CHAPTER

6

Butterfly Diversity and a Preliminary Comparison with Bird and Mammal Diversity

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Butterflies are among the best-known insects—an estimated 90% of the world's species have scientific names. As a consequence, their biology has been extensively investigated (Vane-Wright and Ackery, 1984), and they are perhaps the best group of insects for examining patterns of terrestrial biotic diversity and distribution. Butterflies also have a favorable image with the general public. Hence, they are an excellent group for communicating information on science and conservation issues such as diversity.

Perhaps the aspect of butterfly diversity that has received the most attention over the last century is the striking difference in species richness between tropical and temperate regions. For example, Bates (1875) wrote that it would convey some idea of the diversity of butterflies (in the neighborhood of Belém, a town near the mouth of the Amazon River) when he mentioned that about 700 species are found within a hour's walk of the town, whereas the total number found in the British Islands does not exceed 66, and the whole of Europe supports only 321. This early comparison of tropical and temperate butterfly richness has been well-confirmed (e.g., Owen, 1971; Scriber, 1973).

A general theory of diversity would have to predict not only this difference between temperate and tropical zones, but also patterns within each region, and how these patterns vary among different animal and plant groups. However, for butterflies, variation of species richness within temperate or tropical regions, rather than between them, is poorly understood. Indeed, comparisons of numbers of species among the Amazon basin, tropical Asia, and Africa are still mostly "personal communication" citations, even for vertebrates (Gentry, 1988a). In

Butterflies are conspicuously diverse in tropical forests.

other words, unlike comparisons between temperate and tropical areas, these patterns are still in the documentation phase.

In documenting geographical variation in butterfly diversity, we make some arbitrary, but practical decisions. Diversity, number of species, and species richness are used synonymously; we know little about the evenness of butterfly relative abundances. The New World fauna makes up the preponderance of examples because we are most familiar with these species. By focusing on them, we hope to minimize the errors generated by imperfect and incomplete taxonomy. Although what is and is not a butterfly is technically controversial (e.g., Reuter, 1896; Kristensen, 1976; Scoble, 1986; Scoble and Aiello, 1990), we follow tradition (e.g., Bates, 1861; Kuznetsov, 1915, 1929; Ford, 1945) in which butterflies consist of skippers (Hesperioidea) and true butterflies (Papilionoidea).

The first three sections of this chapter summarize general patterns of butterfly diversity throughout the world, within the conterminous United States, and in the Neotropics, respectively. The fourth section points out, albeit preliminarily, how the distributions of butterflies—and presumably other insects—paint a different biogeographical picture of the world than the distributions of birds and mammals. Finally, we briefly discuss the significance of the observed patterns for conservation and for the study of diversity.

GLOBAL PATTERNS OF BUTTERFLY DIVERSITY

There are about 13,750 species of true butterflies in the world. Ehrlich and Raven (1965) estimated 12,000-15,000, and Robbins (1982) narrowed the range to 12,900-14,600 (including an estimate for undescribed species). Shields (1989) tabulated 13,688 described species. Since Robbins used sources published after 1965 and Shields used post-1982 papers for information, these estimates are somewhat independent, and their similarity indicates that 13,750 species of true butterflies is a reasonable "ballpark" figure, almost assuredly accurate within 10% and probably within 5%.

There are about 17,500 species of butterflies (true butterflies plus skippers) in the world. Ehrlich and Raven did not tabulate numbers of all butterflies, but Robbins estimated 15,900-18,225 species in the world, including estimates of undescribed species. Shields counted 17,280 species, including many synonyms but excluding undescribed species. The estimate of 17,500 species of butterflies in the world is again probably accurate within 10% (15,750-19,250 species).

The number of species of butterflies in each of the world's major biogeographical realms is presented in Figure 6-1, modified from Ackery et al. (1995) for the Ethiopian realm and from Robbins (1982) for the others. The estimates for the Nearctic, Palearctic, and Ethiopian realms are reasonably accurate because their faunas are fairly well-documented. The numbers for the more poorly known Oriental-Australian (innumerable islands) and neotropical realms (literally hundreds of undescribed metalmark, skipper, and hairstreak butterflies) are less accurate, probably within 10% of actual species richnesses.

Species diversity is greater in tropical than temperate areas (Figure 6-1). Of the two northern temperate realms, the Palearctic has greater area and more species than the Nearctic. These temperate realms have fewer species than the primarily tropical neotropical, Ethiopian, and Oriental-Australian realms. Among all realms, the Neotropics has the richest butterfly fauna, approximately equal to that of tropical Africa and Asia combined (Figure 6-1).

The area of lowland rain forest is greatest in the Neotropics (Raven, 1990), but is not responsible for the greater butterfly richness of Latin America. Liberia, the Malay Peninsula, and Panama have similar areas at about the same latitude (Figure 6-2), and their butterfly faunas are documented (Owen, 1971; Robbins, 1982; Eliot and D'Abrera, 1992). Panama is smaller than Liberia and the Malay

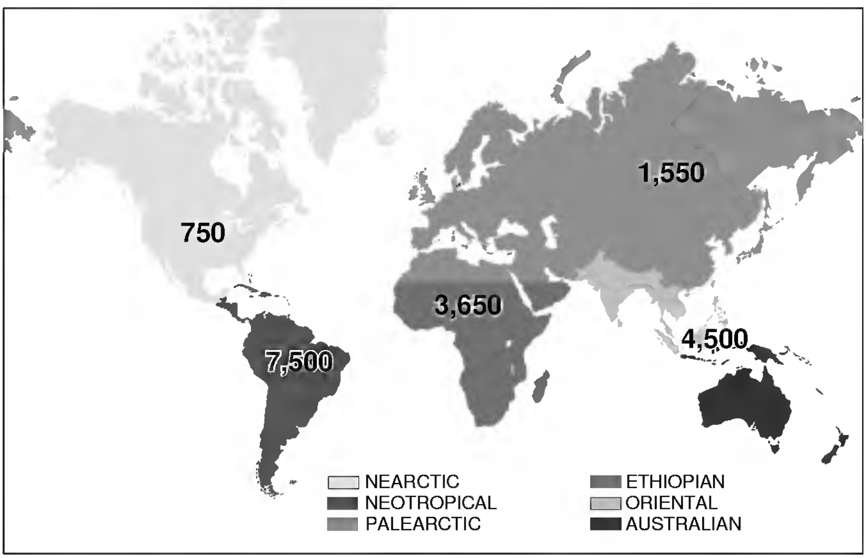

FIGURE 6-1 Number of species of butterflies by biogeographical realm. The 4,500 total is for the Oriental and Australian Realms combined. Ackery et al. (1995) listed 3,607 Ethiopian species. Robbins (1982) gave estimates for the other realms. There are an estimated 17,500 species of butterflies world-wide.

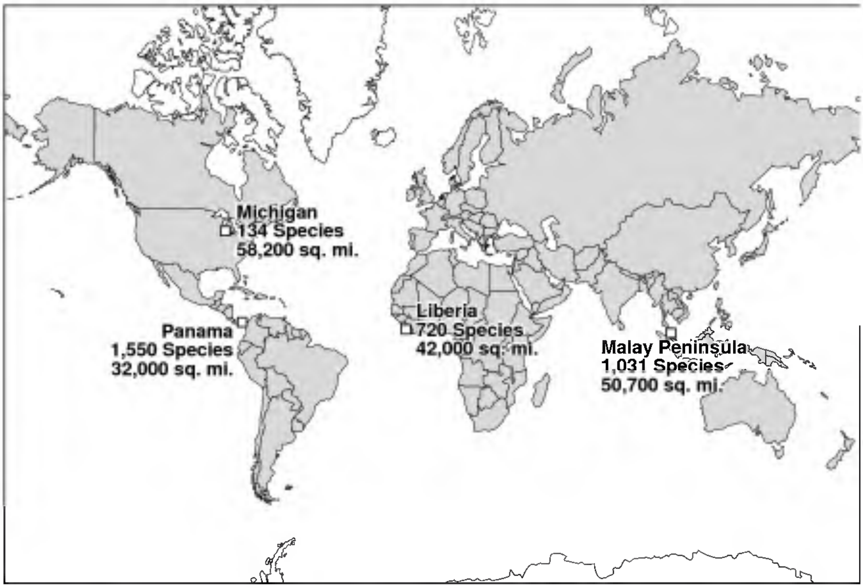

FIGURE 6-2 Area and number of species of butterflies for the Malay Peninsula (Eliot and D'Abrera, 1992), Liberia (Owen, 1971), and Panama (Robbins, 1982). Michigan (see Table 6-1) is included for comparison with an area in the temperate zone.

Peninsula, but has more than twice the number of species of butterflies than the latter areas (Figure 6-2). Since Central America is not an unusually rich part of the Neotropics (see below), its area of lowland rain forest alone is not likely to explain why the Neotropics have a greater butterfly diversity than the Old World tropics.

SPECIES RICHNESS OF U.S. BUTTERFLIES

Species of butterflies have been surveyed relatively well in most of the conterminous United States. For almost all states, it is reasonable to expect that more than 90% of the resident fauna has been discovered. Atlases of the county-by-county distribution of butterflies of the United States have been compiled over the past 20 years from published literature records, data from specimens in museums and private collections, and by conducting field surveys in poorly known geographic areas (Stanford and Opler, 1993; Opler, 1994, 1995).

By reviewing these atlases, we counted the number of true butterflies and skippers that are residents, regular colonists, and vagrants for each state (Table 6-1). Residents are species that reproduce yearly and can survive all seasons. Regular colonists are species that do not survive the winter, but which annually immigrate into the state and usually establish temporary breeding populations. Vagrants are species that have been reported in the state, but do not breed there

TABLE 6-1 The Number of Recorded Species of Butterflies that are Residents, Regular Colonists, and Vagrants for Each State of the Conterminous United States

State	Butterfly Residents and Colonists	Butterfly Vagrants	Breeding Birds[a]
Alabama	132	2	145
Arizona	246	80	246
Arkansas	127	25	130
California	225	25	286
Colorado	230	36	235
Connecticut	101	13	158
Delaware[b]	91	7	160
Florida	163	18	160
Georgia	151	8	160
Idaho[b]	154	6	?
Illinois	121	22	160
Indiana	123	19	151
Iowa	107	19	154
Kansas	133	50	175
Kentucky	116	17	153
Louisiana	117	15	158
Maine	88	13	176
Maryland	121	19	192
Massachusetts	93	19	177
Michigan	134	10	202
Minnesota	132	13	224
Mississippi	134	10	13
Missouri	125	31	175
Montana[b]	184	3	224
Nebraska	170	27	194
Nevada	181	26	224
New Hampshire	92	9	175
New Jersey	120	23	181
New Mexico	272	46	247
New York	119	19	220
North Carolina	140	11	178
North Dakota	132	11	171
Ohio	131	7	180
Oklahoma	146	16	180
Oregon	159	5	232
Pennsylvania	114	20	18
Rhode Island[b]	83	4	141
South Carolina	133	9	152
South Dakota	149	21	207
Tennessee[b]	112	12	160
Texas	290	133	300
Utah	197	18	220
Vermont[b]	66	6	175
Virginia	134	21	179
Washington	140	3	235
West Virginia	112	8	156
Wisconsin	133	12	203
Wyoming	197	13	222

[a]From Peterson (1963).
[b]Incomplete census for butterflies.

except on rare occasions. These categories were based on biology, caterpillar host plants, geographic range, and published reports of breeding. In some cases, category determinations were arbitrary decisions. For example, *Atalopedes campestris* is considered to be a resident in Maryland and Virginia and, although it may not survive every winter, it is judged to be a vagrant where recorded to the north.

The number of species of butterflies recorded per state ranges from 87 for Rhode Island, an incompletely sampled state, to 423 for Texas. Number of species increases from north to south. For example, along the Atlantic seaboard, species richness of butterflies increases steadily from the 101 recorded in Maine to the 181 in Florida. Among the Pacific coastal states, Washington has 143 species, Oregon 164, and California 250.

Texas has the richest butterfly fauna, influenced by the lower Rio Grande Valley. Even though only a few thousand acres of dry tropical forest habitat remain in a few parks, reserves, and refuges, many of Mexico's species of tropical lowland butterflies have been recorded in Cameron, Hidalgo, and Starr counties, largely as vagrants. Nevertheless, quite a few butterflies have their only breeding populations in the United States in the lower Rio Grande Valley.

A second trend is for high species richness to occur in states with greatest topographic diversity. The Rocky Mountain states have the greatest topographic diversity and have faunal connections through the mid-continental cordillera to both the Arctic and species-rich Mexico, through west Texas and southeastern New Mexico to its Sierra Madre Oriental, and through the very rich areas of southeastern Arizona and southwestern New Mexico to the Sierra Madre Occidental. These faunal connections are shown by species with southern biogeographic afffinities that range northward at low to intermediate elevations from Mexico, and those that range southward at high elevations from the arctic and subarctic. All Rocky Mountain states have endemic western North American butterflies, but those bordering the Great Plains also include a significant number of eastern species in their faunas.

Another recognizable trend is for species richness to be greater in the west than in the east. While partly the result of relatively larger size of the states, greater topographic diversity, and their proximity to species-rich Mexico, it is nonetheless true that more butterflies per unit area are found in the richest areas of western states. Florida, the richest eastern state, has 163 species of residents and regular colonists, while the only western states having fewer species are Idaho (154), Oregon (154), and Washington (140).

The poorest region, relative to its latitude, is the alluvial Mississippi drainage, including the states of Arkansas (127), Illinois (121), Iowa (107), Louisiana (117), Mississippi (134), and Missouri (125). The somewhat higher regional species richness in Arkansas, Mississippi, and Missouri is no doubt due to their modest topographic relief. Historical factors such as the relatively recent flooding of the Mississippi embayment also may have had a role.

NEOTROPICAL DIVERSITY

To document how diversity varies within the Neotropics, we tabulated species richness at single localities (Figure 6-3). We did not distinguish tropical breeding residents from strays because, with the exception of some migrants (e.g., Beebe, 1949-1951), there is little evidence that tropical butterflies stray to areas where they do not breed.

La Selva field station is situated in lowland rain forest on the Atlantic side of Costa Rica and is relatively well-collected for the larger butterflies. The number of recorded Papilionidae, Pieridae, and Nymphalidae is 204 species (DeVries, 1994). These three families comprise about one-third of the fauna in Panama (Robbins, 1982), the Amazon Basin (Robbins et al., 1995), and at Itatiaia, a national park primarily above 500 m in Rio de Janeiro state (Zikán and Zikán, 1968). Consequently, 600-650 species is probably a reasonable estimate of La Selva's species richness. Since Belem (Brazil) is not nearly so well-documented, the 700 species recorded by Bates (1875) is a minimal value. For Madre de Dios, Peru, 1,234 species have been recorded since 1979 at the Tambopata Reserve (5,500 ha), and 1,300 species were recorded on five field trips averaging less than 3 weeks each to Pakitza (<4,000 ha), Manu National Park (Robbins et al.,

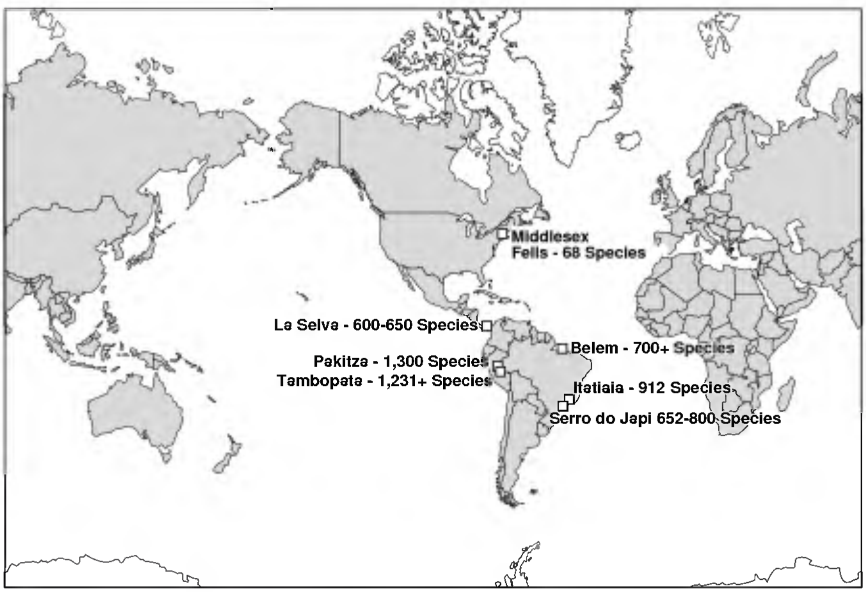

FIGURE 6-3 Number of species of butterflies at neotropical sites. The Middlesex Fells Reservation in Massachusetts is included for comparison with a site in the temperate zone (from Robbins, 1993b).

1995). For southern Brazil, 912 species of butterflies were found over 5 decades at Itatiaia (Zikán and Zikán, 1968; 17 species of Acraeini were omitted in this paper), and 652 species were collected in 8 years at Serra do Japi (750-1,286 m), a reserve near Jundiai, São Paulo (Brown, 1992). Documentation for the Peruvian and Brazilian sites includes museum vouchers.

Even though the number of species at Pakitza and Tambopata continue to increase with each field trip, each of these sites already has more species of butterflies than most, if not all, countries in tropical Africa and Asia (Robbins, 1993a). Clearly, explanations for the greater butterfly diversity of the Neotropics need to account for the extraordinary richness that may occur at single neotropical sites (the within-habitat, alpha, and point diversity concepts of MacArthur, 1969; Whittaker, 1972; Pielou, 1975).

The high butterfly diversity at Pakitza and the Tambopata Reserve is not unique. From what we know about the distribution of neotropical butterflies, there appears to be a band of high butterfly diversity from southern Colombia to the Peru-Bolivia border, ranging eastward from the base of the Andes to the Brazilian states of Acre and Rondônia. This band also appears to extend, with slightly decreased diversity, along the eastern base of the Andes in Venezuela and Bolivia, but documentation is poor.

The upper Amazonian band of high butterfly diversity very roughly consists of two faunal zones and is not uniformly high in diversity. The Rio Madeira drainage in the south has a distinct dry season from about May to September, approximately 2,000 mm annual precipitation (Erwin, 1983, 1991; Terborgh, 1983), and a well-documented high butterfly diversity. Besides Pakitza and the Tambopata Reserve, Jaru and Cacaulandia, Rondônia, Brazil, appear to have similarly high diversities (Brown, 1984; Emmel and Austin, 1990). Alternately, much of the drainage of the Rio Solimões (upper Amazon River) in the north lacks a distinct dry season, has more than 3,000 mm annual precipitation (Gentry, 1988b), and supports a poorly documented butterfly fauna. From museum collections, we infer that parts of eastern Ecuador and the Iquitos, Loreto, Peru, areas are very rich, although sites in the vicinity of Pantoja, Loreto, Peru, on the Rio Napo are relatively poor in species. The faunas of the Rio Solimões and Rio Madeira mix in parts of Acre, Brazil, and Ucayali, Peru, which consequently may be the richest areas in the world for butterflies (Brown and Lamas, personal communications, 1993).

BUTTERFLIES, BIRDS, AND MAMMALS

If patterns of species richness and endemism were similar for different groups of organisms, then knowing these patterns for any group, such as mammals, would be sufficient to determine "biological" priorities among potential sites for conservation. However, at the scale of 100 km^2, butterfly diversity is not well correlated with the diversity of other groups of organisms in temperate

England (Prendergast et al., 1993). For the Neotropics, although lakes and caves do not affect butterfly diversity at a site, they can affect the diversity of bats and freshwater birds. Further, species richness of lowland plants is correlated with precipitation (Gentry, 1988b), and the same is probably true for butterflies. (The data are scanty, but areas with less than 1,500 mm annual precipitation have fewer species of butterflies than wetter areas.) However, the diversity of neotropical mammals does not appear to be correlated with precipitation (Emmons, 1984). Consequently, patterns of butterfly diversity in the Neotropics are not expected to be strongly correlated with the patterns of mammals.

We recorded the number of breeding birds for each state in the United States (Table 6-1). Because diversity is a function of area, we expected the numbers of breeding birds and nonvagrant butterflies for each state to be positively correlated. After omitting incompletely documented states, a Spearman rank correlation coefficient was indeed highly significant ($r=0.606$, $n=42$, $p<0.001$). However, the increase in butterfly diversity from north to south (discussed above) is less pronounced in birds than butterflies. For example, Florida, Georgia, and South Carolina each have fewer breeding birds (152-160) than Maine or Massachusetts (176-177). Whereas the bird fauna of New Mexico is about 10% greater than that of Wyoming, the butterfly fauna is nearly 40% greater.

We graphed the percentage of the world's species of butterflies that occur in each major biogeographical realm (Figure 6-4) with similar percentages for

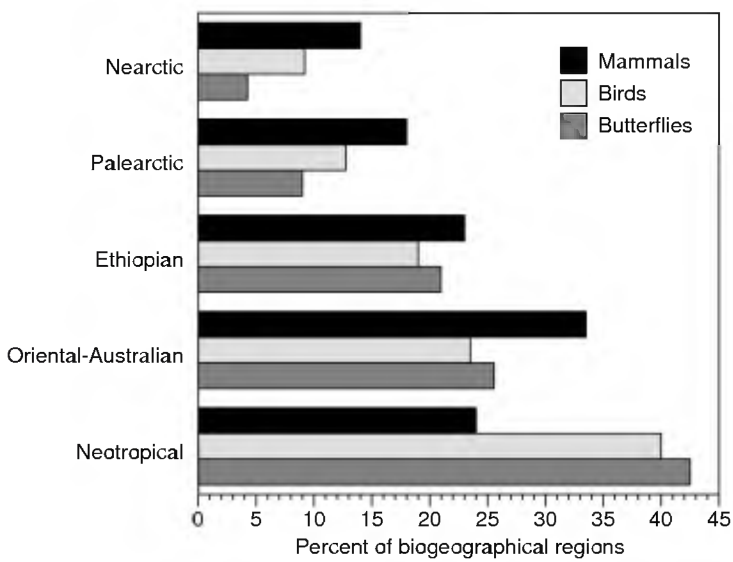

FIGURE 6-4 Proportions of species of butterflies, terrestrial mammals (Cole et al., 1994), and nonmarine birds (Welty and Baptista, 1988) that occur in each of the world's major biogeographical realms.

breeding nonmarine birds (Welty and Baptista, 1988) and terrestrial mammals (Cole et al., 1994). Although slightly different boundaries were used by each author, species richness of butterflies is strongly correlated with diversity of birds, but not with diversity of mammals. For example, the neotropical realm is the richest region for butterflies and birds (40-43%), but fewer than 25% of the world's mammals are neotropical.

Perhaps the major difference between the diversities of butterflies, birds, and mammals is that butterflies are more "tropical" than birds, which, in turn, are more "tropical" than mammals. The percentage of the world's species that occur in the northern temperate Holarctic (including the Nearctic and Palearctic) is 32% for mammals, 21% for birds, and 13% for butterflies. Although there are approximately 2 species of butterflies for every species of bird worldwide, birds greatly outnumber butterflies in the Arctic, have about equal numbers of species as butterflies in temperate North America, and are outnumbered by butterflies in the Neotropics (Table 6-2). Very roughly, an upper Amazonian site will have 3-4 times more species of mammals (including bats)(Emmons, personal communication, 1993), 5 times more species of birds, and 15 times more species of butterflies than a temperate North American site.

DISCUSSION

Among the well-known taxonomic groups of terrestrial animals, butterflies have the greatest number of species. With 17,500 species, they are three to five times more numerous than mammals (Wilson and Reeder, 1993), amphibians (Zug, 1993), mosquitos (Wilkerson, personal communication, 1993), termites (Nickle, personal communication, 1993), or dragonflies (Louton, personal communication, 1993). There are approximately two species of butterflies for every species of nonmarine bird (Welty and Baptista, 1988), and a bit less than three species of butterflies for every one of reptiles (Zug, 1993).

TABLE 6-2 Number of Breeding Birds and Butterflies for Greenland, Georgia, Panama, and Colombia

Locality	Butterflies	Birds
Greenland	5	57
Georgia	151	160
Panama	1,550	710
Colombia	3,100[a]	1,556

[a]Estimate is probably low.

SOURCES: Birds: Panama (Ridgely, 1976); all others (Welty and Baptista, 1988); Butterflies: Greenland (Wolff, 1964); Georgia (this paper); Panama (Robbins, 1982); Colombia (Brown, 1991).

Approximately 90% of the world's species of butterflies have been described taxonomically (Robbins et al., 1995). The great majority of the more than 1,500 undescribed species occur in the Neotropics, which means that diversity studies in this realm, even if restricted to the better-known families (Papilionidae, Pieridae, Nymphalidae), need to include systematists specializing on the neotropical fauna. Since the Papilionidae, Pieridae, and Nymphalidae make up about one-third of this fauna, at least in the lowlands (Robbins et al., 1995), it is possible to focus on these families and still estimate the number of Hesperiidae, Lycaenidae, and Riodinidae.

Although hypotheses can be suggested to explain why butterflies and mammals have different patterns of species richness, we have focused on the implications for conservationists. If butterfly distributions are representative of other insects, then strategies for conserving insects should not be based on the diversity patterns of terrestrial vertebrates, particularly mammals. Further, butterflies are far more "tropical" than mammals, which emphasizes the importance of protecting tropical areas for conserving terrestrial arthropods. From a biological viewpoint, it might be more reasonable to expect a high correlation between butterfly and plant diversity, but this hypothesis appears to be largely unexamined.

The attention given to the magnitude of differences between tropical and temperate areas appears to have had the unfortunate effect of obscuring difficulties in defining, measuring, and comparing diversity. Given that the abundance of tropical insects fluctuates markedly, changing the species composition at a site from year to year (e.g., Wolda, 1992), is the species richness of butterflies in the vicinity of Belem the number of species occurring there in 1 day, 2 months, or 5 years? If the comparison is with England's depauperate fauna, it does not matter which "definition" is used for Belem's species richness. But, if the comparison is with Manaus and Iquitos, then it may first be necessary to understand the dynamics of tropical butterfly communities.

CONCLUSIONS

There is much to be done in developing a general theory that will predict the patterns of diversity that we are beginning to document. We do not know of any current theory that predicted that the upper Amazon basin at the eastern base of the Andes would have the highest species richness in the world or that single sites there might have more species of butterflies than tropical countries on other continents. The Rio Madeira drainage is the richest area for birds and the Rio Solimões has the greatest diversity for canopy trees (Gentry, 1988a); however, neither theory nor correlations of diversity with other groups allows us to predict which of these areas will be richer for butterflies. There is yet a long way to go before we understand tropical butterfly diversity.

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