

Conservation Biology of Malagasy Strepsirhines: A Phylogenetic Approach

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KEY WORDS phylogenetic diversity; complementarity; endemism; protected areas; lemurs; Madagascar

ABSTRACT The phylogenetic diversity of extant lemurs represents one of the most important but least studied aspects of the conservation biology of primates. The phylogenetic diversity of a species is inversely proportional to the relative number and closeness of its phylogenetic relatives. Phylogenetic diversity can then be used to determine conservation priorities for specific biogeographic regions. Although Malagasy strepsirhines represent the highest phylogenetic diversity among primates at the global level, there are few phylogenetic data on species-specific and regional conservation plans for lemurs in Madagascar. Therefore, in this paper the following questions are addressed for extant lemurs: 1) how does the measure of taxonomic uniqueness used by Mittermeier et al. ([1992] Lemurs of Madagascar; Gland, Switzerland: IUCN) equate with an index of phylogenetic diversity, 2) what are the regional conservation priorities based on analyses of phylogenetic diversity in extant lemurs, and 3) what conservation recommendations can be made based on analyses of phylogenetic diversity in lemurs? Taxonomic endemism standardized weight (TESW) indices of phylogenetic diversity were used to determine the evolutionary component of biodiversity and to prioritize regions for conserving lemur taxa. TESW refers to the standardization of phylogenetic diversity indices for widespread taxa and endemism of

species. The phylogenetic data came from recent genetic studies of Malagasy strepsirhines at the species level. Lemur species were assigned as being either present or absent in six biogeographic regions. TESW indices were combined with data on lemur complementarity and protected areas to assign conservation priorities at the regional level. Although there were no overall differences between taxonomic ranks and phylogenetic rankings, there were significant differences for the top-ranked taxa. The phylogenetic component of lemur diversity is greatest for *Daubentonia madagascariensis*, *Allocebus trichotis*, *Lepilemur septentrionalis*, *Indri indri*, and *Mirza coquereli*. Regional conservation priorities are highest for lemurs that range into northeast humid forests and western dry forests. Expansion of existing protected areas in these regions may provide the most rapid method for preserving lemurs. In the long term, new protected areas must be created because there are lemur species that: 1) are not found in existing protected areas, 2) exist only in one or two protected areas, and 3) are still being discovered outside the current network of protected areas. Data on the population dynamics and feeding ecology of phylogenetically important species are needed to ensure that protected areas adequately conserve lemur populations in Madagascar. *Am J Phys Anthropol* 130:238–253, 2006. © 2005 Wiley-Liss, Inc.

Preserving biodiversity is one of the goals of conservation biologists. Biodiversity is usually measured as some aspect of species number and/or patterns of endemism (Cowlshaw and Dunbar, 2000). Conservation priorities can then be assigned to geographically rare species with small population sizes or “hot-spots” consisting of high species number and levels of endemism (e.g., Mittermeier et al., 1998, 1999; Myers et al., 2000). This approach assumes that all species have equal weight or value in terms of their conservation priorities. There has been considerable debate regarding the practical value of assessing conservation priorities based on unweighted indices of species biodiversity (e.g., Prendergast et al., 1993; Harcourt, 2000; Brummitt and Lughadha, 2003). Numerous theoretical and empirical studies revealed that phylogenetic relationships among taxa may be a more inclusive measure than species numbers for conservation biology (May, 1990; Vane-Wright et al., 1991; Williams et al., 1991; Faith, 1992a,b, 1993, 1994a,c, 1996, 2002; Croizer, 1997; Heard and Mooers, 2000; Owens and Bennett, 2000). For conservation purposes, these relationships can be measured as indices of phylogenetic diversity. The phylogenetic diversity of a species is inversely proportional to the relative number and closeness of its phylogenetic relatives (Vane-Wright et al.,

1991). Understanding patterns of phylogenetic diversity is critical for two reasons (Vázquez and Gittleman, 1998). First, phylogenetic diversity tends to favor basal taxa with few sister taxa. These basal taxa are worth more in terms of evolutionary history and conservation biology than more derived taxa with numerous, closely related species (Vane-Wright et al., 1991; Williams and Humphries, 1994). For example, the extinction of *Daubentonia madagascariensis*, a basal lemur species not closely related to any other extant taxa, would result in

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a disproportionately large loss of evolutionary history compared to the loss of *Lepilemur edwardsi*, a species with numerous sister taxa. Second, phylogeny plays an important role in extinction events, and preventing species extinction is one of the main goals of conservation (May, 1990; Vane-Wright et al., 1991; Williams et al., 1991; Crozier, 1997; Nee and May, 1997; Heard and Mooers, 2000; Owens and Bennett, 2000; Faith, 2002; Purvis et al., 2002). For example, Heard and Mooers (2000) found that the probability of extinction for sister taxa within a clade was higher than for taxa between clades. Therefore, conserving species that represent high levels of phylogenetic diversity should be an integral part of conservation biology (e.g., Vane-Wright et al., 1991; Owens and Bennett, 2000; Posadas et al., 2001). Although Malagasy strepsirhines represent the highest phylogenetic diversity among primates at the global level (Sechrest et al., 2002), there are few phylogenetic data on species-specific and regional conservation plans for lemurs in Madagascar.

Primate conservation efforts in Madagascar tend to have focused on either protecting "flagship species" or on iterative exercises in assigning conservation priorities to specific sites or forest fragments. "Flagship species" have charismatic qualities that make them popular with the public and presumably inspire conservation efforts that benefit the local area or habitats (Durbin, 1999). For example, the discovery of the golden bamboo lemur (*Haplemur aureus*) and rediscovery of the greater bamboo lemur (*Haplemur simus*) were key events leading to the creation of Ranomafana National Park in southeast (SE) Madagascar (Wright, 1997). Although the "flagship species" concept was applied successfully in some cases in Madagascar, it has not worked for all species (such as *Propithecus tattersalli*) (Meyers and Ratsirarson, 1988; Vargas et al., 2002), and it does not provide a systematic, scientific method for determining conservation priorities. Thus, various iterative exercises were used by the Global Environment Fund (GEF) of the World Bank, World Wildlife Fund (WWF), and Species Survival Commission Primate Specialist Groups of the International Union for the Conservation of Nature in assigning conservation priorities for primate species (e.g., Mittermeier et al., 1992; GEF, 1996a,b; Oates, 1996). For example, Mittermeier et al. (1992) designed a conservation action plan for extant lemurs. Their conservation priority ratings (1 equals lowest threat; 4 equals highest threat) were based on the following three categories: biological threat (population size), level of protection (presence in protected areas), and taxonomic uniqueness (Table 1). For taxonomic uniqueness, priority in decreasing levels was given to: being the only member of a monotypic family, the only member of a monotypic genus, representing a very distinct monotypic species, and member of a large species group. Recent studies indicate that strict phylogenetic relationships rather than higher-level taxonomic classifications may be a more appropriate tool for conservation biology (e.g., Faith, 1994c, 2002; Owens and Bennett, 2000; Posadas et al., 2001). Therefore, advances in lemur phylogenetics enable this study to address the question of whether phylogenetic diversity is a more appropriate metric than measures of taxonomic uniqueness.

There have been many attempts by researchers, international aid organizations, and conservation groups to determine conservation priorities for forest sites in Madagascar (e.g., GEF, 1996a,b; Ganzhorn et al., 1996/

1997, 1997; ANGAP, 2003). For example, Hannah et al. (1998) and Ganzhorn et al. (1997) described the results of a multidisciplinary conference to assess Madagascar's scientific and conservation priorities. Conference participants observed that many areas of biological significance are located outside protected areas, and that conservation efforts have focused on protected areas in eastern Madagascar to the exclusion of much of the south and southwestern parts of the island. The conclusion of the participants was that there is a need to develop a regional system for biological research and conservation action outside protected areas. A regional approach is needed primarily because of a lack of detailed data on lemur distribution and population dynamics (Gaston and Rodrigues, 2003).

There is little consensus among lemur biologists on regional priorities for conservation action. This lack of consensus is due to the rapidly changing forest landscapes in Madagascar, combined with lack of data on population dynamics and geographic range size for many lemur species (e.g., Green and Sussman, 1990; Du Puy and Moat, 1998; Sussman et al., 2003). For example, Mittermeier et al. (1994) suggested that western dry forests and eastern wet forests are equally endangered. Moreover, deforestation rates for southern dry forests are equal to or exceed those in eastern humid forests in Madagascar (Sussman et al., 1994; Smith et al., 1997). Until recently, there were fewer and generally smaller protected areas in the dry forests of western Madagascar (Du Puy and Moat, 1998). Thus, regional conservation actions could be prioritized for dry forests in Madagascar. However, Ganzhorn et al. (1999) compared lemur communities between eastern wet and western dry forests and documented higher species diversity, lower lemur densities, and lower lemur biomass in eastern wet forests. They also noted that two taxa of endangered lemurs, the only frugivorous species (*Varecia variegata*) and bamboo lemurs (*Haplemur* spp.), are endemic to eastern Madagascar. If the goal of conservation is to preserve species diversity, then these data could be used to prioritize conservation planning for lemurs in eastern Madagascar. Clearly, there is a need for analyses of phylogenetic diversity in lemurs to determine regional conservation priorities in Madagascar. Such data are critical, given the 2003 announcement by the President of Madagascar to triple the coverage of terrestrial protected areas over the next 5 years.

Conservation planning for Malagasy strepsirhines can be systematized by combining existing data on their phylogenetics, biogeography, and community structure at the regional level. Thus, the aims of this paper are to address the following questions: 1) how does the measure of taxonomic uniqueness used by Mittermeier et al. (1992) equate with an index of phylogenetic diversity, 2) what are the regional conservation priorities based on analyses of phylogenetic diversity in extant lemurs, and 3) what conservation recommendations can be made based on analyses of phylogenetic diversity in lemurs?

METHODS

Most biogeographic studies (Nicoll and Langrand, 1989; Langrand, 1990; Mittermeier et al., 1992; Raxworthy and Nussbaum, 1997) on Malagasy flora and fauna have used two main biogeographic regions and associated floristic domains: eastern region (eastern, central, high mountain, and Sambirano domains) and western

TABLE 1. Conservation priority ratings for lemurs in Mittermeier et al. (1992)

Species	Degree of threat	Taxonomic uniqueness	Level of protection	Total Rating	Priority rank ¹
<i>Daubentonia madagascariensis</i>	3	4		7	4
<i>Microcebus murinus</i>	1	2		3	1
<i>Microcebus rufus</i>	1	2		3	1
<i>Mirza coquereli</i>	2	3		5	3
<i>Cheirogaleus medius</i>	1	2		3	1
<i>Cheirogaleus major</i>	1	2		3	1
<i>Allocebus trichotis</i>	4	3		7	4
<i>Phaner f. furcifer</i>	3	2		5	3
<i>P. f. electromontis</i>	3	2		5	3
<i>P. f. pallescens</i>	3	2		5	3
<i>P. f. parienti</i>	3	2		5	3
<i>Lepilemur dorsalis</i>	2	1		3	1
<i>Lepilemur edwardsi</i>	1	1		2	1
<i>Lepilemur leucopus</i>	1	1		2	1
<i>Lepilemur microdon</i>	2	1		3	1
<i>Lepilemur mustelinus</i>	2	1		3	1
<i>Lepilemur ruficaudatus</i>	2	1		3	1
<i>Lepilemur septentrionalis</i>	2	1		3	1
<i>Lemur catta</i>	2	3		5	3
<i>Eulemur coronatus</i>	3	1		4	2
<i>Eulemur m. macaco</i>	2	1		3	1
<i>E. m. flavifrons</i>	4	1	1	6	4
<i>Eulemur mongoz</i>	3	1		4	2
<i>Eulemur rubriventer</i>	2	1		3	1
<i>Eulemur f. fulvus</i>	1	1		2	1
<i>Eulemur f. albifrons</i>	1	1		2	1
<i>Eulemur albocollaris</i>	3	1		4	2
<i>Eulemur f. collaris</i>	2	1		3	1
<i>Eulemur f. mayottensis</i>	2	1	1	4	2
<i>Eulemur f. rufus</i>	1	1		2	1
<i>Eulemur f. sanfordi</i>	2	1		3	1
<i>Varecia variegata variegata</i>	3	2		5	3
<i>Varecia variegata rubra</i>	3	2	1	6	4
<i>Hapalemur g. griseus</i>	1	2		3	1
<i>H. g. alaotrensis</i>	4	2	1	7	4
<i>H. g. occidentalis</i>	2	2		4	2
<i>Hapalemur aureus</i>	4	2		6	4
<i>Hapalemur simus</i>	4	2		6	4
<i>Avahi l. laniger</i>	2	2		4	2
<i>A. l. occidentalis</i>	2	2		4	2
<i>Indri indri</i>	3	3		6	4
<i>Propithecus d. diadema</i>	3	2		5	3
<i>P. d. edwardsi</i>	3	2		5	3
<i>P. d. candidus</i>	4	2		6	4
<i>P. d. perrieri</i>	4	2		6	4
<i>Propithecus tattersalli</i>	3	2	1	6	4
<i>Propithecus v. verreauxi</i>	1	2		3	1
<i>P. v. coquereli</i>	3	2		5	3
<i>P. v. coronatus</i>	4	2	1	7	4
<i>P. v. deckeni</i>	3	2		5	3

¹ Priority rank based on total ranking of conservation priorities in Mittermeier et al. (1992). Highest priority, total scores of 6–7 (ranking of 4); high priority, total score of 5 (ranking of 3); priority, total score of 4 (ranking of 2); and low priority, total score <4 (ranking of 1).

region (western and southern domains). A modified version of this system was used to determine conservation priorities for six biogeographic regions in Madagascar (Fig. 1). This modified system was used because: 1) many areas within the traditional central and western domains no longer contain forests or lemur populations (Godfrey et al., 1999), 2) it is necessary to control for overrepresentation of lemur taxa in the more speciose eastern forests (Ganzhorn et al., 1999), 3) the selected biogeographic regions are large enough to allow accurate data on presence of lemur species (Gaston and Rodrigues, 2003), 4) general floristic composition and forest structure in each region have been documented (Du Puy and Moat, 1996, 1998, 1999; Schatz, 2001), and

5) detailed Geographic Information System (GIS) data are available for each region (Du Puy and Moat, 1996). Although the use of the Sambirano and southern domains (southern dry forest) was maintained, the eastern and western regions were altered. The eastern region was divided into southeast (SE) and northeast (NE) humid forests. The Mangoro River was used to demarcate the two biogeographic regions. This river system is a biogeographic barrier to the distribution of many lemur taxa (Mittermeier et al., 1994; Garbut, 1999; Goodman and Shütz, 1999; Irwin et al., 2000; Lehman and Wright, 2000; Goodman and Ganzhorn, 2003). The western domain was divided into two biogeographic regions: western dry forests and northern

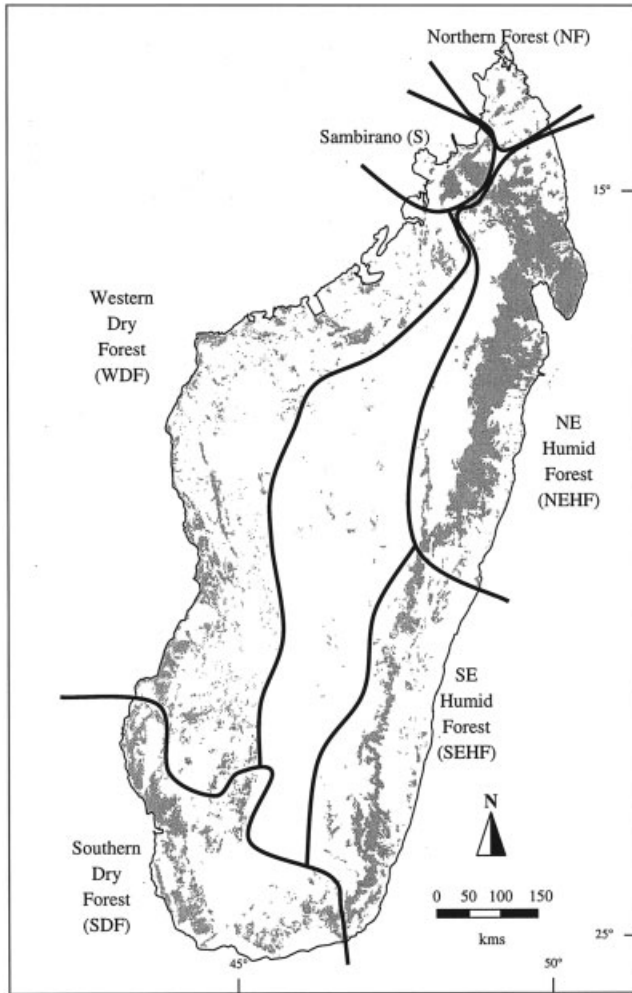


Fig. 1. Locations of six biogeographic forest regions in Madagascar.

forests. Western dry forests and northern forests are separated by the Sambirano and NE humid forests, which represent a major gap in forest cover and are an important biogeographic barrier to dispersal for mammals in Madagascar (Du Puy and Moat, 1996; Garbut, 1999). Presence or absence of lemur species in each region was determined using data from surveys conducted in SE Madagascar (Lehman and Wright, 2000; Lehman et al., 2005) and from published sources (Table 2). Data on the location, number, and size of protected areas were obtained from reports by Association Nationale pour la Gestion des Aires Protégées, le Ministère de l'Eau et de Forêt, and l'Office National pour l'Environnement à Madagascar (ANGAP, 2003).

A consensus phylogeny produced by Yoder (1997) was used as the main source for phylogenetic relationships among lemurs (Fig. 2). This phylogeny was chosen because it is based on a meta-analysis of nine genetic studies on strepsirhines, includes numerous regions of the genome, and supports many of the phylogenetic relationships reported from morphological studies. This phylogeny was supplemented with more recent genetic data for the following clades: *Microcebus* (Yoder et al., 2000), Indriidae (Delpero et al., 2001; Pastorini et al., 2001), and *Eulemur* (Wyner et al., 2000; Delpero et al., 2001).

All analyses were conducted at the species level due to debates regarding phylogenetic relationships and the evolutionary significance of subspecies in extant primates (e.g., Tattersall, 1986; Albrecht and Miller, 1993; Kimbel and Rak, 1993; Shea et al., 1993).

Following Vane-Wright et al. (1991), a node-based method was used to calculate phylogenetic diversity indices (I and W). Index I assigns a value of 1 to each terminal taxon that belongs to a pair of terminal sister taxa. The taxon that constitutes the sister group of this pair receives a value of 2 (equal to the sum of its sister group). Each successive taxon receives a value equal to that of the total sister group. Thus, index I refers to the number of phylogenetic groups to which a taxon belongs (Posadas et al., 2001). The phylogenetic diversity index W measures the proportion that each taxon contributes to the total diversity of the group. Specifically, index W assigns an information value (i) to each terminal taxon. This value is calculated as the number of groups (nodes) to which each taxon belongs. A basic phylogenetic weight (Q) was calculated using the following formula:

$$Q_j = \sum i/i_j$$

where j is equal to each specific taxon in the cladogram. The Q value for each taxon refers to the proportion of total diversity of the group that is contributed by this taxon. The phylogenetic diversity measure (W) was calculated using the following formula:

$$W = Q_j/Q_{\min}$$

where Q_{\min} refers to the lowest Q -value for the entire group.

The phylogenetic diversity indices I and W for lemur species in each region were standardized for widespread taxa and endemism to produce total endemism standardized weights (TESW). Standardization of the phylogenetic index values I and W was necessary to control for differences in species diversity between different clades (Posadas et al., 2001). Standardization was achieved by dividing the taxon value in each clade by the sum of all index values in the clade (I_s and W_s). Variations in levels of endemism between regions were determined by dividing the index value by all regions where a lemur species was present (I_e and W_e). Both standardization and endemism were then incorporated into I and W (I_{es} and W_{es}). These indices control for overweighting of clades that have a large number of taxa and/or one region because of widespread taxa. For example, phylogenetic and biogeographic data for five hypothetical species in four regions are presented in Figure 2. The first step in the process is to determine the unweighted metrics for phylogenetic diversity (I and W). The measures are then standardized for cladistic relationships and biogeographic data (I_{es} and W_{es}). Species A has the highest priority in terms of TESW measures of phylogenetic diversity. TESW metrics for each taxa in a particular region are summed to produce regional measures of phylogenetic diversity. For example, region III contains species A ($W_{es} = 0.21$) and species E ($W_{es} = 0.04$). Thus, the W_{es} score for region III is $0.21 + 0.04 = 0.25$. Each region is then ranked from lowest to highest, controlling for any ties. The final results are that region IV should be prioritized for conservation attention.

TABLE 2. Distribution of 36 lemur species in six biogeographic forest regions in Madagascar

Species	Biogeographic region ¹						Total	Source(s) ²
	NF	NEHF	SEHF	SDF	WDF	S		
<i>D. madagascariensis</i>	X	X	X	—	X	X	5	1–3, 7–10, 11, 15, 20
<i>M. coquereli</i>	—	—	—	—	X	X	2	1–3, 6–10, 11, 19
<i>M. myoxinus</i>	—	—	—	—	X	—	1	12
<i>M. berthae</i>	—	—	—	—	X	—	1	12
<i>M. rufus 1</i>	—	—	X	—	—	—	1	12
<i>M. tavaratra</i>	X	—	—	—	—	—	1	12
<i>M. rufus 2</i>	—	X	—	—	—	—	1	12
<i>M. sambiranensis</i>	—	—	—	—	—	X	1	12
<i>M. ravelobensis</i>	X	—	—	—	—	—	1	12, 19
<i>M. murinus</i>	X	—	—	—	—	—	1	12, 20
<i>M. griseorufus</i>	—	—	—	X	—	—	1	12
<i>A. trichotis</i>	—	X	—	—	—	—	1	1, 4, 8, 10, 11, 13, 14
<i>C. major</i>	X	X	X	—	—	—	3	1, 4, 6–10, 11, 22
<i>C. medius</i>	X	—	—	X	X	—	3	1–10, 11, 18, 19, 20
<i>P. furcifer</i>	X	X	—	—	X	X	4	1, 4, 6–10, 11
<i>L. dorsalis</i>	—	—	—	—	—	X	1	1, 4, 6, 7, 10, 22
<i>L. edwardsi</i>	X	—	—	—	X	—	2	1, 4, 6, 7, 10, 19, 20, 22
<i>L. leucopus</i>	—	—	—	X	—	—	1	1, 4, 6, 7, 10, 22
<i>L. ruficaudatus</i>	—	—	—	X	X	—	2	1, 4, 6, 7, 10, 22
<i>L. septentrionalis</i>	X	—	—	—	—	—	1	1, 4, 6, 7, 10, 22
<i>L. microdon</i>	—	X	X	—	—	—	2	1, 4, 6, 10, 22
<i>P. verreauxi</i>	X	—	—	X	X	—	3	1, 4, 6–10, 11, 18, 19
<i>P. diadema</i>	X	X	X	—	—	—	3	1, 4, 6–10, 11, 15, 22
<i>A. occidentalis</i>	—	—	—	—	X	—	1	1, 4, 6, 7, 10, 19, 20
<i>A. laniger</i>	—	X	X	—	—	—	2	1, 4, 6, 10, 21
<i>I. indri</i>	—	X	X	—	—	—	1	1, 4, 6, 7, 10, 21
<i>V. variegata</i>	—	X	X	—	—	—	2	1, 4, 6, 7, 10, 15, 16, 22
<i>H. griseus</i>	—	X	X	—	X	X	4	1, 3, 4, 6, 7, 10, 15, 22
<i>H. aureus</i>	—	—	X	—	—	—	1	1, 3, 4, 6, 7, 10, 22
<i>H. simus</i>	—	—	X	—	—	—	1	1, 3, 4, 6, 7, 10, 22
<i>L. catta</i>	—	—	—	X	X	—	2	1, 4, 6, 7, 10, 21
<i>E. macaco</i>	—	—	—	—	—	X	1	1, 4–11, 19
<i>E. coronatus</i>	X	—	—	—	—	—	1	1, 4–11, 17
<i>E. rubriventer</i>	—	X	X	—	—	—	2	1, 4–11, 22
<i>E. mongoz</i>	—	—	—	—	X	—	1	1, 4–11, 18, 20
<i>E. fulvus</i>	X	X	X	X	X	X	6	1, 4–11, 15, 17–20, 22
Total	13	13	12	7	14	8		

¹ X = present, — = absent.

² 1, Tattersall, 1982; 2, Sterling, 1993; 3, Sterling and Ramarosoan, 1996; 4, Nicoll and Langrand, 1989; 5, Albrecht et al., 1990; 6, Mittermeier et al., 1994; 7, Thalmann and Rakotoarison, 1994; 8, Ganzhorn et al., 1996/1997; 9, Godfrey et al., 1997; 10, Godfrey et al., 1999; 11, Lehman and Wright, 2000; 12, Rasoloarison et al., 2000; 13, Goodman and Raselimanana, 2002; 14, Rakotoarison et al., 1997; 15, Duckworth et al., 1995; 16, White et al., 1995; 17, Freed, 1996; 18, Muller et al., 2000; 19, Randrianambinina et al., 2003; 20, Schmid and Rasoloarison, 2002; 21, Sussman et al., 2003; 22, Goodman and Ganzhorn, 2003.

Biogeographic definitions and associated computations follow those used by Posadas et al. (2001). Richness was defined as the total number of lemur species in each region. An endemism index was calculated for each region as the quotient between the number of endemic species and the total species in that region. A complementarity index was computed between each pair of biogeographic regions to estimate the shared species between regions. Complementarity was defined as the replication of species presence in different geographic regions (Vane-Wright et al., 1991). Complementarity is a powerful tool for assigning conservation priorities when there are few biological data across large geographic areas, and when a lack of resources requires maximization of the diversity of biological features (Pressey et al., 1996). Thus, measures of complementarity can be used to balance the conservation need to maximize the number of protected species but still deal with the economic reality of minimizing the number of areas protected (Gaston and Rodrigues, 2003). The complementarity index has a maximum value of 1, meaning there are no species in com-

mon between the two biogeographic regions, and a minimum value of 0, meaning both regions considered contain exactly the same species. Complementarity scores were calculated using the RICHNESS software package (Posadas et al., 2001).

Hierarchical cluster analysis was used to convert the standardized, phylogenetic index W_s for each species into four clusters that could be ranked and compared with the taxonomic ranking system used by Mittermeier et al. (1992). Hierarchical cluster analysis identifies relatively homogeneous groups of cases, using an algorithm that starts with each ranking in a separate cluster and combines clusters until only one is left. Species scores for the W_s index were differentiated using squared Euclidean distance methods, and a dendrogram was selected to produce four clusters based on within-group linkages. Phylogenetic rankings (1–4) were then assigned to the four main clusters. Wilcoxon signed-ranks tests were used to determine if there were differences between the taxonomic rankings in Mittermeier et al. (1992) compared to my phylogenetic rankings. This test does not

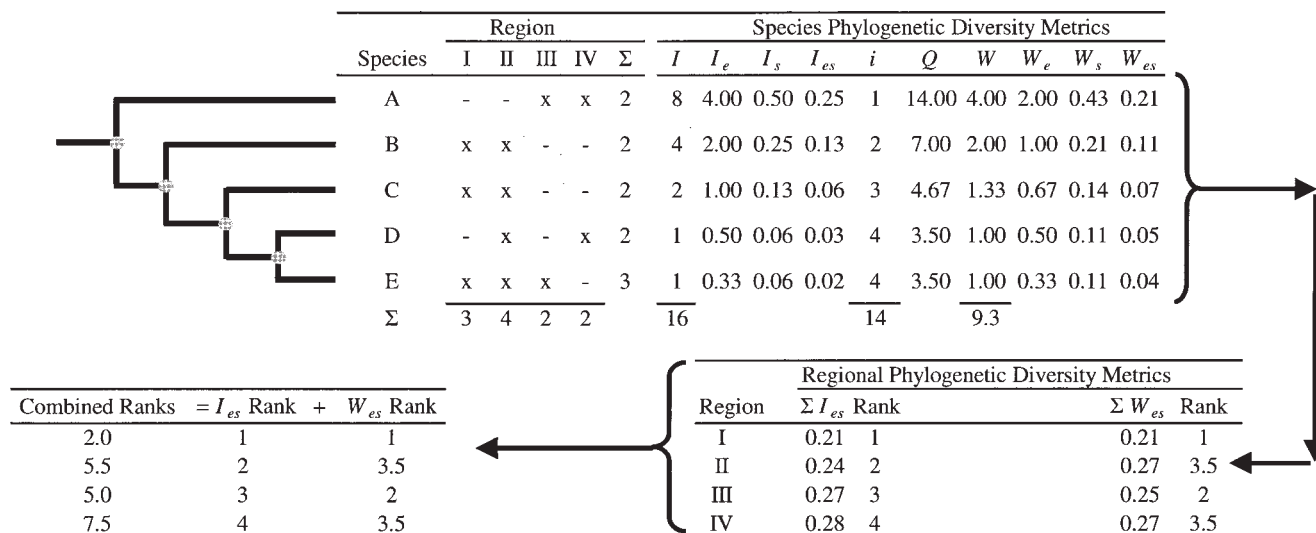


Fig. 2. Hypothetical example of process for determining phylogenetic diversity metrics at species and regional levels. Grey dots on cladogram represent nodes.

require the assumption that the population is normally distributed, and is particularly robust when comparing ordinal data (i.e., ranks). Because of differences in the numbers and kinds of taxa used by Mittermeier et al. (1992) and in this study, only congruent species and associated rankings/scores were used in the tests; thus, the comparative tests make use of 27 lemur taxa.

Regional rankings for species richness, endemism, and protected areas were done by assigning a rank from 1 (lowest richness, endemism, and size of protected area) to 6 (highest richness, endemism, and size of protected area). Complementarity indices were ranked by summing the total scores for each region and then ranking each from 1 (lowest sum value) to 6 (highest sum value). Thus, the complementarity ranking system gives priority to regions that can conserve the most number of species rather than regions that contain highly endemic taxa. Ties were controlled for by averaging the ranks for each tied region.

The basal polytomy for Malagasy strepsirhines will eventually be resolved (Fig. 3). Iterative exercises were used to determine how complete resolution will impact regional *I_{es}* and *W_{es}* metrics. Basal nodes are unresolved for the following four clades: cheirogalidae, indriidae, lepitemuridae, and lemuridae. Regional TESW rankings were created for a series of 24 fully resolved cladograms, which encompass all possible derivations of the four clades. *I_{es}* and *W_{es}* were ranked from 1–6 in each iteration. Overall median rankings were determined based on the total 24 rankings for each region. Total regional rankings for phylogenetic diversity, richness, endemism, and protected areas were reassessed using the median values for measures *I_{es}* and *W_{es}*.

Statistical analyses were conducted using SPSS 11.5. The alpha level was set at 0.05 for all analyses.

RESULTS

At the species level (Fig. 3), the standardized phylogenetic diversity *I_s* was highest for *Phaner furcifer* (4.03), *Allocebus trichotis* (2.00), *Daubentonia madagascariensis*

(1.00), and *Mirza coquereli* (1.00). TESW metrics for *I_{es}* were highest for *A. trichotis* (2.000), *P. furcifer* (1.008), *M. coquereli* (1.000), *Microcebus ravelobensis* (0.485), *M. sambiranensis* (0.242), and *D. madagascariensis* (0.200). The standardized phylogenetic diversity measure *W_s* was highest for *D. madagascariensis* (1.00), *I. indri* (0.270), and *L. microdon* (0.270). TESW measures for *W_{es}* were highest for *I. indri* (0.270), *A. occidentalis* (0.203), *L. septentrionalis* (0.202), and *D. madagascariensis* (0.200). Combined rankings for *I_{es}* and *W_{es}* indicate that the evolutionary component of lemur biodiversity is greatest for *D. madagascariensis*, *A. trichotis*, *L. septentrionalis*, *I. indri*, and *M. coquereli* (Table 3).

The taxonomic uniqueness rankings used by Mittermeier et al. (1992) did not differ significantly from the phylogenetic diversity measure *W_s* for species used in both studies ($z = -1.58, n = 27, P = 0.112$; Fig. 4). However, there were significant differences between studies in species rankings for taxa with a taxonomic ranking above one ($z = -2.76, n = 17, P = 0.006$).

The *I_{es}* metrics were highest for lemurs in NE humid forests (3.37), Sambirano (2.45), and western dry forests (2.26; Table 4). For *W_{es}*, the highest values were for NE humid forests (1.15) and western dry forests (1.01). Species richness was highest for western dry forests (14 taxa) and both the Northeast Humid Forest (NEHF) and Northern Forest (NF) regions (13 taxa). Northern forests contain the highest number of endemic species (5 taxa). Moreover, southern dry forests, Sambirano forests, and northern forests display strong patterns of uniqueness in terms of complementarity in lemur community structure (Table 5). Conversely, NE humid forests and SE humid forests tend to have more species in common between themselves and other biogeographic regions.

Western dry forests contain the largest number of national parks, special reserves, and total protected areas (Tables 6 and 7). Moreover, this region contains the greatest total size of protected areas (597,291 ha). The largest protected areas are found in the Masoala National Park (230,000 ha) in the NE humid forest

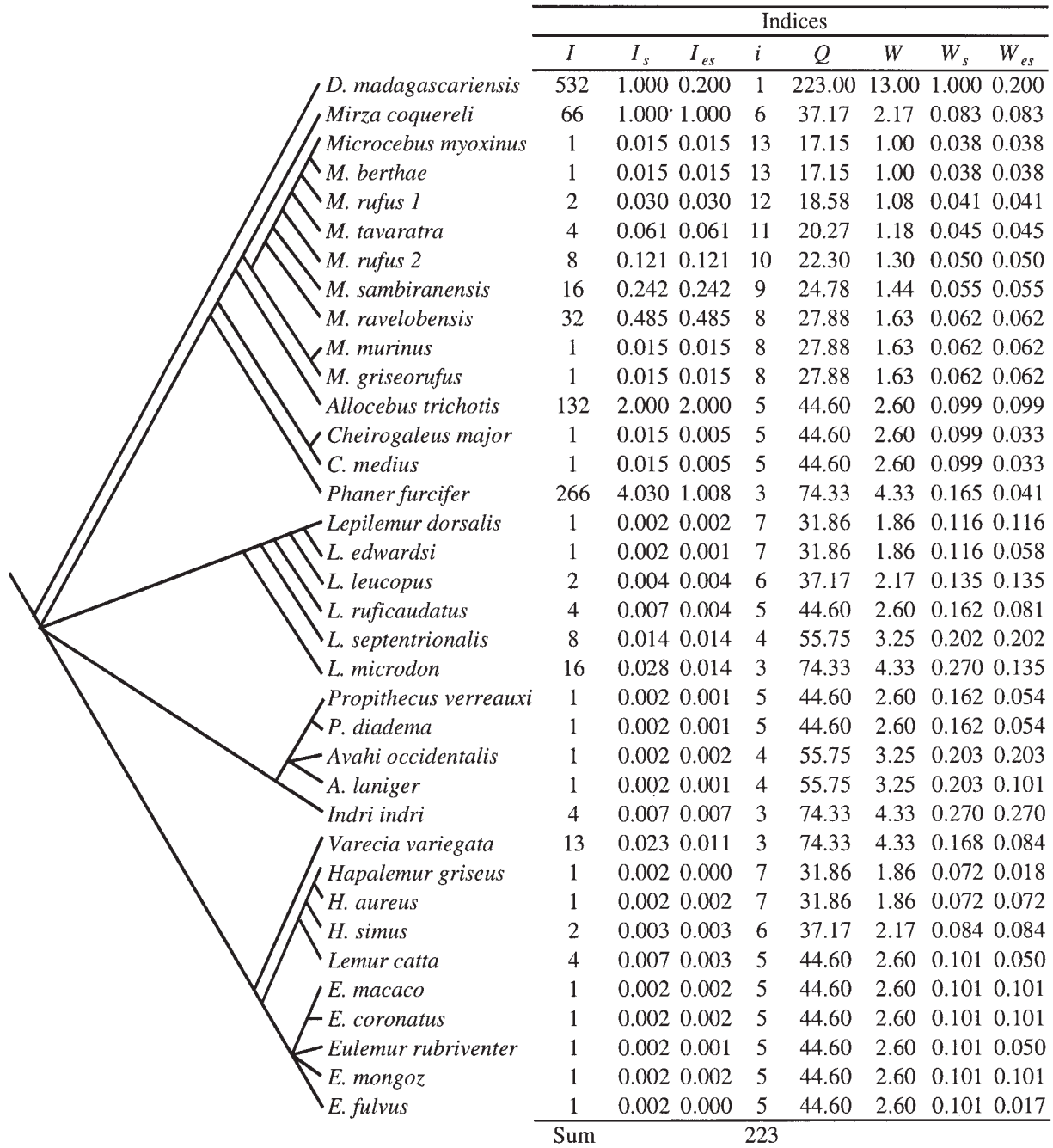


Fig. 3. Phylogeny of extant lemurs and associated node-based phylogenetic indices (phylogeny based on Yoder, 1997).

region and the Midongy-Sud National Park (192,198 ha) in the SE humid forest region. The largest average protected areas are found in the SE humid forest region (mean size = 48,571 ± 65,078.2 ha). Conversely, the southern dry forest and Sambirano regions contain the lowest total amount of protected areas, smallest number of protected areas, and smallest average size of protected areas.

The total combined rankings for standardized endemism scores (*I_{es}* and *W_{es}*), species richness, number of endemic species, complementarity, and protected areas in decreasing priority are: NE humid forests (27.5), west-

ern dry forests (25.0), northern forests (23.0), SE humid forests (20.5), Sambirano (20.0), and southern dry forests (10.0; Table 8). Ranked results for all possible fully resolved trees (n = 24) are found in Appendices A and B. Median phylogenetic measures for *W_{es}* did not alter the ranks for any of the biogeographic regions (Table 9). The only changes were for *I_{es}* rankings: a median ranking of 2 for northern forests (original ranking of 3) and median ranking of 3 for SE humid forests (original ranking of 2). There were no changes in total regional ranks as a result of using the median phylogenetic rankings for the fully resolved trees.

TABLE 3. Total combined ranked scores for TESW measures of I_{es} and W_{es} in 36 lemur species

Species	I_{es} score	Rank	W_{es} score	Rank	Combined ranks
<i>D. madagascariensis</i>	0.200	31	0.200	33	64
<i>A. trichotis</i>	2.000	36	0.099	25	61
<i>L. septentrionalis</i>	0.014	23	0.202	34	57
<i>I. indri</i>	0.007	20	0.270	36	56
<i>M. coquereli</i>	1.000	34	0.083	22	56
<i>L. microdon</i>	0.014	22	0.135	31	53
<i>M. ravelobensis</i>	0.485	33	0.062	19	52
<i>L. leucopus</i>	0.004	17	0.135	32	49
<i>M. sambiranensis</i>	0.242	32	0.055	15	47
<i>V. variegata</i>	0.011	21	0.084	24	45
<i>A. occidentalis</i>	0.002	8	0.203	35	43
<i>L. dorsalis</i>	0.002	13	0.116	30	43
<i>M. murinus</i>	0.015	25	0.062	18	43
<i>P. furcifer</i>	1.008	35	0.041	7	42
<i>M. griseorufus</i>	0.015	24	0.062	17	41
<i>M. rufus 2</i>	0.121	30	0.050	10	40
<i>E. coronatus</i>	0.002	11	0.101	28	39
<i>H. simus</i>	0.003	15	0.084	23	38
<i>M. tavaratra</i>	0.061	29	0.045	9	38
<i>E. rubrienter</i>	0.002	10	0.101	27	37
<i>L. ruficaudatus</i>	0.004	16	0.081	21	37
<i>M. rufus 1</i>	0.030	28	0.041	8	36
<i>E. mongoz</i>	0.002	9	0.101	26	35
<i>A. laniger</i>	0.001	5	0.101	29	34
<i>M. myoxinus</i>	0.015	27	0.038	6	33
<i>H. aureus</i>	0.002	12	0.072	20	32
<i>M. berthae</i>	0.015	26	0.038	5	31
<i>L. catta</i>	0.003	14	0.050	12	26
<i>C. major</i>	0.005	19	0.033	4	23
<i>L. edwardsi</i>	0.001	7	0.058	16	23
<i>C. medius</i>	0.005	18	0.033	3	21
<i>P. verreauxi</i>	0.001	4	0.054	14	18
<i>E. macaco</i>	0.001	6	0.050	11	17
<i>P. diadema</i>	0.001	3	0.054	13	16
<i>H. griseus</i>	0.000	2	0.018	2	4
<i>E. fulvus</i>	0.000	1	0.017	1	2

DISCUSSION

Comparison of taxonomic uniqueness with phylogenetic diversity

Although there were no overall differences between the taxonomic rankings of Mittermeier et al. (1992) and phylogenetic (W_s) rankings, there were significant differences in taxa assigned to the higher rankings (i.e., taxonomic rankings >1). These differences are important because in any prioritized ranking system for conservation, the top-ranked taxa should receive the most rapid and intense attention. In Mittermeier et al. (1992), the highest taxonomic rankings at the species level were given to *D. madagascariensis* (4), *I. indri* (3), *A. trichotis* (3), *M. coquereli* (3), and *Lemur catta* (3), whereas the following taxa have the highest W_s rankings: *D. madagascariensis* (4), *I. indri* (3), and *L. microdon* (3). Thus, *D. madagascariensis* and *I. indri* are the only taxa that have similar ranking scores in both studies, and they are the only top-ranked taxa using both taxonomic and phylogenetic diversity methods. Ultimately, variations in taxonomic and phylogenetic diversity ranks reflect differences in the ranking criteria used in both studies. Mittermeier et al. (1992) employed a taxonomic ranking system based on membership in monotypic taxonomic classifications at the family, genus, and species levels. Higher-level taxonomic categories, such as family and genus, often relate more to the overall grade of evolution than to the evolutionary relatedness among taxa within

the group (de Queiroz and Gauthier, 1994). Theoretical and empirical studies revealed that phylogenetic distinctiveness of taxa should be based on evolutionary relationships (May, 1990; Wiley et al., 1991; Faith, 1992a, 1996, 2002; de Queiroz and Gauthier, 1994; Owens and Bennett, 2000; Faith and Trueman, 2001; Murphy et al., 2001). Therefore, phylogenetic rankings rather than taxonomic rankings should be an important part of any comprehensive conservation plan for lemurs in Madagascar.

There is considerable debate regarding conservation priorities based on different methods of phylogenetic analyses (Owens and Bennett, 2000; Faith et al., 2004; Posadas et al., 2004). In the present study, a node-based analysis was used (Posadas et al., 2001). Node-based analyses of phylogenetic data give priority to basal taxa. Moreover, incorporating regional measures of complementarity, richness, and endemism in the TESW metrics provides an important biogeographic component to setting conservation priorities. However, Faith (1992a, 1994b,c) was critical of TESW metrics and is a strong proponent of the feature-based method for estimating phylogenetic diversity. The feature-based method focuses on relative feature diversity of any nominated set of species rather than nodes separating various taxa between clades. Thus, feature-based methods estimate phylogenetic diversity by summing the lengths of all those phylogenetic branches spanned by a data set (Faith, 1994b). Branch lengths represent inferred evolutionary steps for the character(s) being considered. It is interesting to

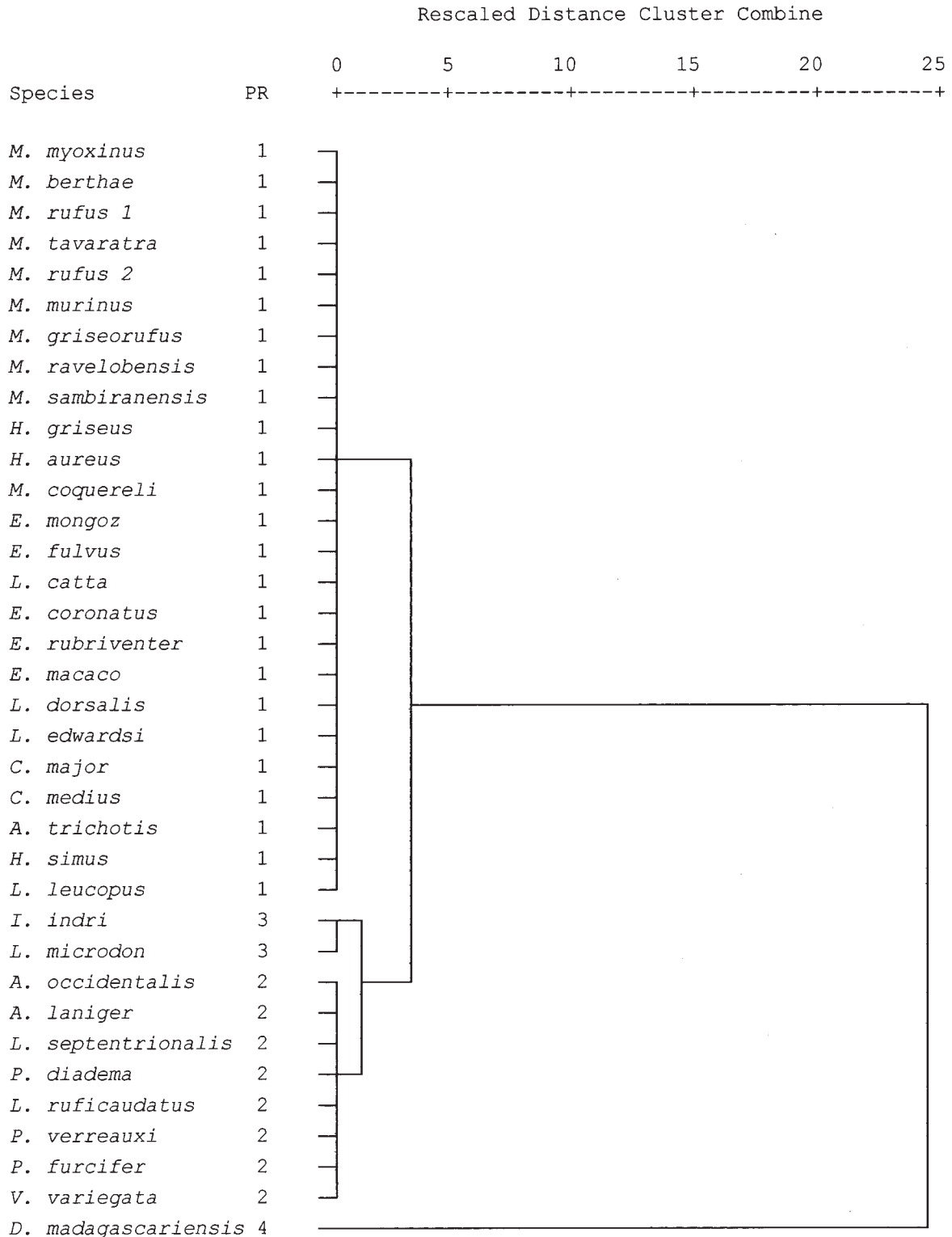


Fig. 4. Hierarchical cluster dendrogram reflecting analyses of phylogenetic index W_s for 36 lemur species in six biogeographic regions in Madagascar. PR, four-point phylogenetic ranking for taxa in each cluster.

note that in a series of published debates on node-based vs. feature-based methods, both phylogenetic methods returned remarkably similar regional conservation rankings based only on phylogenetic diversity metrics (Faith et al., 2004; Posadas et al., 2004). However, differences

in final regional rankings occurred as the result of how the two methods incorporated biogeographic data. In the node-based method, complementarity, richness, and endemism are properties of a specifically defined region. Conversely, in the feature-based method, complementar-

TABLE 4. Phylogenetic values, species richness, and endemism for lemurs in six biogeographic regions in Madagascar¹

Region	<i>I</i>	<i>I_e</i>	<i>I_s</i>	<i>I_{es}</i>	<i>W</i>	<i>W_e</i>	<i>W_s</i>	<i>W_{es}</i>	Richness	Endemism (% endemism)
NF	850.0	220.9	5.64	1.80	42.5	18.8	2.38	0.96	13	5 (13.89)
NEHF	977.0	334.0	7.23	3.37	49.7	23.1	2.76	1.15	13	3 (8.33)
SEHF	572.0	128.5	1.11	0.27	42.3	18.9	2.37	0.89	12	3 (8.33)
SDF	14.0	7.8	0.05	0.03	16.8	8.6	0.82	0.43	7	2 (5.56)
WDF	881.0	248.5	6.10	2.26	44.1	19.9	2.44	1.01	14	4 (11.11)
S	884.0	256.8	6.28	2.45	29.9	11.3	1.69	0.63	8	3 (8.33)

¹ NF, northern forests; NEHF, NE humid forests; SEHF, SE humid forests; SDF, southern dry forests; WDF, western dry forests; S, Sambirano.

TABLE 5. Complementarity scores for lemurs in six biogeographic regions in Madagascar¹

Region	NF	NEHF	SEHF	SDF	WDF
NEHF	0.810				
SEHF	0.800	0.438			
SDF	0.813	0.947	0.944		
WDF	0.750	0.870	0.864	0.667	
S	0.889	0.765	0.824	0.929	0.765

¹ NF, northern forests; NEHF, NE humid forests; SEHF, SE humid forests; SDF, southern dry forests; WDF, western dry forests; S, Sambirano.

ity, richness, and endemism are defined as properties of a set of species, and regions are only arbitrarily defined. Rigorously defined regions are critical to modeling in biogeography and conservation biology (Morrone, 1994; Morrone and Crisci, 1995; Crisci et al., 2003). Also, as noted by Faith et al. (2004), there are a variety of methods for calculating branch lengths, and there are few reliable data on branch lengths for many taxa. For example, Coddington and Scharf (1994) found that morphological and molecular data sets for the same taxa often result in different estimates for the same branch. These issues led many researchers to assume that all branch lengths are equal (Owens and Bennett, 2000; Faith et al., 2004), which seems contrary to the theoretical core of feature-based methods. Finally, one of the strengths of the TESW approach is that it allows information from diverse taxa to be combined (i.e., different cladograms). Thus, phylogenetic and biogeographic data for multiple taxa (e.g., lemurs, reptiles, or amphibians) can be combined to formulate regional conservation priorities. Feature-based methods are not amenable to multispecies comparisons, largely because of issues related to determining branch lengths between different cladograms. Therefore, TESW metrics provide a more expandable measure than feature-based methods for prioritizing regional conservation plans for lemurs.

It should not be assumed that the most basal taxa will always achieve the highest priority rankings when using TESW metrics. Although this is an issue with *I* and *W* metrics, standardization in the *I_{es}* and *W_{es}* indices controls for overweighting only of basal taxa in determining phylogenetic diversity. For example, *P. furcifer* would certainly be considered a top-ranked species based on its basal placement within the highly speciose cheirogalidae clade. However, the combined *I_{es}* and *W_{es}* rankings result in *P. furcifer* being ranked fourteenth out of the total 36 species analyzed in this study. Comparable results can be found for within-family rankings. In the lepilemuridae, the most basal taxon is *L. microdon*.

Combined TESW rankings result in *L. septentrionalis* having a higher phylogenetic diversity ranking (third) than *L. microdon* (sixth). Similar results apply to regional rankings. The presence of basal species in a few regions is balanced by the use of complementarity rankings. High regional rankings are achieved if species representing high levels of phylogenetic diversity are endemic to a particular region.

Regional conservation priorities

NE humid forests and western dry forests are the top priorities for lemur conservation, based on phylogenetic diversity and biogeography metrics. Full resolution of the basal polytomy for lemurs is unlikely to alter prioritizing NE humid forests and western dry forests, provided there are no major changes in in-group relationships. The phylogenetic indices *I_{es}* and *W_{es}* would only be altered to a major extent if one or more species changed family membership. Such major changes in in-group relationships are unlikely, except for changes in subspecies status to/from species status for currently recognized taxa. However, these changes are not necessarily predictable and cannot be tested in this paper. Despite any future changes in in-group relationships for lemurs, high rankings for NE humid forests and western dry forests were not based entirely on their associated phylogenetic scores (*I_{es}* and *W_{es}*). Western dry forests had the second highest number of endemic species, and NE humid forests shared with western dry forests the highest rank for richness. NE humid and western dry forests also contain species that represent high levels of phylogenetic diversity (e.g., *A. trichotis*, *M. coquereli*, and *D. madagascariensis*).

The regional conservation approach presented here is focused only on lemurs. There are other highly endemic taxa requiring immediate conservation attention in Madagascar. The question arises then of how TESW conservation priorities for other animal taxa compare to those for lemurs. To date, there are no published reports on TESW metrics for other animal taxa in Madagascar. However, detailed phylogenetic and biogeographic data are becoming available for some non-primate taxa in Madagascar (Bininda-Emonds et al., 1999; Raxworthy and Nussbaum, 2000; Douady et al., 2002). For example, Raxworthy and Nussbaum (2000) conducted studies of phylogenetic relationships and biogeography in chameleons, including those in Madagascar. Thus, in the near future it may be possible to combine phylogenetic and biogeographic data from cladograms on different taxa into a comprehensive data set for TESW indices and regional conservation priorities in Madagascar.

TABLE 6. Status and size of 47 protected areas located in six biogeographic regions in Madagascar¹

Number	Region	Name	Status	Size (ha)
1	NF	Analamera	SR	34,700
2		Ankarana	SR	18,225
3		Foret d'Ambre	SR	4,810
4		Manongarivo	SR	32,735
5		Montagne d'Ambre	NP	18,200
6	S	Lokobe	INR	740
7		Manangarivo	SR	35,250
8	NEHF	Ambatovaky	SR	60,050
9		Analamazoatra	SR	810
10		Anjanaharibe-Sud	SR	32,090
11		Betampona	INR	2,228
12		Mananara-Nord	NP	23,000
13		Mangervola	SR	11,900
14		Mantadia	NP	10,000
15		Marojejy	NP	60,050
16		Masoala	NP	230,000
17		Nosy Mangabe	SR	520
18		Tsaratanana	INR	48,622
19		Zahamena	NP	41,402
20		Zahamena	INR	22,497
21	SEHF	Andohahela	NP	38,010
22		Andringitra	NP	31,160
23		Kalambatritra	SR	28,255
24		Manombo	SR	5,320
25		Midongy-Sud	NP	192,198
26		Pic d'Ivohibe	SR	3,453
27		Ranomafana	NP	41,601
28	WDF	Ambohijanahary	SR	24,750
29		Andranomena	SR	6,420
30		Ankarafantsika	NP	60,520
31		Baie de Baly	NP	57,418
32		Bemaraha	NP	66,630
33		Bemaraha	INR	85,370
34		Bemarivo	SR	11,570
35		Bora	SR	4,841
36		Isalo	NP	81,540
37		Kasijy	SR	19,800
38		Kirindy-Mitea	NP	72,200
39		Maningoza	SR	7,900
40		Marotandrano	SR	42,200
41		Namoroka	NP	21,742
42		Tampoketsa-Analamaitso	SR	17,150
43		Zombitse-Vohibasia	NP	17,240
44	SDF	Andohahela	NP	38,010
45		Beza Mahafaly	SR	600
46		Cap Sainte Marie	SR	1,750
47		Tsimanampetsotsa	NP	43,200

¹ NF, northern forests; NEHF, NE humid forests; SEHF, SE humid forests; SDF, southern dry forests; WDF, western dry forests; S, Sambirano; NP, national park; SR, special reserve; INR, integrated natural reserve.

Conservation recommendations

A number of preliminary recommendations can be made regarding the conservation of lemur species representing high levels of phylogenetic diversity. Increasing the size of existing protected areas may provide a rapid means of improving conservation protection for lemurs. In existing protected areas, there tend to be some levels of infrastructure (e.g., rules of governance, financial support, camp sites, or trail systems), involvement of local people, and presence of researchers (Wright, 1992, 1997). Because it can take years to set up these infrastructures and develop research programs, expanding existing protected areas may provide the most rapid means for improving lemur protection in the *short term*. For exam-

TABLE 7. Regional summary of protected areas in Madagascar¹

Region	Number of protected areas				Size of protected areas (ha)		
	NP	SR	INR	Total	Total	Mean	SD
WDF	7	8	1	16	597,291.0	37,330.7	28,707.5
NEHF	5	5	3	13	543,169.0	41,782.2	60,420.6
SEHF	4	3	0	7	339,997.0	48,571.0	65,078.2
NF	1	4	0	5	108,670.0	21,734.0	12,251.2
SDF	2	2	0	4	83,560.0	20,890.0	22,868.1
S	0	1	1	2	35,990.0	17,995.0	24,402.2
Total	19	23	5	47	1,708,677	32,145.1	43,859.4

¹ NF, northern forests; NEHF, NE humid forests; SEHF, SE humid forests; SDF, southern dry forests; WDF, western dry forests; S, Sambirano; NP, national park; SR, special reserve; INR, integrated natural reserve.

ple, increasing the size of the Analamazoatra Special Reserve (810 ha), Betampona Integrated Natural Reserve (2,228 ha), Mananara-Nord National Park (23,000 ha), Mantadia National Park (10,000 ha), and Mangervola Special Reserve (11,900 ha) may improve protection for *D. madagascariensis*, *A. trichotis*, and *I. indri* in NE Madagascar. Similarly, increasing the size of Namoroka National Park (21,742 ha), Andranomena Special Reserve (6,420 ha), and Zombitse-Vohibasia National Park (17,240 ha) may enhance lemur conservation for *D. madagascariensis* and *M. coquereli* in western dry forests. *L. septentrionalis* should benefit from increasing the size of Ankarana Special Reserve (18,225 ha) and Analamera Special Reserve (34,700 ha) in northern Madagascar.

Lemurs cannot be preserved only by the expansion of existing protected areas. As of 1997, only 2.8% (16,851.3 km²) of the total remaining forest area (589,185.1 km²) was part of the protected areas system in Madagascar (UNDP, 2002). In the long term, new protected areas must be created because there are lemur species that: 1) are not found in existing protected areas, 2) exist only in one or two protected areas, and 3) are still being discovered, often outside the current network of protected areas. Ultimately, expansion or creation of protected areas requires an answer to the following question: how much habitat is enough to prevent extirpations and extinctions of resident lemur species? For example, Gurd et al. (2001) compared mammal species richness in eastern North American reserves to estimated species-area relationships prior to European settlement to determine if minimal area requirements are being met for extant taxa. Of the 2,355 reserves in the region, only 14 met or exceeded the minimum estimated required area to ensure no loss of mammal species. This study accurately predicted the loss of mammal taxa in many protected areas in eastern North America. Similar studies should be conducted for lemurs and protected areas in Madagascar.

Expanding existing protected areas or creating new protected areas are based on the assumption that protected areas provide adequate levels of protection and that there is no variation in level of protection regardless of status (i.e., special reserve, national park, or integrated natural reserve). There are considerable variations in the actual levels of protection for lemurs and forests in most protected areas in Madagascar (Mittermeier et al., 1992, 1994). Local people often hunt lemurs in protected areas (e.g., Lehman and Wright, 2000; Ran-

TABLE 8. Ranking of six biogeographic regions based on phylogenetic indices, biogeographic indices, and protected areas in Madagascar¹

Region	I_{es} rank	W_{es} rank	Richness rank	Endemism rank	Complementarity rank	Protected areas rank	Total ranks
NEHF	6	6	5.0	3	5.5	2	27.5
WDF	4	5	6.0	5	4.0	1	25.0
NF	3	4	3.5	3	5.5	4	23.0
SEHF	2	3	3.5	6	3.0	3	20.5
S	5	2	2.0	3	2.0	6	20.0
SDF	1	1	1.0	1	1.0	5	10.0

¹ NF, northern forests; NEHF, NE humid forests; SEHF, SE humid forests; SDF, southern dry forests; WDF, western dry forests; S, Sambirano.

TABLE 9. Ranking of six biogeographic regions based on median phylogenetic indices for all possible resolved trees, biogeographic indices, and protected areas in Madagascar¹

Region	Median I_{es} rank	Median W_{es} rank	Richness rank	Endemism rank	Complementarity rank	Protected areas rank	Total ranks
NEHF	6	6	5.0	3	5.5	2	27.5
WDF	4	5	6.0	5	4.0	1	25.0
NF	2	4	3.5	6	3.0	4	22.5
SEHF	3	3	3.5	3	5.5	3	21.0
S	5	2	2.0	3	2.0	6	20.0
SDF	1	1	1.0	1	1.0	5	10.0

¹ NF, northern forests; NEHF, NE humid forests; SEHF, SE humid forests; SDF, southern dry forests; WDF, western dry forests; S, Sambirano.

driamanalina et al., 2000; Goodman and Raselimanana, 2003). For example, Perrier's sifaka (*Propithecus diademata perrieri*) is one of the most critically endangered primates in the world (Konstant et al., 2002). Most *P. d. perrieri* are found only in the Analamera Special Reserve (Lehman and Mayor, 2004). Local people use slingshots to hunt *P. d. perrieri* despite 45 years of protection in a special reserve. Furthermore, deforestation occurs regularly in many protected areas (Lehman, personal observations). This deforestation occurs as the result of slash-and-burn agriculture and the removal of trees for firewood and housing materials. Therefore, regional initiatives to expand or create new protected areas must prioritize the involvement of local people and conservation education if conservation is to succeed in Madagascar (Wright, 1992, 1997; Ratsimbazafy, 2003).

Research needed

Many of the lemur taxa that represent the highest levels of phylogenetic diversity are also among the least-studied of Malagasy strepsirhines (e.g., *D. madagascariensis*, *A. trichotis*, *L. septentrionalis*, and *M. coquereli*). For example, *D. madagascariensis* has only been the subject of one longitudinal study, which was conducted on the small island of Nosy Mangabe (Sterling, 1993, 1994). Moreover, *D. madagascariensis* is extremely difficult to survey using traditional strip transect techniques; most observations are the result of brief, serendipitous encounters (Sterling and Ramarason, 1996; Sterling and McFadden, 2000). Clearly, there is a need to conduct longitudinal studies of *D. madagascariensis*, *A. trichotis*, *L. septentrionalis*, and *M. coquereli*. These studies should focus on identifying sites suitable for intensive studies of population dynamics and feeding ecology.

Data are also required on the population dynamics and feeding ecology of lemurs at the landscape level. These data are critical because theoretical models predict that when the amount of forest cover is less than

20% of the original amount, such as in most of Madagascar, forest fragmentation will have a stronger influence than forest loss on species distribution at the landscape level (Lande, 1987; Andr en, 1994; Fahrig, 1998, 2002). Moreover, one of the most significant consequences of forest fragmentation is an increase in the amount of habitat edge. In Madagascar, ecological gradients between forest and surrounding grasslands (i.e., edge effects) tend to be very abrupt because there are relatively few colonizing tree species found in gaps and edges (e.g., *Cecropia* spp. in South America), and local people often practice slash-and-burn agriculture in the matrix (Lehman et al., in press, a). Colonizing tree species can reduce the penetration distance and intensity of edge effects into the forest. It was speculated that edge effects may extend as far as 250 m into neotropical forests (Malcolm, 2001). Hypothetically, if edge effects penetrate 300 m into a 100-ha square-shaped fragment in Madagascar, then approximately only 16% of the total forest amount will be unaffected by edge effects. Thus, abiotic conditions (e.g., temperature, humidity, wind, and light) in the surrounding matrix may penetrate further and to a greater intensity into forest interiors than those measured for tropical forests in other regions. If this prediction holds true, then edge effects may reduce the abundance and availability of fruit trees (Laurance, 2000), which tend to be patchily distributed, produce few fruit crops, and exist at low densities in Madagascar (Ganzhorn et al., 1999). Alternatively, forest edges may also represent microhabitats with abundant and/or high-quality food resources for some lemur species. Corbin and Schmid (1995) found that female *M. marinus* shifted their range patterns during the dry season to feed on insect secretions from insects that were most abundant near the forest edge. Ganzhorn (1995) documented that low-intensity logging increased light levels in western dry forests, which resulted in a higher protein concentration in leaves. Elevated light levels were documented near forest edges in SE Madagascar (Lehtinen et al.,

2003). Thus, food quality may be higher near forest edges compared to interior forest habitats. Therefore, determining the viability of primate populations in isolated protected areas will require data on how edge effects influence behavior and feeding ecology in lemurs.

Lemur conservation can also be improved by prioritizing the protection of existing forest corridors and creating new corridors between forest fragments (e.g., Laurance and Laurance, 1999; Mech and Hallett, 2001; Couvet, 2002). This prioritization is critical because, based on deforestation rates of -0.9% of total forest cover/year (FAO, 2003), some lemur species may exist only as isolated populations in protected areas completely surrounded by an inhospitable matrix. Long, thin corridors may be completely dominated by edge effects (e.g., Laurance and Laurance, 1999; Lidicker, 1999; Mech and Hallett, 2001). Creation of forest corridors may be particularly critical for lemur survival because most species seem unwilling or unable to traverse matrix habitats between forest fragments (Dehgan, 2003). For example, deforestation resulted in a disjunct distribution for lemurs in the region between Ranomafana National Park and Vohibola III Special Reserve in SE Madagascar (Lehman et al., in press, b). This landscape pattern of habitat loss raises concerns regarding inbreeding of lemur populations within isolated protected areas.

CONCLUSIONS

Conservation rankings based on phylogenetic diversity metrics rather than taxonomic scores may be a more appropriate part of any comprehensive conservation plan for lemurs in Madagascar. In terms of species-specific conservation priorities, the evolutionary component of lemur phylogenetic diversity is greatest for *D. madagascariensis*, *A. trichotis*, *L. septentrionalis*, *I. indri*, and *M. coquereli*. Because these species are also among the least studied of all lemurs, longitudinal studies of their population dynamics must be prioritized. At the regional level, phylogenetic diversity and biogeography metrics indicate that NE humid forests and western dry forests are the top priorities for lemur conservation. Full resolution of the basal polytomy for lemurs is unlikely to alter prioritizing NE humid forests and western dry forests, provided there are no major changes in in-group relationships. In the short term, protection of phylogenetically important taxa can be strengthened by expanding the size of existing protected areas in Madagascar. In the long term, new protected areas must be created to conserve species that do not range near existing protected areas and newly discovered species. Ultimately, conservation plans will succeed only with a greater understanding of how the interactions of forest fragmentation, habitat loss, and edge effects influence the survival and extinction patterns of lemurs in the rapidly disappearing forest landscapes of Madagascar.

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Appendix A. Ranked results of I_{es} for all possible resolved trees ($n = 24$) for Malagasy strepsirhines¹

Number	Pattern	NEHF	WDF	SEHF	NF	S	SDF
1	ABCD	6	4	2	3	5	1
2	ABDC	6	4	3	2	5	1
3	ACBD	6	4	2	3	5	1
4	ACDB	6	5	2	3	4	1
5	ADBC	6	4	2	3	5	1
6	ADCB	6	4	2	3	5	1
7	BACD	6	4	3	2	5	1
8	BADC	6	4	3	2	5	1
9	BCAD	6	4	2	3	5	1
10	BCDA	6	4	2	3	5	1
11	BDAC	6	4	2	3	5	1
12	BDCA	6	4	2	3	5	1
13	CABD	6	4	2	3	5	1
14	CADB	6	4	2	3	5	1
15	CBAD	6	4	1	3	5	2
16	CBAD	6	5	2	3	4	1
17	CDAB	6	4	1	3	5	2
18	CDBA	6	4	2	3	5	1
19	DABC	6	4	2	3	5	1
20	DACB	6	5	2	3	4	1
21	DBAC	6	4	2	3	5	1
22	DBCA	6	5	2	2	5	1
23	DCAB	6	5	2	2	5	1
24	DCBA	6	5	2	3	4	1
Median		6	4	2	3	5	1

¹ Pattern refers to placement of four clades cheirogalidae (A), lepilemuridae (B), indriidae (C), and lemuridae (D).

Appendix B. Ranked results of W_{es} for all possible resolved trees ($n = 24$) for Malagasy strepsirhines¹

Number	Pattern	NEHF	WDF	SEHF	NF	S	SDF
1	ABCD	6	5	2	4	3	1
2	ABDC	6	5	3	4	2	1
3	ACBD	6	5	3	4	2	1
4	ACDB	6	5	3	4	2	1
5	ADBC	6	5	2	4	3	1
6	ADCB	6	5	3	4	2	1
7	BACD	6	5	3	4	2	1
8	BADC	6	5	3	4	2	1
9	BCAD	6	5	3	4	2	1
10	BCDA	6	5	3	4	2	1
11	BDAC	6	5	3	4	2	1
12	BDCA	6	5	2	4	3	1
13	CABD	6	5	3	4	3	1
14	CADB	6	5	3	4	3	1
15	CBAD	6	5	3	4	3	1
16	CBAD	6	5	3	4	3	1
17	CDAB	6	5	3	4	2	1
18	CDBA	6	5	2	4	3	1
19	DABC	6	5	3	4	2	1
20	DACB	6	5	3	4	2	1
21	DBAC	6	5	3	4	2	1
22	DBCA	6	5	3	4	2	1
23	DCAB	6	5	3	4	2	1
24	DCBA	6	5	3	4	2	1
Median		6	5	3	4	2	1

¹ Pattern refers to placement of four clades cheirogalidae (A), lepilemuridae (B), indriidae (C), and lemuridae (D).

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