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THE PERINET EFFECT ? DIVERSITY GRADIENTS IN AN ADAPTIVE RADIATION OF MADAGASCAN BUTTERFLIE (SATYRINAE : MYCALESINA) CONTRASTED WITH OTHER SPECIES-RICH RAINFOREST TAXA

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ABSTRACT.- Satyrine butterflies in the subtribe Mycalesina constitute the largest radiation of butterflies in Madagascar (ca. 63 spp. out of ca. 300). Species definitions in this poorly known group have recently been clarified taxonomically and systematically. The patterns of spatial diversity in mycalesines have been analysed using William's program WORLDMAP on a quarter degree grid (spatial scale 27 x 27 km.). To compensate for sample effort inconsistencies, ranges were interpolated between range limits using two biological and three grid parameters: altitudinal range, habitat type and existing forest cover. The result for the distribution of mycalesine species is a fairly smooth gradient peaking at middle altitudes (ca. 900-1300 m.) and latitudes (ca. 17-20°S and 47-48°E), with a hotspot which falls on the same quarter degree grid square as the well known eastern site of Périnet. Although not displayed by some taxa adapted to other biomes, this general pattern (and the approximate hotspot position) is shown by a wide range of taxa which include pronounced rainforest radiations or a high percentage of rainforest species (e.g. all butterflies other than mycalesines, hesperiid butterflies, frogs, two large radiations of frogs, and chameleons). This medially-centred latitudinal pattern does not reflect habitat area, grid cell altitudinal range or rainfall/temperature gradients, all of which tend to increase northwards. Rather, the pattern corresponds well to a random/uniform distribution of boundary-constrained range positions throughout the Madagascan rainforest. Diversity gradient studies for other taxa in Madagascar or elsewhere in the tropics need to take into account this effect of bounded range overlap richness. Conservation implications are briefly discussed.

KEY WORDS.- Species richness, Butterflies, Frogs, Lemurs

RESUME.- Les papillons Satyrinae de la sous-tribu des Mycalesina représentent la plus importante lignée au sein des Rhopalocères malgaches (environ 63 espèces sur approximativement 300). Dans ce groupe relativement mal connu, la définition des espèces a été récemment clarifiée sur le plan taxonomique. Leurs modes de diversité spatiale ont été analysés en utilisant le logiciel « WORLDMAP » de Williams pourvu d'un quadrillage d'un quart de degré (avec des carrés de ca. 27 km. x 27 km.). Pour compenser l'irrégularité des prélevèments, une interpolation a été effectuée pour établir les distributions entre les limites de répartition en tenant compte de plusieurs paramètres (deux biologiques; trois géographiques): l'altitude, le type d'habitat et la présence d'un couvert forestier. En ce qui concerne la distribution des espèces de Mycalesina, le résultat suivant est obtenu: l'existence d'un gradient à peu près régulier jusqu'à un pic correspondant à des altitudes modérées (vers 900-1300 m.) et des cordonnées comprises entre 17 ° et 20° de latitude sud, 47° et 48° de longitude est; la localisation du point optimal (hotspot) au niveau d'un carré du quadrillage identique à celui du site du Périnet, localité bien connue et située vers le milieu du domaine de l'Est. Bien que ce type de distribution ne se retrouve pas chez certains taxa adaptés à d'autres biomes, il est caractéristique d'un large éventail de taxa (ainsi que la position du hotspot- tout au plus). Ces derniers comprennent soit des lignées typiques des forêts

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humides, soit un fort pourcentage d'espèces adaptées à ces forêts (par exemple, tous les Rhopalocères autres que les Mycalesina, les papillons Hesperiidae, toutes les grenouilles, les deux principales lignées de grenouilles et les caméléons). Ce modèle de distribution avec un hotspot situé vers le milieu de la grande île ne reflêt pas la surface des habitats, ni les rangées altitudinales des carrés, ni encore les gradients pluviométriques et thermométriques, ces paramètres tendant à croître vers le nord. La répartition des Mycalesina ne correspond pas à un réseau de relations bien définies, mais, plus simplement, à une distribution au hasard ou uniforme des dimensions et des emplacements (contraintés par frontières) des aires de répartition le long de la forêt humide de Madagascar. Pour d'autres taxa, qu'elles soient menées à Madagascar ou ailleurs, les études relatives aux variation de la diversité doivent prendre en compte le phénomène d'enrichissement par recouvrement limité d'aires de distribution. Les implications pour la conservation sont brièvement discutées

MOTS CLEFS: Richesse spécifique, Papillons, Batraciens, Lémuriens

INTRODUCTION

MID-ELEVATIONAL AND MID-LATITUDINAL PEAKS IN SPECIES RICHNESS

Various studies have demonstrated mid-gradient peaks in species richness in different taxa, in temperate zones and particularly in the tropics (*e.g.* JANZEN *et al.*, 1976; HOLLOWAY, 1987; ALLEN *et al.*, 1991). In these studies it has been assumed that species richness gradients and peaks reflect underlying environmental gradients, particularly precipitation (*e.g.* GENTRY, 1988), energy (*e.g.* CURRIE, 1991), and habitat area and resource diversity (*e.g.* LAWTON *et al.*, 1987). In contrast, COLWELL and HURTT (1994) modelled species richness gradients from randomly generated biological ranges. These models produced clear mid-latitudinal and mid-elevational peaks, based on what COLWELL and HURTT called non-biological gradients in species richness (to emphasise the absence of assumptions about environmental gradients).

In most parts of the tropics, real data to test such models are hard to find not only because species definitions are generally inadequate, but also because species-rich humid forest habitats are generally complex in shape, making it difficult to separate effects of habitat area on latitudinal and elevational gradients. In Madagascar, however, tropical rainforest is distributed (except in the Sambirano zone, Masoala Peninsula and peripheral patches) in a rather uniform north-south belt, from about 15-25°S. Madagascan rainforest, while it remains mostly contiguous (at least at higher altitudes), provides an excellent opportunity to test environmental and null gradient models for explaining latitudinal species richness. The current study examines latitudinal and elevational gradients of butterflies, and compares them to other groups most rich in humid forest.

Mycalesine radiation

Presumably because of long isolation predating the origin of most modern butterfly higher taxa, the fauna of Madagascar is highly divergent compared to the faunas of

Africa and South-East Asia. For example, the Satyrinae (ca. 100 spp.) represent one third of the butterflies of the island and these, with the exception of two very widespread species, belong to just two subtribes. The present study focuses on one of these groups, the palaeotropical subtribe Mycalesina, which on Madagascar includes one of the largest Lepidopteran evolutionary radiations at the generic level. Including new taxa, and based on a major taxonomic and systematic reappraisal of species definitions (LEES, KREMEN & RAHARITSIMBA, unpublished data), 63 species of mycalesines are currently considered to occur on Madagascar. This research has also clarified the range-sizes of Madagascan species within this group. Geographically, the mycalesines are now amongst the best known of all Madagascan invertebrates. Most species are restricted to rainforest and have graminaceous hostplants.

Interpolating distributions from existing data

It should be possible to predict species richness patterns by summation of well known range sizes and positions. However, existing distributional data points for Madagascar for most organisms are sparse. To make best use of what we know in the face of uneven sampling effort, some kind of treatment of data is required, such as modelling to extrapolate from better-known environmental gradients (see references in WILLIAMS *et al.*, in press). However, in Madagascar, sufficiently detailed and evenly sampled environmental and distributional data are not easy to obtain. A simpler interpolation approach has been adopted here.

METHODS

DATA SOURCES, VERIFICATION AND ANALYSIS

Latitudinal and altitudinal ranges of mycalesines are based on work in progress. Data sources for frogs and chameleons include GLAW and VENCES (1994); for lemurs MITTERMEIER *et al.* (1992); butterfly and other sources are detailed in LEES (submitted), along with further details of methodology. Museum data for butterflies come from Paris, London, Antananarivo and Oxford. Modern field data cover the period 1988-1995 (LEES, KREMEN & RAHARATSIMBA, unpublished). Current data level entry averages 13 independent quarter degree grid cell records per species over 360 butterfly taxa for the Malagasy Region. All localities were checked as far as possible against available map sources. A gazetteer of map and grid cell references was based around VIETTE (1991), to standardise localities across taxa. Species richness patterns have been analysed using WORLDMAP version 3.19 (WILLIAMS, 1994). Species richness is calculated by this program as the raw species count per grid cell. Endemism is calculated as a measure of range-size rarity (expressed as the percentage aggregated reciprocal range size for all species per grid cell).

Correcting for sampling artefacts

Interpolation of species ranges is an attempt to adjust for unevenness in sample effort to look for gross patterns of richness (WILLIAMS *et al.*, in press). Grid cell data on existing forest cover, latitude and eight independent habitat classifications were cross-referenced (for the last two with a table of corresponding biological parameters). Latitudinal and altitudinal distributions were usually assumed to be continuous, unless there was clear evidence for disjunction. Examples are illustrated of a species map (*Admiratio paradoxa* (Mab.): Fig. 3) with empirical records, together with interpolated records, and the corresponding habitat map (rainforest from 1200-2100 m.: Fig. 4) used to assist in interpolation. In Madagascar, altitude ranges up to about 1250-1500 m. along most of the eastern escarpment, and higher in the north (Tsaratanana: 2876 m.) and south (Andohahela: 1951 m.). Fig. 2 displays richness in seven altitudinally banded vegetation classifications used in the interpolations (here not including savannah). Two other kinds of sampling artefacts remain: 1) The biasing effect for species richness and endemism of extreme narrow endemics when not looked for between apparent hotspots and 2) The effect of disturbed area species (*e.g.*, they are prevalent along the road from Antananarivo to Tamatave, which passes next to Périnet). Both of these effects were removed in turn by making use of the hierarchical taxon coding system available in WORLDMAP (LEES, submitted), and for the bias of endemics by simple summation (Figs. 5 and 6).

RESULTS

SPECIES RICHNESS GRADIENTS AND HOTSPOTS

For most taxa, the broad result of interpolation within the rainforest biome was a smoothly increasing latitudinal gradient towards a peak at middle latitudes (cf. Fig. 5). Altitudinal range and latitudinal range are significantly correlated in mycalesines (*e.g.* Fig. 6, $r= 0.686$, $p< 0.001$; see also GASTON 1994), and a pronounced altitudinal gradient was also displayed by most taxa within the eastern rainforest belt. The latitudinal position occupied by the species richness hotspot is of primary interest in this study.

A rainforest hotspot for the grid square at latitude 18° 45'-19° 00'S, which includes the reserves Périnet and Mantady, or immediately adjacent quarter degree squares to the east (the unprotected « Rogez » [= Andekaleka] forest) or to the south (the unprotected Ankeniheny and Lakato forests), was found for mycalesines (63 spp.), all butterflies (299 spp.), butterflies other than mycalesines (236 spp.), hesperiid (55 spp.) and hesperiine butterflies (43 spp.), acraeine butterflies (17 spp.), frogs (182 spp.), mantelline frogs (*Mantidactylus*, *Mantella*: 60 spp.), rhacaphorine frogs in the genus *Boophis* (37 spp.), chameleons (55 spp.) and the chameleon genera *Calumma* and *Brookesia* (see LEES, submitted, for colour figures). For Acraeinae, the hotspot at Périnet was entirely an artefact of disturbed area species since this group of butterflies display a relatively even interpolated richness throughout the eastern biome. In contrast, lemur species (31 spp.) showed a less smooth rainforest species richness gradient varying from ca. 10-14 spp., with a hotspot in the southern square which includes Andohahela (latitude 14° 45-15° S), and a subsidiary hotspot at Zahamena (latitude 17° 30-17°45'S, which was also the primary hotspot for lemur subspecies: 49 taxa, otherwise with similar results to lemur species). No other major groups of organisms have yet been analysed and their ranges interpolated on the quarter degree grid for Madagascar.

Removing disturbed area species

Since disturbed area species could be biasing the figures, these were taken out of the butterfly dataset. This left 192 species (2/3 of butterfly species with records in Madagascar), essentially adapted to primary vegetation habitats. When these were analysed separately, as expected, some effect of disturbed area species was shown, in that species richness was now equal between the Andekaleka square (latitude 18° 30' - 18°45') and the Zahamena square (latitude 17° 30'- 17° 45'). For a similar analysis with mycalesines, the percentage of primary forest species (83%) was sufficiently great not to shift the hotspot from the Périnet square.

Hotspots of endemism

Endemism for mycalesines revealed a similar pattern of hotspots to all non-mycalesine butterflies. For rainforest areas, endemism hotspots for both groups were, from north to south: 1) Montagne d'Ambre, 2) Manongarivo-Tsaratanana, 3) Zahamena, 4) Périnet and 5) Ranomafana. Mycalesines showed higher levels of endemism than non-mycalesine butterflies (reflecting, presumably, lower mean vagility in mycalesines), with Masoala Peninsula/Antongil Bay and Zahamena highlighted as much more distinct entities for mycalesines, whereas the Mananara area was prominent for non-mycalesines. Endemism hotspots for frogs revealed only three hotspots in common with butterflies (Montagne d'Ambre, Périnet area, and Sambirano), with others (better sampled for frogs than for butterflies) unique to frogs (Marojejy, Ambatovaky, and Chaines Anosyennes). This sampling difference between taxa leading to contrasting results emphasises how little is really known about endemism. So how reliable are the hotspots?

Removing narrow endemics

Species richness was summed for the 32 most widespread and 31 rarest species of mycalesines across quarter degree bands of latitude and 50 m. bands of altitude, to produce a species richness profile for all species (Figs. 5, 6). A similar analysis was made using percentiles of range-size rarity (LEES, submitted). The possible bias due to unevenly sampled narrow endemics (lower part of profile) could then be removed.

Species richness gradients of the most widespread 50% of mycalesine species were still broadly similar to results for all species, except that the hotspots were less sharp for both latitude and altitude, with the mid-elevational and especially mid-latitudinal « bulges » much smoother and spread over a wider range (peaking at 18-23 spp. between 500-1350 m and 26-31 spp. between 15-22° S): Figs 5 and 6. Thus, removal of the 50% least widespread species eliminates the possible signal of local endemism; removal of the 25% rarest quartile of range sizes (GASTON, 1994) might represent a better compromise.

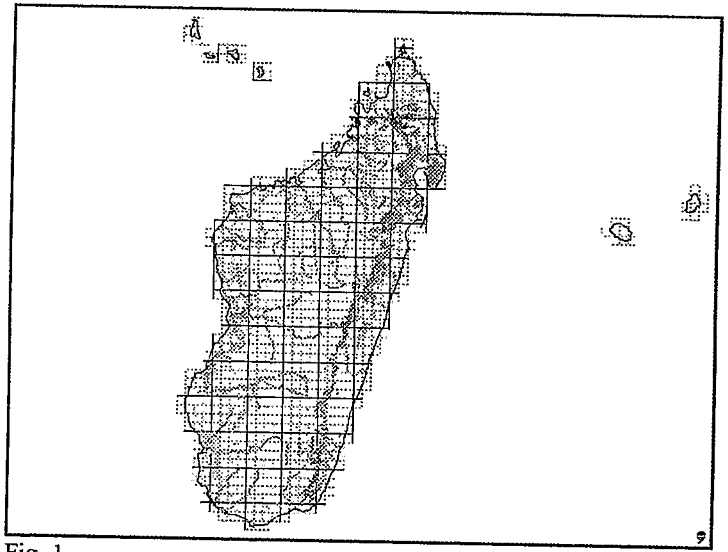


Fig. 1

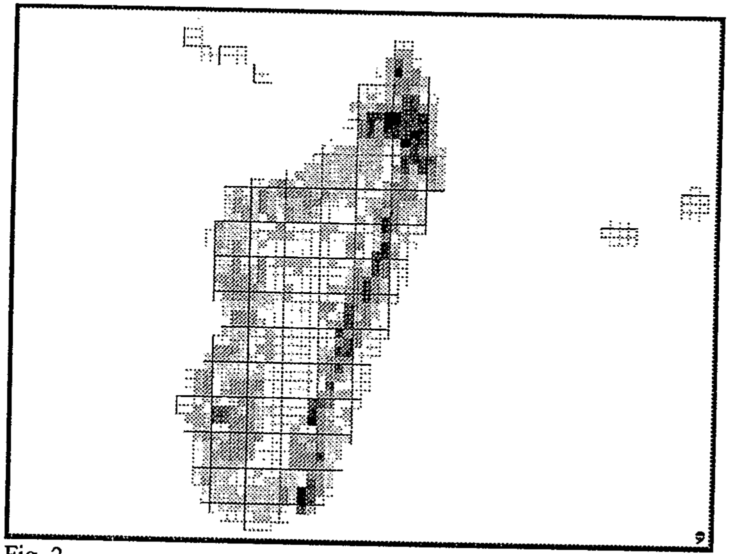


Fig. 2

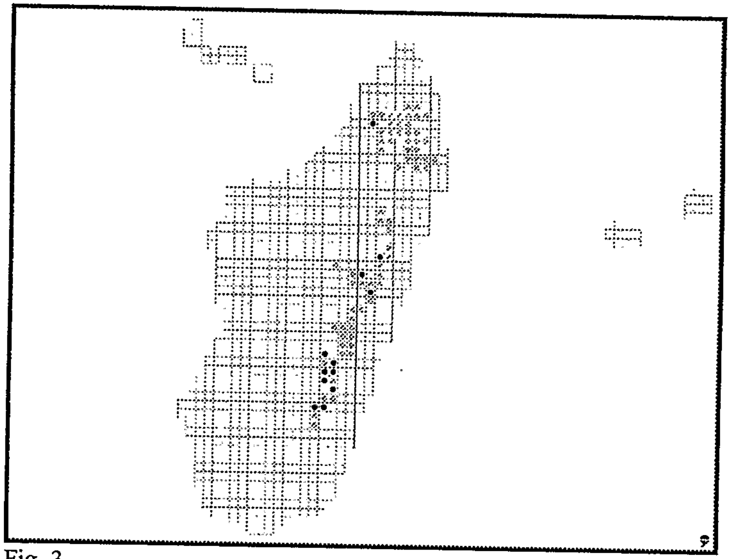


Fig. 3

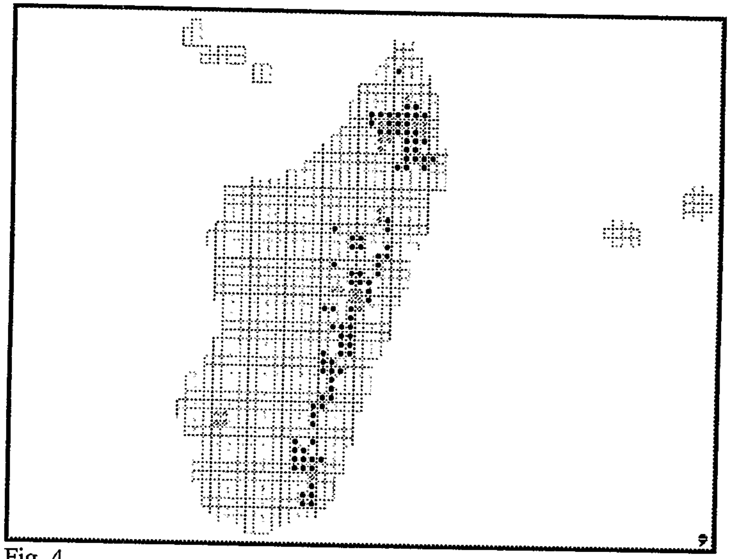


Fig. 4

Fig. 1. Existing primary forest cover in Madagascar (after WCMC 1991). Fig. 2. Richness in seven habitat classifications used in interpolation. Max. (darkest) = 4 types. Fig. 3. Example of a species card. Distribution of *Admiratio paradoxa* (Mycalesina). Bold = original records. Fig. 4. Example of a habitat classification. Primary rainforest 1200-2100 m. Bold = confirmed cover 1989-1990.

DISCUSSION

Because it is the more widespread, and thus better known and more reliably interpolated species, that are predominantly responsible for mid-gradient species richness, it is unlikely that this effect is an artefact of interpolation.

Habitat area has long been considered a fundamental factor explaining geographic differences in species richness, formerly from the perspective of island biogeography, more recently due to the passive sampling effect: the larger the area, the more niches are sampled (JENKINS *In:* GROOMBRIDGE, 1992). Because present relative habitat area (Fig. 1) increases towards northern latitudes of Madagascar, peaking around the latitude of Tsaratanana, this is unable to account for mid-elevational and mid-latitudinal peaks. We do not know enough about the latitudinal distribution of humid forest habitat area in the past to use this as an explanation. However, not only does rainforest cover seem to have been very variable in its upper altitudinal limit and by consequence its habitat area within middle latitudes over the Quaternary (see BURNEY, 1996), but the area that may have been most favourable for past speciation, the topographically diverse eastern escarpment, is restricted to a relatively even north-south band (except at the latitude of the Sambirano zone). Furthermore, northern latitudes from 14 to 16° S are the richest in terms of diversity of altitudinal zones in Madagascar (Fig. 2).

Climatic stability is another assumption which has underpinned much thinking regarding species richness towards the Equator (*e.g.* PIANKA 1966). However, because of the wide band of rainfall-promoting relief at the latitude of the Sambirano zone and the increasing proximity to the Equator of northern Madagascar, middle latitudes are unlikely to have been more stable climatically than northern latitudes.

Similarly, another group of factors more recently considered fundamental to explaining species richness gradients, energy flux and its correlates (including annual temperature, evapotranspiration, and precipitation: CURRIE, 1991), all increase northwards, in the case of rainfall peaking at the latitude of Maroantsetra (DONQUE, 1972), and so cannot explain the observed mid-latitudinal peaks within the rainforest biome.

But why assume that within-biome species ranges are representative at all of underlying environmental gradients?

Species ranges randomly distributed throughout the biome?

Suppose that large radiations, ecologically mostly restricted to one biome (for example, mycalesine butterflies and the two largest radiations of frogs) were more or less randomly distributed in their range positions throughout the biome. What species richness patterns would we then expect to observe in Madagascan rainforest? This would also depend on the frequency distribution of range sizes in a particular group. Clearly if all species had very small ranges, or if all species spanned the entire biome, we would not expect to observe any gradients. In mycalesines, however, altitudinal and latitudinal range sizes conform to a uniform distribution among species (Figs. 5 and 6). Such a distribution does generate a species richness gradient.

For example, Fig. 5 (lower part) shows that mycalesine butterfly species richness increases steadily up to about 1250 metres, but declines rapidly above that altitude. The peak at medium elevations is interpreted as due to range overlap, as shown by the upper part of Fig. 5, where altitudinal range positions and range sizes have been ranked in descending order of overall altitudinal range and subranked by latitudinal range. It is the species more or less intermediate in range size which generate a species richness gradient, whereas the more widespread species contribute disproportionately to overall species richness at medium elevations through range overlap (Fig. 5). The peak in mycalesine species richness for the 50% widest-ranging (and thus best known) species is at a range of elevations (500-1350 m.) consistent with those of the Périnet grid square (ca. 450-1300 m.).

This mid-gradient species-richness effect is repeated (more symmetrically) for latitude (Fig. 6). The latitudinal profile for the 50% most widespread species is smooth and medially domed (the peak occurs at about 17° 45'S, the latitude of Zahamena), but that for the 50% rarest species is uneven. Species richness for the 50% most widespread species corresponds remarkably well to the curve generated by random Model 2 of COLWELL and HURTT (1994). The four largest peaks in the overall distribution represent four apparent endemism hotspots (Manongarivo-Tsaratanana, Masoala, Périnet, and Ranomafana) which are due to the 50% least widespread species.

Thus, the species richness hotspot can be explained simply as the effect of boundaries on species ranges. In groups where wider-ranging species are not restricted to a single biome, however (*e.g.* acraeine butterflies and lemurs), gradients within the rainforest biome are considerably more even. This is because the rainforest boundary presents no « hard » limit to most species in these taxa, and so range overlap continues across the boundary, rather than generating a gradient towards the midpoint of the biome (see COLWELL & HURTT, 1994). Although more species-rich in humid forests, the contrasting result for diversity gradients in lemur species may be explained partly by the fact that many species are not restricted to this biome (so wider-ranging species overlap the rainforest boundary). Thus interpolated species richness varies rather little across the rainforest, and is maximal around Andohahela in the south, where wet and dry biomes meet, reflecting habitat diversity. Furthermore, the lack of any smooth, consistent gradient in this group (despite range interpolation) may be due to dramatic recent declines in the ranges of several species documented from subfossil sites; at least 15 species have become extinct within the last few thousand years (MITTERMEIER *et al.*, 1992).

Any attempt to explain species richness gradients by underlying environmental gradients first needs to first establish the degree of range overlap expected by chance (COLWELL & HURTT, 1994). However, environmental gradients are most pronounced in Madagascar for elevation (*e.g.* DONQUE, 1972) and so of interest is the considerably lower species richness of mycalesines at high than low altitudes (Fig. 5). This trend is well established elsewhere (*e.g.* STEVENS, 1992), and parallels particularly the general decline in habitat area with increasing elevation (*e.g.* LAWTON *et al.*, 1987).

Genus	Species	Altitude range (m.)		Altitude Range size (m.)	Lat. range
Henotesia	subsimilis	0	2050	2050	49
Heteropsis	drepana	400	2005	1605	43
Henotesia	pauper	0	1500	1500	49
Henotesia	strigula	0	1500	1500	41
Henotesia	ankaratra	0	1450	1450	52
Henotesia	*fraterna*	0	1400	1400	47
Henotesia	vola	10	1389	1379	35
Henotesia	bicristata	0	1325	1325	16
Henotesia	iboina	80	1400	1320	51
Henotesia	uniformis	0	1200	1200	38
Henotesia	ankova	880	2030	1150	43
Henotesia	angulifascia	880	2005	1125	38
Houlbertia	38	40	1050	1010	3
Henotesia	32	1035	2030	995	7
Henotesia	28	400	1389	989	33
Henotesia	22	910	1750	840	16
Henotesia	parvidens	1180	2000	820	5
Admiratio	paradoxa	1200	2005	805	33
Henotesia	13B	1200	2005	805	11
Houlbertia	undulosa	650	1420	770	43
Henotesia	*undulans*	100	850	750	43
Masoura	56	740	1475	735	43
Henotesia	turbans	600	1325	725	30
Masoura	antahala	0	700	700	41
Henotesia	exocellata	1000	1700	700	40
Henotesia	maeva	0	700	700	32
Houlbertia	passandava	0	700	700	24
Henotesia	sabas	520	1220	700	2
Henotesia	16	0	675	675	11
Houlbertia	obscura	50	720	670	20
Masoura	ankoma	450	1100	650	25
Henotesia	turbata	1200	1850	650	20
Henotesia	67	750	1400	650	1
Masoura	53	50	550	500	3
Henotesia	parva	980	1475	495	30
Henotesia	laetifica	25	510	485	43
Henotesia	12	1000	1450	450	19
Henotesia	14A	0	400	400	5
Henotesia	63	1100	1475	375	1
Houlbertia	42	*550*	*910*	*360*	1
Houlbertia	erebennis	80	370	290	7
Henotesia	antsianakana	915	1200	285	7
Henotesia	laeta	25	270	245	32
Henotesia	cowani	1130	1350	220	4
Henotesia	20	1000	1220	220	1
Houlbertia	erebina	270	470	200	16
Houlbertia	strato	270	470	200	10
Henotesia	avelona	800	950	150	31
Henotesia	13	1250	1400	150	16
Henotesia	23	1670	1800	130	10
Henotesia	*fuliginosa*	1200	1310	110	2
Henotesia	oxypteron	850	950	100	2
Houlbertia	narova	1000	1100	100	1
Henotesia	62	750	850	100	1
Henotesia	37	*2000*	*2050*	*50*	1
Masoura	masoura	880	910	30	7
Henotesia	26	1080	1100	20	1
Henotesia	49	1389	1400	11	4
Houlbertia	anganavo				11
Henotesia	54				1
Henotesia	anceps				1
Masoura	mabillei				1
Houlbertia	wardi				

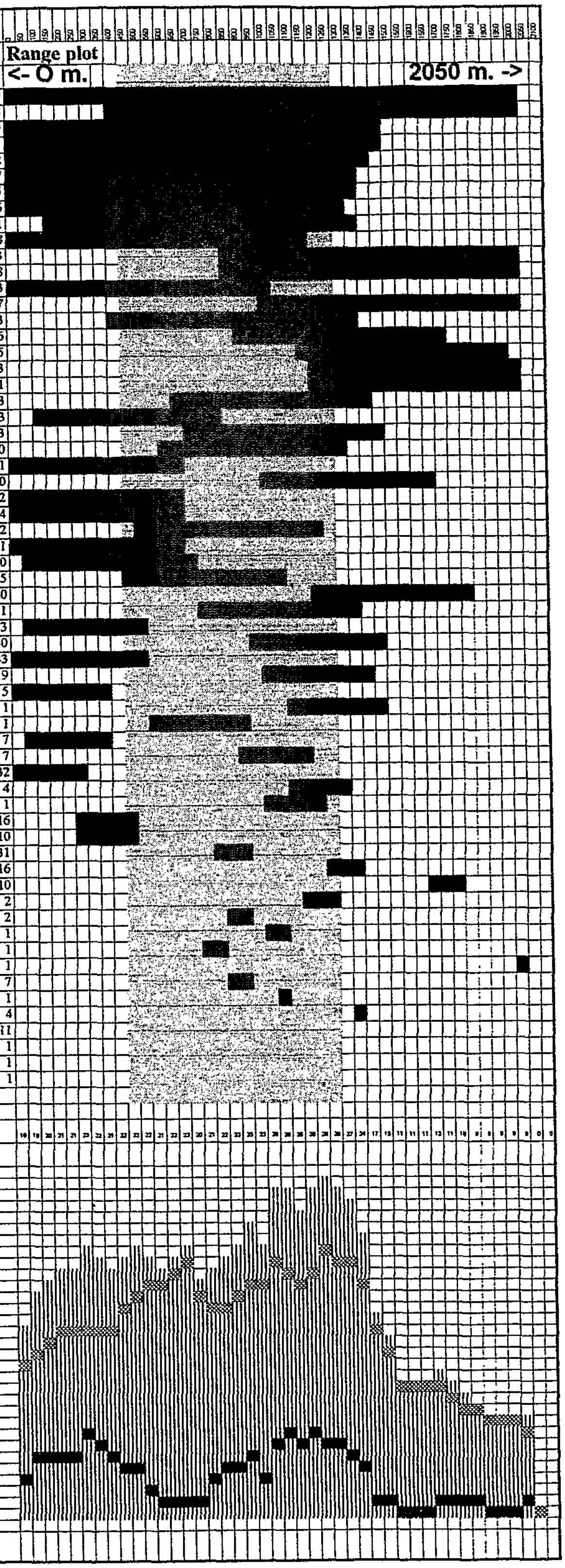
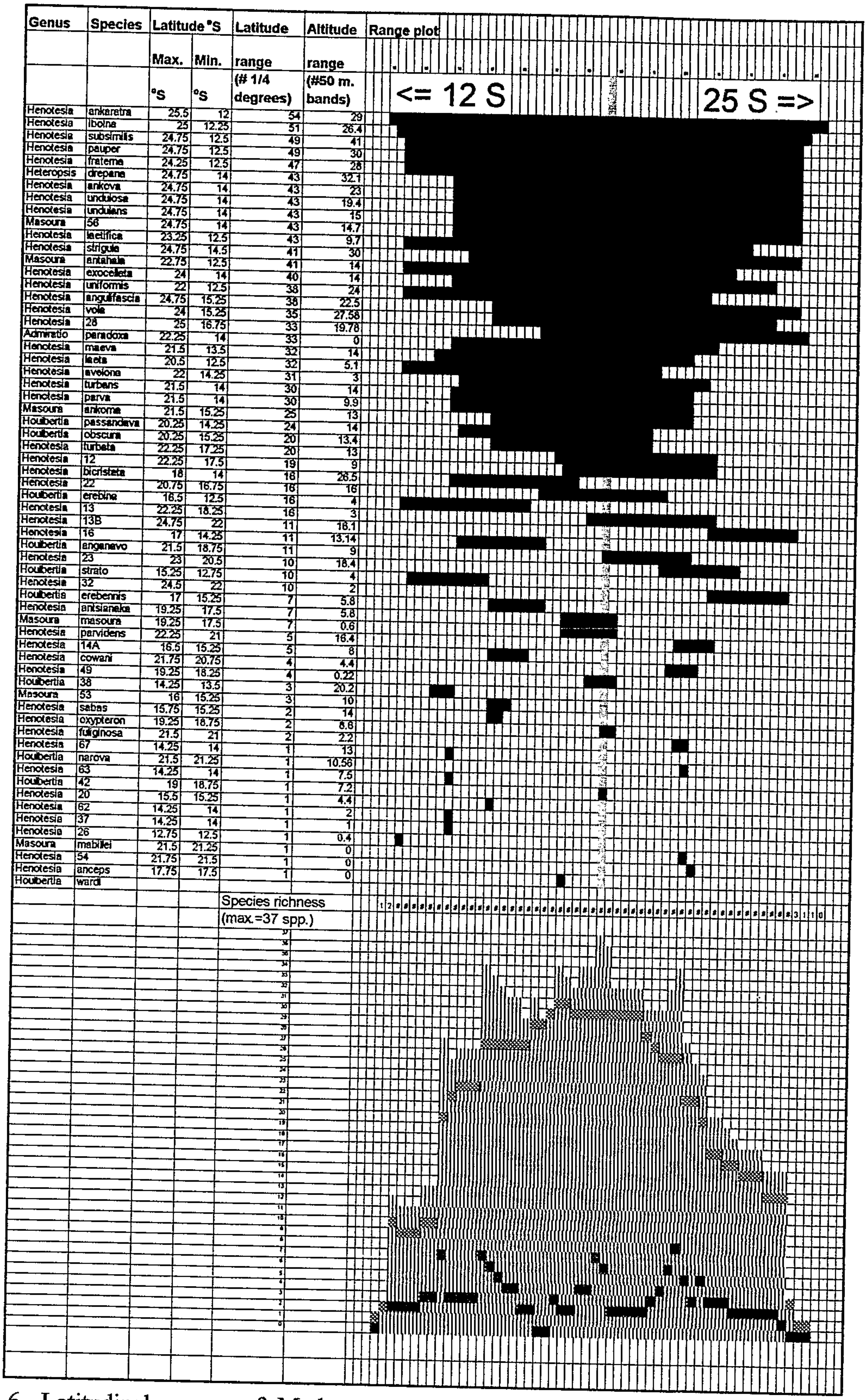


Fig. 5. Altitudinal ranges of Madagascan mycalesines ranked by range size (above) with altitudinal species richness profile (below): all spp. (vertical lines); 50% largest range size spp. (cross-hatched); 50% smallest range size spp. (dark squares). Shaded region = altitudinal range of Périnet/Mantady grid square (Périnet itself is at about 910 m.).



Genus	Species	Latitude °S		Latitude	Altitude
		Max.	Min.	range	range
		°S	°S	(# 1/4 degrees)	(#50 m. bands)
Henotesia	ankaratra	25.5	12	54	29
Henotesia	iboina	25	12.25	51	26.4
Henotesia	subsimilis	24.75	12.5	49	41
Henotesia	pauper	24.75	12.5	49	30
Henotesia	fraterna	24.25	12.5	47	28
Heteropsis	drepana	24.75	14	43	32.1
Henotesia	ankova	24.75	14	43	23
Henotesia	undulosa	24.75	14	43	19.4
Henotesia	undulans	24.75	14	43	15
Masoura	58	24.75	14	43	14.7
Henotesia	laetifica	23.25	12.5	43	9.7
Henotesia	strigula	24.75	14.5	41	30
Masoura	antahala	22.75	12.5	41	14
Henotesia	exocellata	24	14	40	14
Henotesia	uniformis	22	12.5	38	24
Henotesia	angulifascia	24.75	15.25	38	22.5
Henotesia	vola	24	15.25	35	27.58
Henotesia	28	25	16.75	33	19.78
Admiratio	paradoxa	22.25	14	33	0
Henotesia	maeva	21.5	13.5	32	14
Henotesia	laeta	20.5	12.5	32	5.1
Henotesia	avelona	22	14.25	31	3
Henotesia	turbans	21.5	14	30	14
Henotesia	parva	21.5	14	30	9.9
Masoura	ankoma	21.5	15.25	25	13
Houlbertia	passandava	20.25	14.25	24	14
Houlbertia	obscura	20.25	15.25	20	13.4
Henotesia	turbata	22.25	17.25	20	13
Henotesia	12	22.25	17.5	19	9
Henotesia	bicristata	18	14	16	26.5
Henotesia	22	20.75	16.75	16	16
Houlbertia	erebina	16.5	12.5	16	4
Henotesia	13	22.25	18.25	16	3
Henotesia	13B	24.75	22	11	16.1
Henotesia	16	17	14.25	11	13.14
Houlbertia	anganavo	21.5	18.75	11	9
Henotesia	23	23	20.5	10	18.4
Houlbertia	strato	15.25	12.75	10	4
Henotesia	32	24.5	22	10	2
Houlbertia	erebennis	17	15.25	7	5.8
Henotesia	antsianaka	19.25	17.5	7	5.8
Masoura	masoura	19.25	17.5	7	0.6
Henotesia	parvidens	22.25	21	5	16.4
Henotesia	14A	16.5	15.25	5	8
Henotesia	cowani	21.75	20.75	4	4.4
Henotesia	49	19.25	18.25	4	0.22
Houlbertia	38	14.25	13.5	3	20.2
Masoura	53	16	15.25	3	10
Henotesia	sabas	15.75	15.25	2	14
Henotesia	oxypteron	19.25	18.75	2	6.6
Henotesia	fuliginosa	21.5	21	2	2.2
Henotesia	67	14.25	14	1	13
Houlbertia	narova	21.5	21.25	1	10.56
Henotesia	63	14.25	14	1	7.5
Houlbertia	42	19	18.75	1	7.2
Henotesia	20	15.5	15.25	1	4.4
Henotesia	62	14.25	14	1	2
Henotesia	37	14.25	14	1	1
Henotesia	26	12.75	12.5	1	0.4
Masoura	mabillei	21.5	21.25	1	0
Henotesia	54	21.75	21.5	1	0
Henotesia	anceps	17.75	17.5	1	0
Houlbertia	wardi				

Fig. 6. Latitudinal ranges of Madagascan mycalesines ranked by range size (above) with altitudinal species richness profile (below): all spp. (vertical lines); 50% largest range size spp. (cross-hatched); 50% smallest range size spp. (dark squares). Shaded region = latitude of Périnet.

CONSERVATION IMPLICATIONS

Conserving hotspots of species richness or endemism?

As far as conservation strategies are concerned, the current study does not suggest that conservation effort should necessarily be focused at mid-latitudes and altitudes, even where species richness hotspots overlap multiply between taxa, because wider-ranging species often have lower risks of extinction (GASTON, 1994: 104). Rather, it suggests that the prevalent prison-network approaches to both species protection (which strangles flexibility for future range-shifting in response to climate change) and to bioinventory (which by focusing sampling effort within reserves makes no attempt to estimate real range sizes), need to be readdressed. While we do need to prioritise conservation of endemics we already know about through enhanced reserve protection and augmentation, we also need to plan for habitat continuity, so as to maintain and restore connectivity, ecosystem viability and range overlap richness. If we do not do this, intermediate areas like Périnet (which is already a fragment) will not only decline in species richness (due particularly to edge effects, minimum population viability problems and cessation in immigration of all but wide-ranging « tramp » species), but they will also lose their role as viaducts for genetic diversity. Future evolutionary adjustments in Madagascar, through range-shifting in adaptive response to shifting gradients, such as those caused by climate change, will then become impossible.

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