

existing primate communities may enable the prevention of drastic and unforeseen changes to extant ecosystems (Wright and Jernvall, 1999).

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