Biogéographie de Madagascar, 1996 : 369-383

PATTERNS OF ENDEMISM FOR TERRESTRIAL VERTEBRATES IN EASTERN MADAGASCAR

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ABSTRACT.- Patterns of endemism were determined for four vertebrate groups: amphibians, reptiles, birds, and non-volant mammals in Eastern Madagascar. A total of 360 species endemic to Eastern Madagascar were included in a Parsimony Analysis of Endemism (PAE) for 26 survey sites. Patterns of endemism are largely congruent between each vertebrate group, although the classic phytogeographic classification of HUMBERT (1955) is not well supported by any of the vertebrate groups.

KEY WORDS.- Madagascar, Biogeography, Vertebrates, Endemism, Ecology

RESUME.- Des modèles d'endémisme ont été établis pour quatre groupes de vertébrés: Amphibiens, Reptiles, Oiseaux et Mammifères non volants, dans la région est de Madagascar. Un total de 360 espèces endémiques pour l'est de Madagascar ont été incluses dans une analyse parsimonieuse de l'endémisme (APE) pour un total de 26 zones observées. Les modèles d'endémisme sont largement conformes entre chaque groupe de Vertébrés, bien que la classification phytogéographique classique D'HUMBERT (1955) ne soit pas bien appuyée par aucun des groupes de Vertébrés.

MOTS-CLES.- Madagascar, Biogéographie, Vertébrés, Endémisme, Ecology

INTRODUCTION

Despite the substantial biogeographic interest in Madagascar, there have been surprisingly few studies of biogeographic patterns of endemism for the vertebrate groups within the island. The only detailed studies to date have been restricted to lemurs and reptiles. MARTIN (1972) used lemur distributions to propose seven areas of endemism; LANG (1990) described patterns of endemism of cordylid lizards; and RAXWORTHY and NUSSBAUM (1995) suggested new biogeographic divisions in northern Madagascar based on distributions of chameleons of the genus *Brookesia*. Most recently, reptile patterns of endemism have been analyzed for Eastern Madagascar by RAXWORTHY and NUSSBAUM (in press). Other studies have described more general patterns of vertebrate endemism in Madagascar. For example, bird endemism supports an Eastern and Western-Southern division (LANGRAND, 1990), amphibian endemism supports an Eastern, Southern and Western division (BLOMMERS-SCHLÖSSER & BLANC, 1993) and reptile endemism supports an Eastern, Southern, Western and Central division (BLANC, 1972). No attempt has yet been made to test if patterns of patterns of endemism are congruent between all these groups.

The first (and only) detailed biogeographic classification of Madagascar was proposed by HUMBERT in 1955, and his phytogeographic zones have subsequently

In: W.R. LOURENÇO (éd.)
Editions de l'ORSTOM, Paris

formed the basis of many zoogeographic studies (*e.g.* PAULIAN, 1961; MARTIN, 1972; LANG, 1990). HUMBERT (1955) used a combination of climatic data, topography, and vegetation types to establish a hierarchical division of Madagascar into regions, domains, sub-domains, and sectors. The hierarchical classification of these biogeographic units is an explicit feature of Humbert's classification, and any site in Madagascar can be assigned to four different categorical ranks. This hierarchical classification is presented in Table I and figure 1.

Surprisingly, HUMBERT's phytogeographic hypothesis, although widely accepted as a model in zoogeographic discussions, has not yet been tested using biogeographic data for all the major group of vertebrates. If this phytogeographic hypothesis accurately describes congruent patterns of plant and animal endemism (a product of vicariance speciation, dispersal, or extinction) then it should be supported by each vertebrate group.

The aim of this paper is to describe patterns of vertebrate endemism using zoogeographic data from amphibians, reptiles, birds, and mammals, and test Humbert's phytogeographic hypothesis.

DESCRIBING PATTERNS OF ENDEMISM

Patterns of endemism are the product of historical events associated with speciation (*e.g.* time, place, and type of speciation event), as well as the responses of species to variable or changing ecological conditions (*e.g.* climatic change, competition). Evidence of highly congruent patterns of endemism between radically different groups implies a common response to historical events. In the case of Madagascar, an island isolated for at least 80 M years (STOREY *et al.*, 1995), it seems probable that many groups must have experienced similar histories, and, therefore, congruent endemism patterns are expected.

Although identifying areas of endemism is widely recognized as critical in all methods of biogeographic analysis (*e.g.* AXELIUS, 1991; HAROLD & MOOI, 1994), few methods of determining patterns of endemism exist. Phenetic clustering methods have been used to analyse species similarity between sites, but this technique is plagued with problems, with different similarity indices and clustering methods producing different dendrograms. More recently, parsimony analysis, developed for phylogenetic studies, has been used to determine hierarchical patterns of endemism. This method, Parsimony Analysis of Endemicity (or Endemism) (PAE), was first described by ROSEN (1988) and ROSEN and SMITH (1988).

PAE resembles cladistic phylogenetic analysis, except that the Operational Taxonomic Units in PAE are geographical areas rather than taxa, and the characters used in PAE are species distributions. The character state for each species distribution is either present or absent. Shared presence of species provides evidence of biogeographic affinity between different sites, and is used to produce a hierarchical pattern of endemism. We use the term « synendemic » to signify the equivalent of synapomorphy, as used in phylogenetic topologies. PAE reversals either represent species that have gone extinct or were missed during surveying. A non-unique synendemic represents a species distribution that is « polyendemic » (equivalent to homoplasy is phylogenetics). Parsimony reveals the best supported pattern of endemism by minimizing the number of « polyendemic » species.

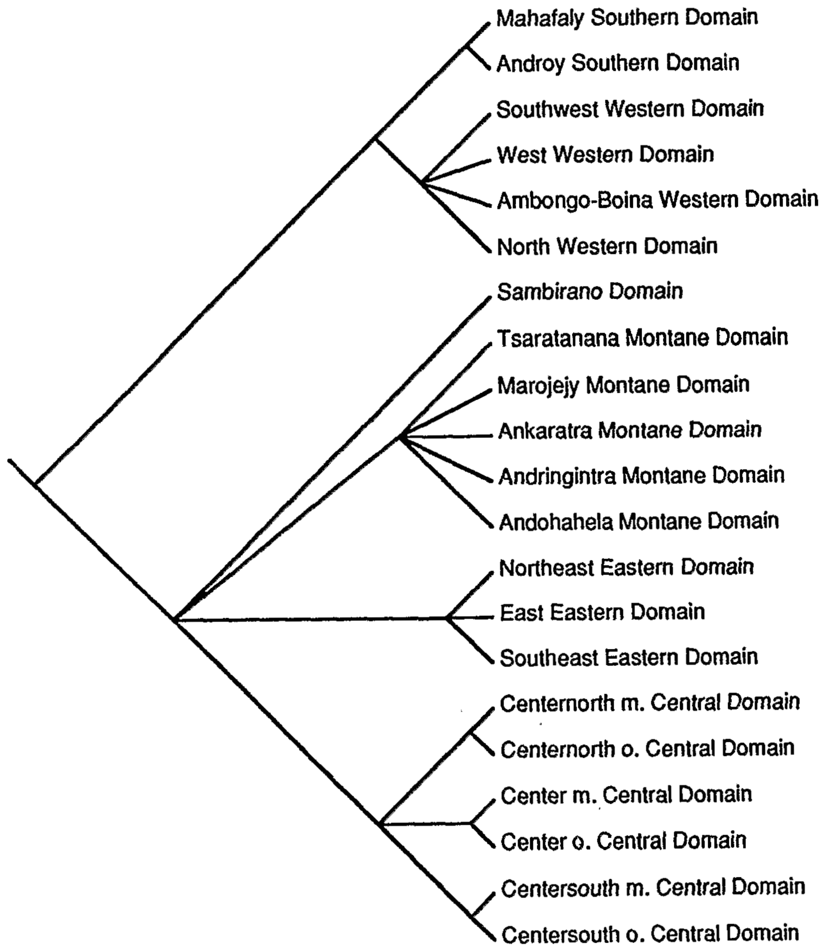

Fig. 1. HUMBERT'S (1955) phytogeographic zones of the Eastern Region of Madagascar.

METHODS

To determine the degree of congruence in patterns of vertebrate endemism, we restricted this analysis to species endemic to the eastern region of Madagascar. We selected this region based on the: 1) high species diversity in all groups; 2) high local endemism, and 3) availability of recent inventory and taxonomic data, collected by ourselves and others. Four vertebrate groups were included: amphibians, reptiles, birds, and non-volant mammals. Distributional data for each vertebrate group was obtained from our own field surveys of amphibians, reptiles, and small mammals at each survey site (see RAXWORTHY & NUSSBAUM, 1994 for survey methods) and the following sources: amphibians and reptiles (GLAW & VENCES, 1994), birds (LANGRAND, 1991; NICOLL & LANGRAND, 1989), and mammals (NICOLL & LANGRAND, 1989; MITTERMEIER *et al.,* 1994; CARLETON, 1994; MACPHEE, 1987; JENKINS, 1992, 1993; JENKINS, GOODMAN & RAXWORTHY, in press).

The twenty-six sites that have been surveyed for each vertebrate group are distributed throughout the complete elevational and latitudinal range found in Eastern

Madagascar (Fig. 2). Site coordinates are given by RAXWORTHY and NUSSBAUM (in press). To control for elevation, sites were limited to the following elevational bands: 1) 0-800 m, 2) 800-1500 m, and 3) above 1500 m (16). The elevational band for each site is indicated by either 1, 2, or 3 after the site name. These survey sites include many of the humid forest reserves in Madagascar, and, based on current deforestation trends (GREEN & SUSSMAN, 1990), are likely to be the main sites where native forest will survive in Eastern Madagascar.

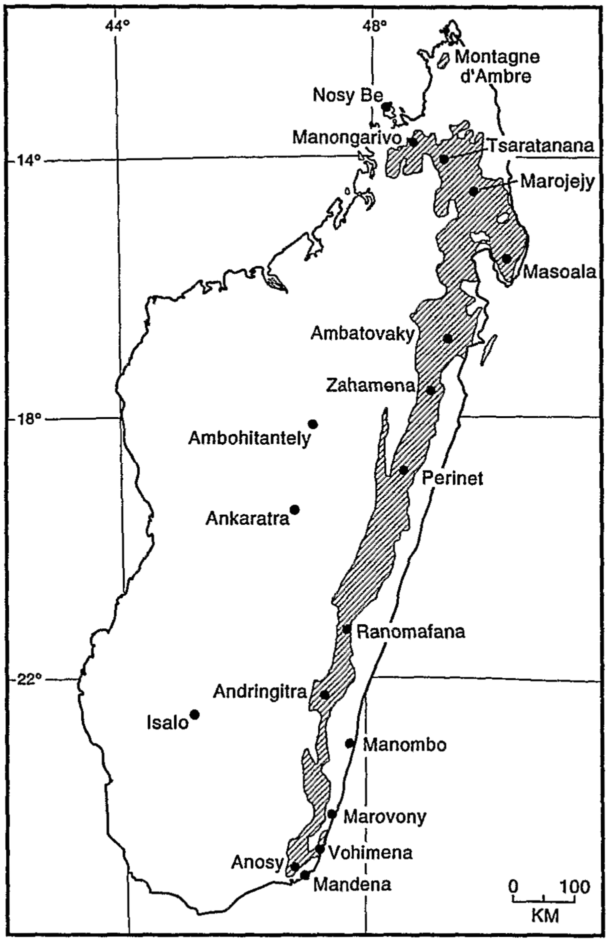

Fig. 2. Sites surveyed in the Eastern Region of Madagascar. The shaded area represents the approximate limit of the eastern rainforest belt.

Parsimony analysis of endemism was done using PAUP (Phylogenetic Analysis Using Parsimony) version 3.1 (SWOFFORD, 1993) using the following options: Character-state optimization=ACCTRAN, search=HEURISTIC, with 10 replications for stepwise addition. Trees were rooted using a hypothetical outgroup area devoid of all species (see ROSEN & SMITH, 1988). No upper limit was imposed on the maximum number of trees saved. All characters were analysed unordered, without differential character weighting.

RESULTS

Table II gives the site species diversity of Eastern Madagascar endemics for each vertebrate group. The data matrix for each group consisted of: 131 species of amphibians (30 uninformative), 152 reptiles (52 uninformative), 38 birds (none uninformative), and 39 non-volant mammals (5 uninformative). Uninformative species are restricted to single sites (site endemic in this analysis) and therefore do not contribute to the PAE pattern. The data matrix used in this analysis is available from the authors.

The PAE strict consensus cladogram for each group is shown in figure 3. The statistics associated with each cladogram are given in Table III. The amphibian cladogram has four major endemic clades: Montane High Plateau, Isalo, Northwest/Tsaratanana/Ambohitantely, and the Eastern Escarpment. The reptile cladogram also has four major endemic clades: Montane High Plateau, Isalo, Northwest, and the Eastern Escarpment. By contrast, the bird and mammal cladograms are poorly resolved, which probably reflects the much lower species diversity in both these groups. Two clades shown in the bird cladogram are Tsaratanana/Andringitra and the Eastern Escarpment. Two major clades found in the mammal cladogram correspond approximately to the northern mid-elevation section of the Eastern Escarpment, and the southern low elevation section of the Eastern Escarpment.

DISCUSSION

CONGRUENCE WITHIN AND BETWEEN GROUPS

The degree of congruence exhibited by the species within the most parsimonious PAE pattern can be represented by the consistency index of FARRIS and KLUGE (1969). The consistency index for each PAE vertebrate pattern is given in Table III, and is similar for each of the four vertebrate groups (between 0.32-0.38, excluding uninformative species), with reptiles and birds being the most consistent, and mammals being the least consistent. These similar degrees of consistency demonstrate that the most parsimonious pattern of endemism is equally well supported by species within each vertebrate group.

There is a strong degree of congruence shown between the amphibian and reptile PAE cladograms. Both vertebrate groups support the recognition of the following four regions of endemism: Ambre/Northwest, Eastern Escarpment, Central High Plateau, and Isalo. The only significant difference concerns the relationship of Tsaratanana and Ambohitantely, which is placed either with the Eastern Escarpment sites (reptiles), or with the Northwest/Ambre sites (amphibians). Because the bird pattern of endemism is poorly resolved, it is largely congruent with the amphibian and reptile patterns. The most significant difference found in the bird endemism pattern is the close relationship between Tsaratanana and Andringitra. The mammal endemism cladogram is poorly resolved, and therefore is also largely congruent with the other patterns of endemism. The mammal data places Tsaratanana with other Eastern Escarpment sites, in agreement with the reptile pattern.

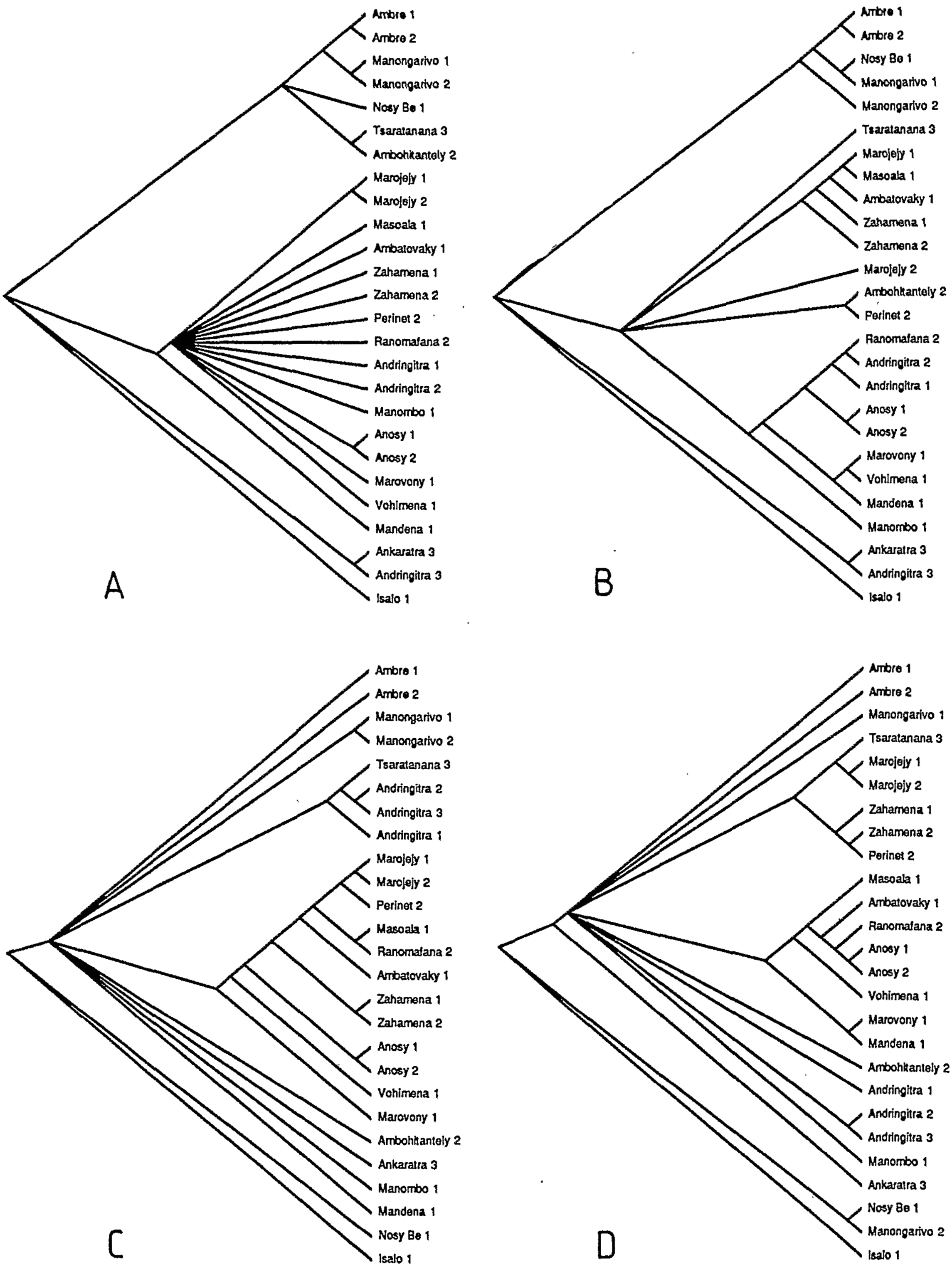

Fig. 3. Strict consensus PAE cladograms for Eastern endemic vertebrates: A) amphibians, B) reptiles, C) birds, and D) mammals.

The degree of congruence exhibited between the four vertebrate groups broadly supports the hypothesis of a common pattern of endemism. The one site that appears to be problematic is Tsaratanana, which shares regionally endemic species with the Northwest, Ambre, the Eastern Escarpment, and Andringitra.

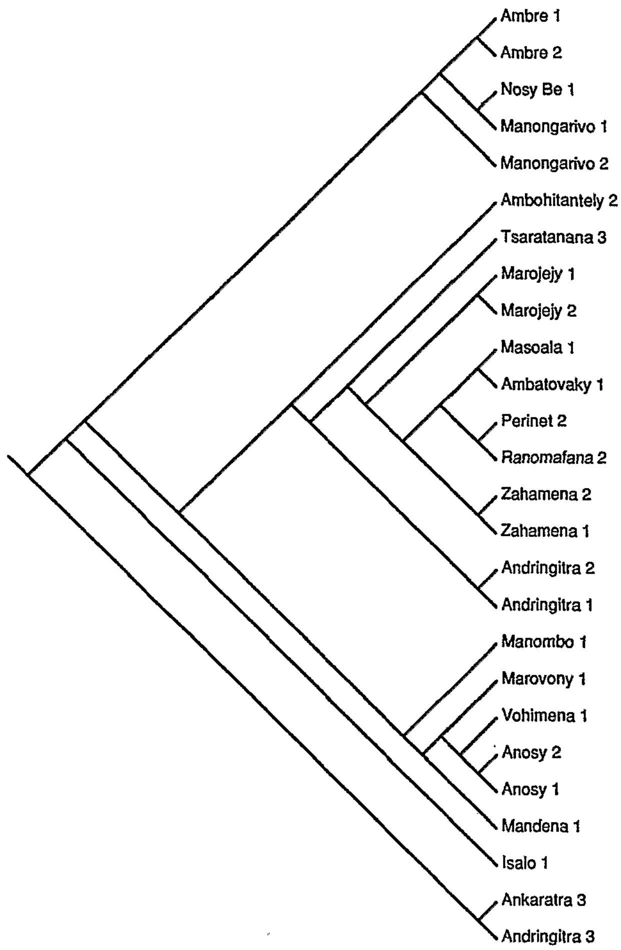

Fig. 4. Most parsimonious PAE cladogram for Eastern endemic amphibians, reptiles, birds, and non-volant mammals.

COMBINED PATTERN OF VERTEBRATE ENDEMISM

The vertebrate data set, when combined together (360 species, 87 species uninformative), gives a completely resolved PAE pattern of endemism (Fig. 4). Four major endemic regions are recognised: Montane High Plateau, Isalo, Northwest/Ambre, and the Eastern Escarpment. Within the Eastern escarpment, two endemic clades are identified: Northeast (between 14-23°S), and Southeast (between 23-25°S). The consistency index (excluding uninformative species) is 0.32 (which is within the range recorded when each vertebrate group was analyzed separately).

In order to compare the overall vertebrate pattern of endemism with each vertebrate group pattern of endemism, we compared the tree length (number of steps) of both patterns using the distributional data for each group separately (Table III). This analysis was performed using MacClade (MADDISON & MADDISON, 1992). The percentage increases in tree length using the overall endemism pattern were: 6% (amphibians), 10% (reptiles), 14% (mammals) and 33% (birds). The bird distribution data most seriously conflicts with the overall pattern of endemism. The most obvious explanation for this type of result centres on the superior dispersal ability of birds, compared to non-volant mammals, reptiles and amphibians.

COMPARISON WITH OTHER PAE PATTERNS

Only one other Madagascan PAE study has been made to date, and is based on reptile distributions (RAXWORTHY & NUSSBAUM, in press). Although this study included additional survey sites (Ankarana, Bekakazo, Ambohijanahary, Mantady, Tolongoina) and reptile species not endemic to Eastern Madagascar, the pattern of endemism is very similar to that described above. The only difference in the regional clades is that Isalo is placed with the Northwest/Ambre/Ankarana clade based on the presence of shared species that are not endemic to Eastern Madagascar. The Consistency Index was 0.33 (excluding uninformative species), which is very similar to that found in this study.

TESTING HUMBERT'S PHYTOGEOGRAPHIC HYPOTHESIS

Figure 5 shows Humbert's phytogeographic classification of the survey sites included in this study (see Fig. 1 and Table I). The tree length for Humbert's hypothesis can be calculated using each of the vertebrate groups separately, and also all groups combined, to test how well each data set supports this hypothesis. Minimum tree lengths were calculated using MacClade, and are given in Table III.

Humbert's phytogeographic hypothesis is not supported by any of the vertebrate data sets. The percentage tree length increase using Humbert's hypothesis (compared to the most parsimonious PAE tree) is 17% (reptiles), 27% (amphibians), 39% (mammals), and 118% (birds). For every vertebrate group, the combined vertebrate PAE pattern of endemism had a shorter tree length (and therefore is better supported) than Humbert's hypothesis (Table III).

For the combined vertebrate data set, the minimum tree length of Humbert's hypothesis (1123 steps) is 21% longer than the PAE pattern (925 steps). The combined vertebrate PAE pattern is a much better supported hypothesis of endemism than Humbert's phytogeographic hypothesis. The major differences shown by the combined PAE pattern compared to Humbert's hypothesis are:

1) Tsaratanana does not show a close affinity to the other two high montane areas, Andringitra and Ankaratra.

2) Ambre and Manongarivo (above 800 m elevation) share many species with Humbert's Sambirano Domain sites (Nosy Be and Manongarivo below 800 m elevation). A close affinity between both Ambre and Manongarivo (above 800 m elevation) and Humbert's Central Domain sites (such as Marojejy, Zahamena, Ambohitantely) is not well supported.

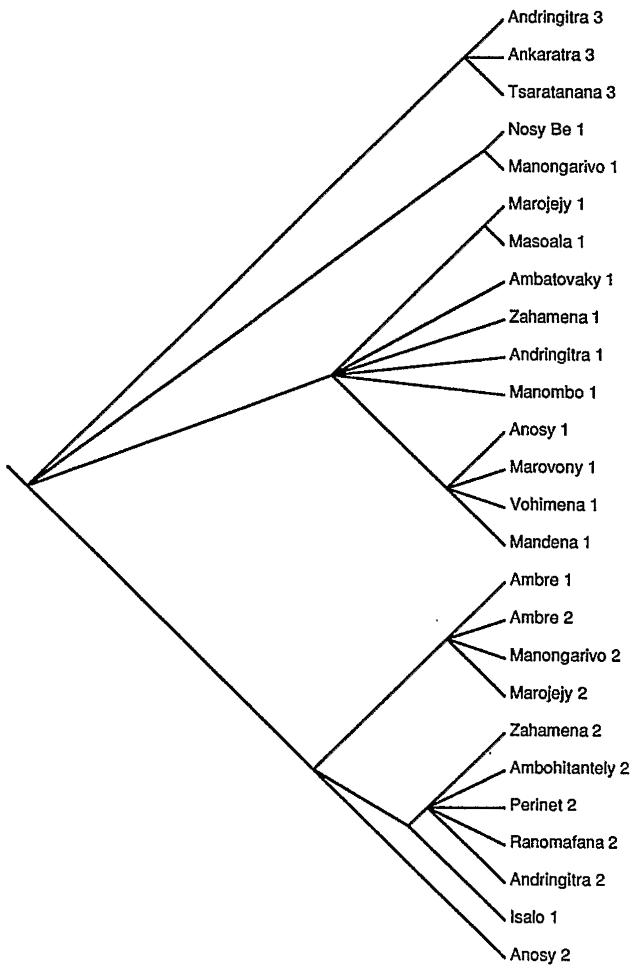

Fig. 5. Cladogram of endemism for the 26 survey sites, based on the hierarchical phytogeographic classification proposed by HUMBERT (1955).

3) Low elevation sites (below 800 m) in the Eastern Domain do not all group together. The Central Domain mid-elevation sites (800-1500 m) also do not group together. Thus, Humbert's division of the eastern escarpment rainforest into two domains, above and below 800 m, is not supported. Instead, two major clades distinguished largely by latitude are identified from the PAE results. The northern clade includes all sites between Tsaratanana and Andringitra. The southern clade includes all sites between Manombo and Mandena. This result demonstrates that latitude-based biogeographic divisions of the eastern escarpment rainforest are more important than divisions based on elevation.

4) Isalo does not group with other Central Domain sites such as Ranomafana or Andringitra.

CONCLUSIONS

Vertebrate patterns of endemism are not congruent with Humbert's phytogeographic hypothesis in Eastern Madagascar. This means either plant and vertebrate distributions are incongruent, or that Humbert's hypothesis does not accurately reflect patterns of plant endemism. The only way to address this issue will be by analyzing plant and animal distribution data together. However, Humbert's phytogeographic hypothesis can no longer be assumed as an adequate zoogeographic model. It is far more appropriate that faunal distribution patterns are analyzed independently, rather than being used to modify Humbert's hypothesis.

Patterns of endemism in amphibians, reptiles, birds, and mammals appear to be largely congruent in Eastern Madagascar, but obvious differences also exist, especially in the case of Tsaratanana. Although it is unlikely that perfect congruence will ever be found in distribution patterns for different groups, it may still be appropriate to describe a 'best-fit' pattern of regional endemism that can be used in conservation planning.

In other regions of the world, areas with high local endemism are now being ranked as sites of high conservation priority, based on the substantial evidence that recent global patterns of extinction are dominated by regions rich in endemic species (MYERS, 1988, 1990; PIMM, *et al.*, 1995). Until our understanding of patterns of endemism is complete, we will be unable to determine which species are most vulnerable to extinction in Madagascar.

ACKNOWLEDGEMENTS

This research was made possible with the help of Jean-Baptiste Ramanamanjato, Achille Raselimanana, Angelin and Angeluc Razafimanantsoa, and the cooperation of the Ministère de l'Enseignement Supérieur, the Ministère de la Production Animale et des Eaux et Forêts and the Ministère de la Recherche Scientifique et Technologie pour le Developpement. This research was funded in part by grants from the National Science Foundation (DEB 90 24505 and 93 22600), the National Geographic Society (5396-94), and Earthwatch. Logistic support was provided by World Wide Fund for Nature, Conservation International, and CARE.

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Table I.- Distribution of survey sites within Humbert's (1955) phytogeographic divisions. Survey sites numbers are: 1 = Montagne d'Ambre 1, 2 = Montagne d'Ambre 2, 3 = Nosy Be 1, 4 = Manongarivo 1, 5 = Manongarivo 2, 6 = Tsaratanana 3, 7 = Marojejy 1, 8 = Marojejy 2, 9 = Masoala 1, 10 = Ambatovaky 1, 11 = Zahamena 1, 12 = Zahamena 2, 13 = Ambohitantely 2, 14 = Périnet 2, 15 = Ankaratra 3, 16 = Ranomafana 2, 17 = Andringitra 1, 18 = Andringitra 2, 19 = Andringitra 3, 20 = Isalo 1, 21 = Manombo 1; 22 = Marovony 1, 23 = Vohimena 1, 24 = Anosy 1, 25 = Anosy 2, 26 = Mandena 1. Elevation bands for each site indicated by: 1 (below 800 m), 2 (800-1500 m), or 3 (above 1500 m).

Region	Domain	Sub-domain	Sector	Survey Site
Eastern	Sambirano	Sambirano	Sambirano	3, 4
	Montane	Montane	Tsaratanana	6
			Marojejy	
			Ankaratra	15
			Andringitra	19
			Andohahela	
	Central	Centernorth	Montane	1, 2, 5, 8
			Occidental	
		Center	Montane	12, 13, 14, 16, 18
			Occidental	20
		Centersouth	Montane	25
			Occidental	
	Eastern	Eastern	Northeast	7, 9
			East	10, 11, 17, 21
			Southeast	22, 23, 24, 26
Western	Western	Western	North	
			Ambongo-Boina	
			West	
			Southwest	
	Southern	Southern	Mahafaly	
			Androy	

Table. II. Site diversity of vertebrate spécies endemic to Eastern Madagascar.

	Eastern endemic species diversity				
Site	Amphibians	Reptiles	Birds	Mammals	Total
Ambre 1	25	23	7	7	62
Ambre 2	18	22	7	5	52
Nosy Be 1	10	26	0	2	38
Manongarivo 1	20	24	4	7	55
Manongarivo 2	14	9	4	4	31
Tsaratanana 3	22	13	15	7	57
Marojejy 1	40	41	30	12	123
Marojejy 2	41	8	32	10	91
Masoala 1	28	28	20	13	89
Ambatovaky 1	37	30	18	13	98
Zahamena 1	31	29	31	25	116
Zahamena 2	36	21	19	15	91
Ambohitantely 2	17	19	4	7	47
Perinet 2	63	30	32	18	143
Ankaratra 3	13	9	4	4	30
Ranomafana 2	35	22	23	11	91
Andringitra 1	30	15	9	2	56
Andringitra 2	32	21	11	19	83
Andringitra 3	16	8	9	8	41
Manombo 1	18	12	4	3	37
Isalo 1	7	1	0	0	8
Anosy 1	34	21	21	13	89
Anosy 2	35	21	21	14	91
Vohimena 1	21	21	11	7	60
Marovony 1	19	20	11	4	54
Mandena 1	13	18	3	4	38

Table. III. Statistics for Parsimony Analysis of Endemism (PAE) in Eastern Madagascar.

Character	Vertebrate Data Set Amphibians	Reptiles	Birds	Mammals	All Combined
Number of species	131	152	38	39	360
Number of informative species	101	100	38	34	273
Number of unique synendemics	25	33	12	4	74
Number of most parsimonious trees	32	14	14	28	1
Consistency Index	0.41	0.49	0.38	0.36	0.38
Consistency Index (excluding uninformative species)	0.35	0.38	0.38	0.32	0.32
Homoplasy Index	0.59	0.51	0.62	0.68	0.68
Retention Index	0.57	0.55	0.77	0.59	0.53
Number of steps in most parsimonious tree	315	304	100	110	925
Number of steps in combined taxa PAE tree[1]	333	334	133	125	925
Minimum number of steps in Humbert's hypothesis[2]	399	353	218	153	1123

1) Fig. 4; 2) Fig. 5.