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Butterfly biogeography and endemism on tropical Pacific islands

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Butterfly distributions on 26 tropical Pacific archipelagos were analysed to examine the effects of geography on diversity and endemism. The total butterfly fauna for each archipelago was divided into continental (found also on continental areas), Pacific (found within more than one archipelago but not outside of the study area), and endemic species (restricted to a single archipelago). Numbers and proportions of each species were related to eight geographic variables by stepwise multiple linear regression analysis. Total area of an archipelago and distance from other land masses were important predictors of the number of species within an archipelago. Proportions of butterfly species in each category were related differently to the geographic variables, with endemism being promoted by the number of large islands within an archipelago. Relative to birds, butterflies have been less successful in colonizing remote archipelagos and have much lower levels of endemism. Even if colonization is successful, butterfly speciation may be constrained by the mechanics of coevolution with available host plants.

ADDITIONAL KEY WORDS:—Archipelagos – birds – butterflies – diversity – Pacific Ocean – speciation.

CONTENTS

INTRODUCTION

Endemism on islands and archipelagos is strongly correlated with geographic features (Williamson, 1981; Adler, 1992). Among birds on tropical Pacific archipelagos, for instance, the level of endemism is related positively to archipelago isolation and the number of large islands—circumstances in which both intra- and inter-archipelago speciation can proceed (Mayr, 1965; Diamond, 1977; Adler, 1992). Moreover, taxa isolated on the same island may respond differently over evolutionary time to geographic features of that island.

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Such differential responses have been attributed to taxon-specific dispersal ability, susceptibility to extinction, and the ability to change habitat affinities and dispersal (e.g. Mayr, 1965; Diamond, 1984). Thus, the poor dispersal ability of lizards relative to birds is at least partly responsible for the much higher proportion of endemic lizards (0.62; Bauer & Vindum, 1990) than of birds (0.27; Adler, 1992) on New Caledonia. While there are many other examples of differences in island endemism among distantly related taxa (e.g. Diamond, 1984), geographic correlates of endemism and differences among organisms have received little quantitative analysis.

Butterflies on the geographically diverse tropical Pacific islands provide an excellent opportunity to examine patterns of endemism. These butterfly faunas are sufficiently known to permit robust statistical analysis. By comparing butterflies with birds, it is possible to discern patterns in speciation and endemism among distantly related taxa that employ a similar dispersal mechanism, namely flight. Accordingly, patterns of distribution and endemism for butterflies were examined and compared with those of birds on the same archipelagos (Mayr, 1965; Diamond, 1980; Adler, 1992).

MATERIAL AND METHODS

Following archipelago definitions of Adler (1992), species lists of indigenous butterflies (Papilionoidea) were compiled from the literature (Table 1) for 26 oceanic archipelagos and isolated islands in the tropical Pacific Ocean (Figure 1). A conservative approach was used when assessing butterfly distributions, and questionable records were omitted. Distributional data for the Bismarcks, Solomons, and Vanuatu were taken principally from D'Abrera (1971). Detailed single-archipelago surveys of the butterfly fauna were used for Fiji (Robinson, 1975) and New Caledonia (Holloway & Peters, 1976). All danaine records for the study area were taken from Ackery & Vane-Wright (1984). Records for the monarch butterfly (*Danaus plexippus*) were ignored because of widespread human introduction (e.g. Scudder, 1875). Although precise numbers of butterfly species on particular Pacific archipelagos may deviate from the values given here depending upon taxonomic treatment and intensity of collection (Table 1), the magnitude of such variation is likely to be small compared to the substantial differences in species numbers between archipelagos.

For each island group, the total number of species and the numbers of continental (species found also on continental areas including New Guinea), Pacific (species endemic to tropical Pacific islands but found within more than

TABLE 1. Butterfly families of the tropical Pacific islands

Family	Island groups occupied	Number of species			
		Total	Continental	Pacific	Endemic
Papilionidae	10	30	16	2	12
Pieridae	13	29	14	1	14
Nymphalidae	26	115	62	7	46
Lycaenidae	18	111	65	18	28

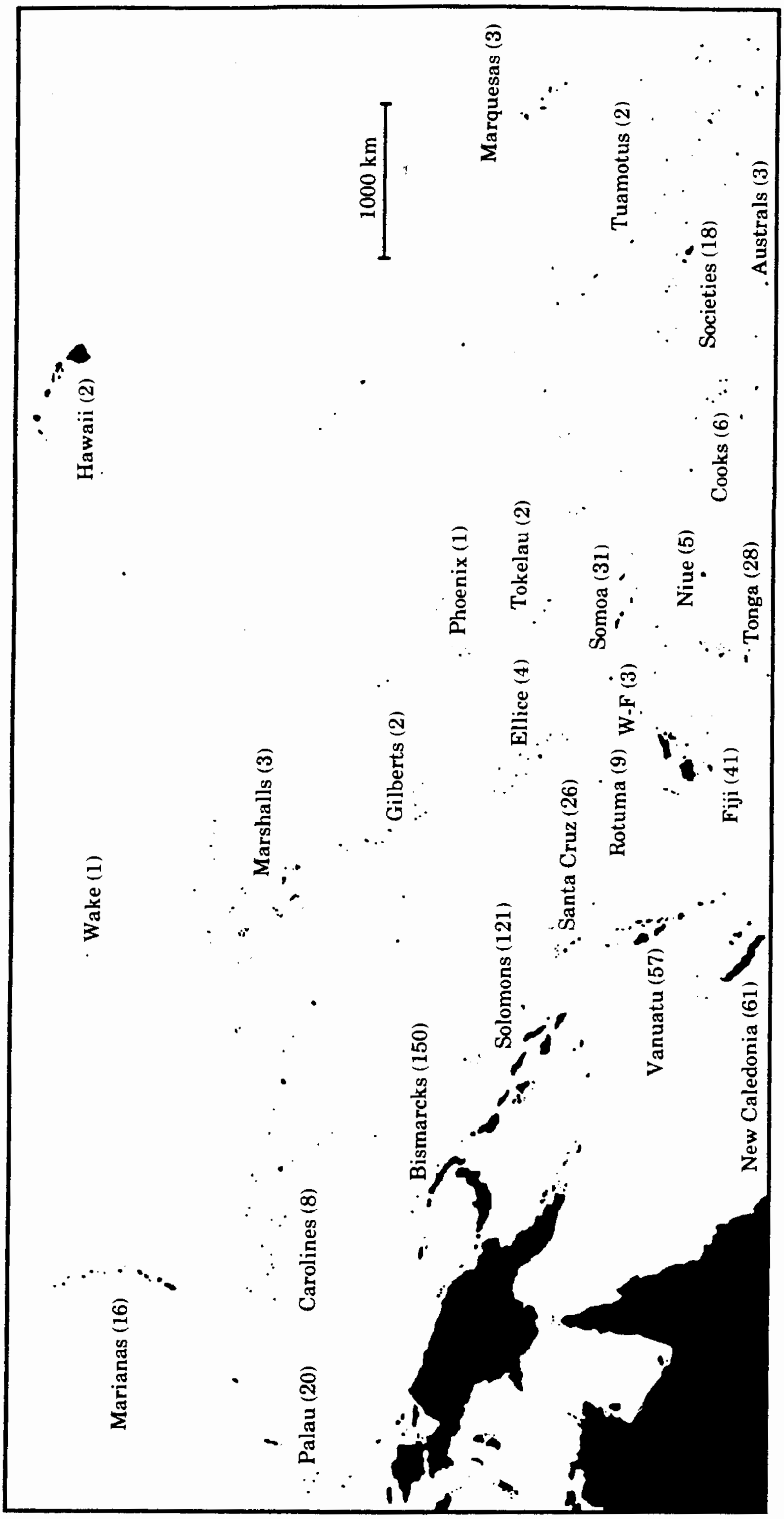

Figure 1. Map of the study area in the tropical Pacific Ocean with numbers of butterfly species within each archipelago in parentheses. New Guinea and eastern Australia appear in the lower left of the map, and archipelago limits follow Adler (1992). The map is bounded to the north and south by the Tropics of Cancer and Capricorn, respectively. W-F signifies Wallis and Futuna.

one archipelago), and endemic species (species endemic to a single archipelago or isolated island) were tabulated. Eight physical variables were used to describe the geography of each archipelago or isolated island: total land area of the archipelago; numbers of islands > 1000 km^2, 500 km^2, and 100 km^2; maximum elevation; and distances to the nearest continental source area including New Guinea, the nearest adjacent land mass, and the nearest adjacent larger land mass (see Adler, 1992). All geographic variables except numbers of islands were $\log_{10}$ transformed to reduce variance.

Distributions of each family among the 26 island groups and numbers of species in each species category were examined first, and then linear regression analysis was used to construct species-area power curves (log–log plots) for the total species pool and for each of the three species categories. Each of the 26 archipelagos or isolated islands represented a single observation. Stepwise multiple linear regression analysis was used to relate the numbers and proportions of species in each category to the eight geographic variables. A variable was included in a regression model if its P value was < 0.05 and was removed if the P value fell above 0.10. Only those island groups with at least 10 total species were included in the regressions of species proportions; all proportions were arcsine transformed. Numbers of butterflies among the three species categories (continental, Pacific, and endemic) were compared with those of birds using chi-square analysis. This analysis was conservative since several dozen species of endemic birds were extirpated apparently by early human settlers (e.g., James & Olson, 1991; Olson & James, 1991; Milberg & Tyrberg, 1993).

RESULTS

The tropical Pacific butterfly fauna consists of 285 species in four families, of which 157 are continental and 100 are endemic to a single island or archipelago. The Nymphalidae and Lycaenidae are the most widespread and species-rich families (Table 1). Every island group in this study has at least one native nymphalid, and only the most remote and species-poor archipelagos lack lycaenids. The other families extend eastward from New Guinea, Australia, and Asia to varying degrees; papilionids have reached Samoa and the Marianas and pierids have reached Tonga and the Marianas. Among the Nymphalidae, satyrines extend to the Society Islands and the Marianas, and the danaines extend all the way to the Society, Cook, and Ellice Islands. A lone libytheine has inexplicably reached the Marquesas, but the subfamily is absent from all other archipelagos except the Bismarcks, Solomons, and New Caledonia (Holloway, 1983). The only amathusiine in the region is confined to the Bismarcks and Solomons. The four families of the region have similar numbers of endemic species relative to continental species ($\chi^2 = 5.28$, $P = 0.152$, df $= 3$).

The small low-lying atolls of Micronesia (Marshalls, Gilberts, Ellice, Phoenix, Tokelau, and Wake) and remote easternmost archipelagos (Tuamotus, Australs, Marquesas, and Hawaii) all have fewer than five species of butterflies. Most of these species are continental, and only three are endemic (Table 2). The large near archipelagos (Bismarcks and Solomons) are rich in both total species and endemics. All other island groups have a small or moderate number of total species and are poor in endemics.

Total land area of an island group accounts for over 50% of the variation in

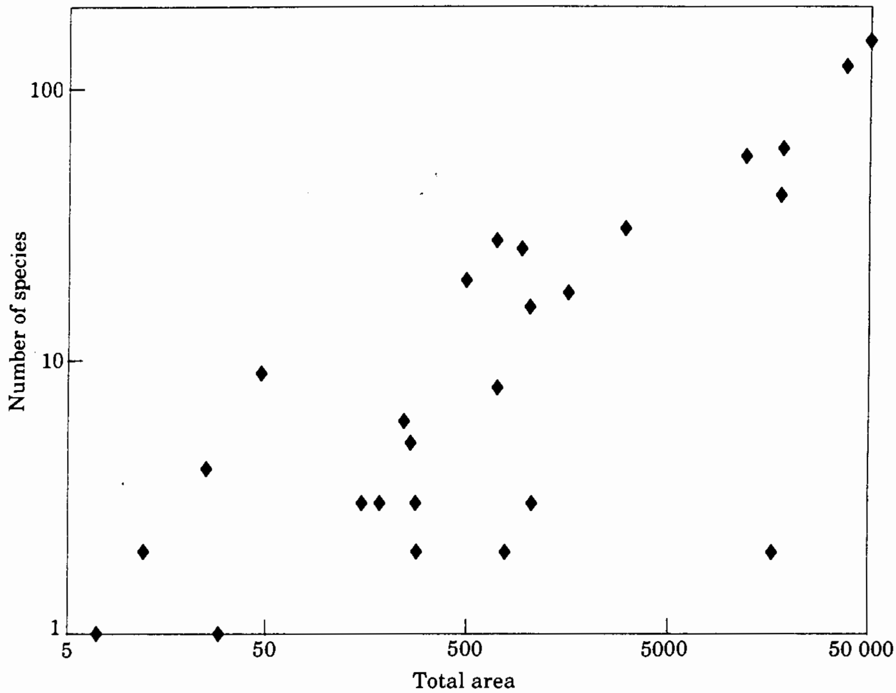

Figure 2. Plot of the relationship between $\log_{10}$ number of species within an archipelago and $\log_{10}$ total land area (km^2).

the numbers of species in each species category (Table 3). In the regression for all species, Hawaii (the fifth largest archipelago) has only two species and lies far below other archipelagos of similar size (Figure 2). The slope of the species-area regression is steepest for endemic species and most gradual for Pacific species. Thus, similar increases in area result in greater increases in the number of endemic species than in Pacific and continental species. When other geographic variables are considered, however, island isolation (either from continental source areas or adjacent archipelagos) is a better predictor of the number of all and Pacific species than area or elevation (Table 4). In the total species regression on isolation, the two least isolated archipelagos (the Bismarcks and Solomons) and the most isolated archipelago (Hawaii) are far removed from the other more tightly clustered archipelagos (Figure 3). If these three archipelagos are removed from analysis, the remaining 23 archipelagos nonetheless show a strong relationship between numbers of species and distance to the nearest archipelago ($R^2 = 0.50$, $F = 20.89$, $P = 0.0002$). Isolation and area together account for 75% of the variation in the total number of species within an archipelago. For continental and endemic species, area enters the regression model first, but distance to other land masses remains an important predictor. Thus, the number of species within an archipelago is related negatively to isolation and positively to total land area. Isolation and area together account for at least 60% of the variation in species numbers for each species category.

In contrast to species numbers, species proportions within categories were much less dependent on total land area and showed significant relationships with

TABLE 2. Numbers of butterfly species on each of the 26 archipelagos or isolated islands included in this study and references used to compile the butterfly lists

Archipelago	Number of species				References
	Total	Continental	Pacific	Endemic	
Tuamotus	2	2	0	0	Viette, 1950; Holloway & Peters, 1976
Australs	3	3	0	0	Poulton & Riley, 1928; Viette, 1950; Clarke, 1971; Robinson, 1975; Holloway & Peters, 1976
Cooks	6	4	2	0	Druce, 1892; Hopkins, 1927; Poulton & Riley, 1928; Robinson. 1975; Holloway & Peters, 1976; Samson, 1979; Ackery & Vane-Wright, 1984
Marquesas	3	1	1	1	Hopkins, 1927; Poulton & Riley, 1928, 1934; Holloway, 1983
Societies	18	11	5	2	Druce, 1892; Hopkins, 1927; Poulton & Riley, 1928, 1934; Viette, 1950; Given, 1968; Robinson, 1975; Holloway & Peters, 1976; Samson, 1979; Holloway, 1983; Ackery & Vane-Wright, 1984; Hara & Hirowatari, 1989; Hirowatari, 1990a, b, 1992
Niue	5	4	1	0	Given, 1968; Robinson, 1975; Samson, 1979; Ackery & Vane-Wright, 1984
Samoa	31	21	6	4	Druce, 1892; Swezey, 1921; Hopkins, 1927; Comstock, 1966; Robinson, 1975; Holloway & Peters, 1976; Samson, 1979; Ackery & Vane-Wright, 1984
Wallis-Futuna	3	1	2	0	Hopkins, 1927; Ackery & Vane-Wright, 1984
Tonga	28	20	7	1	Druce, 1892; Hopkins, 1927; Poulton & Riley, 1928; Comstock, 1966; D'Abrera, 1971; Robinson 1975; Holloway & Peters, 1976; Samson, 1979; Ackery & Vane-Wright, 1984
Fiji	41	28	7	6	Druce, 1892; Hopkins, 1927; D'Abrera, 1971; Robinson, 1975; Holloway & Peters, 1976; Samson, 1979; Ackery & Vane-Wright, 1984
Rotuma	9	7	2	0	Robinson, 1975; Holloway & Peters, 1976
Vanuatu	57	46	11	0	Druce, 1892; Hopkins, 1927; Viette, 1950; Howarth, 1962; D'Abrera, 1971; Robinson, 1975; Holloway & Peters, 1976; Samson, 1979; Ackery & Vane-Wright, 1984
New Caledonia	61	45	5	11	Druce, 1892; Viette, 1950; D'Abrera, 1971; Robinson, 1975; Holloway & Peters, 1976; Samson, 1979; Ackery & Vane-Wright, 1984
Santa Cruz	26	21	5	0	Ackery & Vane-Wright, 1984; Samson, 1979

TABLE 2.—*continued*

Archipelago	Number of species: Total	Continental	Pacific	Endemic	References
Solomons	121	70	16	35	Howarth, 1962; D'Abrera, 1971; Holloway & Peters, 1976; Samson, 1979; Ackery & Vane-Wright, 1984
Bismarcks	150	102	12	36	D'Abrera, 1971; Holloway & Peters, 1976; Samson, 1979; Ackery & Vane-Wright, 1984
Palau	20	20	0	0	Semper, 1906; Matsumura, 1915a, b; Nakamura, 1929a; Hirose, 1934
Carolines	8	8	0	0	Semper, 1906; Matsumura, 1915a; Hirose, 1934
Marianas	16	13	1	2	Matsumura, 1915a, b; Schultze, 1925; Nakamura, 1929b; Hirose, 1934; Swezey, 1942; Zimmerman, 1958; Robinson, 1975; Samson, 1979; Ackery & Vane-Wright, 1984
Marshalls	3	3	0	0	Matsumura, 1915a; Hirose, 1934; Clark, 1951; Samuelson & Nishida, 1987
Gilberts	2	2	0	0	Butler, 1885; Woodford, 1885; Hopkins, 1927; Van Zwaluwenburg, 1943; Holloway & Peters, 1976
Ellice	4	2	2	0	Butler, 1885; Woodford, 1885; Hopkins, 1927; Robinson, 1975; Holloway & Peters, 1976; Ackery & Vane-Wright, 1984
Phoenix	1	1	0	0	Van Zwaluwenburg, 1955
Tokelau	2	2	0	0	Comstock, 1966; Holloway & Peters, 1976
Wake	1	1	0	0	Swezey, 1926
Hawaii	2	0	0	2	Zimmerman, 1958

additional geographic factors (Table 4). The proportion of continental species in an archipelago fauna decreases as island elevation increases, while endemism is enhanced by an increased number of large islands within an archipelago. The Bismarcks and Solomons, both with several large islands > 1000 km^2, thus have the highest levels of endemism among the archipelagos considered. The proportion of Pacific species in an archipelago increases with distance to source

TABLE 3. Species-area power regressions for butterflies on tropical Pacific archipelagos. N is the number of archipelagos with at least one species in the species group, c is the intercept, and z is the slope

Group	N	c	z	R^2	F	P
All species	26	−0.34	0.45	0.57	32.43	0.0001
Continental species	25	−0.51	0.49	0.67	47.16	0.0001
Pacific species	16	−0.36	0.29	0.54	16.39	0.0012
Endemic species	10	−1.98	0.70	0.75	24.46	0.0011

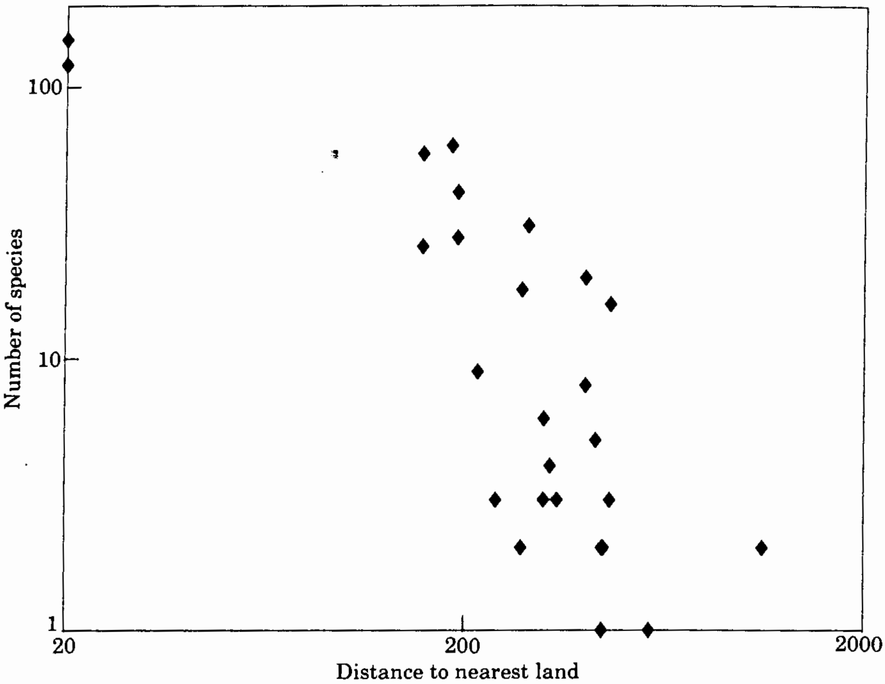

Figure 3. Plot of the relationship between $\log_{10}$ number of species within an archipelago and $\log_{10}$ distance (km) to the nearest body of land.

areas and elevation and decreases with area; the relatively small but high islands of Samoa, Tonga, and the Societies have the greatest proportions of Pacific species. Relative to birds, there is a significant excess of continental butterflies and a deficiency of species endemic to a single archipelago or island (Table 5). By contrast, proportions of butterflies and birds in the Pacific category are similar.

TABLE 4. Regression models of $\log_{10}$ number of butterfly species or proportion of species and the geographical variables. Variables are listed in the order entered into a stepwise regression. n is the number of archipelagos with at least one species in a particular species category (numbers of species) or the number of archipelagos with at least 10 species (proportions of species)

Category	n	Regression model	R^2	F	P
		Numbers of species			
All species	26	2.12 − 0.83 (nearest land) + 0.29 (area)	0.75	33.63	0.0001
Continental species	25	1.30 + 0.39 (area) − 0.46 (source)	0.75	33.38	0.0001
Pacific species	16	2.29 − 0.76 (nearest land)	0.60	21.40	0.0004
Endemic species	10	0.14 + 0.46 (area) − 0.54 (nearest land)	0.94	51.87	0.0001
		Proportions of species			
Continental species	11	2.89 − 0.65 (elevation)	0.76	28.09	0.0005
Pacific species	11	− 0.52 + 0.05 (source) + 0.26 (elevation) − 0.08 (area)	0.89	18.00	0.0011
Endemic species	11	0.04 + 0.04 (number islands > 1000 km^2)	0.67	18.41	0.0020

TABLE 5. Statistical distribution of birds and butterflies among three species categories of the tropical Pacific archipelagos. Observed and expected numbers and χ^2 values are given for each cell. Model $\chi^2 = 52.49$ (df = 2, $P < 0.001$)

		Continental	Pacific	Endemic
Birds	observed	143	50	292
	expected	189	49	247
	χ^2	11.18	0.02	8.23
Butterflies	observed	157	28	100
	expected	111	29	145
	χ^2	19.02	0.03	14.01

DISCUSSION

Some species of butterflies are highly mobile and capable of long-distance trans-oceanic dispersal (e.g. Holzapfel & Harrell, 1968; Fox, 1978; Farrow, 1984). Even the most remote archipelagos of the tropical Pacific have been colonized by butterflies. The Pacific butterfly fauna is derived originally from Australia, New Guinea, and Asia and secondarily from adjacent archipelagos through successive invasions along stepping-stone routes (Robinson, 1976; Holloway, 1983). Despite their dispersal powers, however, butterflies are less likely than birds to become established on remote archipelagos. Numbers of bird and butterfly species are remarkably similar on the less remote archipelagos east of New Guinea (e.g. Bismarcks: birds 168, butterflies 150; Vanuatu: birds 56, butterflies 57; Samoa: birds 33, butterflies 31). On the most remote archipelagos, however, the numbers of bird species are far greater than of butterflies. For instance, Hawaii has been colonized successfully many times by birds but only twice by butterflies.

The lesser ability of butterflies to become established on remote archipelagos is also reflected in the relationships between numbers of bird and butterfly species and the geographic variables. Archipelago area is the most important of the geographic variables in explaining variation in bird species richness (Adler, 1992), whereas isolation generally is the most important for butterflies. The greater effect of island isolation on butterfly establishment may simply reflect the lesser flight capacities of butterflies compared to birds (see below). Interestingly, the relationships between species numbers in the three species categories and island area (Table 3) illustrate an effect also described by Scott (1972) for Antillean butterflies. Namely, the number of endemic species increases more quickly with island area than does the number of more widely distributed categories (continental or Pacific). Birds on tropical Pacific archipelagos show a similar pattern. If speciation and endemism follow directly from effects of genetic isolation over time, larger island areas would be more conducive to differentiation between populations because of a decreased probability of extinction and consequently a longer population lifetime (Mayr, 1965). Relative to more widely dispersed species, there would be more endemic species on larger islands, as is empirically the case.

Presence of a species within an archipelago is a function of both dispersal and colonizing ability. By virtue of their smaller size, butterflies have much lower flight speeds than do birds (Greenewalt, 1962, 1975). Directed dispersal by flight will therefore be less effective, although butterflies may be more susceptible to random dispersal by ambient atmospheric motions that exceed maximum flight speeds. In any dispersal scenario involving time-dependent mortality, however, butterflies will be less likely to survive because of their much shorter lifespans. Pre-adult stages passively dispersing on floating debris will be similarly affected. Moreover, successful butterfly colonization following arrival at an archipelago is constrained by the availability of suitable host plants. Butterflies are generally specialized herbivores, feeding as larvae only on a narrow range of host plants or even on a single species (Ehrlich & Raven, 1964; Ackery & Vane-Wright, 1984). The flora of Pacific islands is as constrained biogeographically as are insect distributions and is characterized by reduced species numbers and high rates of endemism (e.g. Balgooy, 1971). Thus, plant species composition of islands provides an additional constraint against which butterfly colonization must operate. An analogous constraint will apply to myrmecophilous lycaenids (Balduf, 1974). This constraint is of much less significance for birds, which will interact with the flora only at community-wide dietary levels. It is noteworthy that two of the most geographically widespread butterfly species, namely *Hypolimnas bolina* (found on 24 archipelagos), and *Precis villida* (17 archipelagos) are polyphagous and accept a wide variety of host plants (Common & Waterhouse, 1972; Ackery, 1988).

Although the nymphalids and lycaenids are the most dominant families in terms of distribution and numbers of species, neither family accounts for a disproportionate number of endemic species. Speciation within the tropical Pacific has accounted for only 45% of the present butterfly fauna, and 22% of those species that are endemic to the region are widespread. The remaining 55% of the fauna is comprised of continental forms that have not speciated after arrival on the islands. This magnitude of speciation contrasts sharply with that of birds; over 70% of the tropical Pacific avifauna is endemic to the region, and only 13% of those endemics is widespread in the Pacific (Adler, 1992). If the extirpated endemic birds are included, the difference between birds and butterflies is even more extreme.

Butterflies have not undergone the extensive adaptive radiations (via intra-archipelago speciation) that have resulted in the numerous endemic birds of Hawaii and other remote archipelagos (Diamond, 1977). Butterfly speciation in the Pacific archipelagos (as manifested by rates of endemism) is primarily a result of limited inter-archipelago speciation and some intra-archipelago speciation in the Bismarcks and Solomons (Table 2). These archipelagos are both the largest in land area and closest to a continental source. Even if butterfly colonization is successful, speciation may be constrained by the mechanics of insect-plant coevolution that prevent rapid diversification. Closely related host plants simply may not be available for the evolution of new plant associations, thereby impeding the formation of new butterfly species. At present, host plant data for the tropical Pacific butterfly fauna are insufficiently detailed to evaluate this hypothesis. In the context of island biogeography, detailed correlations of host plant availability and endemism may yield considerable insight into the process of speciation in butterflies.

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