

# Endemic butterflies on Grande Comore: habitat preferences and conservation priorities

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## Abstract

The island of Grande Comore (Comoro Islands, western Indian Ocean) has an endemic butterfly fauna threatened by rapid habitat change. Transect counts were used to assess the abundance and species richness of butterflies in different habitats, and along an elevational gradient. Species richness of non-endemic butterflies was highest in low elevation, man-modified habitats. In contrast, most endemic butterflies were confined to forest habitats, which only remain above 500 m elevation. Richness and abundance of endemic butterflies were highest at the lower elevational limits of the remaining forest. Controlling for elevation, the richness of endemic butterflies was highest in mature forest where the gross structure of the forest remained intact, lower in scrubby secondary forest, and lowest in pioneer forest on old lava flows. The survival of the majority of the endemic butterflies may depend on forest conservation measures in the rapidly diminishing areas of mature forest at mid elevations. © 1998 Elsevier Science Ltd. All rights reserved

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## 1. Introduction

Unlike most insects in tropical forests, butterflies are taxonomically tractable, occur at moderate levels of species richness, and are easy to sample (Gilbert, 1984; Brown, 1991; New, 1991; Sparrow et al., 1994). These characteristics have made tropical butterflies a popular group for investigations into the effects of small-scale disturbance (Bowman et al., 1990; Spitzer et al., 1997), selective logging (Hill et al., 1995) and forest fragmentation (Daily and Ehrlich, 1995).

For conservationists, patterns in the richness of geographically restricted or endemic butterflies will often be of particular interest (e.g. Thomas and Mallorie, 1985). In regions where existing habitat protection is sparse, habitats rich in endemic taxa may be potential priority areas for reserves, particularly if other plant and animal taxa can be shown to follow similar patterns. Several studies have revealed consistent differences in the

responses of butterflies with large and small geographical ranges to human disturbance of tropical forest habitats. Whereas widespread butterfly species typically become more abundant in man-modified tropical forests, endemic or geographically restricted species decline (Thomas, 1991; Spitzer et al., 1993; Hill et al., 1995). Such anthropogenic effects will often be superimposed on natural patterns in richness and abundance resulting from abiotic gradients such as geology or elevation. Therefore, studies of the combined influences of human habitat modification and abiotic gradients on butterfly richness and abundance may be needed to set conservation priorities.

Here we investigate the effects of both anthropogenic factors (forest clearance and underplanting) and natural factors (successional stage and elevation) on the richness and abundance of butterflies on Grande Comore, a tropical, oceanic island in the western Indian Ocean. The Comoro Islands, of which Grande Comore is the largest, have *c.* 32 endemic butterfly taxa (Turlin, 1993–1996), including four that are listed as globally threatened (Baillie and Groombridge, 1996). The Comoros were identified as a key area for the conservation of

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swallowtail butterflies by New and Collins (1991), and are also recognised as a 'hotspot' for bird endemism (Bibby et al., 1992), with 16 endemic taxa (Louette, 1988). However, despite rapid loss of natural habitats, no terrestrial protected areas have been designated on the islands, and in the face of rapid habitat change there is an urgent need to identify key areas for conservation (Viette, 1980; Sayer et al., 1992).

## 2. Methods

### 2.1. Study area

Grande Comore (known locally as Ngazidja) lies in the Mozambique Channel between Madagascar and east Africa, 11°20'S and 43°11'E. It has an area of 1146 km<sup>2</sup>, and reaches a maximum elevation of 2361 m at the summit of the volcano, Kartala. Grande Comore is separated from the neighbouring islands of Anjouan (Ndzuan), Moheli (Mwali) and Mayotte (Maore) by distances of 48 to 230 km, from east Africa by 300 km, and from Madagascar by 500 km. All the islands are volcanic, and have never been linked to Africa or Madagascar. Grande Comore has a tropical climate with a hot, wet season from October to May and a slightly cooler, drier season from June to September. Monthly mean temperatures at sea level vary between 23 and 27°C, and the annual rainfall on the dry north east coast is 1900 mm, rising to 5900 mm in the forest on the west slopes of Kartala (Battistini and Vérin, 1984). The results presented are based on 10 weeks of fieldwork on Grande Comore in July–September 1992 (during the cool, dry season), and six weeks of fieldwork in March and April 1994 (during the hot, wet season).

At low and mid-elevations, the island is heavily cultivated or covered by sparsely-vegetated lava flows. At higher elevations, and particularly above 800 m on the slopes of Kartala, areas of rainforest remain (Fig. 1). However, except above 1200 m, this forest has been largely underplanted with crops, particularly bananas. The human population is expanding rapidly (47% of the population is under 15 years old: Battistini and Vérin, 1984) forcing the expansion of subsistence and small-scale commercial agriculture higher up the mountain slopes. Of the four islands of the Comoros archipelago, Grande Comore has the largest remaining forest area, estimated in 1986 to total 8658 ha of primary forest and 10083 ha of forest underplanted by crops (Agrar-Und Hydrotechnik, 1987).

### 2.2. Butterflies of Grande Comore

In contrast to most of the island's flora and fauna, the butterflies of Grande Comore have been subject to extensive study (Voeltzkow, 1917; Viette, 1980; Lewis et

al., 1993; Turlin, 1993–1996; Harper et al., 1996), and the species list is probably almost complete except for the families Hesperidae and Lycaenidae where several taxa have been added in the last five years (Turlin, 1993–1996). This study focused on the three other butterfly families represented on the Comoros, the Papilionidae, Pieridae and Nymphalidae. Like most oceanic islands (Williamson, 1981), the Comoros have an impoverished butterfly fauna, but high levels of endemism. Of 83 butterfly species, 17 are classified as full species endemic to the Comoros, and a further 15 are classified as subspecies endemic to the Comoros (Turlin, 1993–1996). Four butterfly species are listed as globally 'Threatened' (Collins and Morris, 1985; Baillie and Groombridge, 1996). Ten of the endemic species and eight of the endemic subspecies from the Papilionidae, Pieridae and Nymphalidae occur on Grande Comore (Table 1). The endemic butterflies are taxonomically diverse, representing many different genera rather than radiation within one genus. As such they would collectively receive high 'value' in conservation rankings which take into account taxonomic distinctiveness (Vane-Wright et al., 1991). For the same reason, any broad distinction between endemics and non-endemics

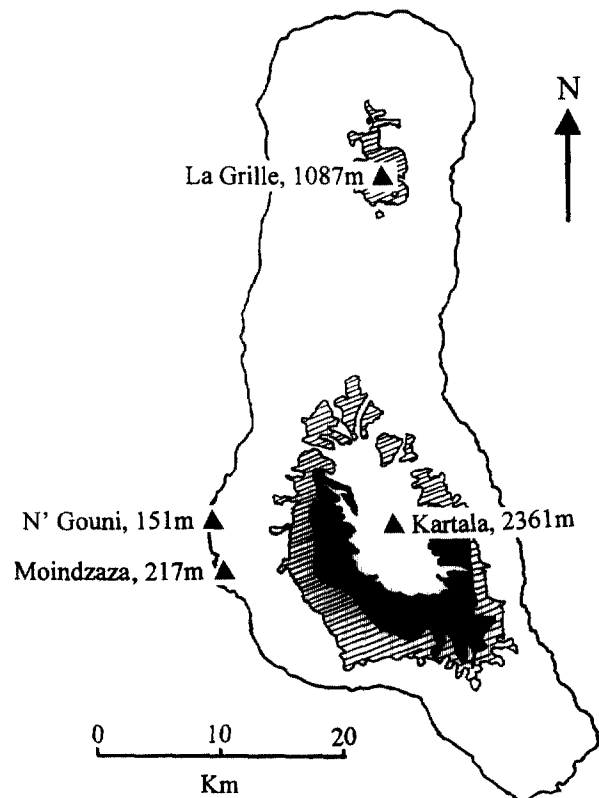


Fig. 1. Forest cover on Grande Comore. Hatching represents areas of underplanted and regenerating secondary forest (mostly above 500 m). Black areas represent mature non-underplanted forest (mostly above 1200 m), on the upper slopes of the volcano, Kartala. N'Gouni, Moindzaza and La Grille are elevated areas resulting from historic volcanism.

Table 1  
Endemic Papilionidae, Pieridae and Nymphalidae of Grande Comore

Species	Endemicity	Distribution
<b>Papilionidae</b>		
<i>Papilio dardanus</i> Oberthür 1888, ssp. <i>humbloti</i>	Ess	GC
<i>Papilio epiphorbas</i> Boidsuval 1833 ssp. <i>praedicta</i>	Ess	GC, (An)
<i>Papilio aristophontes</i> Oberthür 1897	Es	GC
<sup>a</sup> <i>Graphium levassori</i> (Oberthür) 1890	Es	GC
<b>Pieridae</b>		
<i>Eurema floricola</i> (Butler) 1879 ssp. <i>anjuana</i>	Ess	GC, Mo, An, Ma
<i>Belenois creona</i> (Vollenhoven) 1869 ssp. <i>elisa</i>	Ess	GC, Mo, An, Ma
<i>Mylothris ngaziya</i> (Oberthür) 1888	Es	GC
<b>Nymphalidae</b>		
<i>Antanartia dimorphica</i> Howarth 1966 ssp. <i>comoroica</i>	Ess	GC
<i>Neptis cormilloti</i> Turlin 1994	Es	GC
<i>Charaxes castor</i> Rothschild 1903 ssp. <i>comoranus</i>	Ess	GC
<sup>a</sup> <i>Charaxes paradoxa</i> Lathy 1925	Es	GC
<i>Pseudacraea lucretia</i> Cramer 1775 ssp. <i>karthala</i>	Ess	GC, (An)
<i>Amauris ochlea</i> Boisduval 1847 ssp. <i>affinis</i>	Ess	GC, (An)
<i>Amauris comorana</i> Oberthür 1897	Es	GC
<i>Acraea masaris</i> Oberthür 1893 ssp. <i>jodina</i>	Es	GC, (Mo, An)
<sup>a</sup> <i>Acraea comor</i> Pierre 1992	Es	GC
<i>Henotesia comorensis</i> Oberthür 1916 ssp. <i>salimi</i>	Es	GC, (Mo, An)
<i>Henotesia comorana</i> Oberthür 1916	Es	GC

Taxonomy follows Turlin (1993–1996) and Ackery et al. (1995).

<sup>a</sup> Represents species listed for Grande Comore, but not recorded during the two periods of fieldwork. Es = endemic species (species known only from the Comoro Islands). Ess = endemic subspecies (subspecies unique to the Comoro Islands). 'Distribution' indicates the islands of the archipelago from which each taxon has been recorded (Turlin, 1993–1996, pers. observ.): GC = Grande Comore, An = Anjouan, Mo = Moheli, Ma = Mayotte. Brackets indicate that the populations on those islands are classified as representing separate subspecies. Full species lists for the islands are given by Turlin (1993–1996).

is unlikely to be the consequence of taxonomic relatedness of the species investigated (cf. Harvey and Pagel, 1991).

We focus on the subset of butterfly species and subspecies endemic to the Comoros. The non-endemic butterflies are all widespread in continental Africa, Madagascar or both, and are not of high conservation priority. Although rare species have traditionally been the cause of more conservation concern than rare subspecies (Mallet, 1996), we do not distinguish in the analyses between taxa classified as endemic species and endemic subspecies; the two are treated together as 'endemics'. If endemic subspecies were given lower conservation priority than endemic species, there is a danger that the division would reflect the bias introduced by taxonomists who focus attention on certain taxa, and may be more likely to classify them as full species.

### 2.3. Census technique

A modified transect walk technique (Pollard, 1977; Thomas, 1983) was used to assess butterfly abundance and richness. All butterflies entering an imaginary box (5 m long × 5 m wide × 2 m high) in front of the observer were identified and counted as he walked at a slow, steady pace along a track. A second observer recorded butterflies in an equivalent zone from 2 m to

the forest canopy, where present, using 8×30 binoculars to check identifications if necessary. Transects were standardised for duration (8 min or 4 min), and distance (500 m or 250 m) to ensure consistency among transects. Since the Comoran butterfly fauna has relatively few species, compared with most tropical areas, all species from the families investigated were distinguishable in flight.

In 1992, 71 transects, each of 8 min duration, were carried out in a representative selection of habitats over a range of elevations, and an additional 46 transects of 4 min duration were carried out in forest habitats. Analyses use either 8-min transects or 4-min transects; the two were not combined. In 1994, the 46 4-min forest transect routes were repeated, and an additional 91 (total = 137) transects of 4 min duration were carried out in the forest zone on the western slopes of Kartala (Fig. 1). Four forest habitat sub-categories were identified (Table 2). Transects that were assessed as being intermediate between forest sub-categories, or which passed through two different categories of habitat, were not used in the analyses.

### 2.4. Data analysis

We use the number of endemic taxa or non-endemic taxa recorded on a transect, *R*, as our measure of butterfly

Table 2  
Categories of forest on Grande Comore

Forest Category	Description
Pioneer forest on old lava flows	Canopy 3–8 m with scattered taller trees and a variety of shrub species on a substrate of lava.
Regenerating secondary forest	Canopy 3–8 m with scattered taller trees in areas which have been subject to selective logging. <i>Psidium</i> sp. constitute 80% or more of cover.
Underplanted mature forest	Canopy 8 m or higher with understorey composed largely of banana or other crops.
Mature non-underplanted forest	Canopy 8 m or higher with understorey composed largely of native plants

richness. Each transect provides a 'snapshot' sample of the butterflies present in the surrounding habitat, and is not intended as a comprehensive inventory. Richness was used in preference to an index of diversity for several reasons. First, the small numbers of species recorded on each transect make the interpretation of any diversity statistic difficult. Second, choice of an index of diversity is an arbitrary decision, giving different weightings to species number and species evenness; richness is less ambiguous and easier to interpret (Magurran, 1988). Finally, while diversity indices are less sensitive to variations in sample size, in this study a large sample (which would tend to increase recorded richness) is a valuable attribute of a site for conservation evaluations, i.e.  $R$  takes into account not only the species present, but also their abundance. For statistical analyses we used  $\sqrt{(R+0.5)}$ . This transformation is appropriate where the data are counts (Sokal and Rohlf, 1995), and in all cases it improved homogeneity of variance as judged by Levene's Test and analysis of residuals, so that the data met the assumptions necessary for parametric tests. Statistical analyses use Minitab 10.

### 3. Results

#### 3.1. General patterns of richness for endemic and non-endemic butterflies

Excluding hesperiid and lycaenid butterflies (see above), 33 butterfly taxa (18 non-endemics, 7 endemic species, and 8 endemic subspecies) were recorded on transects, and three additional species (all non-endemics) were recorded during casual recording. Full species lists are given by Lewis et al. (1993) and Harper et al. (1996). Species discovery curves for endemics and non-endemics reached an asymptote after *c.* 45 transect walks of 8 min (360 min of recording), suggesting that a longer fieldwork period would not have increased greatly the number of species recorded. Only five additional species from the Papilionidae, Pieridae and Nymphalidae have ever been recorded from Grande

Comore (Turlin, 1993–1996), so we are confident that the results give a fairly comprehensive impression of the status of the butterflies of the island.

For the 46 transect routes that were identical in 1992 (cool, dry season) and 1994 (hot, wet season),  $\sqrt{(R_{\text{endemic}}+0.5)}$  was significantly higher during the hot, wet season (two-tailed paired *t*-test;  $t=4.387$ ,  $n=46$ ,  $p<0.001$ ), consistent with previous studies of tropical insect seasonality (Wolda, 1987). For this reason, data from the two periods are not pooled. Broad patterns in richness were investigated using the 1992 data, when recording occurred over the full elevational range; the detailed analysis of forest habitats uses the data from 1994, when forest habitats were targeted.

Across the elevational range 0–1400 m, the 1992 data revealed a significant decrease with elevation in the total number of species recorded ( $\sqrt{(R_{\text{total}}+0.5)}=2.4405-6.72\times 10^{-4}$  elevation,  $n=71$ ,  $p<0.001$ ). However, this pattern masks contrasting elevational patterns for non-endemics and endemics (Fig. 2). Non-endemics

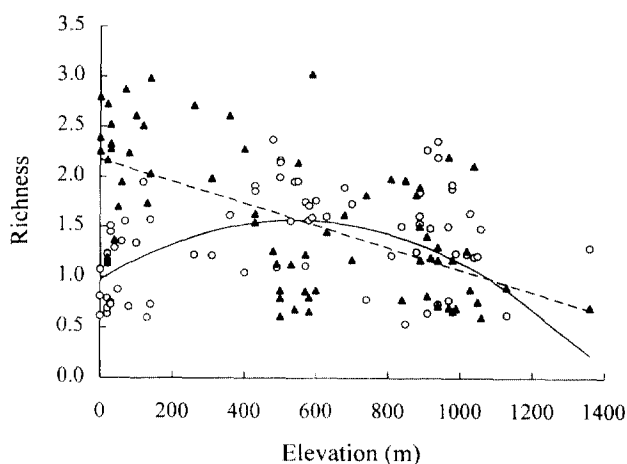


Fig. 2. Patterns in richness of endemic and non-endemic butterflies with elevation in the 0–1400 m elevation zone (1992 data, 8-min transects). Richness is plotted separately for endemic butterflies ( $\sqrt{(R_{\text{endemic}}+0.5)}$ ; open circles) and non-endemic species ( $\sqrt{(R_{\text{non-endemic}}+0.5)}$ ; filled triangles), and the best-fitting lines for endemics (solid line) and non-endemics (broken line) are shown. Data points have been displaced slightly to allow multiple points at the same value to be plotted.

Table 3  
Elevational effects on the richness of endemic butterflies in forest habitats

Forest category	<i>n</i>	Minimum elevation (m)	Maximum elevation (m)	<i>r</i>	<i>p</i>
Pioneer forest on old lava flows	26	780	1070	−0.018	ns
Regenerating secondary forest	49	500	1000	−0.238	ns
Underplanted mature forest	34	840	1180	−0.442	< 0.05
Mature non-underplanted forest	10	1040	1330	−0.523	ns
All categories	137	780	1810	−0.216	< 0.05

Forest habitat subcategories are defined in Table 2. Minimum and maximum elevations indicate the range of elevations within which transects were carried out for each forest category. *r* is the Pearson correlation coefficient between  $\sqrt{(R_{\text{endemic}} + 0.5)}$  and elevation.

have peak richness at low elevations, and richness declines with elevation ( $\sqrt{(R_{\text{non-endemic}} + 0.5)} = 2.1739 - 0.001107 \text{ elevation}$ ,  $n = 71$ ,  $p < 0.001$ ). Endemic richness shows a significantly humped pattern, with few endemics at low elevation, and a peak at mid elevations corresponding to the lower levels of the remaining forest habitats ( $\sqrt{(R_{\text{endemic}} + 0.5)} = 0.9710 + 0.002170 \text{ elevation} - 2 \times 10^{-6} \text{ elevation}^2$ ,  $n = 71$ ,  $p = 0.021$ ).

For endemics and non-endemics where there were at least five observations in total, we calculated elevational ranges for each taxon as the difference between the maximum and minimum elevations at which the taxon was recorded. Although endemics and non-endemics did not differ in the width of the elevational range occupied (Mann Whitney  $W = 192.5$ ,  $n_{\text{endemic}} = 12$ ,  $n_{\text{non-endemic}} = 15$ ,  $p = 0.2404$ ), the elevation at the mid point of their elevational range was significantly higher for endemics (Mann Whitney  $W = 230.0$ ,  $n_{\text{endemic}} = 12$ ,  $n_{\text{non-endemic}} = 15$ ,  $p = 0.0027$ ), again illustrating the importance of mid elevation (forest) habitats.

### 3.2. Changes with elevation within the forest

Across all forest habitat categories, there was a significant overall decrease in endemic richness with elevation ( $r = -0.216$ ,  $n = 137$ ,  $p < 0.05$ ). The trend within forest habitat categories was also for a decrease in endemic richness with elevation (Table 3), although this decrease was statistically significant only for underplanted forest, probably because of the narrow elevational range occupied by each forest type (Table 3). The decrease in richness with elevation reflects a general decrease in the abundance of individual endemic species with elevation (Fig. 3). Seven of the 10 endemics for which sufficient data exist peak in abundance below 900 m, and five of these peak in the very lowest elevational zone, where very little forest now remains.

### 3.3. Comparison of forest types

To compare forest types while avoiding the confounding effects of elevation, we focused recording

effort on a narrow elevational zone (800–1000 m elevation) within which the number of endemic species and subspecies recorded was unlikely to be affected significantly by elevation. Insufficient mature, non-underplanted forest remained at these elevations to assess the importance of completely undisturbed habitats, but pioneer forest on old lava flows, regenerating secondary forest and underplanted mature forest could all be compared. Full lists of endemic species and subspecies for the three forest types were very similar, but the habitats differed significantly in endemic richness (Fig. 4). Analysis of covariance using the General Linear Model (GLM) command confirmed that elevation had no significant effect on endemic richness within this zone ( $f_{1,55} = 0.55$ ,  $p = 0.461$ ), but habitat had a strong effect ( $f_{2,55} = 17.71$ ,  $p < 0.001$ ). In the full model, there was no significant habitat  $\times$  elevation

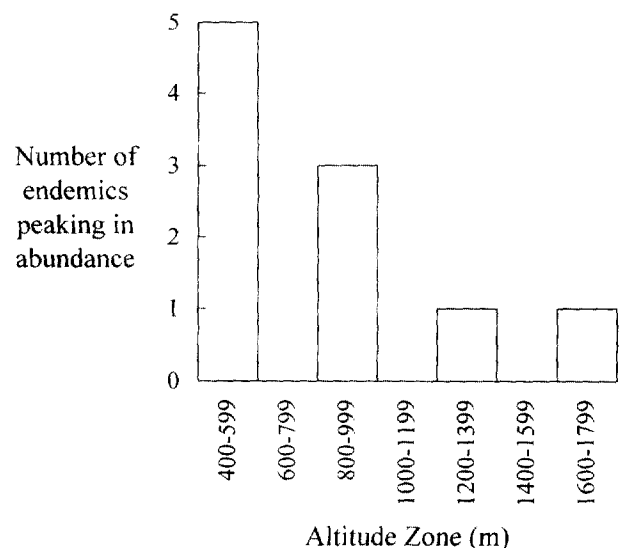


Fig. 3. Elevational zones in which the abundance of endemic butterfly species peaks in the forest (1994 data). Abundance was calculated for each species as the total number of individuals recorded in an elevational zone, divided by the total number of transects in the zone. No species peaked in abundance in the 600–799 m, 1000–1199 m and 1400–1599 m zones.

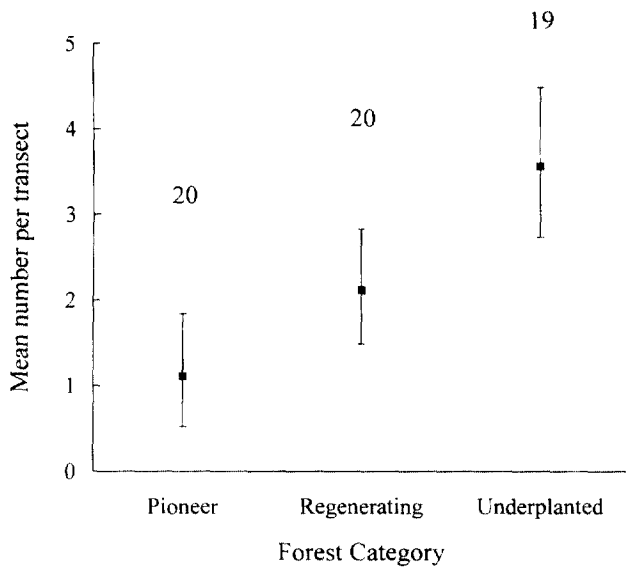


Fig. 4. Endemic richness in three forest habitat categories for the 800–1000 m elevation zone (1994 data). Values plotted are the mean number (with 95% confidence intervals) of endemics recorded on 4-min transects, back-transformed from means of  $\sqrt{(R_{\text{endemic}} + 0.5)}$ ; calculated in statistical analyses. Forest categories are defined in Table 2. Each of the three forest habitats differs significantly from the other two (Tukey–Kramer method for multiple comparisons). The value above means are sample sizes (number of 4-min transects) in each forest category.

interaction ( $f_{2,53} = 0.19, p = 0.827$ ). Multiple comparison tests (Tukey–Kramer method; Sokal and Rohlf, 1995) revealed that each habitat differed significantly from the other two in terms of endemic richness. Underplanted mature forest had the highest endemic richness, and pioneer forest on old lava flows had the lowest (Fig. 4).

To gain some indication of the relative importance of mature, non-underplanted forest, each of 10 transects in mature non-underplanted forest was paired with a transect in underplanted mature forest at the same elevation (selected at random if more than one had been carried out at the same elevation), and the habitats were compared for  $\sqrt{(R_{\text{endemic}} + 0.5)}$  using a two-tailed paired *t*-test ( $t = 0.372, n = 10, p = 0.718$ ). Although the sample size was small because so little mature non-underplanted forest remained below 1200 m, the lack of significance suggests that endemic richness may be rather similar in the two habitats.

### 3.4. Habitat preferences for individual endemics

Again using data from the 800–1000 m elevation zone to control for elevation, all endemics occurring in this zone (except the two *Henotesia* species) occurred at higher density in underplanted mature forest than in pioneer forest on old lava flows or regenerating secondary forest (Table 4). In contrast, of the eight non-endemic

Table 4  
Relative abundance of endemic butterflies in three forest habitat categories, within the 800–1000 m elevational zone

Species	Forest Category		
	Pioneer forest old lava flows (20)	Regenerating secondary forest (20)	Underplanted mature forest (19)
<i>Papilio d. humbloti</i>	0.00	0.07	0.16
<i>Papilio aristophontes</i>	0.50	0.27	0.84
<i>Mylothris ngaziya</i>	0.80	1.67	4.63
<i>Neptis cormilloti</i>	0.15	0.50	2.00
<i>Amauris comorana</i>	0.00	0.08	0.42
<i>Henotesia comorensis</i>	0.30	0.28	0.16
<i>Henotesia comorana</i>	0.05	1.67	1.42
Total	1.80	4.54	9.63

Number of transects in parentheses. Abundance values are the mean number of individuals observed per 4-min transect. Only species with at least five individuals recorded in this zone are listed.

mic taxa recorded on forest transects, all but two (*Melanitis leda* and *Bicyclus anynana*) had highest abundance in pioneer forest on old lava flows or regenerating secondary forest. The remaining 10 non-endemic species observed during fieldwork were not recorded at all on forest transects. This broad difference between endemics and non-endemics is reflected by a significant negative correlation between  $\sqrt{(R_{\text{endemic}} + 0.5)}$  and  $\sqrt{(R_{\text{non-endemic}} + 0.5)}$  for 8-min transects in 1992 ( $r = -0.316, n = 71, p < 0.01$ ) and no significant correlation for 4-min transects in 1994 ( $r = -0.093, n = 137, n.s.$ ).

## 4. Discussion

### 4.1. Endemics and non-endemics compared

On Grande Comore, and elsewhere (Thomas and Mallorie, 1985; Spitzer et al., 1993), geographically restricted or endemic butterfly species are often biotope specialists, although they can be among the most abundant species at the sites where they occur. However, the situation on Grande Comore contrasts with previous studies of butterflies and other organisms (e.g., Järvinen, 1982; Thomas and Mallorie, 1985; Wheeler, 1988) which have found that geographically restricted species tend to occur in the most species-rich communities. On Grande Comore, the most species-rich communities are in man-modified habitats, where very few endemics occur. Conversely, the habitats that are richest in endemic species (forests) support very few non-endemics, and there is a significant negative correlation or no significant correlation between endemic richness and non-endemic richness, depending on the range of habitats and elevations considered. If the goal

is to set conservation priorities, endemics and non-endemics must be considered separately.

The elevational pattern in richness of endemic and non-endemic taxa (Fig. 2) must to a large extent result from human interference with habitats, highlighting the fact that ecological (e.g. MacArthur, 1972) and non-biological (Colwell and Hurtt, 1994) explanations for elevational patterns in richness are appropriate only in uniform, relatively undisturbed habitats. Originally, much of Grande Comore, including coastal areas, was covered by forest (Benson, 1960; Battistini and Vérin, 1984). It seems likely that the endemics evolved at a time when almost all of the island was covered by forest, and that most endemic butterflies would originally have occurred at lower elevations than at present. Support for this hypothesis comes from the observation of two endemics, *Mylothris ngaziya* and *Charaxes castor comoranus* at 200 m or below on two of the extinct coastal volcanoes (N'Gouni and Moindzaza: Fig. 1), which retain elements of the original forest cover on the steep inner slopes of their cones. These species were not otherwise recorded below the lower forest fringes at 500 m. In contrast, many of the non-endemics may be relatively recent additions to the Comoran fauna, and would have been able to move in to colonise the open habitats created as humans began to clear the forests, perhaps 1000 years ago (Battistini and Vérin, 1984).

#### 4.2. Threats and priorities on Grande Comore

Loss of forest habitats on the Comoros is a gradual process, driven largely by agricultural expansion rather than timber exploitation. Selective tree-felling, burning and banana-planting in previously uncultivated forests was frequently observed during fieldwork. This habitat change is rapidly encroaching on the elevational zone where the richness of endemic butterflies is greatest, and where the abundance of individual endemics is highest. The situation on Grande Comore may be comparable to that in many other parts of the tropics where endemic species survive in 'islands' of forest on steep mountain slopes surrounded by flatter land where the forest has been destroyed. Some of these endemics will have evolved in the high elevation zones, but many if not most will be lowland species which have survived on the mountain slopes simply because these are the only places where forests remain. In the latter case, the maximum elevation at which populations are self-supporting may be relatively low. If habitat change is pushing back the lower limits of the forest, these species are likely to be among the first to go extinct.

On Grande Comore, by controlling for elevational effects, we are able to compare habitats that have been subjected to different forms and varying degrees of human disturbance in terms of their 'value' for endemic butterflies. At present, the underplanted forest habitats

resulting from low-intensity agriculture, where the canopy of the forest remains intact, have the highest abundance and richness of endemic butterflies, probably comparable with the few remaining areas of undisturbed forests at the same elevation. Endemic birds (Louette, 1988; Louette and Stevens, 1992) also appear to be thriving in these underplanted forests. Provided that human activity in this zone does not intensify—and provided that forest can regenerate where the understorey is composed of dense banana cover—this habitat seems likely to remain of importance for endemic butterflies.

However, observations from lower elevations on Grande Comore and from elsewhere on the archipelago (Benson, 1960; Battistini and Vérin, 1984), suggest that low-impact agriculture is invariably the precursor of more intensive human activity, which results either in plantations with no forest cover, or regenerating secondary forest. Neither habitat supports many endemic butterflies. Furthermore, regenerating secondary forests probably lack many host plants, but are rich in nectar plants, so many of the butterflies observed there may be temporary visitors from nearby areas where the structure of the forest remains more intact. The final forest category, pioneer forest on old lava flows, is unlikely to be exploited rapidly, since the soils are too thin for most crops. Unfortunately, this habitat is unlikely to provide a refuge for the endemic butterflies: abundance and richness was even lower than in regenerating secondary forests (Fig. 4). However, as succession progresses, pioneer forests will develop into mature forests. In the longer term (hundreds of years), their conservation is of great importance, but to ensure survival of most endemic butterfly taxa in the short term, mature forests may need to be prioritised for conservation.

At present there are no protected terrestrial areas in the Comoros, a characteristic shared by only a handful of the world's nations (Balmford and Long, 1995). A UNEP/UNESCO/IUCN project on the Comoros is currently drafting proposals for environmental legislation. In the face of continuing rapid habitat loss, it should be a priority to designate a forest reserve which would ensure the survival of the forest endemics. Butterflies should not be assumed to provide an indicator group for other endemic animals and plants (Thomas and Mallorie, 1985; Kremen, 1992), but equivalent data for other taxa are lacking, and the key habitat zone for endemic butterflies (mature forest, particularly below 1000 m elevation) is being destroyed rapidly. Inevitably, any future reserve designation in the Comoros is likely to be opportunistic, with the choice of designated areas constrained by criteria other than pure conservation value, for example ease of access, current land-use and the impact on the local human population of taking a large area of forest out of cultivation. Studies such as this one may be of value in suggesting the importance

of zones or broadly defined habitat areas rather than specific sites.

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