CHAPTER ONE

Biogeography and Primates: A Review

Shawn M. Lehman and John G. Fleagle

ABSTRACT

In this paper, we present an introduction to primate biogeography at a continental level and then review the literature as it pertains to primate studies. Primate species diversity is highest in the Neotropics and Asia. Most primates range into rain/humid forests in Africa, Asia, and the Neotropics. Asia contains the highest total number of primate species (N = 38) that are considered to require conservation attention, followed closely by the Neotropics (N = 33 species). These biogeographic patterns reflect complex phylogenetic, geologic, and ecological processes. The various biogeographic theories and models used to explain these patterns can be organized into several broad categories (1) descriptive studies, (2) comparative-quantitative approaches, (3) refugia theory, (4) phylogenetic approaches, (5) community ecology, and (6) conservation biology. Descriptive models have been derived from distribution data obtained during collecting expeditions. These models focused on geographic variations in species characteristics and barriers to dispersal (e.g., Gloger's Rule, Bergmann's Rule, Allen's Rule, river barrier hypothesis). With the advent of digitized statistical procedures, these barriers became testable biogeographic hypotheses using comparative-quantitative models. Thus, many researchers have noted the importance of rivers as

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geographical subdivisions of populations of a species. Comparative-quantitative models have also involved studies of species-area and distribution-abundance relationships. Generally, larger areas are more species rich and widely distributed primates tend to exist at higher densities. Many researchers have also investigated various ecological correlates (e.g., rainfall, latitude) to patterns of primate species richness. There has been considerable debate regarding the importance of Pleistocene Refugia for understanding the historical biogeography of primates. Phylogenetic or cladistic biogeography focuses on shared derived characters, which can be used to reconstruct biogeographical history. The presence or absence of species within a geographic area has been investigated extensively through studies of community ecology. Similarities between primate communities are most likely if they share a common biogeographic history. Composition of primate communities can also reflect evolutionary niche dynamics. Finally, researchers studying primate conservation biology have synthesized methods from various biogeographic models to understand and predict primate rarity and extinction events. Much of the renewed interest in primate biogeography tends to focus on the spatial and temporal patterns that influence species origins and diversity.

Key Words: Primates, ecological biogeography, historical biogeography, diversity, Neotropics, Africa, Madagascar, Asia.

INTRODUCTION

Biogeography is the study of the distribution and diversity of organisms in space and time (Cox and Moore, 2005). There are two main approaches to producing and testing hypotheses of species distribution and diversity: (1) ecological biogeography and (2) historical biogeography (Lomolino *et al.*, 2005). Ecological biogeography is used to investigate distribution and diversity patterns based on the interactions between an organism and its physical and biotic environment (Huggett, 2004). Historical biogeography determines the series of events that led to the origin, dispersal, and extinction of tropical taxa (Crisci *et al.*, 2003). Using this approach, researchers have explained the biogeography of plants and animals as the result of the appearance of barriers and the disappearance of barriers (Wiley, 1988). The biogeography of many organisms is likely the result of a complex relationship between ecological and historical factors (e.g., Bush, 1994; Tuomisto and Ruokolainen, 1997; Lomolino *et al.*, 2005). In this paper, we present an introduction to primate biogeography at a continental level and then review the literature as it pertains to primate studies in order to put the papers from this volume in a broader historical perspective.

Primate Biogeography at the Continental Level

There are approximately 348 exant primate species in the world (Appendix 1), although this number varies depending on which taxonomy is used (e.g., Rylands *et al.*, 2000; Groves, 2001; Grubb *et al.*, 2003; Brandon-Jones *et al.*, 2004; Isaac *et al.*, 2004). Morever, there have been at least 46 new species discovered or redescribed in the last 10 years (Rylands, 1998; Silva and Noronha, 1998; van Roosmalen, 1998; Kobayashi and Langguth, 1999; Rasoloarison *et al.*, 2000; Thalmann and Geissmann, 2000; van Roosmalen *et al.*, 2000; Rylands *et al.*, 2002; van Roosmalen *et al.*, 2002; Mayor *et al.*, 2004; Jones *et al.*, 2005). Extant primates are found almost exclusively in one of the following four tropical regions: Neotropics (Central and South America), Africa, Madagascar, and southern and eastern Asia. In an effort to obtain a broad overview of primate ecology in a biogeographical perspective we have summarized broad patterns of primate ecology of living primates by continent (Table 1). In our overall semi quantitative review of primate adaptations and biogeography, we have relied heavily on secondary sources (e.g., Rowe, 1996) because they provide a breadth of data reduced to a common format.

Species diversity is highest in the Neotropics and Asia. At higher taxonomic levels, the most genera are located in Africa whereas the most families are found in Madagascar and the Neotropics. The high taxonomic diversity for Madagascar is remarkable because it is considerably smaller in area (587,040 km^2) than any of the other regions (Reed and Fleagle, 1995) and only 10–20% of the original forest cover remains in this country (Green and Sussman, 1990; Du Puy

Table 1. Primate species, genera, and family diversity in four main biogeographic regions

Region	Species	Genera	Families
Neotropics	116	18	5
Africa	83	21	4
Madagascar	59	14	5
Asia	90	16	4
Total	348	69	18

and Moat, 1998). There are also extremely high levels of endemicity (81%–100%) for primates, vascular plants, reptiles, and amphibians in Madagascar (e.g., Ganzhorn *et al.*, 1999; Garbut, 1999; Goodman and Benstead, 2005).

Most primates range into rain/humid forests in Africa, Asia, and the Neotropics (Table 2). Patterns of forest use are somewhat different for lemurs. Of the 48 lemur species for which there are habitat data, 64.0% (N = 31) range into dry forests. Exploitation of woodlands and wooded grasslands is most common among African primates, which allows these animals to range over a wider area than that covered only by forests. Neotropical and African primates use riparian habitats more often than taxa in either Madagascar or Asia. Use of swamp and montane habitats is common among Neotropical and Asian primates. In the Neotropics, numerous primate species, particularly those in the Callitrichidae, exploit secondary/edge habitats.

Fruit is exploited by many primate species in each region, and particularly in the Neotropics where all species studied to date eat at least some fruit (Table 3). Leaves are eaten by many primates in all regions, but are exploited by only a few taxa in the Neotropics. Conversely, a higher proportion of primates exploit gums and tree exudates in the Neotropics. Insects and fauna are eaten commonly by primates in the Neotropics, Africa, and Asia; but infrequently by those in Madagascar. Although few lemurs exploit seeds as food, many species eat flowers.

Primate conservation priorities at the species level differ between regions (Table 4). Asia contains the highest total number of primate species (N = 38) that are considered to require conservation attention, followed closely by the Neotropics (N = 33 species). The Neotropics contain 42.8% (N = 9) of the 21 total primate species that are critically endangered worldwide (*Ateles hybridus*, *Brachyteles hypoxanthus*, *Callicebus barbarabrownae*, *C. coimbrai*, *Cebus xanthosternos*, *Leontopithecus caissara*, *L. chrysopygus*, *Oreonax flavicauda*, and *Saguinus bicolor*). There are six primate species listed as critically endangered in Asia (*Hylobates moloch*, *Macaca pagensis*, *Pongo abelii*, *Rhinopithecus avunculus*, *Trachypithecus delacouri*, and *T. poliocephalus*). There are four critically endangered primates in Madagascar (*Eulemur albocollaris*, *Hapalemur aureus*, *Prolemur simus*, and *Propithecus tattersalli*) and two in Africa (*Piliocolobus rufomitratus* and *P. tephrosceles*). Of the 51 primate species considered to be endangered, 21 are located in Asia and 13 in Africa. The Neotropics contain 33.3% (N = 14) of the 42 primate species listed as vulnerable worldwide.

Table 2. Percentage of primate species that range into eight main habitats in the Neotropics, Africa, Madagascar, and Asia

Region	N species	% total recognized species	Wet/humid forests	Dry/deciduous forests	Woodland forests	Riparian forests	Spiny forests/scrub	Swamp forests	Montane forests	Edge/secondary forests
Neotropics	84	72.4	91.7	22.6	3.6	33.3	3.6	21.4	14.3	44.0
Africa	60	72.3	80.0	43.3	30.0	38.3	10.0	11.7	8.3	31.7
Madagascar	50	84.7	54.0	64.0	8.0	22.0	8.0	2.0	8.0	30.0
Asia	62	68.9	91.9	27.4	1.6	11.3	1.6	19.4	32.3	24.2
Total	256	73.6	81.6	36.7	10.2	27.0	5.5	14.8	16.0	33.6

Table 3. Percentage of primate species that exploit seven main food categories in the Neotropics, Africa, Madagascar, and Asia

Region	N species	% total recognized species	Fruit	Leaves	Exudate	Insects/fauna	Seeds	Flowers	Other
Neotropics	70	60.3	100.0	38.6	38.6	67.1	40.0	38.6	30.0
Africa	55	66.3	81.8	65.5	10.9	67.3	34.5	25.5	10.9
Madagascar	55	93.2	69.1	52.7	16.4	32.7	9.1	56.4	25.5
Asia	52	57.8	96.2	84.6	3.8	59.6	42.3	57.7	46.2
Total	232	66.7	89.8	60.2	19.5	58.8	32.7	45.1	28.8

Table 4. Number of primate species at three levels of conservation risk in the Neotropics, Africa, Madagascar, and Asia

Region	No. critically endangered	No. endangered	No. vulnerable	Total	% total recognized species
Neotropics	9	10	14	33	28.4
Africa	2	13	7	22	26.5
Madagascar	4	7	10	21	35.6
Asia	6	21	11	38	42.2
Total	21	51	42	114	32.8

The above biogeographic patterns reflect complex phylogenetic, geologic, and ecological processes (Eisenberg, 1979; Terborgh and van Schaik, 1987; Ayres and Clutton-Brock, 1992; Reed and Fleagle, 1995; Fleagle and Reed, 1996; Pastor-Nieto and Williamson, 1998; Wright, 1999; Harcourt, 2000b; Laws and Eeley, 2000; Harcourt *et al.*, 2005). For organizational structure, we have grouped biogeographic theories and models into several broad categories (1) descriptive studies, (2) comparative-quantitative approaches, (3) refugia theory, (4) phylogenetic approaches, (5) community ecology, and (6)conservation biology. Historically, descriptive models have been derived from distribution data obtained during collecting expeditions (e.g., Wallace, 1853; Darwin, 1859; Bates, 1863; Wagner, 1868). These models focus on differences in species distribution and abundance due to barriers to dispersal at the continental level. The comparative and quantitative models enable researchers to narrow the geographic focus to patterns of local species richness. Two primary variables have been extensively examined in these models: species number and some ecological characteristic(s) of the environment (e.g., area, latitude, and rainfall). An especially important series of biogeography theories have emphasized the importance of Pleistocene refugia. The phylogenetic approach to biogeohraphy developed from Hennig's (1966) method of analyzing taxa with respect to shared characters which have been derived from an ancestor common only to themselves. In phylogenetic or cladistic biogeography, shared characters were replaced by shared geographic regions. The resulting area cladograms could then be used to reconstruct the biota of a historic region. Community ecology incorporates the perspective on how species composition and interactions relate to biogeographic processes. Conservation biology synthesizes methods from other biogeographic approaches to understand and predict primate rarity and extinction events at various levels (e.g., species, sites, landscape, regions, continent, and global). From these models, precise predictions of the distribution and diversity of species could be generated and tested.

Descriptive Models

There has been an explosion of research interest on the identification, classification, and study of mammals during the last 150 years (Wallace, 1853; Darwin, 1859; Grandidier, 1875–1921; Hesse *et al.*, 1937; Mayr, 1942; Darlington, 1957; Simpson, 1965; Futuyma, 1998; Groves, 2001). As researchers catalogued and analyzed new species, they began to develop rules and general descriptive models to explain biogeographic processes. For example, geographic differences in climate were used to explain clinal variations in skin pigmentation (Gloger's Rule), body size (Bergmann's Rule), and appendage length (Allen's Rule). Increased research interest into allopatric speciation led researchers to investigate how barriers, such as rivers, caused geographical subdivision of populations of a species. Rivers have long been thought to influence the biogeography of tropical taxa (e.g., Wallace, 1853; Darwin, 1859; Bates, 1863; Wagner, 1868). Wallace (1853) is credited with first proposing that rivers influence the geographic distribution of tropical species:

> During my residence in the Amazon district, I took every opportunity of determining the limits of species, and I soon found that the Amazon, Rio Negro and the Madeira formed the limits beyond which certain species never passed (p. 5).

Observations such as this led to the formulation of the river theory of biogeography. River theory holds that differentiation of tropical biota occurred as the result of populations being split into isolated subpopulations by networks of rivers. The constant processes of erosion and silt deposition cause changes in the course of a tropical river. Forest habitats along the riverbanks are also altered as a river changes course. The combination of meandering rivers and mosaic forests creates habitat heterogeneity, which is associated with increased opportunities to specialize and avoid interspecific competition (Salo *et al.*, 1986; Räsänen *et al.*, 1987). River based explanations have been used by researchers studying the distribution and diversity of birds (e.g., Sick, 1967;

Remsen and Parker, 1983; Caparella, 1992), reptiles (Rodrigues, 1991), and non-volant mammals (Eisenberg, 1981; Eisenberg, 1989). However, recent studies of patterns of genetic population differentiation in rodents (Patton *et al.*, 1994) and frogs (Gascon *et al.*, 1996, 1998) along the Jurua River in Brazil do not support the river barrier hypothesis. Although the population structure for some loci in the rodents and frogs were consistent with differentiation along opposite river banks, the results were due largely to substantial differentiation at one or a few collecting localities. Gascon and co-workers (1998) concluded that patterns of geographic variation in four frog species were the result of the sampling region being a zone of secondary contact.

Rivers and their floodplains have been shown to influence the adaptive radiation and distribution of Malagasy strepsirhines (Martin, 1972; Tattersall, 1982; Meyers *et al.*, 1989; Thalmann and Rakotoarison, 1994; Goodman and Ganzhorn, 2003), New World monkeys (Hershkovitz, 1968; Hershkovitz, 1977; Eisenberg, 1979; Hershkovitz, 1984; Ayres, 1986; Hershkovitz, 1988; Cheverud and Moore, 1990; Froehlich *et al.*, 1991; Ayres and Clutton-Brock, 1992; Peres *et al.*, 1996; Wallace *et al.*, 1996; Peres, 1997; Lehman, 1999; Lehman, 2004), Old World monkeys (Booth, 1958; Grubb, 1990; Colyn and Deleporte, 2002), and apes (Hill, 1969; Gonder *et al.*, 1997). For example, Ayres and Clutton-Brock (1992) conducted a preliminary biogeographic survey of the distribution of Amazonian primates and found that similarity of species across riverbanks was negatively correlated with river discharge, length/discharge, and width. There was also a negative correlation between the distance from the headwaters of the Amazon River and the similarity of primate species between its banks. However, some studies of Old World monkeys do not support the river barrier hypothesis. Colyn (1988) and Oates (1988) reviewed data on the distribution of guenons in western Africa and in Zaire. They concluded that although rivers may somewhat impede gene flow in guenons, there is little evidence that rivers are major barriers to the dispersal of forest monkeys in western and central Africa (but see Colyn and Deleporte, 2002). Similarly, Meijaard and Groves (this volume) emphasize that the effect of specific rivers as biogeographic barriers is influenced by a variety of other factors, including their history.

In the mid-20th century, new data on tropical geology and animal distribution lead to the theory of panbiogeography. Panbiogeography focuses on the coevolution of geographic barriers and biotas (Croizat, 1958, 1976). This theory employs the notion that biotas evolve together with barriers (Cracraft, 1988; Cracraft and Prum, 1988b). Thus, the barrier cannot be older than the disjunction. Darwin (1859) recognized the role of vicariance in evolution when he proposed that: "barriers of any kinds, or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions" (p. 347). If populations are isolated by vicariance events for extended periods of time, then speciation may occur via allopatry (reviewed in Wiens and Graham, 2005). The basic method is to plot the distributions of organisms on maps and connect the disjunct distribution areas together with lines called tracks. A track is the spatial coordinates of a species or groups of species. If the superimposed tracks of unrelated species overlap, the resulting overlapped lines indicate the presence of ancestral biotas that were fragmented by geologic or climatic change. For example, Croizat (1976) suggested that faunal differences to the east and west of the Andes are due to the uplift of this mountain range.

Comparative-Quantitative Approaches

Quantitative approaches developed since the middle of the mid-20th century have vastly improved our understanding of biogeography. One of the first and best examples of ecological patterns that grew out of analyses of these data was the relationship between species number and area (Rosenzweig, 1995). Species-area relationships predict that there is a positive relationship between the number of species and the size of an area (Preston, 1962; Williams, 1964; MacArthur and Wilson, 1967). This relationship is expressed as the equation:

$$S = CA^{z}$$

which is usually expressed in the log-transformed form,

$$\log S = \log C + z \log A$$

where S is the number of species, A is the area, z the slope of the line, and C is a constant usually referred to as the intercept. Species-areas relationships have been investigated at various biogeographic levels in primates (Reed and Fleagle, 1995; Jones, 1997; Bates *et al.*, 1998; Eeley and Laws, 1999; Harcourt, 1999; Laws and Eeley, 2000; Lomolino, 2000; Biedermann, 2003; Lehman, 2004; Harcourt and Doherty, 2005). For example, Reed and Fleagle

(1995) documented a high correlation ($R^2 = 0.87$) between the number of primate species and the area of rain forest for major continents (South America, Africa, and SE Asia) and large islands (Madagascar, Borneo, Sumatra, and Java).

Increased understanding of species-area relationships and the role of behavior and diet in determining an animal's ability to persist in habitats of varying size led to the ecological specialization hypothesis (Hanski, 1982; Brown, 1984; Hanski *et al.*, 1993; Hanski and Gyllenberg, 1997; Irschick *et al.*, 2005). According to this hypothesis (Brown, 1984), species that exploit a wide range of resources (generalists) are both locally common (high density) and widely distributed, whereas species that exploit a narrow range of resources (specialists) have a limited distribution and tend to be locally uncommon (low density). Studies of ecological specialization in primates have provided conflicting results (Arita *et al.*, 1990; Jones, 1997; Eeley and Foley, 1999; Peres and Janson, 1999; Harcourt *et al.*, 2002; Harcourt, 2004; Lehman, 2004; Harcourt *et al.*, 2005). At the global level, Wright and Jernvall (1999) found a "remarkably linear" relationship between the geographic range of primates and habitat breadth, but not dietary breadth. Conversely, Harcourt *et al.* (2002) found that dietary breadth was the only trait to covary with rarity in primate genera. Finally, Eely and Foley (1999) documented positive relationships between species range size and both habitat breadth ($r = 0.851$) and dietary breadth ($r = 0.634$) in African anthropoid primates. Recent studies have revealed the need to refine methods used to test species-area relationships and associated models, such as ecological specialization (Vazquez and Simberloff, 2002; Fernandez and Vrba, 2005a; Irschick *et al.*, 2005). For example, dietary niche breadth is often measured by summing the total number of food categories (fruit, leaves, flowers, insects, etc.) exploited by a species (Eeley and Foley, 1999; Wright and Jernvall, 1999; Harcourt *et al.*, 2002). It is important to note that this dietary categorization does not discriminate between dietary type breadth (number of food categories exploited) and dietary species diversity (number of plant species exploited). For example, a hypothetical primate species could be a dietary type specialist if it exploits only two food categories (e.g., fruits and leaves) but a dietary species generalist if it exploits hundreds of plant species within each of these two food types. Irschick *et al.* (2005) argued that specialization should be measured using data on resource availability and exploitation, and that researchers should integrate phylogenetic data into their models.

Ecological gradients also influence the biogeography of many tropical organisms. Many abiotic and biotic factors form a gradient within the environment (Hutchinson, 1957). Although some species are eurytopic (ecologically tolerant) and others are stenotopic (ecologically intolerant), each can survive within only a certain environmental range (range of optimum). This range is bounded at both ends of the gradient by zones of physiological stress, which are areas where a species finds it increasingly difficult to survive. Thus, a variety of environmental gradients (e.g., temperature, humidity, and latitude as well as geological features) may influence primate biogeography (Stevens and O'Conner, this Volume; Kamilar, this volume).

Correlates between rainfall and primate diversity have been investigated at the continental level (Reed and Fleagle, 1995; Cowlishaw and Hacker, 1997; Kay *et al.*, 1997; Peres and Janson, 1999). Reed and Fleagle (1995) found a high correlation between species diversity and mean annual rainfall for Africa ($R^2 = 0.75$), Madagascar ($R^2 = 0.70$), and South America ($R^2 = 0.67$). They concluded that although more data are needed on specific abiotic and biotic factors, primate diversity at the global and continental levels is highly correlated with geography and climate. In another example, Kay *et al.* (1997) found that primate species richness in South America exhibits a unimodal relationship with rainfall; peaking at *ca.* 2500 mm and then declining. They then reanalyzed Reed and Fleagle's (1995) data for Asia and found similar results. Kay and co-workers (1997) concluded that in areas with very high rainfall, soil leaching depletes nutrient levels and cloud cover reduces the light available for solar radiation for plants. Thus, plant productivity and primate species richness actually decline in areas of highest rainfall. Peres and Janson (1999) conducted a zoogeographical review of primate species distribution and environmental factors at 185 forest sites in the Neotropics. Their data did not support the hypothesis that primate richness is correlated with rainfall. Instead, they suggested that this relationship holds only in deciduous (dry) closed canopy forests where precipitation may be a limiting abiotic factor. In evergreen rain forests, where rainfall is not a limiting factor, precipitation is not a major determinant of primate richness in the Neotropics. Many researchers have cited geographic variation in rainfall as the proximate factor influencing lemur evolutionary ecology (Albrecht *et al.*, 1990; Godfrey *et al.*, 1990; Albrecht and Miller, 1993; Ravosa *et al.*, 1993, 1995; Wright, 1999; Ganzhorn, 2002; Godfrey *et al.*, 2004; Lehman *et al.*, 2005). For example, resource seasonality may apply to some extant Indriidae (*Indri, Avahi*, and *Propithecus*) in that the largest *Propithecus* are found in the eastern humid forests with progressively smaller forms being found in the dry forests of western, northern, and southern Madagascar (Albrecht *et al.*, 1990; Ravosa *et al.*, 1993, 1995). Seasonal fluctuations in rainfall are more pronounced and the length of the dry season tends to be longer in dry forests compared to humid forests (Ganzhorn, 1994; Ganzhorn *et al.*, 1997; Ganzhorn, 2002). Based on these biogeographic data, low annual rainfall and a long dry season should produce strong selective pressures for larger adult body size in indriids (Ravosa *et al.*, 1995). However, Lehman *et al.*, (2005) investigated ecogeographic size variations in sifakas and found a positive rather than negative correlation between body size and rainfall. This positive relationship may reflect reduced leaf and fruit quality due to nutrient leaching from soils in areas of high rainfall in Madagascar.

Latitudinal gradients have been suggested to influence primate richness and diversity (Cowlishaw and Hacker, 1997; Gaston *et al.*, 1998; Peres and Janson, 1999; Harcourt, 2000b; Böhm and Mayhew, 2005). The mechanisms controlling latitudinal variation in species richness and range size are poorly understood (for review, see Gaston *et al.*, 1998 and Willig, 2003). Brown (1984) argued that range size decreases in areas of high species richness because of increased levels of interspecific competition. Conversely, Stevens (1989) suggested that greater ecological flexibility of high-latitude species enables them to exist in ephemeral populations at lower altitudes. Many researchers have linked patterns of species richness to the combined effects of latitude and rainfall (Schall and Pianka, 1978; Stevens, 1989; Pagel *et al.*, 1991; Ruggiero, 1994; Cowlishaw and Hacker, 1997; Kay *et al.*, 1997; Pastor-Nieto and Williamson, 1998; Conroy *et al.*, 1999; Harcourt, 2000b; Harcourt and Schwartz, 2001; Harcourt *et al.*, 2002; Fernandez and Vrba, 2005b). Regions close to the equator exhibit increased habitat heterogeneity and rainfall, which tend to result in more niches and higher mammalian species richness (Emmons, 1999). However, in a recent study, Böhm and Mayhew (2005) used historical biogeography techniques to investigate patterns of species richness for primates in Africa and Asia. They found that these patterns result from the passage of time since colonization and rates of cladogenesis rather than latitude. Cowlishaw and Hacker (1997) tested Rapoport's rule, that latitudinal ranges of species become progressively smaller toward the equator, using the distribution and diversity of 64 species of African primates. Although latitude only influenced the geographical range of species south of the equator, rainfall was a better predictor of the geographic range of African primates north of the equator and south of the equator. Peres and

Janson (1999) reviewed the effect of latitudinal gradients on primate species richness in the Neotropics. They found that within latitudinal belts the number of primate species found in Central and South America was very weakly correlated with latitude.

Dispersal biogeography developed from attempts to correlate present day distribution patterns with dispersal of ancestral species (i.e., historical biogeography). Dispersal biogeography holds that species move from a center oforigin and undergo jump dispersal across pre-existing barriers to outlying areas (Cox and Moore, 2005). Understanding the distribution of fossils is essential because the oldest fossils are presumed to be located near the center of origin. This model requires dispersal to occur after the development of isolating barriers (Gaston, 1994). These barriers are often polarized, allowing migration in only one direction (Por, 1978). Polarization is due to ecological conditions, such as species richness and composition on either side of the barrier(s). Colonizing individuals may become isolated for such an extended period of time that they undergo speciation. Dispersalism relies on biotic factors, such as differential abilities of some species to colonize an outlying area (Myers and Giller, 1988).

Dispersal biogeography has been used to explain the distribution and diversity of primates in eastern Venezuela, Guyana, Suriname, and French Guiana (Eisenberg, 1989; Norconk *et al.*, 1997). For example, Eisenberg (1989) proposed dispersal of primates into Venezuela and Guyana via two routes: (1) from the SW through western Amazonia (Brazil and Colombia); and (2) across the Andes bordering Venezuela and Colombia. Norconk *et al.* (1997) elaborated further on this theory by suggesting that widespread tropical savannas, rivers, and mountain ranges represent contemporary barriers to the dispersal of primates in Guyana. There have been many criticisms of the dispersalist approach (Craw and Weston, 1984). Dispersal explanations for species distribution often constitute untestable hypotheses that do not provide a general framework for the analyses of multiple taxa. Thus, *ad hoc* explanations for the disjunct distribution of one taxon cannot be applied to other taxon or taxa.

Refugia Theory

Increased understanding of the historical biogeography of tropical flora and fauna led to the formation of the refuge hypothesis (Mayr and O'Hara, 1986;

Brown, 1987; Prance, 1987). Analyses of several groups of South American plants and animals showed overlapping areas of endemism as well as hybridization zones located between these areas (Vanzolini and Williams, 1970; Haffer, 1982). Haffer (1969) and Vanzolini and Williams (1970) hypothesized that varying humid and arid conditions since the Quaternary period resulted in speciation and subspeciation among tropical organisms. Forest areas contracted whereas savannas expanded during arid periods. In humid periods, the forest refuges re-expanded and joined. Some animal populations that became isolated in the restricted forest areas differentiated at the species or subspecies level before geographical overlap was reestablished with other isolated populations (Haffer, 1982). The resulting species then colonized new habitats following expansion of forest biota. This theory has four assumptions: (1) allopatry is required for geographic differentiation; (2) allopatry leads to differentiation; (3) differentiation takes many thousands of generations; and (4) differentiating characters are selectively neutral (Prance, 1987). The refuge theory has been used to model species diversity in numerous taxa and biogeographic regions (Kingdon, 1971; Diamond and Hamilton, 1980; Prance, 1987; Avise and Walker, 1998). However, the refuge hypothesis has been criticized by many researchers (Endler, 1982; Colinvaux, 1987; Cracraft and Prum, 1988b; Bush *et al.*, 1990; Bush, 1994; Colinvaux *et al.*, 1996; Knapp and Mallet, 2003; Bridle *et al.*, 2004). Colinvaux (1987) and Bush (1994) reviewed data on the paleoecological record in the Amazon basin of South America. They concluded that glacial cooling and reduced atmospheric CO_2caused disturbance of refuge areas. Thus, it was proposed that refugia were areas of maximal disturbance rather than areas of minimal disturbance. Furthermore, the refuge theory has, at times, been supported using biased or inadequate patterns of endemism and character change across geographic areas (Mayr and O'Hara, 1986; Prance, 1987; Gentry, 1989; Nelson *et al.*, 1990). Researchers have found that species level diversification for many tropical organisms occurred before the Pleistocene (Endler, 1977; Heyer and Maxson, 1982; Cracraft, 1988; Cracraft and Prum, 1988a; Bush *et al.*, 1990).

There is considerable debate regarding the influence of forest refugia on primate biogeography (e.g., Kinzey and Gentry, 1979; Kinzey, 1982; Froehlich *et al.*, 1991; Evans *et al.*, 2003). For example, Kinzey and Gentry (1979) suggested that the distribution of dusky titi monkeys (*Callicebus moloch*) and collared titi monkeys (*Callicebus torquatus*) are the result of these taxa being restricted to different forest refugia during the Pleistocene and that they consequently developed species-specific adaptations to flora and fauna associated with different soils that have persisted. However, the habitat differences have been questioned (Defler, 1994). Researchers conducting genetic studies of chimpanzees (*Pan troglodytes*) have also questioned the role of Pleistocene refugia in primate biogeography in Africa (Morin *et al.*, 1994; Goldberg, 1996; Gonder *et al.*, 1997). Morin *et al.* (1994) documented that populations of chimpanzees exchanged genes across large geographic regions regardless of forest refugia. Collins and Dubach (2000) found similar results for *Ateles*, in that most speciation events predated the Pleistocene in the Neotropics, and Disotell and Raaum (2002) suggest dates for many guenon taxa in the Miocene, well before Pleistocene climatic fluctuations.

Phylogenetic Approaches

Phylogenetic or cladistic biogeography focuses on shared derived characters which can be used to reconstruct biogeographical history (Brooks, 1990; Hovenkamp, 1997; Humphries and Parenti, 1999). Phylogeography uses results of molecular systematics to infer biogeography (Avise, 2000). Brooks (1990) suggests two reasons why a species lives where it lives: (1) it may live in an area because its ancestor lived in that area and the descendant evolved there; or (2) it may have evolved elsewhere and dispersed into the area where it now resides. If the first case holds true, then the history of the species should coincide with the history of the area (association by descent). In the second case, there should no relationship between species history and area history (association by colonization). Thus, areas that have been connected most recently share more species and characters in common than those areas that have been separated for longer periods of time.

Cladistic biogeography has been used extensively in studies of living and fossil primates (Froehlich *et al.*, 1991; Albrecht and Miller, 1993; Da Silva and Oren, 1996; Goldberg and Ruvolo, 1997; Grubb, 1999; Ron, 2000; Jensen-Seaman and Kidd, 2001; Cortés-Ortiz *et al.*, 2003), and is well-represented in this collection of articles (Ellsworth and Hoelzer, this volume; Gonder and Disotell, this volume; McGraw and Fleagle, this volume; Yoder and

Heckman, this volume; Heesy *et al.*, this volume; Beard, this volume; Rossies and Seiffert, this volume). Phylogenetic studies of primate biogeography have employed many types of data. Froehlich *et al.* (1991) analyzed 76 craniodental measurements on 284 spider monkeys. They concluded that the craniodental morphology of spider monkeys is the result of a complex relationship among dispersal from Pleistocene refugia, adaptation to non-flooded forest near seasonal swamp forest, and isolation by rivers and habitat barriers. However, other investigations of the distribution of Amazonian primates with cladistic methods revealed that diversity patterns do not match those predicted by the refugia model (Da Silva and Oren, 1996; Ron, 2000). Instead, there was consistent support for rivers acting as barriers to dispersal that ultimately led to allopatric speciation. In another example, Grub (1999) theorized that speciation that occurred due to cladogenesis required more than one vacariance event. Thus, the evolutionary history of large-bodied primates may have been in response to a series of vicariance events in Africa. If this theory finds support from, for example, molecular data, then researchers must consider determining environmental conditions before, during, and after a sequence of variance events (Hovenkamp, 1997). Researchers have often looked at only one vicariance event when studying the evolutionary biology of primates (e.g., Brandon-Jones, 1996; Medeiros *et al.*, 1997; Cropp *et al.*, 1999). Moreover, researchers investigating colonization abilities in extant taxa tend to have utilized a constant dispersal rate or distance (e.g., Zagt *et al.*, 1997; Losos *et al.*, 1998; Berggren *et al.*, 2002). Grubb (1999) hypothesized that expansion and contraction of African biomes led to changes in dispersal rates for many species. Finally, Grubb (1999) theorized that increased forest fragmentation actually leads to heightened geographical variation in species. He suggested that primate data support this model in that the number of taxa within zoogeographical primate species seem to be significantly positively correlated with total range.

Community Ecology

The presence or absence of species within a geographic area has been investigated extensively through studies of community ecology (Gee and Giller, 1987; Schoener, 1988; Wiens, 1989; Findley, 1993; Ricklefs and Schluter, 1993;

Thiollay, 1994; Pugesek *et al.*, 2002). Species may rely on each other, or one upon another, for a variety of things (e.g., food, shelter, predator detection, and parasite protection). Thus, the biogeography of one species may be positively influenced by the distribution and density of another species (Huston, 1996). In other cases, competitive exclusion may occur whereby the presence of one species prevents one or more species from occupying an area (Lotka, 1925; Volterra, 1926; Gause, 1934). This phenomenon can occur naturally or as the result of native species being displaced by an invader (Connell, 1961; Silander and Antonovics, 1982).

There have been numerous biogeographic studies of primate community structure (Fleagle and Mittermeier, 1980; Bourliere, 1985; Soini, 1986; Waser, 1986; Terborgh and van Schaik, 1987; Peres, 1988; Ganzhorn, 1992; Peres, 1993a, b; Fleagle and Reed, 1996; Ganzhorn, 1997; Godfrey *et al.*, 1997; Peres, 1997; Tutin *et al.*, 1997; Julliot and Simmen, 1998; Cowlishaw and Dunbar, 1999; Fleagle *et al.*, 1999; Fleagle and Reed, 1999; Janson and Chapman, 1999; Peres and Janson, 1999; Reed, 1999; Lehman, 2000; Peres and Dolman, 2000; Ganzhorn and Eisenbeiss, 2001; Fleagle and Reed, 2004; Haugaasen and Peres, 2005). Similarities between primate communities are most likely if they share a common biogeographic history (Fleagle and Reed, 1996; Ganzhorn, 1998). Composition of primate communities can also reflect evolutionary niche dynamics (e.g., Webb *et al.*, 2002; Desdevises *et al.*, 2003; Wiens and Graham, 2005). For example, the presence of species in a primate community, such as those in eastern Madagascar, can represent assemblages of functional groups of omnivores, frugivores, and folivores (Ganzhorn, 1997). Species entering a community following extinctions or climatic changes seem to fill adaptive or functional gaps. These cycles of adding new species continue until each functional group is represented in a community.

Many researchers have noted that the collections of species in relatively depauperate communities are not random subsets of larger assemblages. Rather they are often ordered, nested subsets of species from species-rich sites (Darlington, 1957; Patterson, 1987). Different communities of a faunal area are considered to be nested if each species in community A, which has few species, is also represented in the larger, more species-rich community B. The size and isolation of the habitat plays a critical role in determining nestedness (Yiming *et al.*, 1998). A large habitat will tend to contain more species than, for example, three small habitats of the same total size. Nestedness is thought to be due to three mechanisms: (1) differential colonization abilities of species, (2) nested distribution of habitats, and (3) differential extinction of species associated with reduced habitat area (Patterson and Atmar, 1986; Boecklen, 1997). For example, Ganzhorn (1998) documented that species-poor communities tend to represent nested subsets of species-rich communities in Madagascar and Lehman (this volume) provides a similar analysis of the primates of Guyana. However, there have been no other studies of nestedness patterns in primate communities.

Conservation Biology

Although specifics of primate evolutionary ecology are widely debated, there is consensus that primate evolution is closely linked to the use tropical forest habitats (e.g., Cartmill, 1972; Sussman, 1991; Cartmill, 1992; Martin, 1993). Forest-dwelling primates are increasingly threatened by logging, agriculture, and hunting (Cowlishaw and Dunbar, 2000; Chapman and Peres, 2001). Numerous studies have provided insights into how primates respond to habitat disturbances and hunting pressures (Johns and Skorupa, 1987; Mittermeier *et al.*, 1994; Ganzhorn *et al.*, 1996/1997; Ganzhorn, 1997; Chiarello, 1999; Peres, 1999; Lehman and Wright, 2000; Onderdonk and Chapman, 2000; Peres, 2000; Peres and Dolman, 2000; Radispiel and Raveloson, 2001; Laurance *et al.*, 2002; Goodman and Raselimanana, 2003; Marsh, 2003; Sussman *et al.*, 2003; Paciulli, 2004; Johnson *et al.*, 2005; Lehman *et al.*, this volume). For example, frugivorous lemurs may be particularly susceptible to habitat disturbance because there are few fruiting trees in Madagascar (Ganzhorn *et al.*, 1999). Of the fruiting trees available, most tend to produce small crops with long intervals between fruiting periods (Ganzhorn, 1997). In southeast Madagascar, White *et al.* (1995) found that density estimates for *Varecia variegata variegata* dropped from 1.6 individuals/ha in primary forests to 0.01 individuals/ha in disturbed forests. Sympatric *Eulemur fulvus* and *E. rubriventer* were less affected by forest disturbance because of their greater locomotor flexibility for vertical clinging and leaping, and because they exploit smaller fruit trees than *V. v. variegata*. This disparity in the size of feeding trees is important because one of the consequences of fragmentation is a reduction in the number of large trees, particularly near fragment edges (Laurance *et al.*, 1997).

Many researchers have investigated the effects of forest fragmentation on primate biogeography (Jones, 1997; Estrada *et al.*, 1999; Oka *et al.*, 2000; Onderdonk and Chapman, 2000; Passamani and Rylands, 2000; Ganzhorn *et al.*, 2001; Ganzhorn and Eisenbeiss, 2001; Evans *et al.*, 2003; Ganzhorn *et al.*, 2003; Marsh, 2003; Norconk and Grafton, 2003; Sussman *et al.*, 2003; Baranga, 2004; Mbora and Meikle, 2004; Chapman *et al.*, 2005; Harcourt and Doherty, 2005). Larger fragments tend to have more habitats and larger total population limits, which in turn allow them to host more species (Rosenzweig, 1995). However, this positive relationship between fragment size and species richness can mask important ecological information when species are lumped together without regard to variations in rarity, habitat requirements, or range limits (Zanette, 2000). Ideally, species should be categorized according to several ecological variables, which provide more deterministic analyses and predictions. This approach is important because there is not a consistent positive relationship between species richness and fragment size (Matthiae and Stearns, 1981; Onderdonk and Chapman, 2000; Harcourt and Doherty, 2005). For example, Ramanamanjato and Ganzhorn (2001) found that capture rates and population characteristics of *Microcebus rufus* were not affected by fragment size in the littoral forests of southern Madagascar. Harcourt and Doherty (2005) investigated how forest fragmentation influenced primate richness at global, continental, and site scale. They found that primate richness declined with fragment area at all spatial scales, except in Africa. Most importantly for conservation biology, Harcourt and Doherty (2005) noted that estimates of minimum area requirements for primate species tend to exceed the size of most forest fragments. Moreover, a recent edited volume contains data that indicates that there is species-specific or even individual flexibility in how primates respond to forest fragmentation (Marsh, 2003). Clearly, more data are needed to understand why and how some primate species do better than others in terms of their population dynamics in fragmented forest landscapes.

Forest fragmentation causes a dramatic increase in the amount of habitat edge (Lovejoy *et al.*, 1986; Laurance and Yensen, 1991; Chen *et al.*, 1992). Edges are dynamic zones characterized by the penetration, to varying depths and intensities, of abiotic conditions (e.g., wind, temperature, humidity, solar radiation) from the matrix into the forest interior (Chen *et al.*, 1992; Malcolm, 1994). The penetration of abiotic factors into the forest interior results in changes to vegetation structure, microclimate, and food resources

(Lovejoy *et al.*, 1986; Laurance and Yensen, 1991; Malcolm, 1994; Murcia, 1995; Laurance *et al.*, 1997; Woodroffe and Ginsberg, 1998; Fagan *et al.*, 1999; Cadenasso and Pickett, 2001). For example, trees in forest edges are prone to higher rates of canopy-gap formation, damage, and mortality because of microclimatic changes and increased wind turbulence (Laurance *et al.*, 1997; Laurance, 2000). When the total area of a forest fragment decreases linearly, the relative amount of interior forest decreases more rapidly than forest edge (e.g., Laurance and Yensen, 1991; Murcia, 1995; Zheng and Chen, 2000). Thus, smaller fragments will contain a relatively higher proportion of edge to interior forest than larger fragments. Although there have been numerous studies of the influence of forest edges on tropical taxa (Murcia, 1995; Ries *et al.*, 2004; Harper *et al.*, 2005), there are relatively few studies of edge effects on primates (e.g., Norconk and Grafton, 2003; Lehman *et al.*, 2006a; Lehman *et al.*, 2006b). Increased use of secondary forests/edges in Neotropical primates is driven largely by habitat selection in the speciose Callitrichidae (*Cebeulla*, *Mico*, *Callithrix*, *Saguinus*, *Leontopithecus*, and *Callimico*). Callitrichidae may exploit these habitats because they contain an abundance of insect prey (Rylands and de Faria, 1993). Conversely, use of edge habitats may be an artifact of the number of studies conducted in these habitats versus those on conspecifics in natural habitats (Rylands, 1996). Edge effects are particularly relevant to lemurs. Madagascaran forests are highly fragmented and, therefore, may be prone to extreme edge effects (Green and Sussman, 1990; Du Puy and Moat, 1998; Lehtinen *et al.*, 2003; Watson *et al.*, 2004). Lehman *et al.* (2006a) found that density estimates for *Avahi laniger* and *Microcebus rufus* were higher in edge habitats in SE Madagascar. Clinal variations in food quality rather than abundance represents a possible covariate to the distribution and abundance of *A. laniger*. Specifically, Ganzhorn (1995) documented higher protein concentration in leaves near forest edges. Thus, the quality of leaves may be highest near forest edges which results in higher *A. laniger* densities in these habitats. The density and distribution of *M. rufus* and their food trees were positively correlated. Preference for edge habitats can have significant negative impacts on primate conservation. For example, there is evidence for increased hunting pressures by humans in edge habitats, which may place edge tolerant lemurs at greater risk for species extirpations (Lehman, in press).

Conservation biologists have applied biogeographic models to questions on rarity and extinction patterns in primates (Arita *et al.*, 1990; Jones, 1997;

Jernvall and Wright, 1998; Mittermeier *et al.*, 1998; Harcourt, 1999; Mittermeier *et al.*, 1999; Wright, 1999; Myers *et al.*, 2000; Harcourt and Schwartz, 2001; Harcourt *et al.*, 2002; Ratsimbazafy, 2002; Dehgan, 2003; Harcourt, 2004; Whittaker *et al.*, 2005). Harcourt and Schwartz (2001) investigated what biological traits distinguish taxa susceptible to extinction from less susceptible taxa among primates in SE Asia. They found that traits associated with extinction risk appear to be large body mass, low density, large annual home range, and low maximum latitude. Expected traits that did not correlate with susceptibility were low interbirth interval, high percent frugivory, high group mass, low altitudinal range, and small geographic range. Jernvall and Wright (1998) sought to answer this question by analyzing the ecological characteristics of extant primates in various categories of endangerment of extinction. They used these data to predict the ecological integrity of communities in the future, assuming extinctions proceed according to current rankings of endangerment. The most severe change in ecological range is projected to happen in Madagascar, while Africa has less severe, but ecologically specific extinctions. Loss in the ecological range of Asian primates is severe but only a little more severe than would be expected based on the decline in Asian primate species richness. South American extinctions affect taxonomic more than ecological aspects of diversity. Despite advances made in applying biogeographic models to primate conservation, we have few longitudinal data on correlates to species rarity (Coppeto and Harcourt, 2005). For example, Chapman *et al.* (2005) analyzed primate survey data collected over 28 years in Kibale, Uganda. They found that primate recovery in logged areas was either slow or did not occur for some species. Thus, future biogeographic studies should investigate how forest fragmentation, habitat loss, and edge effects operate synergistically to influence the survival and extinction patterns of primates.

Biodiversity hotspots are used by some conservation biologists to assign conservation priorities when a lack of resources requires maximization of thediversity of biological features (Prendergast *et al.*, 1993; Pressey *et al.*, 1996; Mittermeier *et al.*, 1998; Mittermeier *et al.*, 1999; Myers *et al.*, 2000; Hamilton *et al.*, 2001; Meijaard and Nijman, 2003; Watson *et al.*, 2004). Although definitions of hotspots vary widely, they are typically defined as geographic areas characterized by high numbers of rare, endemic species (Myers, 1988; Vane-Wright *et al.*, 1991). Application of hotspot methodology indicates that 34 biogeographic regions, which comprise only 2.3% of the Earth' surface, contain approximately 75% of the world's most threatened mammals, birds, and amphibians (Mittermeier *et al.*, 2005).

There has been considerable debate regarding the practical value of assessing conservation priorities based solely on unweighted indices of species biodiversity (e.g., Prendergast *et al.*, 1993; Harcourt, 2000a; Brummitt and Lughadha, 2003). The biodiversity hotspot approach assumes that each endemic species has equal weight or value in terms of conservation priorities. Numerous theoretical and empirical studies have revealed that phylogenetic relationships among taxa are also an important measure for conservation biology (May, 1990; Vane-Wright *et al.*, 1991; Williams *et al.*, 1991; Faith, 1992a, b, 1993, 1994a, c, 1996; Croizer, 1997; Heard and Mooers, 2000; Owens and Bennett, 2000; Faith, 2002). For conservation purposes, these relationships can be measured as indices of phylogenetic diversity. Phylogenetic diversity of a species can be measured either as the inverse proportion of the relative number and closeness of its phylogenetic relatives (Vane-Wright *et al.*, 1991) or by summing the lengths of all those phylogenetic branches spanned by a data set (Faith, 1994b). For example, a novel application of hotspot and phylogenetic diversity methods revealed that lemurs represent the world's highest conservation priority for primates (Sechrest *et al.*, 2002). Furthermore, Lehman (in press) found that the phylogenetic component of lemur diversity is greatest for *Daubentonia madagascariensis*, *Allocebus trichotis*, *Lepilemur septentrionalis*, *Indri indri*, and *Mirza coquereli*. It is unfortunate that many of these high-priority lemur taxa are also amongst the least-studied of all primates.

Numerous studies have been conducted on the behavioral ecology of a few species at well-established sites, with relatively little attention paid to determining the geographic distribution for each species (Scott *et al.*, 2002). Despite a lack of data on the distribution of many tropical mammals, range maps are often produced in articles and books. Ultimately, distribution limits represent hypotheses that must be tested with fieldwork (MacArthur, 1972). As such, many researchers have investigated methods for determining the geographical range of species (e.g., Fortin *et al.*, 1996; Lidicker, 1999; Peterson, 2001; Bauer and Peterson, 2005). Range limits for some species are abrupt and can be demarcated by a barrier to dispersal (Caparella, 1992). However, many species exhibit a clinal decrease in their distribution, with no observable barrier to dispersal (Terborgh, 1971). Fortin *et al.* (2005) reviewed methods for quantifying distribution patterns and suggested that the following questions need to be addressed for many species: (1) how large are geographic ranges?; (2) how can geographic range boundaries be identified?; (3) are range boundaries gradual or sharp transitions?; (4) are the shapes of species' boundaries jagged or smooth?; (5) how much variation in the use of the landscape is found within range boundaries?; (6) are there internal boundaries?; and (7) is the range fragmented? Furthermore, it is important to realize that range limits for a species are not static and tend to change through time. Many primate species have experienced a drastic reduction in their geographic distribution within the last 2,000 years (e.g., Jungers *et al.*, 1995; Godfrey *et al.*, 1997; Godfrey *et al.*, 1999; Harcourt and Schwartz, 2001; Miller *et al.*, 2004; Lehman *et al.*, 2006c). For example, skeletal remains of *Indri indri* have been recovered from sites thousands of kilometers past the range limits of extant conspecifics (Jungers *et al.*, 1995). Range contractions in mammals are often the direct result of human disturbance (Channell and Lomolino, 2000), although global warming can also alter habitat structure and primate distributions (Jungers *et al.*, 1995; Dunbar, 1998). The question arises as to the long-term consequences of range contraction on population dynamics of primates (Cowlishaw, 1999).

Current Issues

Primate biogeography is entering a period of intense research and synthesis. Much of this interest tends to focus on documenting the spatial patterns of species in the world today and changes that can be reconstructed from records of the past in an effort to identify past trends and predict patterns for the future (e.g., Wright and Jernvall, 1999). Hoever our ability to reconstruct the processes that drive primate biogeography depend heavily on our understanding of several basic, but poorly aspects of primate biology:

1. **The dispersal abilities of individual primate taxa and the factors that influence these abilities.**

   All primate taxa (except possibly humans) are surrounded by areas where the species cannot maintain a population because of different physical conditions or a scarcity of required resources (Fortin *et al.*, 1996; Legendre *et al.*, 2002; Fagan *et al.*, 2003; Bauer and Peterson, 2005; Stevens and O'Connor, this volume). These dispersal barriers may be related to a variety of topographic and ecological conditions. For example, species can be limited in their distribution by topographic barriers. Thus, mountain ranges act as efficient barriers because their elevation can present conditions too cold for most primates that have adapted to the warmer conditions found at lower elevations. The ultimate barrier to primate dispersal is the physiology of primate species, which tends to be adapted to a limited range of environmental conditions. Researchers tend to invoke the multidimensional niche concept (MNC) when discussing dispersal patterns and limitations of a species. The MNC is a theoretical explanation of how different environmental factors limit abundance and distribution (Hutchinson, 1957). Because each species has a range of tolerances and preferences along every niche axis (habitat, diet, rainfall, etc.), a species can only occur in those areas where niche axes are within ranges of tolerance. Population growth rates are highest where the greatest number of niche axes is closest to most optimal conditions (Brown, 1995). Thus, there is great interest in determining how the physical limitations of a primate species and environmental gradients interact to form historical and ecological patterns of dispersal.

2. **Reconstructing the history and influence of disturbances upon primate taxa.**

   Reconstructive studies place our understanding of distribution patterns of primate species, and the habitats they range into, in a temporal context. In biogeography, a disturbance is any ecological or human-related process that disrupts the structure and/or composition of a habitat type. The effects of the disturbance can be either temporary or permanent. It is informative to divide disturbances into two classes: (1) those that influence the structure of a ecosystem, and (2) those that affect primate community structure within a habitat, region, and/or ecosystem. For example, primatologists tend to focus on how anthropogenic disturbances (e.g., fire, logging, and human land-clearing activities) influence primate community structure. Disturbances can also influence extinction and extirpation patterns of certain species. Although anthropogenic disturbances are often cited in discussions of primate biogeography and conservation, the effects of natural disturbances (e.g., flooding regimes, tree falls) on primate community structure have rarely been studied.

APPENDIX 1. Distribution, habitat use, diet, and conservation ratings for 348 species of extant primates ("+" indicates use of that habitat or food category by a species)

		Habitat use[2]								Diet[3]							
Species[1]	Region	WHF	DDF	WF	RF	SSF	SF	MF	ESF	FR	LE	EX	I/F	SE	FL	OT	Threat[4]
Allenopithecus nigroviridis	Africa	+					+			+			+		+		
Arctocebus calabarensis	Africa	+											+				
Cercocebus atys	Africa	+	+		+					+			+	+			
Cercocebus galeritus	Africa	+	+							+	+			+			
Cercocebus sanjei	Africa																
Cercocebus torquatus	Africa	+	+							+	+		+		+		
Cercopithecus albogularis	Africa	+	+														
Cercopithecus ascanius	Africa	+	+	+					+	+	+		+				
Cercopithecus campbelli	Africa	+	+		+				+	+	+		+		+		
Cercopithecus diana	Africa	+							+	+	+			+	+		EN
Cercopithecus doggetti	Africa																
Cercopithecus erythrogaster	Africa	+	+						+	+	+		+				EN
Cercopithecus erythrotis	Africa	+								+	+		+				VU
Cercopithecus hamlyni	Africa	+								+	+		+				
Cercopithecus kandti	Africa																
Cercopithecus lhoesti	Africa	+						+	+	+	+		+				
Cercopithecus lowei	Africa																
Cercopithecus mitis	Africa	+	+					+		+	+		+				
Cercopithecus mona	Africa	+	+		+			+	+	+	+		+				
Cercopithecus neglectus	Africa	+	+		+			+	+	+	+		+	+			
Cercopithecus nictitans	Africa	+			+					+	+		+				
Cercopithecus petaurista	Africa	+	+			+	+		+	+			+		+		
Cercopithecus pogonias	Africa	+							+	+	+		+				
Cercopithecus preussi	Africa	+							+	+	+		+				EN
Cercopithecus roloway	Africa																
Cercopithecus solatus	Africa	+															VU
Cercopithecus sclateri	Africa	+	+		+		+			+	+		+				EN

(*cont.*)

APPENDIX 1. (*Continued*)

Species[1]	Region	Habitat use[2]								Diet[3]							Threat[4]
		WHF	DDF	WF	RF	SSF	SF	MF	ESF	FR	LE	EX	I/F	SE	FL	OT	
Chlorocebus aethiops	Africa	+	+						+	+	+		+	+			
Chlorocebus cynosuros	Africa																
Chlorocebus djamdjamensis	Africa																
Chlorocebus pygerythrus	Africa																
Chlorocebus sabaeus	Africa																
Chlorocebus tantalus	Africa																
Colobus angolensis	Africa	+							+	+	+			+			
Colobus guereza	Africa	+	+	+	+				+	+	+						
Colobus polykomos	Africa	+									+			+			
Colobus satanas	Africa	+					+		+		+			+	+		VU
Colobus vellerosus	Africa	+	+		+					+	+				+		VU
Erythrocebus patas	Africa			+	+					+			+	+		+	
Euoticus pallidus	Africa	+															
Galago alleni	Africa	+			+					+			+				
Galago cameronensis	Africa																
Galago cocos	Africa																
Galago demidoff	Africa	+	+		+					+		+	+				
Galago gallarum	Africa		+	+	+					+			+	+			
Galago granti	Africa																
Galago matschiei	Africa	+								+		+	+				
Galago moholi	Africa			+	+							+	+				
Galago nyasae	Africa																
Galago orinus	Africa																
Galago rondoensis	Africa																EN
Galago senegalensis	Africa		+	+	+	+						+	+				
Galago thomasi	Africa																
Galago zanzibaricus	Africa	+								+			+				
Galagoides granti	Africa																
Gorilla beringei	Africa	+						+			+					+	EN

Gorilla gorilla	Africa	+					+		+		+					+	EN
Lophocebus albigena	Africa	+								+	+		+	+			
Macaca sylvanus	Africa		+										+	+			VU
Mandrillus leucophaeus	Africa	+								+				+			EN
Mandrillus sphinx	Africa	+								+	+			+			VU
Miopithecus talapoin	Africa	+								+			+				
Otolemur crassicaudatus	Africa		+	+	+					+		+	+				
Otolemur garnettii	Africa			+	+					+			+				
Otolemur monteiri	Africa																
Pan paniscus	Africa	+							+	+	+					+	EN
Pan troglodytes	Africa	+	+	+	+				+	+	+				+		EN
Papio anubis	Africa	+	+	+	+	+				+			+	+			
Papio cynocephalus	Africa		+	+	+					+	+			+	+		
Papio hamadryas	Africa			+	+	+								+		+	
Papio papio	Africa	+	+	+						+			+	+	+		
Papio ursinus	Africa			+	+	+				+	+		+		+		
Perodicticus potto	Africa	+	+	+	+					+		+	+				
Piliocolobus badius	Africa	+	+	+	+				+		+				+		EN
Piliocolobus foai	Africa																
Piliocolobus gordonorum	Africa																VU
Piliocolobus kirkii	Africa																EN
Piliocolobus pennantii	Africa	+		+	+	+	+		+	+	+				+		EN
Piliocolobus preussi	Africa	+								+	+						
Piliocolobus rufomitratus	Africa				+					+	+				+		CR
Piliocolobus tephrosceles	Africa																CR
Procolobus verus	Africa	+					+				+			+			
Theropithecus gelada	Africa			+							+		+			+	
Bunopithecus hoolock	Asia	+								+	+		+		+	+	EN
Hylobates agilis	Asia	+					+			+	+		+		+		EN
Hylobates albibarbis	Asia	+															
Hylobates klossii	Asia	+								+	+		+				VU
Hylobates lar	Asia	+	+					+	+	+	+		+		+	+	EN
Hylobates moloch	Asia	+							+	+	+		+		+	+	CR
Hylobates muelleri	Asia	+							+	+	+		+		+		

(*cont.*)

APPENDIX 1. (*Continued*)

Species[1]	Region	Habitat use[2]								Diet[3]							Threat[4]
		WHF	DDF	WF	RF	SSF	SF	MF	ESF	FR	LE	EX	I/F	SE	FL	OT	
Hylobates pileatus	Asia	+						+		+	+		+		+	+	VU
Loris lydekkerianus	Asia	+	+				+					+	+		+		
Loris tardigradus	Asia	+	+				+	+			+		+		+		EN
Macaca arctoides	Asia	+	+							+			+	+	+	+	VU
Macaca assamensis	Asia	+	+					+		+	+		+			+	VU
Macaca fascicularis	Asia	+					+			+	+		+	+	+	+	
Macaca fuscata	Asia	+	+					+		+	+		+	+		+	
Macaca hecki	Asia																
Macaca leonina	Asia	+	+							+			+	+	+	+	VU
Macaca maura	Asia	+								+							EN
Macaca mulatta	Asia																
Macaca nemestrina	Asia	+					+	+		+			+	+	+	+	VU
Macaca nigra	Asia	+								+	+		+				EN
Macaca nigrescens	Asia	+								+				+	+	+	
Macaca ochreata	Asia	+								+				+	+	+	
Macaca pagensis	Asia																CR
Macaca radiata	Asia	+	+							+	+		+	+	+	+	
Macaca siberu	Asia																
Macaca silenus	Asia	+								+	+		+		+		EN
Macaca sinica	Asia		+							+	+		+	+	+		VU
Macaca thibetana	Asia	+						+		+	+		+	+		+	
Macaca tonkeana	Asia	+								+	+		+	+	+		
Nasalis larvatus	Asia	+			+		+			+	+						EN
Nomascus concolor	Asia																EN
Nomascus gabriellae	Asia																VU
Nomascus hainanus	Asia																
Nomascus leucogenys	Asia																
Nomascus siki	Asia																
Nycticebus bengalensis	Asia	+											+				

Nycticebus coucang	Asia	+	+				+									
Nycticebus pygmaeus	Asia	+									+	+				VU
Pongo abelii	Asia	+		+		+			+							CR
Pongo pygmaeus	Asia	+		+		+	+		+							EN
Presbytis chrysomelas	Asia															
Presbytis comata	Asia	+					+		+	+				+	+	EN
Presbytis femoralis	Asia	+				+		+	+	+			+			
Presbytis frontata	Asia	+							+	+						
Presbytis hosei	Asia	+							+	+		+	+			
Presbytis melalophos	Asia	+						+	+	+			+	+		
Presbytis natunae	Asia															
Presbytis potenziani	Asia	+				+		+	+	+			+		+	VU
Presbytis rubicunda	Asia	+							+	+		+	+	+		
Presbytis siamensis	Asia															
Presbytis thomasi	Asia	+						+	+	+			+	+		
Pygathrix cinerea	Asia															
Pygathrix nemaeus	Asia	+					+	+	+	+			+	+	+	EN
Pygathrix nigripes	Asia	+							+	+						EN
Rhinopithecus avunculus	Asia	+							+	+			+			CR
Rhinopithecus bieti	Asia		+				+		+	+					+	EN
Rhinopithecus roxellana	Asia		+				+		+	+					+	VU
Semnopithecus ajax	Asia															
Semnopithecus dussumieri	Asia															
Semnopithecus entellus	Asia	+	+		+		+	+	+	+		+	+	+	+	
Semnopithecus hector	Asia															
Semnopithecus hypoleucos	Asia															
Semnopithecus priam	Asia															
Semnopithecus schistaceus	Asia															
Simias concolor	Asia	+				+	+		+	+						EN
Symphalangus syndactylus	Asia	+						+								
Tarsius bancanus	Asia	+										+				
Tarsius dentatus	Asia															
Tarsius pelengensis	Asia															
Tarsius pumilus	Asia						+					+				

(*cont.*)

APPENDIX 1. (*Continued*)

		Habitat use[2]								Diet[3]							
Species[1]	Region	WHF	DDF	WF	RF	SSF	SF	MF	ESF	FR	LE	EX	I/F	SE	FL	OT	Threat[4]
Tarsius sangirensis	Asia																
Tarsius syrichta	Asia	+											+				
Tarsius tarsier	Asia																
Trachypithecus auratus	Asia	+							+	+	+		+		+		EN
Trachypithecus barbei	Asia																
Trachypithecus cristatus	Asia	+			+		+		+	+	+					+	
Trachypithecus delacouri	Asia	+									+						CR
Trachypithecus ebenus	Asia																
Trachypithecus francoisi	Asia	+								+	+						EN
Trachypithecus geei	Asia	+	+	+	+					+	+				+		EN
Trachypithecus germaini	Asia																
Trachypithecus hatinhensis	Asia																
Trachypithecus johnii	Asia	+	+		+			+		+	+				+	+	EN
Trachypithecus laotum	Asia																
Trachypithecus obscurus	Asia	+						+	+	+	+			+	+		
Trachypithecus phayrei	Asia	+						+	+	+	+					+	
Trachypithecus pileatus	Asia	+	+							+	+		+	+	+		EN
Trachypithecus poliocephalus	Asia	+								+	+					+	CR
Trachypithecus shortridgei	Asia																
Trachypithecus vetulus	Asia	+	+		+			+	+	+	+				+		EN
Allocebus trichotis	Madagascar	+								+		+	+				EN
Avahi laniger	Madagascar	+							+		+				+		
Avahi occidentalis	Madagascar		+		+				+		+				+		VU
Avahi unicolor	Madagascar		+		+												
Cheirogaleus adipicaudatus	Madagascar																
Cheirogaleus crossleyi	Madagascar																
Cheirogaleus major	Madagascar	+	+							+	+		+		+		
Cheirogaleus medius	Madagascar		+		+	+				+		+	+		+	+	
Cheirogaleus minusculus	Madagascar																

Cheirogaleus ravus	Madagascar																
Cheirogaleus sibreei	Madagascar																
Daubentonia madagascariensis	Madagascar	+	+							+	+	+	+	+			EN
Eulemur albifrons	Madagascar	+								+	+				+		
Eulemur albocollaris	Madagascar	+															CR
Eulemur cinereiceps	Madagascar																
Eulemur collaris	Madagascar	+															
Eulemur coronatus	Madagascar		+						+	+	+		+		+	+	VU
Eulemur fulvus	Madagascar	+	+	+					+	+	+		+		+	+	
Eulemur macaco	Madagascar	+								+	+		+	+	+	+	VU
Eulemur mongoz	Madagascar		+			+			+	+	+	+			+		VU
Eulemur rubriventer	Madagascar	+						+	+	+	+		+		+		VU
Eulemur rufus	Madagascar	+	+							+	+		+		+		
Eulemur sanfordi	Madagascar	+	+							+	+				+	+	
Hapalemur alaotrensis	Madagascar						+										
Hapalemur aureus	Madagascar	+														+	CR
Hapalemur griseus	Madagascar	+	+					+	+	+						+	
Hapalemur occidentalis	Madagascar	+	+														
Indri indri	Madagascar	+								+	+					+	EN
Lemur catta	Madagascar		+	+	+	+			+	+	+				+	+	VU
Lepilemur dorsalis	Madagascar	+	+		+					+	+					+	VU
Lepilemur edwardsi	Madagascar		+		+					+	+			+	+		
Lepilemur leucopus	Madagascar		+		+						+						
Lepilemur microdon	Madagascar	+						+			+				+		
Lepilemur mustelinus	Madagascar	+						+		+	+				+		
Lepilemur ruficaudatus	Madagascar		+							+	+						
Lepilemur septentrionalis	Madagascar	+	+							+	+						VU
Microcebus berthae	Madagascar		+														
Microcebus griseorufus	Madagascar		+							+			+		+		
Microcebus murinus	Madagascar	+	+		+	+			+	+		+	+		+		
Microcebus myoxinus	Madagascar		+							+			+		+	+	EN
Microcebus ravelobensis	Madagascar		+		+					+			+		+	+	EN
Microcebus rufus	Madagascar	+							+	+			+				

(*cont.*)

APPENDIX 1. (*Continued*)

		Habitat use[2]								Diet[3]							
Species[1]	Region	WHF	DDF	WF	RF	SSF	SF	MF	ESF	FR	LE	EX	I/F	SE	FL	OT	Threat[4]
Microcebus sambiranensis	Madagascar		+							+			+				
Microcebus tavaratra	Madagascar		+							+			+				
Mirza coquereli	Madagascar		+		+					+		+	+		+	+	VU
Phaner electromontis	Madagascar																
Phaner furcifer	Madagascar		+		+					+	+	+	+		+	+	
Phaner pallescens	Madagascar																
Phaner parienti	Madagascar																
Prolemur simus	Madagascar	+															CR
Propithecus coquereli	Madagascar		+						+	+	+				+		
Propithecus deckenii	Madagascar		+						+	+	+				+		
Propithecus diadema	Madagascar	+								+	+			+	+		EN
Propithecus edwardsi	Madagascar	+							+	+	+			+	+		
Propithecus perrieri	Madagascar		+	+					+	+	+				+		
Propithecus tattersalli	Madagascar		+	+						+	+				+		CR
Propithecus verreauxi	Madagascar		+						+	+	+				+		VU
Varecia rubra	Madagascar	+								+		+			+		
Varecia variegata	Madagascar	+								+		+			+		EN
Alouatta sara	Neotropics																
Alouatta belzebul	Neotropics																
Alouatta caraya	Neotropics	+	+		+	+				+	+				+	+	
Alouatta coibensis	Neotropics	+					+			+	+						
Alouatta guariba	Neotropics	+							+	+	+				+	+	
Alouatta niggerima	Neotropics																
Alouatta palliata	Neotropics	+	+				+	+	+	+	+				+	+	
Alouatta pigra	Neotropics	+							+	+	+				+		EN
Alouatta seniculus	Neotropics	+	+	+	+	+	+		+	+	+				+	+	
Aotus azarai	Neotropics																
Aotus nigriceps	Neotropics	+						+	+	+	+				+	+	
Aotus nancymaae	Neotropics																

Aotus trivirgatus	Neotropics	+	+				+	+	+	+		+		
Aotus hershkovitzi	Neotropics													
Aotus lemurinus	Neotropics	+				+								VU
Aotus miconax	Neotropics	+				+								VU
Aotus vociferans	Neotropics													
Ateles paniscus	Neotropics	+			+			+		+		+	+	
Ateles belzebuth	Neotropics	+	+	+				+	+			+	+	VU
Ateles fusciceps	Neotropics	+				+		+	+					
Ateles geoffroyi	Neotropics	+	+		+	+		+	+		+	+	+	
Ateles hybridus	Neotropics	+												CR
Ateles marginatus	Neotropics	+						+			+			EN
Brachyteles arachnoides	Neotropics	+	+				+	+	+	+	+			EN
Brachyteles hypoxanthus	Neotropics	+						+	+		+	+	+	CR
Cacajao calvus	Neotropics			+	+			+			+	+	+	
Cacajao calvus	Neotropics	+		+	+			+		+	+	+	+	
Callicebus brunneus	Neotropics	+		+			+	+	+	+		+		
Callicebus cinerascens	Neotropics			+			+							
Callicebus cupreus	Neotropics	+						+			+			
Callicebus donacophilus	Neotropics	+						+						
Callicebus hoffmannsi	Neotropics				+		+	+						
Callicebus moloch	Neotropics			+	+		+	+	+	+				
Callicebus baptistia	Neotropics													
Callicebus pallescens	Neotropics													
Callicebus torquatus	Neotropics	+		+			+	+	+	+	+			
Callicebus medemi	Neotropics													
Callicebus barbarabrownae	Neotropics	+												CR
Callicebus coimbrai	Neotropics	+												CR
Callicebus melanochir	Neotropics	+												VU
Callicebus modestus	Neotropics	+		+										VU
Callicebus nigrifrons	Neotropics	+												
Callicebus oenanthe	Neotropics	+				+								VU
Callicebus olallae	Neotropics	+												VU
Callicebus ornatus	Neotropics	+	+											VU
Callicebus personatus	Neotropics	+					+	+	+			+		VU

(*cont.*)

APPENDIX 1. (*Continued*)

		Habitat use[2]								Diet[3]							
Species[1]	Region	WHF	DDF	WF	RF	SSF	SF	MF	ESF	FR	LE	EX	I/F	SE	FL	OT	Threat[4]
Callimico geoldii	Neotropics	+								+		+	+				
Callithrix acariensis	Neotropics																
Callithrix argentata	Neotropics	+	+		+					+		+	+				
Callithrix aurita	Neotropics	+	+							+		+	+				EN
Callithrix flaviceps	Neotropics	+	+							+		+	+	+			EN
Callithrix geoffroyi	Neotropics	+	+						+	+		+	+				VU
Callithrix humilis	Neotropics																
Callithrix jacchus	Neotropics			+	+	+	+		+	+		+	+				
Callithrix kuhlii	Neotropics	+	+						+	+		+					
Callithrix manicorensis	Neotropics																
Callithrix mauesi	Neotropics	+															
Callithrix melanura	Neotropics																
Callithrix nigriceps	Neotropics	+							+	+		+	+	+			
Callithrix penicillata	Neotropics	+		+					+	+		+	+				
Callithrix pygmaea	Neotropics				+				+	+		+	+				
Callithrix saterei	Neotropics																
Cebus albifrons	Neotropics		+		+		+			+		+	+	+		+	
Cebus apella	Neotropics	+	+		+			+		+		+	+	+		+	
Cebus capucinus	Neotropics	+	+		+			+	+	+	+		+	+	+	+	
Cebus libidinosus	Neotropics																
Cebus nigritus	Neotropics																
Cebus olivaceus	Neotropics	+	+		+		+	+		+			+	+			
Cebus robustus	Neotropics	+															VU
Cebus xanthosternos	Neotropics	+							+	+			+	+	+		CR
Chiropotes albinasis	Neotropics	+			+					+				+	+		
Chiropotes satanas	Neotropics	+			+		+			+			+	+	+		EN
Lagothrix brunneus	Neotropics																
Lagothrix cana	Neotropics	+															
Lagothrix lagotricha	Neotropics	+			+			+		+	+	+		+		+	

Lagothrix lugens	Neotropics	+						+	+						VU
Lagothrix poeppiggi	Neotropics	+						+	+		+				
Leontopithecus caissara	Neotropics	+						+		+	+		+		CR
Leontopithecus chrysomelas	Neotropics	+			+		+	+		+	+				EN
Leontopithecus chrysopygus	Neotropics	+		+				+		+	+				CR
Leontopithecus rosalia	Neotropics	+					+	+		+	+		+		EN
Mico humeralifer	Neotropics	+					+	+		+	+				
Mico leucippe	Neotropics														
Mico melanurus	Neotropics														
Mico intermedius	Neotropics														
Mico emiliae	Neotropics														
Mico nigriceps	Neotropics														
Mico marcai	Neotropics														
Mico chrysoleucus	Neotropics														
Mico saterei	Neotropics														
Oreonax flavicauda	Neotropics	+				+		+	+		+	+	+		CR
Pithecia aequatoralis	Neotropics	+		+				+	+			+			
Pithecia albicans	Neotropics	+		+				+	+		+	+		+	
Pithecia irroratra	Neotropics														
Pithecia monachus	Neotropics	+		+				+	+		+	+			
Pithecia pithecia	Neotropics	+		+			+	+	+		+	+	+		
Saguinus martinsi	Neotropics														
Saguinus pileatus	Neotropics														
Saguinus tripartitus	Neotropics	+						+			+				
Saguinus nigricollis	Neotropics	+					+	+		+	+	+	+	+	
Saguinus mystax	Neotropics	+			+		+	+		+	+				
Saguinus midas	Neotropics	+			+		+	+		+	+	+			
Saguinus labiatus	Neotropics	+		+	+		+	+		+	+			+	
Saguinus inustus	Neotropics	+													
Saguinus imperator	Neotropics	+						+		+	+		+	+	
Saguinus bicolor	Neotropics				+		+	+		+	+		+		CR
Saguinus fuscicollis	Neotropics	+		+			+	+		+	+			+	
Saguinus geoffroyi	Neotropics	+	+				+	+		+	+		+	+	
Saguinus graellsi	Neotropics														

(*cont.*)

APPENDIX 1. (*Continued*)

		Habitat use[2]								Diet[3]							
Species[1]	Region	WHF	DDF	WF	RF	SSF	SF	MF	ESF	FR	LE	EX	I/F	SE	FL	OT	Threat[4]
Saguinus leucopus	Neotropics	+							+	+							VU
Saguinus oedipus	Neotropics	+							+	+		+	+	+			EN
Saimiri ustus	Neotropics	+							+	+			+				
Saimiri vanzolinii	Neotropics						+			+			+				VU
Saimiri boliviensis	Neotropics	+							+	+			+	+			
Saimiri oerstedii	Neotropics	+	+							+	+		+	+			EN
Saimiri sciureus	Neotropics	+			+				+	+			+				

[1] Species from Groves (2001), supplemented with information from Brandon-Jones *et al.* (2004) and Rylands *et al.* (2000).

[2] Habitat and diet data taken from Chapman *et al.* (1999), Gupta and Chivers (1999), Sussman (1999), Rowe (1996), Ganzhorn *et al.* (1997), Garbut (1999), and Eeley and Foley (1999). WHF = wet/humid forests, DDF = deciduous/dry forests, WF = woodland forests, RF = riparian forests, SSF = spiny forests/scrub, SF = swamp forests, MF = montane forests, and ESF = Edge/secondary forests.

[3] FR = fruits, LE = leaves, EX = exudate/gum, I/F = insects/fauna, SE = seeds, FL = flowers, OT = others (grasses, bark, fungi, buds).

[4] Threat follows the IUCN (2005) categories; CR = critically endangered, EN = endangered, VU = vulnerable.

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