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COMPOSITION AND CHARACTERISTICS OF BIRD COMMUNITIES IN MADAGASCAR

Lucienne WILME

Missouri Botanical Garden - Madagascar Research and Conservation Program, BP 3391, Antananarivo 101, MADAGASCAR

ABSTRACT.- Current knowledge of the taxonomic and geographic composition of Madagascar's resident avifauna is reviewed, with particular emphasis on forest birds. Distribution patterns in the avifauna do not match those of the botanical communities, and especially the domains of floristic endemism in the Eastern Region. The tolerance of the endemic forest avifauna to habitat degradation is proportional to its degree of taxonomic endemism. The 21 species belonging to the two endemic families and the two endemic subfamilies are clearly the most sensitive to forest degradation. The members of these higher taxonomic groups could serve as useful biological indicators of Madagascar's forest habitats.

KEY WORDS.- Madagascar, Birds, Endemism, Ecological niche, Biological indicator

RÉSUMÉ.- Ce travail présente un résumé de la connaissance actuelle de la composition taxinomique et géographique de l'avifaune résidente de Madagascar et plus particulièrement de l'avifaune forestière. Les schémas de distribution de l'avifaune ne se superposent pas à ceux des communautés botaniques et notamment en matière de description des domaines d'endémisme floristiques de la Région Est de Madagascar. En considérant l'avifaune endémique forestière de Madagascar, la tolérance à la dégradation des forêts est proportionnelle au degré d'endémisme taxinomique, et il apparaît que les 21 espèces appartenant aux deux familles et deux sous-familles endémiques à Madagascar sont certainement les plus sensibles à la dégradation des forêts. L'ensemble des éléments appartenant à ces taxons supérieurs devraient constituer les indicateurs biologiques des milieux forestiers de Madagascar.

MOTS-CLES.- Madagascar, Oiseaux, Endémisme, Niche écologique, Indicateur biologique

INTRODUCTION

On the basis of floristic and ecological data, Madagascar can be divided into two major phytogeographic regions, the East Malagasy Region and the West Malagasy Region (HUMBERT, 1955). According to WHITE (1983), the East Malagasy Region is divided into four domains: Eastern (escarpment and coastal zone), Central (eastern part of central highlands), High Mountain, and Sambirano; and the West Malagasy Region into the Western and Southern Domains (Table I, Fig. 1). Details on sites within the existing protected areas system and those of biological interest are reviewed in NICOLL and LANGRAND (1989).

A total of 204 breeding species of birds are recognized in Madagascar. This includes the 201 species listed in LANGRAND (1990), minus the Snail-eating Coua *Coua*

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delalandei, now regarded as an extinct species (GOODMAN, 1993a), plus four new additions to the list: the Common Quail *Coturnix coturnix* and the Harlequin Quail *Coturnix delegorguei* now considered as nesting species (LANGRAND & APPERT, in press.), a new Sylviidae being described (GOODMAN *et al.*, in press.), and *Nesillas typica lantzii*, which is being elevated to the rank of species (SCHULENBERG *et al.*, 1993). Three of these 204 species have been introduced to the island: Common Myna *Acridotheres tristis* (at the end of last century), Common Waxbill *Estrilda astrild* in 1983, and House Sparrow *Passer domesticus* in 1984 (LANGRAND, 1990). A total of 106 (53%) of the 201 non-introduced species are endemic to Madagascar and another 25 species (just over 12%) have a distribution limited to a wider region including Madagascar and the neighboring islands (Comoros, Mascarenes, and the Seychelles) (LANGRAND, 1990).

In view of the declining forests of Madagascar (JENKINS, 1987; GREEN & SUSSMAN, 1990; NELSON & HORNING, 1993a, 1993b) an understanding of the resident avifauna's geographic distribution, niche occupancy and tolerance to habitat disturbance might help to identify conservation priorities and to predict responses of the avifauna to human disturbance. The high degree of endemism among this rather mobile group of animals not only justifies special attention in terms of conservation efforts, but also offers an ideal set of species to test models in community ecology.

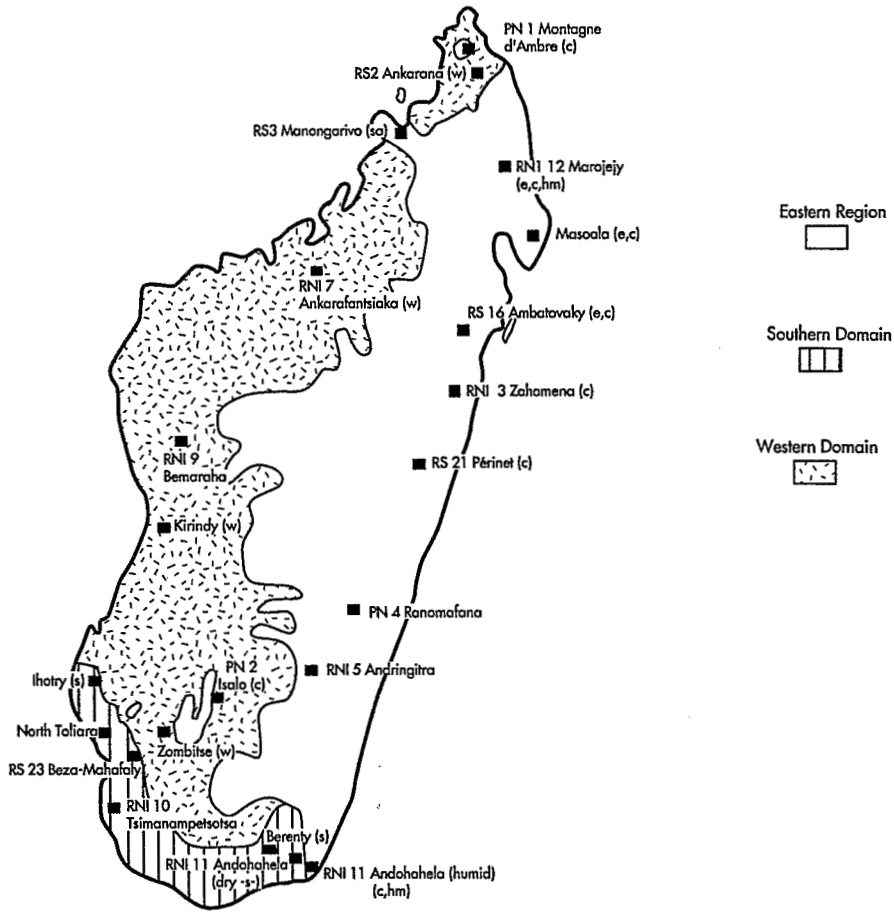

Fig. 1. Location of study sites within phytogeographic divisions; Eastern Region; Southern Domain; Western Domain; Abbreviation as in Table II.

TAXONOMIC AND GEOGRAPHIC DISTRIBUTION

Of the 201 non-introduced breeding species 66 are Passeriformes, which are under-represented outside forest habitats. Within forests they comprise a high percentage (90.5%) of the endemic passerine species in Madagascar (Fig. 2). Within each of Madagascar's regions and domains breeding species are mainly found in forest habitats emphasizing the predominant role of this type of habitat for the Malagasy avifauna. This role is highlighted by the fact that 85 (80%) of all endemic species rely on forest habitats. Considering only the 114 forest birds species, this means that three out of four species in Malagasy forests are endemic (Fig. 2). For this reason, the present analysis is restricted to species occuring in natural forests, though other habitats certainly also deserve special attention (LANGRAND & WILME, 1993).

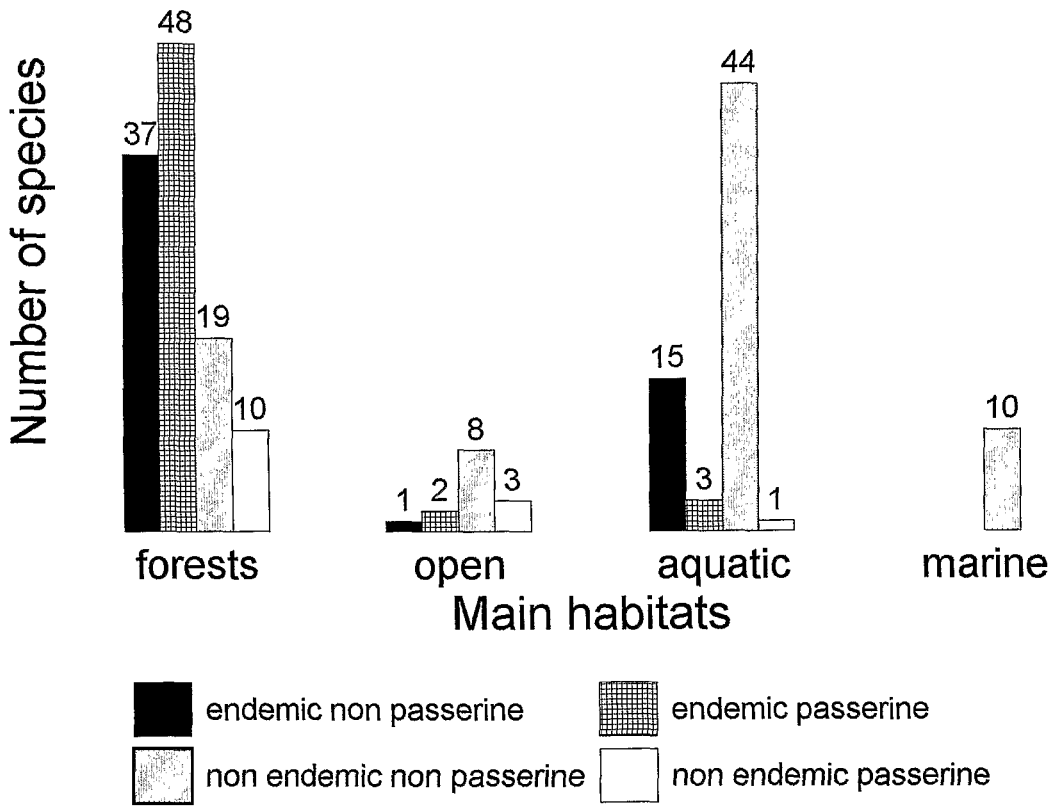

Fig. 2. Composition of Madagascar nesting bird species according to main habitat (numbers are total number of species per habitat).

The classification summarized in Table II shows the distribution of forest birds according to the phytogeographic regions and domains. The Eastern Region as a whole contains more species and more regional endemism than the Western Region; 99 species, with 36 endemic in the East, versus 77 and 15 regional endemics in the West. This pattern holds for all forest bird taxa, but is more marked for passerines. Neither the

Eastern, Sambirano, nor High Mountains Domains hold any local endemics. Only the Central Domain contains local endemics (five species). In contrast both domains of the Western Region have local endemic species (two in the Western Domain and nine in the Southern Domain).

To understand similarities in species composition and assess species turnover, Jaccard's index was calculated separately for endemic, non-endemic, non-passerine and passerine species for each of the 22 sites studied (Table III). This index for comparison between two sites is calculated as

$$JI = \frac{N_C}{N_A + N_B - N_C}$$

where N_C is the number of species common at both sites; and N_A and N_B are the numbers of species present at site A and site B respectively (MUELLER-DOMBOIS & ELLENBERG, 1974). The sites used in this calculation are shown in Figure 1 along with the domain in which they occur. Species lists are based on at least 30 days of intensive surveys per site.

Cluster analysis with Jaccard's indices of similarity between sites does not produce geographically distinct clusters when applied to non-endemic species. This means that among non-endemic birds, there is no distinct set of species inhabiting dry forests versus those predominantly in wet forest areas. Non-endemic species have broad distributions and low turnover rates, indicating more generalized habit requirements.

Applying cluster analysis to similarity indices of Madagascar endemic species reveals three distinct clusters. The geographic extent and characteristics of species similarities within and between these clusters are shown in figure 3.

The endemic avifauna differs little between sites of the eastern rainforest. The humid forest parcel of Andohahela (Parcel 1) in the extreme south holds the same island endemic bird species as Marojejy in the northeast. This homogeneity in species composition ends abruptly along the western watershed of Andohahela. Here species turnover is almost complete between the humid Eastern Region and the dry Southern Domain, which is itself homogeneous in terms of endemic species in general and passerines in particular (two non-passerines species have a limited range in the Southern Domain, *Monias benschii*, *Uratelornis chimaera*, and *Coua verreauxi* does not occur in the eastern part of the Domain). The avifauna of Isalo, with its locally endemic passerine (*Pseudocossyphus bensoni*) is more closely related to that of the south and the west than to that of the Central Domain, contrary to expectations on phytogeographic grounds.

The species assemblage, especially for passerines, changes between sites of the Southern Domain and the Western Domain, as represented by Zombitse, Kirindy, Bemaraha, Ankarafantsika and Ankarana. Montagne d'Ambre and Manongarivo do not cluster with the other sites: Montagne d'Ambre is an isolated island of rainforest within the Western Domain and its avifauna is depauperate; Manongarivo belongs to the Sambirano Domain and its bird composition shows affinities with both eastern and western sites. Here we find eastern species such as *Coua caerulea*, *C. serriana* and *Phyllastrephus zosterops* together with western species such as *Falculea palliata* and *Philepitta schlegeli*. Even though the species list for Manongarivo is not complete, the site's geographic position seems to overide phytogeographic effects.

DISTRIBUTION ACCORDING TO NICHES

Species were assigned to niches according to their main food items, and their feeding and nesting habits (Table II). On the basis of these niche variables, the 114 forest bird species are distributed among 28 different niches. To facilitate comparisons, each of the 28 niches was assigned to one of the 16 categories listed in Table IV. The absolute numbers of birds species increase with increasing structural and floristic diversity of the forest, from the drier western forests to the wet forests of the center and east. However the number of guilds and the relative number of species in each guild remain similar in both phytogeographic regions. Insectivores, followed by small predators, are the dominant groups throughout the island. The main difference between the Eastern and the Western Region is the higher representation of insectivores in the east. Whereas the east holds 39 of the 45 strictly insectivorous forest species, the west contains only 23 of 45. Though forest structure is correlated with bird species diversity, it alone is insufficient to explain the greater species richness in the east, which is mainly due to an increase in arboreal species. This is exemplified by the higher number of strictly arboreal insectivorous species in the Central Domain with a forest height of up to 25 m, compared to the lower number of species in this guild in forests of approximately the same height in the Eastern Domain and the Sambirano.

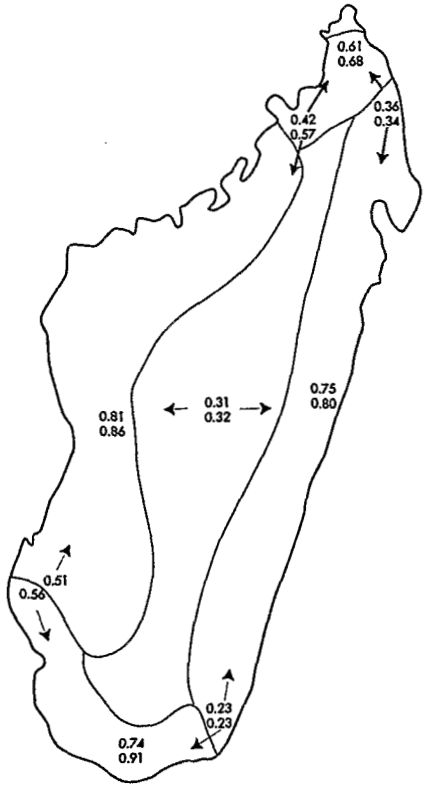

Fig. 3. Species similarities within and between separate units of the endemic avifauna as identified by cluster analysis. Values are means of Jaccard's indices. The upper and lower value of each pair of numbers refer to endemic non passerine and endemic passerine respectively.

Within the Eastern Region, the Eastern Domain is somewhat depauperate in insectivores (Table IV). Seven of the 10 species common to the Eastern region, but not present in the Eastern Domain itself, are insectivores. The Sambirano links and combines niche elements belonging to the Eastern or to the Western Region. Both the High Mountain Domain and the Sambirano hold a reduced set of species that are widespread across the island, and contain no local endemic bird species. Among the forest bird species, taxonomical endemism at the species level is particularly high in the guild of exclusively arboreal insectivorous passerines. The geographic distribution of these groups of endemic species is uneven. Whereas insectivores (such as the genus *Phyllastrephus*) and predators reached higher species numbers in the east, omnivores and « vegetarian » species have about the same number of species in the east and in the west, respectively 16 (16%) and 10 (10%) for the east, and 15 (19%) and 10 (13%) for the west. This difference might be linked to the pronounced dry season of the west, favoring species which are able to feed on a greater variety of food items.

TOLERANCE TO FOREST DISTURBANCE

Four categories are recognized to describe the quality of forest habitats: undisturbed forest, slightly disturbed forest, secondary growth and anthropogenic wooded grassland. Forest species are defined as those occurring in undisturbed forest, although they may also exist in other forest types (Table II). Out of the 114 species occurring in undisturbed forest, 22 (19%) rely exclusively on this habitat, whereas 38 species (33%) also occur in slightly disturbed forest, and another 54 (47%) also occur in secondary growth or anthropogenic grassland.

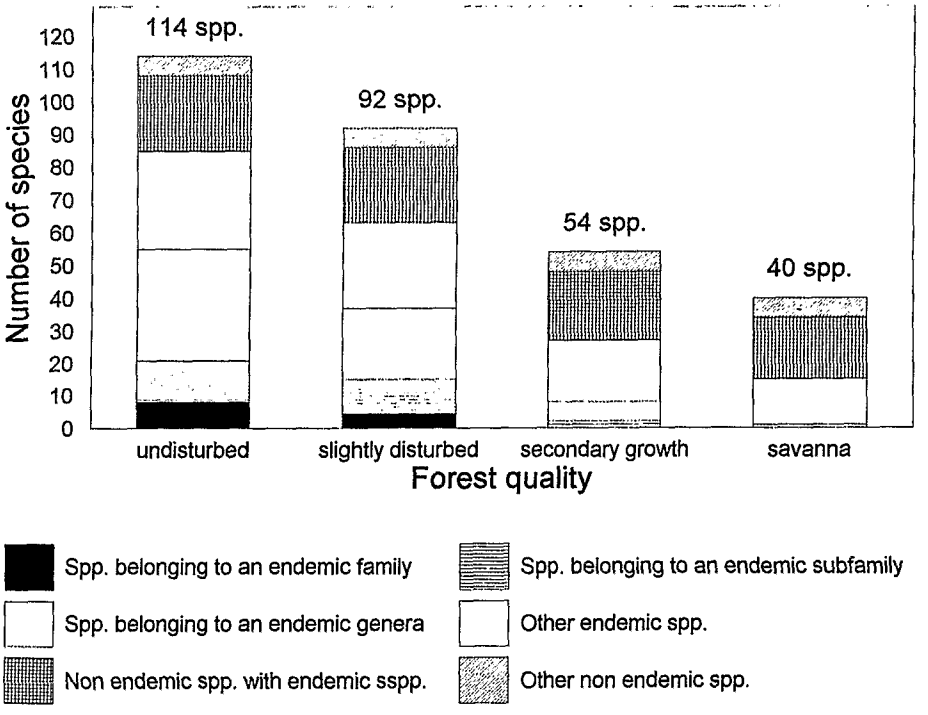

Figure 4. Taxonomic level of endemism and tolerance to forest disturbance of Madagascar forest bird species (numbers are total number of species per forest habitat).

Members of Madagascar's endemic bird families and subfamilies are not tolerant of forest disturbance. Of the 32 endemic forest genera, 27 do not occur in secondary growth or anthropogenic grassland. Only eight species (out of 55), belonging to 5 endemic genera occur in secondary habitats. At the sub-family level, only two species of *Coua* are tolerant of some forest disturbance. The eight species belonging to the two endemic families occur only in undisturbed and slightly disturbed forest (Table V, Fig. 4). Studied forests that are not isolated, that cover at least several hundred km^2, with altitudes starting at least at 800 meters above sea level hold at least 60% of the species in endemic genera within their respective phytogeographic region.

The information at hand is not sufficient to reveal causal factors in the patterns of species distributions across Madagascar. Current fragmentation and previous corridors between the east and the west (*e.g.* Sambirano) confound the analysis with cases such as the presence of an « eastern » rainforest species of rail (*Canirallus kioloides*) in the deciduous dry forests of Bemaraha or the western species of mesite (*Mesitornis variegata*) in Ambatovaky rainforest in the east. The Malagasy avifauna does not reflect the phytogeographic patterns seen among the botanical communities, especially in the Eastern Region.

CONCLUSION

Despite some uncertainties and ambiguities, the present analysis of the Malagasy avifauna re-emphasizes the pending threat to the island's higher endemic bird taxa, especially the endemic families and sub-families. Species belonging to endemic families (Mesitornithidae, Brachypteraciidae) already have a patchy distribution, and the modern distribution of three of eight species in these families (*Monias benschi*, *Mesitornis variegata*, *Uratelornis chimaera*) is highly restricted. The endemic sub-families (Couinae, Phillepittinae) are widespread, although the latter is relatively sensitive to forest disturbance and fragmentation. The Couinae contain a single genus (*Coua*) with nine extant species that are broadly distributed in different types of forest; they feed on a variety of food and occupy different forest strata. But the largest species within this sub-family (*Coua delalandei*, *Coua primavea* and *Coua berthae*) are all extinct (GOODMAN, 1993a, 1993b). Undisturbed forests with an area of several thousand ha hold at least three species of *Coua* belonging to at least two different ecological niches. The distribution pattern of the remaining species is not simple; for example the southern endemic *Coua verreauxi* has a narrow distribution, while the eastern species *C. serriana* and eastern subspecies of *C. cristata* are more common at lower elevation (below 500 m). These higher endemic taxa, with eight genera, 21 species, and six sub-species, may serve as biological indicators or key elements to define conservation priorities. The ecological niches utilized by these two families and two subfamilies include insectivores, omnivores, vegetarians and small predators as well as terrestrial, arboreal, and terrestrial/arboreal species when considering feeding and nesting habits. Using these species and subspecies for conservation purposes may provide a useful predictive indicator of forest conditions and thus offers a tool for improved management and preservation of Malagasy natural forest ecosystems.

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Table II. Distribution of forest birds according to phytogeographic regions and domains and their ecological niches. Distribution: 1 = species present; W: Western Region, subdivided in Western (w) and Southern (s) Domains; E: Eastern Region, subdivided in Easte (e), Central (c), Sambirano (sa), and High Mountains (hm) Domains. Level of endemism, geographic: Mad. = Madagascar, s, w, W, c, E as before. Tolerance = Tolerance to forest degradation: 0 = Undisturbed forest; 1 = slightly disturbed forest; 2 = secondary growth; 3 = savanna. Ecological niches: Food: gastropods (G), insects (I), vertebrates (V), nectar, fruit and/or seeds (vegetarian) (Veg); Feeding habit: arboreal (Ar), terrestrial (T), aerial (Ae), raptor (R); Nest: arboreal (Ar), terrestrial, holes on ground or in cliffs (T), parasitic (P).

	Distribution:								level of endemism			Ecological niche:		
	w	s	W	e	c	sa	hm	E	geographic	taxonomic	Tole-rance	Food	Feeding habit	Nest
NON-PASSERINE SPECIES														
Lophotibis cristata	1	1	1	1	1	1	1	1	Mad.	genera	2	I G V	T	Ar
Aviceda madagascariensis	1	1	1	1	1			1	Mad.	species	3	I V	R	Ar
Machaeramphus alcinus	1		1	1	1			1		subspecies	3	I V	R	Ar
Eutriorchis astur				1	1			1	E	genera	0	V	R	Ar
Polyboroides radiatus	1	1	1	1	1	1	1	1	Mad.	species	2	V	R	Ar
Accipiter henstii	1		1	1	1			1	Mad.	species	2	V	R	Ar
Accipiter madagascariensis	1	1	1	1	1	1		1	Mad.	species	3	I V	R	Ar
Accipiter francesii	1	1	1	1	1	1	1	1			3	I V	R	Ar
Buteo brachypterus	1	1	1	1	1	1	1	1	Mad.	species	3	V	R	Ar
Falco zoniventris	1	1	1	1	1	1		1	Mad.	species	3	I V	R	Ar
Falco peregrinus	1	1	1	1	1		1	1			3	V	R	F
Numida meleagris	1	1	1	1	1	1		1			3	Veg	T	T
Mesitornis variegata	1		1	1				1	Mad.	family	0	I Veg	T	Ar
Mesitornis unicolor				1	1			1	E	family	0	I Veg	T	Ar
Monias benschi		1	1						s	family	0	I Veg	T	Ar
Turnix nigricollis	1	1	1	1	1			1	Mad.	species	3	I Veg	T	T
Canirallus kioloides	1		1	1	1	1		1	Mad.	species	1	I	T	Ar
Sarothrura insularis				1	1		1	1	E	species	3	I Veg	T	T
Pterocles personatus	1	1	1						W	species	3	Veg	T	T
Streptopelia picturata	1	1	1	1	1	1		1		subspecies	3	Veg	T	Ar
Treron australis	1	1	1	1	1	1		1		subspecies	3	Veg	Ar	Ar
Alectroenas madagascariensis				1	1	1	1	1	E		2	Veg	Ar	Ar
Coracopsis vasa	1	1	1	1	1	1		1		subspecies	3	Veg	Ar	Ar
Coracopsis nigra	1	1	1	1	1	1	1	1		subspecies	3	Veg	Ar	Ar
Agapornis cana	1	1	1	1	1	1		1	Mad.	species	3	Veg	Ar	Ar
Cuculus audeberti				1	1			1		subspecies	1	I	Ar	P
Cuculus rochii	1	1	1	1	1	1		1	Mad.	species	3	I	Ar	P
Coua gigas	1	1	1						W	subfamily	1	I Veg	T	Ar
Coua coquereli	1		1			1		1	Mad.	subfamily	1	I Veg	T	Ar
Coua serriana				1	1	1		1	E	subfamily	1	I Veg	T	Ar
Coua reynaudii				1	1	1	1	1	E	subfamily	1	I Veg	T	Ar
Coua cursor		1	1						s	subfamily	1	I	T	Ar
Coua ruficeps	1	1	1						W	subfamily	1	I Veg	T	Ar
Coua cristata	1	1	1	1	1	1		1	Mad.	subfamily	2	I Veg G V	Ar	Ar
Coua verreauxi		1	1						s	subfamily	1	I Veg	Ar	Ar
Coua caerulea	1		1	1	1	1	1	1	Mad.	subfamily	2	I Veg V	Ar	Ar
Centropus toulou	1	1	1	1	1	1		1		subspecies	3	I V	Ar	Ar
Tyto soumagnei				1	1			1	E	species	0	V	R	Ar
Otus rutilus	1	1	1	1	1	1		1		subspecies	3	I	R	Ar
Ninox superciliaris	1	1	1	1	1			1	Mad.	species	2	I	R	T
Asio madagascariensis	1	1	1	1	1	1		1	Mad.	species	3	V	R	Ar
Caprimulgus madagascariensis	1	1	1	1	1	1		1		subspecies	3	I	Ar	T
Caprimulgus enarratus	1		1	1	1			1	Mad.	species	1	I	Ar	T
Zoonavena grandidieri	1	1	1	1	1	1		1		subspecies	1	I	Ae	Ar

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Table I. Biogeographic regions and domains in Madagascar

Regions and Domains	Elevation	Rainfall	Dry season	Character	Species diversity	endemism	canopy
Eastern Malagasy Region							
Eastern Domain	0-800m	> 2000 mm	no	evergreen	very high	high	25-30 m
Central Domain	800-1300m	> 1500 mm	no	evergreen	high	high	20-25 m
	1300-2000 m						10-12 m
High Mountain Domain	> 2000m	substantial	no	evergreen	low	very high	6 m
Sambirano Domain	0-1876m	> 2000 mm	no	evergreen	high	high	25-30 m
Western Malagasy Region							
Western Domain	0-800m	500-2000 mm	< 7 months	deciduous	medium	very high	12-15 m
Southern Domain	0-400m	350-750 mm	7 months	deciduous	medium	very high	3-6 m

adapted from Phillipson (1994)

	Distribution:								level of endemism			Ecological niche:		
	w	s	W	e	c	sa	hm	E	geographic	taxonomic	Tole-rance	Food	Feeding habit	Nest
Apus melba	1	1	1	1	1	1	1	1		subspecies	3	I	Ae	C
Apus barbatus	1	1	1	1	1	1	1	1		subspecies	3	I	Ae	C
Ispidina madagascariensis	1	1	1	1	1	1		1	Mad.	species	1	I V	Ar	T
Merops superciliosus	1	1	1	1	1	1		1			3	I	Ae	T
Eurystomus glaucurus	1	1	1	1	1	1		1		subspecies	3	I	Ae	Ar
Brachypteracias leptosomus				1	1			1	E	family	1	I G V	T	T
Brachypteracias squamiger				1	1			1	E	family	1	I G V	T	T
Atelornis pittoides				1	1	1	1	1	E	family	1	I V	T	T
Atelornis crossleyi				1	1			1	E	family	0	I	T	T
Uratelornis chimaera		1	1						s	family	1	I	T	T
Leptosomus discolor	1	1	1	1	1	1		1			3	I V	Ar	Ar
Upupa epops	1	1	1		1	1		1			3	I	T	Ar
PASSERINE SPECIES										subspecies				
Philepitta castanea				1	1	1	1	1	E	subfamily	1	Veg	Ar	Ar
Philepitta schlegeli	1		1			1		1	Mad.	subfamily	1	Veg	Ar	Ar
Neodrepanis coruscans				1	1		1	1	E	subfamily	0	I	Ar	Ar
Neodrepanis hypoxantha					1		1	1	E	subfamily	0	I	Ar	Ar
Phedina borbonica	1	1	1	1	1	1	1	1		subspecies	3	I	Ae	C
Coracina cinerea	1	1	1	1	1	1	1	1		subspecies	2	I	Ar	Ar
Phyllastrephus madagascariensis	1	1	1	1	1	1		1	Mad.	species	1	I	Ar	Ar
Phyllastrephus zosterops				1	1	1		1	E	species	1	I	Ar	Ar
Phyllastrephus apperti	1		1						w	species	0	I	Ar	Ar
Phyllastrephus tenebrosus				1	1			1	E	species	0	I	Ar	Ar
Phyllatrephus cinereiceps					1			1	c	species	0	I	Ar	Ar
Hypsipetes madagascariensis	1	1	1	1	1	1	1	1		subspecies	3	I Veg	Ar	Ar
Copsychus albospecularis	1	1	1	1	1	1		1	Mad.	species	2	I	Ar	Ar
Pseudocossyphus sharpei				1	1		1	1	E	genera	1	I Veg	Ar	Ar
Pseudocossyphus imerinus		1	1						s	genera	1	Veg	Ar	Ar
Pseudocossyphus bensoni					1			1	c	genera	2	I Veg	Ar	Ar
Nesillas typica	1	1	1	1	1	1	1	1		subspecies	3	I	Ar	Ar
Nesillas lantzii		1	1						s	species	3	I	Ar	Ar
Thamnornis chloropetoides		1	1						s	genera	1	I	Ar	Ar
Dromaeocercus brunneus					1			1	c	genera	0	I	Ar	Ar
Randia pseudozosterops				1	1			1	E	genera	1	I	Ar	Ar
Sp. nov.				1	1			1	E	genera	1	I	Ar	Ar
Newtonia amphichroa				1	1			1	E	genera	0	I	Ar	Ar
Newtonia brunneicauda	1	1	1	1	1	1	1	1	Mad.	genera	1	I	Ar	Ar
Newtonia archboldi		1	1						s	genera	1	I	Ar	Ar
Newtonia fanovanae				1	1			1	E	genera	0	I	Ar	Ar
Neomixis tenella	1	1	1	1	1	1		1	Mad.	genera	3	I	Ar	Ar
Neomixis viridis				1	1		1	1	E	genera	0	I	Ar	Ar
Neomixis striatigula	1	1	1	1	1	1		1	Mad.	genera	1	I	Ar	Ar
Hartertula flavoviridis					1			1	c	genera	0	I	Ar	Ar
Pseudobias wardi				1	1		1	1	E	genera	0	I	Ar	Ar
Terpsiphone mutata	1	1	1	1	1	1	1	1		subspecies	3	I	Ar	Ar
Oxylabes madagascariensis				1	1			1	E	genera	1	I	Ar	Ar
Crossleyia xanthophrys					1			1	c	genera	1	I	T	T
Mystacornis crossleyi				1	1			1	E	genera	1	I	T	Ar
Nectarinia souimanga	1	1	1	1	1	1	1	1		subspecies	3	I Veg	Ar	Ar
Nectarinia notata	1	1	1	1	1	1	1	1		subspecies	3	I Veg	Ar	Ar
Zosterops maderaspatana	1	1	1	1	1	1	1	1			3	I Veg	Ar	Ar
Calicalicus madagascariensis	1		1	1	1	1	1	1	Mad.	genera	1	I V	Ar	Ar
Schetba rufa	1		1	1	1			1	Mad.	genera	0	I V	Ar	Ar
Vanga curvirostris	1	1	1	1	1	1		1	Mad.	genera	1	I V	Ar	Ar
Xenopirostris xenopirostris		1	1						s	genera	1	I V	Ar	Ar
Xenopirostris damii	1		1						w	genera	0	I	Ar	Ar
Xenopirostris polleni				1	1			1	E	genera	1	I	Ar	Ar
Falculea palliata	1	1	1			1		1	Mad.	genera	2	I G V	Ar	Ar
Leptopterus viridis	1	1	1	1	1	1	1	1	Mad.	genera	2	I V	Ar	Ar
Leptopterus chabert	1	1	1	1	1	1		1	Mad.	genera	2	I Veg	Ar	Ar
Cyanolanius madagascarinus	1		1	1	1	1		1		subspecies	2	I Veg	Ar	Ar
Oriolia bernieri				1	1			1	E	genera	0	I	Ar	Ar
Euryceros prevostii				1	1			1	E	genera	0	I V	Ar	Ar
Hypositta corallirostris				1	1			1	E	genera	0	I	Ar	Ar
Tylas eduardi	1		1	1	1			1	Mad.	genera	1	I	Ar	Ar
Dicrurus forficatus	1	1	1	1	1	1		1		subspecies	3	I	Ar	Ar
Hartlaubius auratus	1	1	1	1	1	1		1	Mad.	species	3	Veg	Ar	Ar
Ploceus nelicourvi				1	1	1	1	1	E	species	1	I	Ar	Ar
Ploceus sakalava	1	1	1						W	species	3	I Veg	Ar	Ar
Foudia madagascariensis	1	1	1	1	1	1	1	1	Mad.	species	3	I Veg	Ar	Ar
Foudia omissa				1	1		1	1	E	species	1	I Veg	Ar	Ar
TOTAL	68	63	77	89	95	59	33	99						

Table III. Similarities between sites according to Jaccard. Indices above diagonal refer to endemic species and non-endemic species; indices below the diagonal refer to to non-passerine species and passerine species.

Sites	RNI 11	RNI 5	PN 4	RS 21	RNI 3	RS 16	Maso	RNI 12	PN 1	RS 3	PN 2	RS 2	RNI 7	RNI 9	Kiri	Zomb	Ihot	Toli	RS 23	RNI 10	Bere	RNI 11'
RNI 11 (humid)		.67	.77	.72	.78	.67	.72	.76	.46	.41	.23	.34	.32	.34	.35	.31	.23	.25	.23	.21	.29	.23
Andohahela		.78	.96	.96	.85	.88	.92	1.00	.93	.85	.78	.93	.82	.82	.85	.93	.67	:78	.74	.70	.82	.78
RNI 5	.68		.74	.65	.61	.54	.60	.69	.49	.35	.20	.30	.29	.31	.29	.25	.23	.23	.23	.19	.25	.21
Andringitra	.73		.74	.74	.69	.73	.70	.78	.71	.76	.69	.71	.62	.62	.64	.71	.58	.57	.54	.62	.62	.57
PN4	.77	.67		.86	.71	.61	.71	.81	.52	.39	.19	.32	.29	.33	.31	.27	.22	.22	.22	.18	.25	.20
Ranomafana	.89	.79		1.00	.88	.92	.92	.96	.96	.85	.67	.89	.85	.85	.88	.96	.69	.81	.77	.73	.79	.81
RS 21	.71	.62	.92		.69	.63	.78	.81	.48	.38	.18	.32	.29	.31	.31	.28	.22	.23	.20	.17	.26	.20
Périnet	.87	.73	.89		.88	.92	.96	.96	.96	.88	.74	.89	.85	.85	.88	.96	.69	.81	.77	.73	.79	.81
RNI 3	.78	.59	.72	.67		.70	.75	.78	.48	.45	.24	.38	.31	.38	.36	.30	.25	.26	.23	.22	.30	.23
Zahamena	.81	.67	.80	.82		.88	.84	.85	.85	.91	.69	.85	.88	.88	.84	.85	.64	.83	.72	.68	.81	.76
RS 16	.65	.51	.60	.63	.64		.70	.71	.36	.39	.21	.28	.26	.31	.33	.27	.23	.23	.19	.16	.23	.19
Ambatovaky	.82	.68	.80	.78	.85		.88	.88	.88	.88	.67	.81	.85	.85	.81	.88	.62	.80	.69	.65	.78	.73
Maso	.74	.61	.81	.84	.74	.66		.84	.46	.43	.24	.37	.33	.37	.38	.34	.26	.28	.26	.21	.31	.26
Masoala	.82	.64	.76	.82	.81	.86		.92	.92	.84	.70	.85	.81	.81	.85	.92	.65	.77	.73	.69	.75	.77
RNI 12	.79	.66	.81	.84	.74	.67	.95		.45	.40	.23	.34	.31	.35	.35	.32	.24	.26	.24	.20	.30	.24
Marojejy	.87	.77	.89	.87	.86	.86	.78		.93	.85	.78	.93	.82	.82	.85	.93	.67	.78	.74	.70	.82	.70
PN 1	.63	.49	.75	.69	.58	.43	.60	.61		.46	.26	.51	.37	.40	.34	.32	.23	.26	.26	.24	.31	.23
Mont. Ambre	.61	.68	.60	.58	.63	.64	.60	.58		.85	.78	.93	.89	.89	.92	1.00	.73	.85	.81	.77	.82	.85
RS 3	.57	.42	.55	.55	.60	.51	.55	.56	.53		.34	.56	.51	.51	.51	.46	.42	.41	.35	.33	.44	.38
Manongarivo	.53	.54	.52	.51	.59	.56	.56	.51	.72		.69	.85	.81	.81	.84	.85	.64	.76	.72	.68	.74	.76
PN 2	.50	.36	.41	.39	.41	.38	.42	.47	.50	.47		.40	.45	.50	.41	.48	.39	.42	.48	.41	.45	.48
Isalo	.33	.39	.33	.32	.37	.35	.35	.32	.48	.54		.78	.68	.68	.70	.78	.71	.63	.65	.75	.68	.69
RS 2	.63	.42	.57	.57	.58	.43	.57	.61	.69	.62	.59		.72	.62	.66	.56	.43	.46	.39	.42	.53	.43
Ankarana	.44	.47	.43	.42	.48	.46	.46	.42	.70	.77	.57		.89	.89	.92	.93	.73	.85	.81	.70	.89	.85
RNI 7	.52	.33	.48	.48	.51	.41	.48	.49	.57	.54	.56	.79		.71	.79	.65	.51	.54	.47	.46	.61	.51
Ankarafantsika	.44	.49	.43	.43	.45	.47	.47	.43	.59	.75	.56	.80		1.00	.88	.89	.69	.88	.77	.67	.92	.81
RNI 9	.53	.35	.52	.49	.56	.45	.52	.53	.54	.47	.57	.66	.82		.79	.65	.51	.54	.47	.46	.61	.51
Bemeraha	.47	.50	.45	.44	.51	.49	.49	.44	.68	.88	.61	.87	.84		.88	.89	.69	.88	.77	.67	.92	.81
Kiri	.53	.38	.49	.49	.52	.45	.52	.53	.54	.51	.57	.75	.82	.83		.74	.51	.58	.51	.43	.64	.55
Kirindy	.48	.44	.47	.46	.49	.50	.50	.46	.58	.81	.50	.80	.85	.84		.92	.72	.92	.88	.69	.81	.92
Zomb	.51	.35	.47	.47	.43	.40	.50	.51	.56	.49	.70	.64	.71	.71	.76		.54	.66	.59	.49	.64	.64
Zombitse	.50	.46	.49	.48	.51	.52	.52	.48	.61	.79	.54	.84	.81	.81	.88		.73	.85	.81	.77	.82	.85
Ihot	.40	.33	.39	.39	.38	.35	.40	.41	.42	.47	.53	.54	.60	.57	.61	.69		.81	.64	.63	.69	.69
Ihotry	.33	.36	.32	.31	.36	.34	.34	.31	.42	.55	.52	.58	.59	.56	.57	.61		.71	.82	.77	.69	.78
Toli	.43	.28	.39	.40	.42	.39	.43	.44	.46	.47	.58	.58	.69	.69	.69	.78	.77		.76	.65	.80	.81
Toliara	.38	.40	.38	.37	.42	.40	.40	.37	.48	.63	.44	.67	.66	.64	.71	.69	.76		.87	.68	.88	.91
RS 23	.48	.35	.47	.43	.43	.36	.47	.48	.56	.49	.65	.59	.66	.71	.71	.81	.64	.78		.79	.79	.93
Beza-Mahafaly	.30	.30	.29	.29	.33	.31	.31	.29	.35	.50	.46	.52	.50	.50	.57	.55	.78	.83		.71	.77	.95
RNI 10	.45	.35	.40	.38	.40	.30	.38	.40	.49	.45	.62	.53	.59	.56	.56	.63	.61	.61	.73		.73	.79
Tsimanampetsotsa	.29	.30	.29	.28	.32	.30	.30	.28	.39	.48	.50	.56	.50	.48	.50	.53	.78	.73	.78		.67	.75
Bere	.52	.34	.45	.45	.48	.38	.48	.52	.53	.50	.60	.68	.80	.81	.76	.85	.59	.77	.74	.63		.84
Berenty	.38	.40	.38	.37	.42	.40	.40	.37	.48	.63	.50	.67	.66	.64	.66	.69	.83	.92	.83	.80		.81
RNI 11' (dry)	.48	.32	.43	.43	.43	.36	.47	.48	.51	.53	.65	.64	.71	.71	.76	.87	.69	.84	.93	.73	.79	
Andohahela	.32	.33	.31	.31	.35	.33	.33	.31	.39	.53	.50	.56	.55	.54	.61	.59	.78	.88	.95	.83	.88	

Table IV. Distribution of forest species among ecological niches in different Phytogeographic Regions and Domains (abbreviation as in Table II).

Ecological niches:			Domains and Regions								
Food	Feeding habit	Nest	w	s	W	e	c	sa	hm	E	Madagascar
I	Ar	Ar/P	13	14	16	26	30	13	9	30	34
I	T	Ar	2	2	3	2	3	2		3	4
I	T	T		1	1	1	2			2	3
I	Ar	T	3	2	3	3	4	1		4	4
Subtotal Insectivores			**18**	**19**	**23**	**32**	**39**	**16**	**9**	**39**	**45**
I, Veg	Ar	Ar	8	8	9	9	9	7	7	9	11
I, Veg	T	Ar	4	3	5	4	3	3	1	5	8
I, Veg	T	T	1	1	1	2	2		1	2	2
Subtotal Omnivores			**13**	**12**	**15**	**15**	**14**	**10**	**9**	**16**	**21**
Veg	Ar	Ar	6	6	7	7	7	8	3	8	9
Veg	T	Ar	1	1	1	1	1	1		1	1
Veg	T	T	2	2	2	1	1	1		1	2
Subtotal Vegetarians			**9**	**9**	**10**	**9**	**9**	**10**	**3**	**10**	**12**
nV	Ar	Ar	15	11	16	16	16	11	4	17	19
nV	T	Ar	1	1	1	1	1	1	1	1	1
nV	T	T	1	1	1	4	4	2	1	4	4
nV	Ar	T	1	1	1	1	1		1	1	1
Subtotal small predators			**18**	**14**	**19**	**22**	**22**	**14**	**7**	**23**	**25**
Large predators			**4**	**3**	**4**	**5**	**5**	**3**	**2**	**5**	**5**
Aerial insectivores			**6**	**6**	**6**	**6**	**6**	**6**	**3**	**6**	**6**
TOTAL			**68**	**63**	**77**	**89**	**95**	**59**	**33**	**99**	**114**

Table V. Tolerance to forest degradation of Malagasy forest bird species (numbers are number of species within taxa)

Taxonomic level of endemism	Number of species in forest types: undisturbed	slightly disturbed	secondary growth	anthropogenic grassland
Species belonging to an endemic family	8	4	0	0
Species belonging to an endemic subfamily	13	11	2	0
Species belonging to an endemic genera	34	22	6	1
Sub total	**55**	**37**	**8**	**1**
Other endemic species	30	26	19	14
Non endemic species with endemic subspecies	23	23	21	19
Other non endemic species	6	6	6	6
Sub total	**59**	**55**	**46**	**39**
TOTAL	**114**	**92**	**54**	**40**