Atlantic Forest Butterflies: Indicators for Landscape Conservation[1]

Keith S. Brown Jr.[2] and **André Victor L. Freitas**

Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 6109, Campinas, São Paulo, Brazil 13.083-970

ABSTRACT

The Atlantic Forest region (wide sense) includes very complex tropical environments, increasingly threatened by extensive anthropogenic conversion (>90%). Ecologically specialized, short-generation insects (butterflies) are evaluated here as indicators for monitoring community richness, landscape integrity, and sustainable resource use in the region. The > 2100 butterfly species in the Atlantic Forest region have been censused in many sites over 35 years, giving comparable daily, weekly, monthly, and long-term site lists. The 21 most thoroughly studied sites include 218–914 species, of which half can be censused in a week or less. The butterfly communities are divided into six relatively distinct faunal regions, centered in the northeast, the central coastal tablelands, the southeast coastal plain, the mountains plus interior of the southeastern states, the central plateau, and the southern states. Species richness shows the highest values in coastal mountains from 15 to 23°S. Local butterfly communities show a high turnover, with 20 to 40 percent of the species, especially small Lycaenidae and Hesperiidae, recorded only as unstable populations or "tourists." Easily sampled species in the family Nymphalidae, and especially its bait-attracted subfamilies, are best correlated with the entire butterfly fauna and can be used as surrogates for species diversity. In most butterfly groups, species richness is well predicted by landscape connectivity alone, or by composite indices of environmental heterogeneity, natural disturbance, and (negatively) anthropogenic disturbance. Principal components and redundancy analyses showed that the richness and proportions of different butterfly groups in the local fauna are variably explained by disturbance, seasonality, temperature, vegetation, soils, and landscape connectivity. Various groups thus can be used as rapid indicators of different types of change in the community, its environment, and the landscape. Threatened and rare species also can be used as indicators of the most unique Atlantic Forest communities (paleoenvironments), which need special attention.

RESUMO

A região da Mata Atlântica *latu sensu* inclui ambientes tropicais muito complexos, cada vez mais ameaçados por extensa conversão antrópica (>90%). Insetos pequenos, especializados, e de ciclo rápido (borboletas) são avaliados neste trabalho como indicadores para o monitoramento da riqueza de comunidades, integridade de paisagens, e uso sustentável de recursos na região. As >2100 espécies de borboletas na região da Mata Atlântica têm sido recenseadas em muitos sítios durante os últimos 35 anos, dando listas comparáveis diárias, semanais, mensais e totais para cada sítio. Os 21 sítios mais intensivamente estudados incluem 218–914 espécies, das quais metade pode ser amostrada em uma semana ou menos. As comunidades de borboletas são divididas em seis subregiões faunísticas relativamente distintas, centradas no nordeste, nos tabuleiros baianos, no litoral do sudeste, nas regiões montanhosas no interior dos estados do sudeste, no Planalto Central, e no estados do sul. A riqueza de espécies é maior nas serras costeiras entre 15 e 23°S. As comunidades locais de borboletas possuem alta reposição, com 20 a 40 por cento das espécies, especialmente os pequenos Lycaenidae e Hesperiidae, registradas em populações instáveis ou sendo apenas "turistas." As espécies facilmente amostradas na família Nymphalidae, especialmente as atraídas a iscas fermentadas, são mais correlacionadas com a riqueza total e podem ser usadas como estimadores da riqueza total no ambiente. Na maior parte dos grupos de borboletas, a riqueza de espécies é altamente correlacionada com conectividade simples da paisagem, e com índices compostos de heterogeneidade, perturbação natural, e (negativamente) perturbação total no ambiente. As análises de Componentes Principais e de Redundância mostram que as riquezas e proporções de diferentes grupos de borboletas são variavelmente explicadas por perturbação, sazonalidade, temperatura, vegetação, solos, e conectividade. Vários grupos podem assim ser úteis como indicadores rápidos de diferentes tipos de mudanças na comunidade, no seu ambiente, e na paisagem. Espécies raras e ameaçadas podem também ser usadas para indicar os sistemas mais únicos na região (paleoambientes), que necessitam de atenção especial.

THE BRAZILIAN ATLANTIC FOREST REGION (in the wide sense) includes very complex natural landscapes, due to its highly diverse terrain, climate, and vegetation (Oliveira-Filho & Fontes 2000). During the past 500 years of occupation by European, African, and Asian peoples, >90 percent of the original Atlantic Forests have been converted to anthropic systems (Brown & Brown 1992, Coimbra-Filho &

Câmara 1996, Dean 1995). In most of the region, the remaining forest vegetation occurs as small fragments isolated from each other by agriculture or non-forest systems (São Paulo–Kronka *et al.* 1993; Fig. 1 in Morellato & Haddad 2000). Thus, effective conservation (*i.e.*, the wise, equitable, and sustainable use of the land and its resources) of the Atlantic Forests is a difficult task, requiring extensive knowledge of landscape dynamics, community ecology, and metapopulation biology (Wiens 1997). In practice, physical and biological indicators must be found to rapidly track landscape-scale factors and processes, and thus serve as early warnings of unsustainable resource use, excessive land occupation, species disappearance, and ecosystem disintegration (Kremen *et al.* 1993, 1994; Brown 1996a, 1997a, b).

In this study, we sought to discover simple, adequate, and consistent inventory and monitoring methods for Atlantic Forest systems. We used indicators to provide quantitative measures of changes in species diversity, community structure, and various aspects of the environment. Many groups of insects have been suggested as possible indicators for inventorying and monitoring the diversity and integrity of natural landscapes (Brown 1991; Kremen 1992; Pearson & Cassola 1992; Halffter & Favila 1993; Kremen *et al.* 1993, 1994; Longino 1994; Favila & Halffter 1997). Among these, butterflies may be especially useful indicators of many aspects of changing environment at the landscape level, because of their rapid reproduction, tight association with specific physical factors and plant resources, and resulting sensitivity to environmental changes (Brown 1991, 1996a, b, 1997a, b; Kremen 1992; New *et al.* 1995; New 1997). In Atlantic Forest systems, butterflies are diverse, well known, and easily attracted, sampled, and identified, thus forming an ideal group for monitoring conservation practice in this system (Brown 1991, 1992, 1993a–c, 1997a, b; Brown & Freitas 1999).

Here we examine the feasibility of using Atlantic Forest butterfly communities for conservation planning and monitoring, seeking to answer the following questions: (1) how can the variation in composition of Atlantic Forest butterfly communities among different seasons, regions, and landscapes be measured?; (2) are the structure and richness of local butterfly communities related to specific environmental variables, including anthropogenic disturbance and landscape connectivity?; and (3) how can the answers to these questions be applied to monitor natural systems and aid in landscape management and conservation?

Our approach was to determine the consistency and relative importance of numerous environmental factors in structuring the variation of butterfly communities in the Atlantic Forest region. To do this, we repeatedly inventoried sites over several years, using standardized methods to establish cumulative lists of species and estimate the short- and long-term variation in composition, richness, and abundance of species within each community (Brown 1972a). We then quantified general patterns of diversity and community structure of butterflies in many sites throughout the region. We used multivariate statistics to establish the relative importance of local climate, topography, soils, vegetation, connectivity, and natural and anthropogenic disturbance in structuring these communities. Finally, we will discuss the conservation implications of these results in light of the impacts that different land-use patterns have on butterflies.

MATERIALS AND METHODS

COMPARABLE DATA SETS: CENSUSES AND SPECIES AND SITE LISTS.—Butterfly presence and abundance were monitored through daily "maximized recording" visual surveys, as described by Ebert (1969), Brown (1972a, 1991, 1996b, 1997a), Clench (1980), and Brown and Hutchings (1997). Daily censuses were conducted intensively over large and small areas, using baits and traps to increase their efficiency. Paths or roads beside or through all recognizable ecotypes in an area were covered repeatedly in visual inventories, which included the use of binoculars to discover and identify as many of the butterflies present as possible. This usually required an intensive training *in situ,* to permit secure and rapid recognition of 500 or more species by color, pattern, behavior, and habitat. For each daily census (3–12 hours; the time counted for periods of warm, cloudy weather was reduced by 50% and rainy periods were not counted, following Brown & Hutchings 1997), a single observer moved about rapidly in a 1- to10-km^2 area (walking up to 15 linear km), covering many different habitats and resources; two or more persons covered separate sectors (10–50 ha) more intensively, meeting occasionally to compare notes. Special attention was devoted to forest edges, streams or their banks, rich soil and flower patches, small clearings, and any other highly heterogeneous environments. Points with notable concentrations of butterflies were observed until no additional species had been recorded after five to ten minutes.

Excrement, carcasses, and rotting fruit baits

also were placed on the ground and in cylindrical net traps at eye level (up to 10/linear km along edges or paths; Austin & Riley 1995, DeVries *et al.* 1997). When available, sheaves of drying *Heliotropium indicum* (Boraginaceae) were hung in shady, humid, and open undergrowth to attract Ithomiinae males (Beebe 1955, Brown 1985), and up to 100 tissue paper/saliva baits were placed on leaves within dense forest to attract skippers (Austin *et al.* 1993, Lamas *et al.* 1993). Skippers and other groups also were sought on moist soil and on flower patches, including especially Verbenaceae, Rubiaceae, Asteraceae, flowering trees (*Inga* and *Schinus*), and vines.

Any individual not immediately identifiable (usually < 2% of those seen; mostly Satyrinae, Theclinae, and Hesperiinae) was captured (if possible), verified, and released with minimum handling; a few difficult-to-identify individuals or important new records for a site were collected for later study (voucher specimens have been deposited in the Museu de História Natural, UNICAMP). For rare or threatened species, handling was limited to occasional males. Abundance, including approximate numbers of each sex seen, captured, and released, was tallied for all species observed, as well as data on their behavior and resources.

Suitable combination of adjacent daily lists in a single site gave 14-hour weekly standard censuses, which could be compared to those of other weeks or sites, or further combined to monthly or seasonal lists. Additional joining of lists from many visits to a site (at least 100 observer-hours) gave preliminary site lists. Twenty-one of these sites had sufficiently complete lists (adequate representation of all families with few species being added in new visits) for comparison of faunas and environments in these sites (Table 1; Fig. 1). Twelve of these site lists were mostly from our own field surveys over 35 years. Lists for nine other sites were compiled and published by other Brazilian lepidopterists using similar methods; seven of these sites also were visited and the lists complemented by us. An additional ten sites (footnote a, Table 1; Fig. 1) were used for analyzing patterns in a small, well-sampled Nymphalid group, the Ithomiinae.

For multivariate analysis, the Nymphalidae on the site lists were divided into ten tribal or subfamily groups as in Table 1, with the small Libytheinae (monotypic) and Danainae (five species) united with the Ithomiinae. Along with the small families Pieridae and Papilionidae, this gave 12 taxonomic units of Nymphalidae + Pieridae + Papilionidae (NPP), most of which also showed reasonable eco-

logical coherence through shared host plant families, habitat preferences, and color patterns. The entire butterfly fauna also was divided into six larger taxonomic–ecological groups: (1) bait-attracted Nymphalidae (Morphinae through Eurytelinae in Table 1); (2) the remaining, often sun-loving or model/mimetic Nymphalid species, plus all the Pieridae and the Papilionidae (these first two large groups included all the NPP, the previous 12 small ones); (3) the Lycaenidae subfamily Riodininae; (4) the remaining Lycaenidae (Theclinae + Polyommatinae); (5) the largest skipper subfamily (Hesperiinae, with monocot-feeding larvae); and (6) all the remaining skippers (Pyrrhopyginae + Pyrginae; almost all dicot feeders as larvae). Many of the groups used for analysis corresponded roughly to one or another of the major color/behavior divisions of the Mexican butterfly fauna used for environmental monitoring and comparison by Maza and Soberón (1998); better examples included Papilionidae ("black-red"), Charaxinae ("closed-reflecting"), Satyrinae ("dark-cryptic"), and Apaturinae + Limenitidini + Cyrestidini + Coloburini (ALCC; "Adelpha").

Calculations of similarities among total lists of butterflies and their smaller component groups used presence/absence. For daily, weekly, and monthly lists, the Sorensen index $[2c/(a + b)]$ was used; for full site lists, simple Euclidean distances were grouped by Ward's algorithm, which minimizes the sum of squares (variance) of the clusters, usually of small size (Ward 1963).

Environmental factors and their effects on butterfly communities.—For each of the 21 well-studied sites in Table 1, the sampling intensity (total time and area covered) and an additional 21 environmental factors and parameters were scored (Table 2): 2 of geographic position, 3 of topography, 4 of climate (DNMet 1992), 3 of soils (Projecto RADAMBRASIL 1975–1987), 4 of vegetation (previous source and also more recent and detailed publications) including 2 indicators of disturbance and heterogeneity (vines and bamboos), and 5 of landscape (from direct observation during visits; permanent surface water, principal type of disturbance, pollution levels, total proportion of secondary vegetation, and connectivity). The last was quantified as a sum of four factors averaged in the landscape sectors in between forest patches, defined as follows: (1) humidity: 0 = dry earth, 1 = variably dry and humid, 2 = always humid with a high water table, 3 = swamp or gallery vegetation with much standing or flowing water; (2) height

and density: 0 = denuded urban or open fields, grasslands, or agriculture, 1 = scrub or low bushy vegetation, 2 = open or disturbed forest, 3 = dense forest; (3) linkage: 0 = scattered and unlinked small forest patches, 1 = mosaic with many linked or larger forest fragments, 2 = all fragments effectively interconnected; and (4) width of forest corridors: 0 = none present, 1 = narrow strips (1–5 m wide), 2 = broad corridors (5–30 m wide), 3 = very broad links (30–100 m wide), 4 = essentially continuous forest.

The environmental variables were chosen and coded primarily to emphasize independent ecological factors that possibly varied with human occupation of the system, as explained in the footnotes of Table 2. Topography, soils, and vegetation variables were scored to make higher values reflect either greater richness or higher heterogeneity in the environment, resulting in more different microhabitats which are presumably favorable for maintenance of a higher number of species in the site (Brown 1997a).

Collinearity and relationships among the species richness of butterfly groups (including various combinations, up to the total fauna per site) and environmental factors (including combinations of factors to give composite indices of heterogeneity and disturbance) were examined through correlation coefficients (Spearman's r) using STATISTICA (StatSoft 1995). Regression parameters (R^2, intersects and slopes, and probabilities), including those for nonlinear models of interaction, also were determined and the relationships plotted.

Principal components analysis (PCA) was used (FITOPAC software; Shepherd 1995) to identify combinations of environmental factors especially useful in explaining the variation in species richness for the 12 smaller (NPP) and additional 4 larger (2 Lycaenid and 2 Hesperid) butterfly groups among sites. To avoid effects of collinearity among the environmental variables, a PCA of the environmental data (except latitude) in the 21 sites was performed, and the first three axes were selected to represent the combination of the environmental data. This form of reduction in variables may "eliminate collinearity problems without compromising the biological questions to be asked" (Philippi 1993).

Interactive multivariate analysis (canonical community ordination or CANOCO, Version 3.12; ter Braak 1987–1992; Kremen 1992) was used to identify factors of the physical environment that were most correlated with the proportions of (a) the 12 smaller groups of NPP, and (b) the 6 larger groups of butterflies in each site. The first ordination axis for the proportions of the 12 small divisions of NPP (including mostly larger and easily recognized species; about a third of the fauna) had a gradient (measured by detrended canonical analysis) of only 0.511, well below the 1.5 recommended for standard canonical ordination; the same occurred in the analysis of the 6 large groups including the entire fauna (gradient 0.585). This required the use of redundancy analysis (RDA). All environmental data were standardized (maximum values adjusted to 1), and each significant vector was defined statistically by 999 Monte Carlo permutations. Triplots were produced to show the relative positions of the eigenvectors for all significant environmental factors determining the community structure (as shown by the divergent eigenvectors of the butterfly groups) over the site positions, in relation to two major axes defined by the interaction of all three sets of information (proportions of butterfly groups and values for 20 environmental factors, except latitude, in the 21 sites).

RESULTS: ATLANTIC FOREST BUTTERFLY COMMUNITIES

Sampling methods, efficiency, and comparability.—Not all butterfly groups were easy to inventory. The Lycaenidae and Hesperiidae were especially erratic and difficult to sample, with slow accumulation of species over long sampling periods (see Table 3 for data from 26 years of standard inventories in the 251-ha Santa Genebra forest reserve in Campinas, location CP in Fig. 1). The Nymphalidae, Pieridae, and Papilionidae were easiest to recognize in the field and sample to near-asymptotes (Table 3, values in bold). In general, standard weekly lists (14-hour) included about half the species present and could be compared among each other for composition and abundance. A cumulative list including 80 percent or more of the fauna, adequate for comparisons among sites, could be achieved with *ca* 500 observer-hours of census (Table 3); this preferably would be in several different seasons that included the yearly flower peaks. Coastal sites tended to be richest from April to September and poorer in spring and summer (October–March), while the species richness of montane communities peaked from January to March, and interior sites (Table 3) from March to June, as noted by Ebert (1969).

In the Santa Genebra site, only 34.5 percent (238) of the 690 species recorded, including a larger proportion of the Pieridae (68%), Papilionidae

TABLE 1. *Diversity and community composition of butterflies recorded in 21 Atlantic Forest sites.*

Butterfly group	Atlantic spp. (endemic)	Site codes: Endemic genera	JP João Pess.	PE E. Per- namb.	MC Ma- ceió	CG Chap. Guim.	BR Bra- sília
Nymphalidae	**461 (204)**	**18**	**86**	**139**	**86**	**223**	**216**
Libytheinae/Danainae	6 (0)	0	3	4	3	4	4
Ithomiinae[a]	54 (22)	2	8	19	11	24	22
Morphinae	10 (7)	0	3	4	2	2	6
Brassolinae	36 (19)	4	8	9	8	10	15
Satyrinae	130 (70)	12	11	27	14	[b]55	[b]52
Charaxinae	34 (9)	0	9	16	3	20	19
Apat/Lim/Cyr/Col[c]	45 (17)	0	10	13	10	21	21
Eurytelinae	77 (20)	0	15	25	15	[b]50	38
Nymphalinae	28 (16)	0	7	7	9	17	18
Acraeini	21 (19)	0	1	2	1	5	8
Heliconiini	20 (4)	0	11	13	10	15	13
Pieridae	**50 (16)**	**2**	**18**	**21**	**17**	**24**	**27**
Papilionidae	**43 (18)**	**0**	**5**	**6**	**3**	[b]**21**	**15**
Lycaenidae	**679 (305)**	**7**	**88**	**178**	**57**	**270**	**268**
Polyommatinae	5 (2)	1	3	3	1	3	4
Theclinae	306 (151)	?	43	99	28	115	130
Riodininae	368 (152)	6	42	76	28	[b]152	[b]134
Papilionoidea	**1233 (543)**	**27**	**197**	**344**	**163**	**538**	**526**
Pyrrhopyginae	51 (26)	4	1	2	2	16	6
Pyrginae	351 (116)	4	61	116	35	160	120
Hesperiinae	485 (263)	33	48	76	18	160	124
Hesperioidea	**887 (405)**	**41**	**110**	**194**	**55**	**336**	**250**
Total butterflies	**2120 (948)**	**68**	**307**	**538**	**218**	**874**	**776**
(predicted total if Nymph = 0.27 T)			319	515	319	826	800
(predicted total if Ithom. = 0.040 T)			*200*	*475*	*275*	*600*	*550*
Threatened species[d]			**3**	**7**	**1**	**6**	**4**
Data sources (References) for site:[e]			1,2	1,3	4	1,5	1,6,7

[a] Reasonably complete Ithomiinae lists are available for ten more localities, included in Figure 1 and in the similarity analysis in Figure 2a: (**GO**) Goiânia to Leopoldo Bulhões, GO = 20 species and (**PP**) Paraopeba, MG = 16 (refs. *1,6*), (**CM**) Camacã to Itaimbé, BA = 33 (*1*), (**IM**) Itamaraju, BA = 25 (*1,10*), (**BG**) Baixo Guandu, ES = 35 (*1,10*), (**MS**) Mirassol, SP = 19 (*1*), (**PT**) Petrópolis, RJ = 26 (*1*), (**IG**) Iguaçu, PR = 12 (*1,18*), (**AG**) Agrolândia, SC = 12 (*1*), and (**RS**) Caxias do Sul, RS = 11 (*1,19*). Note that the lower values for Ithomiinae occur in dry environments in the northeast (JP and MC, also urban as is SP), interior (CG, BS, GO, PP, MS), or seaside (DS), or in sites below the tropic with winter frosts (CT, JV, IG, AG, RS).

[b] In these two sites, these groups include some species from the southern Amazonian fauna, not found farther south in the Mata Atlântica region or included in Figure 1.

[c] Apaturinae, Limenitidini, Cyrestidini, and Coloburini, four small bait- and mud-attracted groups, most with larvae that feed on plants in the order Urticales.

[d] Lists of threatened species: Brazil, Bernardes *et al.* 1990, Brown 1993a; Paraná, Casagrande & Mielke 1993; Minas Gerais, Brown *et al.* 1998, Casagrande *et al.* 1998; Rio de Janeiro, Otero *et al.* 2000; and São Paulo, in preparation. Most of these contain illustrations and range information for the species listed.

[e] Sources for the site data: 1 = K. Brown 1991, 1996a, 1996c, 1997a; 2 = Kesselring & Ebert 1982; 3 = Ebert 1969; 4 = Cardoso 1949; 5 = Brown 1987; 6 = Brown & Mielke 1967a, b; 7 = Collections of David Gifford (now in the DZ-UFPr) and material in the UnB, Brasília; 8 = Brown & Mielke 1968; 9 = Data from W. Benson and the collections of the Reserva Florestal de Linhares, CVRD, and the UFPr; 10 = Material collected by C. and P. C. Elias in the collections of KB and the UFPr; 11 = Mielke & Casagrande 1998; 12 = Brown 1992; 13 = G. Accacio, doctoral dissertation 1997; 14 = Data of A. V. L. Freitas and Ronaldo B. Francini; 15 = Zikán & Zikán 1968; 16 = C. Mielke 1996; 17 = unpublished list from C. H. C. Mielke 1998; 18 = Köhler 1929 (revised); 19 = Material in the collections of the Colégio Anchieta, Porto Alegre, RS.

(53%), and Nymphalidae except Satyrinae (47%), could be considered common or abundant residents (present on more than one-fourth of the 244 independent daily census lists of 3 to 12 hours analyzed; Table 3). Of the 360 species that appeared erratically only in certain seasons or years (recorded on less than one-eighth of the daily censuses, including 58% of the Hesperiidae and 73% of the Lycaenidae), 194 (28% of the total community) have been recorded so rarely (<2% of the lists) that

TABLE 1. *Extended.*

BH Belo Horiz.	LI Linha-res	ST Santa Teresa	PC Poços Caldas	MD Morro Diabo	SJ Serra Japi	CP Cam-pinas	SP USP camp.	AS Alto Serra	SV São Vi-cente	IT Ita-tiaia	RJ Rio de Janeiro	XE Xe-rem	DS Delta S. João	CT Curi-tiba	JV Join-ville
159	**218**	**244**	**168**	**156**	**208**	**210**	**91**	**165**	**174**	**228**	**168**	**177**	**159**	**149**	**190**
4	5	5	5	4	5	6	4	5	6	6	5	5	5	6	6
21	32	36	23	21	31	28	16	25	25	27	23	27	19	15	16
3	4	9	5	2	6	5	3	5	6	7	6	5	4	4	7
10	13	21	7	12	14	13	6	14	11	19	13	9	10	12	18
20	42	48	34	23	30	29	7	25	22	46	20	27	22	29	25
13	20	21	8	15	15	17	7	10	14	16	16	17	12	9	17
19	27	25	20	20	25	27	7	15	20	24	18	22	20	10	32
31	41	36	29	34	38	43	17	20	27	35	30	32	31	24	28
15	14	18	19	15	18	18	14	20	18	17	15	14	15	18	20
11	4	8	9	1	13	12	1	12	10	18	6	6	7	10	7
12	16	17	9	9	13	12	9	14	15	13	16	13	14	12	14
30	25	36	35	19	36	28	23	25	26	38	31	29	24	30	31
14	19	17	16	15	19	17	11	14	16	22	24	22	19	13	21
114	**197**	**150**	**134**	**73**	**166**	**131**	**36**	**65**	**97**	**260**	**183**	**103**	**89**	**85**	**184**
4	2	3	3	3	4	4	2	2	2	4	3	3	2	3	3
75	90	61	84	32	108	85	22	28	57	140	100	40	45	42	96
35	105	86	47	38	54	42	12	35	38	116	80	60	42	40	85
317	**459**	**447**	**353**	**263**	**429**	**386**	**161**	**269**	**313**	**548**	**406**	**331**	**291**	**277**	**426**
5	8	10	11	10	6	9	4	4	2	18	4	4	8	12	13
90	167	152	100	90	125	144	47	26	78	148	120	70	35	58	148
75	201	160	113	97	122	151	39	60	108	200	126	57	16	140	209
170	**376**	**322**	**224**	**197**	**253**	**304**	**90**	**90**	**188**	**366**	**250**	**131**	**59**	**210**	**370**
487	**835**	**769**	**577**	**460**	**682**	**690**	**251**	**359**	**501**	**914**	**656**	**462**	**350**	**487**	**796**
589	**807**	**904**	**619**	**578**	**770**	**778**	**337**	**611**	**644**	**844**	**622**	**656**	**589**	**552**	**704**
500	*800*	*900*	*575*	*525*	*775*	*700*	*400*	*500*	*625*	*675*	*575*	*675*	*475*	*375*	*400*
3	**9**	**11**	**6**	**1**	**9**	**2**	**0**	**3**	**0**	**17**	**14**	**2**	**6**	**4**	**16**
1,8	1,9,10	1,10	1,3	1,11	1,12	1	13	1,14	1,14	1,15	1	1	1	1,16	1,17

they can be considered accidental members of the community, or "tourists." Some of these erratic species were common residents in sites only a few kilometers away (Brown 2001), and at least one (the myrmecophilous riodinine *Adelotypa malca*) had a dense population just 100 m across an orchard from a swamp forest on the reserve border, in identical habitat.

Standard weekly lists in Santa Genebra separated by 5 to 17 days (normally sampling the same populations and even individuals) showed an average similarity of > 0.85 for the larger and more common Nymphalidae, Pieridae, and Papilionidae, but only 0.73 for the mostly smaller or rarer Lycaenidae and Hesperiidae. After 18 to 40 days (sampling the same communities in the same season) the average similarities were still high (near 0.82 and 0.70, respectively); these values were consistent among years at the same peak season (April). In different seasons, however, the indices dropped to near 0.77 and below 0.60, respectively.

A test of the accuracy and utility of the standard surveys was undertaken in the peak season of 2000, comparing six weekly lists from Santa Genebra to six taken during the same weeks in a similarly sized forest fragment (Ribeirão Cachoeira, 207 ha) only 16 km to the east. The second fragment was at the same elevation but on a very different substrate (rocky eutrophic soils, dissected by a rushing stream) that produced a very different vegetation (F. Martins, pers. comm.). The previous year's (1999) lists in Santa Genebra were used as a control. The results (Table 4) clearly and consistently segregated the two butterfly communities; this was especially evident in the very dissimilar Ithomiinae, Satyrinae, ALCC, Acraeini, Riodininae, and Pyrginae lists, on both weekly and cumulative levels.

GEOGRAPHICAL PATTERNS OF BUTTERFLY COMMUNITY RICHNESS AND COMPOSITION.—Butterfly species are distributed unevenly in the Atlantic Forest sites (Fig. 1). Although some groups are most diverse in the southeastern coastal mountains near the Tropic of Capricorn (Morphinae, Brassolinae, Acraeini, Papilionidae, and Pieridae), others are richest near
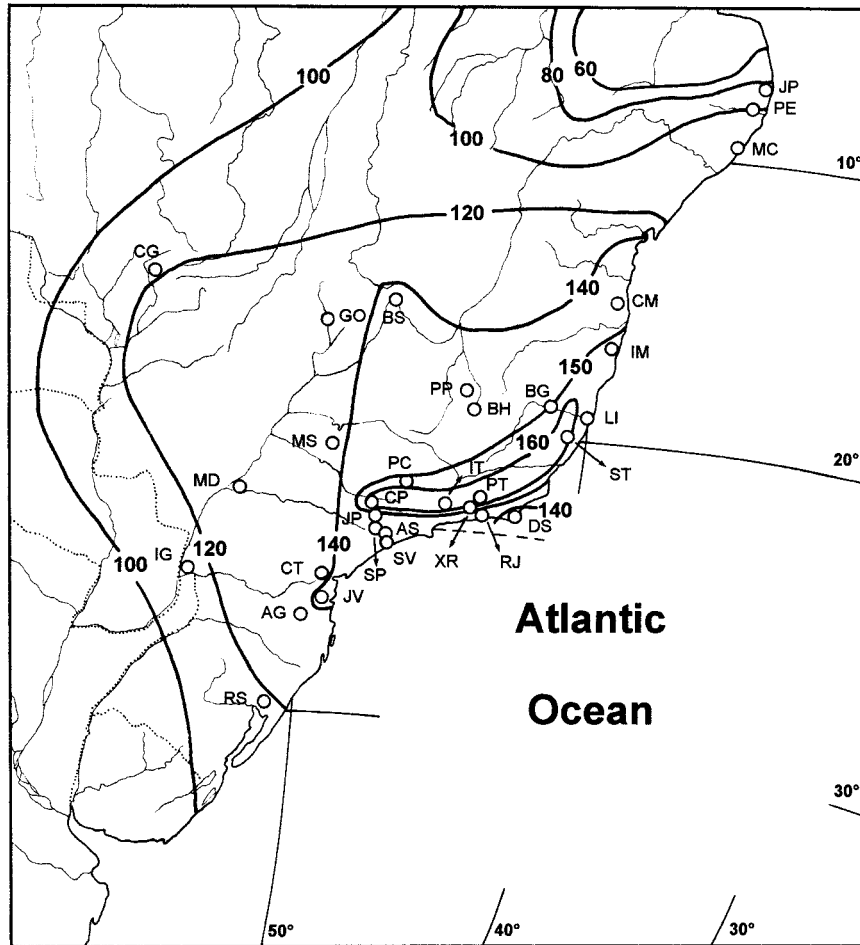
FIGURE 1.   Geographical positions of 31 Atlantic Forest study sites used for analysis of butterfly communities and environment with isoclines of species richness, for a total of eight butterfly groups in the Atlantic Forest region (based on data and codes in Table 1): Ithomiinae, Morphinae, Brassolinae, Eurytelinae, Acraeini, Heliconiini, Pieridae, and Papilionidae. Primarily Amazonian species occurring in Chapada (24 species) and Brasília (3 species) but not farther south in the Atlantic Forest region were not included in the values.

20°S in subcoastal Espírito Santo state (Ithomiinae, Satyrinae, and Heliconiini); others peak in more seasonal interior forests (Eurytelinae and Charaxinae). Almost all drop off sharply north of 12°S where the coastal forests become narrow (Table 1; Fig. 1); in all other regions, forest sites can be expected to include 550 to >900 species (Table 1).

Similarity analysis of species and subspecies in well-sampled butterfly groups from many sites (Table 1) separated the Atlantic Forests into six subregions (Fig. 2): coastal tablelands in the northeast (coded N) and east-central sectors (B, for Bahia state), southeast coastal lowlands (L), southeast montane areas (M), the central plateau back of

these mountains (mostly with semi-deciduous forest [D southward] and cerrado [C north of 18°]), and frost-prone areas (S) at various elevations south of 24°S. Some of the sites were clearly marginal to two regions and included species from both (double letters in the dendrograms).

PRINCIPAL CORRELATIONS AMONG RICHNESS VALUES IN BUTTERFLY GROUPS.—Highly significant correlations ($r > 0.70$) were found logically between combined groups and their included subdivisions, with notable exceptions of the tribe Heliconiini ($r = 0.64$ with the mimetic group) and the subfamily Morphinae ($r = 0.53$ with the bait group). Both of

these small groups (Table 1) were also poorly correlated with the total list (0.56 and 0.53, respectively), as were the other small groups Papilionidae ($r = 0.66$), Ithomiinae ($r = 0.64$), Pieridae ($r = 0.60$), Nymphalinae ($r = 0.47$), and Acraeini ($r = 0.45$), which reflected the progressively divergent richness determinants, preferences, and resources of these groups from those of the reamaining fauna. The best correlations between the total list and its components were seen in the six largest groups: Pyrginae ($r = 0.95$), Hesperiinae ($r = 0.91$), Theclinae ($r = 0.86$), Riodininae ($r = 0.84$), Satyrinae ($r = 0.83$), and Eurytelinae ($r = 0.80$), and also in one small group, the Charaxinae ($r = 0.82$). The large correlations between the two subdivisions of the Hesperiidae ($r = 0.89$) and the Lycaenidae ($r = 0.79$) were not found among the subfamilies of Nymphalidae, except in the bait-attracted groups: Eurytelinae with Charaxinae, $r = 0.82$; with Satyrinae, $r = 0.78$; with ALCC, $r = 0.74$; and was also seen in Charaxinae with ALCC, $r = 0.74$ and Heliconiini, $r = 0.69$ (the highest value for this tribe). The Ithomiinae were surprisingly best correlated with the entire bait-attracted group ($r = 0.76$) and its components Eurytelinae ($r = 0.70$), ALCC ($r = 0.69$) and Charaxinae ($r = 0.68$). The Riodininae (a Lycaenid subfamily) showed strong correlation with two Nymphalid subfamilies, the Satyrinae ($r = 0.86$) and the Charaxinae ($r = 0.74$), as well as the entire bait-attracted group ($r = 0.79$). The Pieridae were highly correlated with the Acraeini ($r = 0.78$) and the Morphinae ($r = 0.77$).

COLLINEARITY AMONG ENVIRONMENTAL FACTORS.—Highly significant correlations ($r > 0.7$) were observed for only altitude with mean temperature ($r = -0.82$, a well-known relationship) and both these with bamboos ($r = 0.73$ and -0.72, respectively), of disturbance with pollution ($r = 0.74$), connectivity with topography ($r = 0.73$), and temperature range with vegetation mosaic ($r = 0.70$). High covariation also occurred for vegetation category with connectivity ($r = 0.69$) and topography ($r = 0.65$), total secondary vegetation with bamboos ($r = 0.67$), and continentality (distance from the coast) with dry months ($r = 0.65$), the last also noted in this region by Oliveira-Filho and Fontes (2000).

CORRELATIONS BETWEEN BUTTERFLY RICHNESS AND ENVIRONMENTAL FACTORS.—The matrix of cross correlations (Table 5) showed highly significant negative associations of temperature with the richness of three cold-hardy groups: Acraeini, $r = -0.74$ (also correlated with bamboos and connectivity, both with $r = 0.70$); Nymphalinae, $r = -0.71$ (also with temperature range, $r = 0.74$, and latitude, $r = 0.80$); and Pieridae, $r = 0.70$ (also with topography, $r = 0.72$, and connectivity, $r = 0.70$). These three, along with Morphinae, seemed relatively insensitive to disturbance, pollution, and secondary vegetation; these three anthropic factors gave significant negative correlations with almost all groups, especially Satyrinae ($r = -0.75$, -0.71, and -0.60, respectively) and the combined bait-attracted groups ($r = -0.66$, -0.72, and -0.66). The Heliconiini uniquely showed very low correlation with secondary vegetation ($r = -0.09$). Connectivity was significantly correlated with the 12 smaller groups of NPP ($r = 0.43$–0.71, with Eurytelinae just below significance at $r = 0.39$), but less with Lycaenidae or Hesperiidae. The Eurytelinae, mostly vine feeders as larvae, were best correlated with vines ($r = 0.64$) and secondary vegetation ($r = -0.62$). Dry months and permanent water gave only negative significant correlations, although with low positive values in the first case for several bait-attracted groups, Theclinae, Riodininae, and Pyrginae; mean annual rainfall and soil fertility gave no significant correlations (Table 5). Lycaenidae and Hesperiidae were significantly sensitive to sampling area and effort (not included in Table 5), and area also showed significant effects on many bait-attracted groups.

Using the richness of eight easily sampled taxa as dependent variable (as in Fig. 1) and the single landscape factor connectivity as the independent variable, a quadratic plot ($y = a + bx + cx^2$; convex) gave the very high $R^2 = 0.718$. No other single factor (Table 2) came anywhere close to this significance, and connectivity did not explain the variation in richness of Lycaenidae or Hesperiidae (Table 5). With a composite heterogeneity index of the sum of the values in Table 2 for topography, dry months, soil mosaic, vegetation mosaic, and half the value for temperature range, a linear plot of richness showed that $R^2 = 0.37$ ($P = 0.002$) and the convex quadratic model, $R^2 = 0.48$. With natural disturbance in the environment (approximated as a sum of topography, temperature range, vines, and bamboos), the linear R^2 was 0.42 ($P = 0.001$), and the quadratic, 0.56. In contrast, a strong negative correlation was seen between richness and an index for anthropogenic disturbance, estimated (see above) as the sum of disturbance type, pollution, and one-tenth of the percentage of

TABLE 2. *Environmental factors in 21 sites of Atlantic Forest analyzed for determinants of butterfly fauna richness and composition.*

Environmental and physical factors Sites:	João Pessoa	E. Per- namb.	Ma- ceió	Chap. Guim.	Bra- sília	Belo Horiz.	Linha- res	Santa Teresa
Sampling effort ($< 20 < 60 < 200 <$ total days)	4	3	3	4	4	3	3	4
Area sampled ($\log_{10}$ ha)	2.8	3.2	3.3	4.2	3.5	3.4	4.3	4.0
Latitude (degrees south of Equator)	7	8	10	15	16	20	19	20
Distance from the coast ($\log_3$ km)	1.4	3.2	3.3	6.4	6.2	5.3	3.1	3.5
Mean altitude of site (m elev.)	20	100	5	400	1000	1000	20	700
Range of altitudes sampled (m)	50	200	10	300	700	500	40	400
Topography: principal relief type[a]	2	3	1	3	3	5	2	5
Mean annual temperature (°C)	25	25	25	23	21	21	24	19
Variation in mean monthly temperature (°C)	1	1	1	7	7	6	6	7
Mean annual rainfall in dm	18	20	15	17	16	15	12	16
Mean number of dry months/year	3	3	3	4	4	2	1	0
Principal soil/texture category[b]	5	5	5	3	5	6	4	4
Soil fertility (base availability)[c]	4	5	3	4	3	2	5	2
Soil mosaic in site[d]	2	4	2	5	5	5	5	3
Principal vegetation category[e]	3	3	3	3	2	3	3	6
Vegetation mosaic: complexity[f]	2	2	2	4	3	3	3	5
Vines and lianas: importance[g]	3	3	1	5	4	4	4	5
Bamboos: abundance in site[h]	1	2	2	4	3	3	2	4
Permanent surface water in area[i]	4	2	5	3	4	3	3	2
Type and intensity of disturbance[j]	6	4	6	2	3	5	1	2
Level of agricultural/industrial pollution[k]	3	2	4	1	1	4	2	1
Total percent of secondary vegetation	60	80	90	50	40	60	50	50
Connectivity of site (see text for calculation)	2	4	2	7	7	9	6	9

[a] Principal relief type, coded as 1 = level, 2 = depression or gently rolling, 3 = rolling, 4 = strongly rolling, and 5 = steep or mountainous.

[b] Soil categories, averaged: 1 = rock or hardpan, 2 = sand or concretionary, 3 = Cambisol or plinthic, 4 = moderate-texture Latosol, 5 = moderate-texture podzolized, and 6 = very argyllic or humic soil.

[c] Soil bases and fertility: 1 = hardpan or coarse sand, 2 = alic, 3 = alic + dystrophic, 4 = dystrophic, 5 = dystrophic + eutrophic, and 6 = eutrophic soil.

[d] Soil mosaic: 1 = >80 percent of one type of soil, 2 = 50–80 percent of one type, 3 = at least three types, 4 = four types, and 5 = five or more soil types in mosaic.

[e] Vegetation categories, corresponding to aspect diversity: 1 = principally anthropic systems, 2 = mangrove, oceanside restinga, open savanna systems including high-altitude pseudoparamo, or white sand campina; 3 = poor dense forest, floodable forest or bamboo forest; 4 = open palm or liana forest, or semi-deciduous/deciduous forests; 5 = alluvial terrace, delta, or cloud forest; and 6 = rich mixture of dense and open forest (see Brown 1997a and following footnote).

[f] Vegetation mosaic (per 100-ha patch): 1 = relatively uniform vegetation; 2 = only two major types, 3 = three subequal, 4 = four major vegetation types, and 5 = five or more types in complex mosaic.

[g] Abundance of lianas from 1 = almost absent in tree dominated system to 6 = occupying almost half of basal area of vegetation covering many trees.

[h] Abundance of bamboos in system from 1 = essentially absent to 6 = present in many large patches, up to 30% of the vegetation mosaic.

[i] Presence of permanent water bodies (perennial rivers, lakes, swamps) coded as: 1 = minimal, 2 = small ponds or streams, 3 = some larger rivers or lakes, 4 = many lakes, and 5 = oceanside.

[j] Type of disturbance or anthropic use in region: 1 = mostly continuous forest with some agroforestry, 2 = limited small agriculture, 3 = some suburban or commercial agricultural use, 4 = mosaic landscape with extensive human presence, 5 = also with industrial use of land, and 6 = basically anthropic or urban landscape.

[k] Cumulative effects of agricultural or industrial pollution in site: 1 = negligible, 2 = light, 3 = moderate, and 4 = heavy.

secondary vegetation (linear $R^2 = 0.39$, $P = 0.002$; Table 5).

PRINCIPAL ENVIRONMENTAL COMPONENTS AFFECTING BUTTERFLY RICHNESS.—Principal components analysis (PCA) of the environmental data from the 21 sites (Table 2) gave three axes explaining 62 percent of the cumulative variation (Table 6). These axes were used to represent the environmental variation explaining the richness of the 12 smaller butterfly groups, and the 2 subfamilies each of Lycaenidae and Hesperiidae in a new PCA.

The first axis (dominated by topography, temperature, and vegetation) explained 33 percent of the environmental variation among the sites, and most of the between-site variation in the richness

TABLE 2.   *Extended.*

Poços Caldas	Morro Diabo	Serra Japi	Cam-pinas	USP campus	Alto Serra	São Vi-cente	Ita-tiaia	Rio de Janeiro	Xe-rem	Delta S. João	Curi-tiba	Join-ville
2	2	3	4	3	2	4	4	3	2	3	4	4
3.9	4.3	3.3	2.4	2.0	3.3	3.7	4.1	3.5	3.3	3.2	2.7	3.0
22	22.5	23	23	23.5	24	24	22.5	23	23	22.5	25	26
5.0	5.7	4.2	4.5	3.7	2.7	2.0	3.9	1.5	2.9	1.0	4.7	2.5
1200	350	900	600	800	900	50	1400	400	100	10	1000	100
1000	300	600	40	50	350	400	2400	800	200	10	400	200
5	2	5	2	3	5	5	5	5	5	1	3	3
18	24	17	21	19	17	21	16	24	24	24	16	20
5	9	7	6	6	8	7	11	5	5	5	6	5
17	13	14	14	14	26	25	20	14	26	10	14	15
1	3	1	2	0	0	0	1	0	0	2	0	0
6	4	4	5	4	4	2	4	4	4	2	4	3
4	3	3	4	2	2	2	2	5	2	4	2	3
3	3	2	2	2	2	4	3	4	2	3	3	4
4	3	4	3	1	5	6	5	6	6	3	4	5
3	3	3	2	3	3	4	5	3	2	2	3	3
3	5	5	6	3	3	1	3	2	2	2	3	1
5	4	6	4	1	6	2	6	2	3	1	5	2
2	4	3	2	2	4	5	3	1	4	5	4	3
4	4	4	5	6	2	6	1	6	5	3	6	6
3	2	1	3	4	2	4	1	3	2	1	3	2
50	40	30	40	90	60	60	20	80	30	80	60	50
8	5	8	6	1	12	6	12	10	12	6	6	7

of Acraeini, Pieridae, Nymphalinae (the cold-hardy groups), Ithomiinae, Morphinae, Brassolinae, Papilionidae, both groups of skippers, the total bait-attracted and model-mimetic groups (but not their sum, NPP), and the total fauna (Table 6). The second axis (dominated by dry months and continentality) explained an additional 18 percent of the environmental variation, and the largest part of the richness for Eurytelinae and Lycaenidae. The third axis (dominated by soils) explained an additional 11 percent of the environmental variation, and a majority of the variation in Heliconiini. Charaxinae and Satyrinae richness were associated with all three axes (Table 6).

BUTTERFLY COMMUNITY STRUCTURE AND ENVIRONMENT: CANONICAL ORDINATION.—Redundancy analysis (RDA) of the data for the twenty-one sites in Tables 1 and 2, within the context of CANOCO 3.12, showed for the 12 smaller groups (Fig. 3a) a predominant influence of distance from the coast (continentality), explaining 20 percent of the among-site variation in the proportions of the groups (Table 7). This was followed by disturbance (12%), mean temperature (12%), temperature range in the site (10%), and vegetation category (5%, not quite significant); the five together explained 59 percent of the variation. All other fac-

tors were not significant ($F < 2.5$, $P > 0.05$). When continentality (a geographical number, not necessarily an ecological factor) was removed, its closest correlate (dry months; Oliveira-Filho & Fontes 2000) replaced it, explaining 15 percent of the variation as the second most influential vector. Disturbance moved to first place, explaining 19 percent. Third, fourth, and fifth places remained the same, all significant (Table 7). The five vectors explained 58 percent of the variation in butterfly proportions. Subsequent removal of anthropogenic disturbance led to its substitution by the nearly equivalent pollution (Table 5), explaining along with the same three subsequent vectors, a total of 53 percent of the variation (Table 7). Continentality (or dry months) and disturbance vectors opposed each other along one canonical axis, temperature and its variation (or altitude) along the other (Fig. 3a), which corresponded closely with the results of the PCA.

The second RDA, using the six larger divisions of the entire butterfly fauna (Fig. 3b), included seven significant vectors with F between 2.66 and 4.8, explaining 74 percent of the total variation. Soil mosaic on the first axis explained 16 percent, and dry months on the second, 13 percent. These were followed by five disturbance-related vectors of landscape and vegetation: permanent water and second-

TABLE 3. *Cumulative total of species over time on the total butterfly site list for the Mata de Santa Genebra, Campinas, São Paulo, Brazil, by groups of butterflies (**families** and subfamilies; Table 1). The "1975" column includes information in local collections and early visits to the site in 1973 and 1974; the next column includes early censuses and mark-recapture projects, and the first five standard inventories (April of 1988 to 1992). The point at which 90 percent of the presently recorded species had already been sampled is shown in **bold**.*

Butterfly group	Sampled until: Daily lists to number: Cumulative obs/h:	1975	16/4/92 5 200	19/6/97 16 340	9/3/98 36 477	2/7/98 62 614	21/10/98 93 752	18/1/99 119 892	2/4/99 145 1032	17/6/99 173 1172	15/10/99 205 1312	17/4/00 231 1452
Nymphalidae (total)		123	176	188	**193**	198	203	205	206	208	209	210
Ithomiinae + Danainae + Liby.		19	26	29	29	**31**	32	32	33	34	34	34
Morphinae + Brassolinae		5	15	**16**	16	17	17	17	17	17	17	18
Satyrinae		15	22	25	**27**	28	29	29	29	29	29	29
Charaxinae		7	14	**15**	16	16	17	17	17	17	17	17
Apaturinae + Lim. + Col. + Cyr.		14	22	**24**	25	26	27	27	27	27	27	27
Eurytelinae		30	36	38	**39**	39	40	42	42	42	43	43
Nymphalinae		16	**17**	17	17	17	17	17	17	18	18	18
Heliconiini + Acraeini		16	**24**	24	24	24	24	24	24	24	24	24
Pieridae		20	**27**	27	27	28	28	28	28	28	28	28
Papilionidae		10	**16**	16	16	17	17	17	17	17	17	17
Lycaenidae (total)		33	67	84	98	105	115	**118**	122	126	128	131
Theclinae + Polyommatinae		19	49	57	67	69	76	79	**82**	85	87	89
Riodininae		14	26	28	33	36	**39**	39	40	41	41	42
PAPILIONOIDEA (total)		186	286	315	334	**348**	363	368	373	379	382	386
Pyrrhopyginae		2	5	6	6	6	7	7	**8**	8	9	9
Pyrginae		58	116	124	**130**	134	135	136	139	141	143	144
Hesperiinae		40	89	104	119	132	**136**	138	145	150	151	151
HESPERIOIDEA (total)		100	210	234	255	272	**278**	281	292	299	302	304
Total list (butterflies)		286	496	549	589	620	**641**	649	665	678	684	690

TABLE 4. *Similarities (Sorensen) among three 14-h standard weekly censuses, and cumulative lists for six weeks (84 h) taken during March–May 2000 period in two forest fragments 16 km apart in Campinas, SP. Both fragments were of similar size but with different topography, soils, and vegetation (SG = Santa Genebra, CP in Table 1; RC = Ribeirão Cachoeira), with controls in SG for the same period in 1999. The six groups with the most divergent indices (site × year) are shown in **bold**.*

| | Three 14-h standard weekly censuses | | | | | Cumulative list (six weeks) | | | | |
| | Number of species (min–max) | | | Average 3 similarity indices | | Number of species (total) | | | Global similarity index | |
Butterfly group	RC 2000	SG 2000	SG 1999	RC 2000 × SG 2000	SG 2000 × SG 1999	RC 2000	SG 2000	SG 1999	RC 2000 × SG 2000	SG 2000 × SG 1999
Total of all butterflies	266–303	269–305	293–318	0.71	0.79	447	431	448	0.77	0.83
Papilionidae	7–9	7–10	7–11	0.81	0.84	13	11	12	0.92	0.87
Pieridae	15–19	18–23	20–23	0.80	0.89	22	26	26	0.87	0.92
Danainae + Libytheinae	3–4	4–5	3–5	0.84	0.90	5	5	6	1.00	0.91
Ithomiinae	14–17	15–16	14–16	**0.82**	**0.87**	21	18	19	**0.82**	**0.92**
Morphinae + Brassolinae	2–5	2	4–5	0.40	0.60	9	4	8	0.62	0.67
Satyrinae	11–16	8–10	9–12	**0.54**	**0.79**	19	14	15	**0.67**	**0.90**
Charaxinae	7–10	7–9	9–12	0.84	0.87	12	10	13	0.73	0.78
Apat+ Lim + Cyr + Col (= ALCC)	5–7	5–10	10–11	**0.43**	**0.65**	13	14	14	**0.67**	**0.86**
Eurytelinae	21–22	22–23	25–28	0.84	0.86	27	30	32	0.91	0.90
Nymphalinae	10–12	11–13	13	0.87	0.96	17	15	15	0.88	0.93
Heliconiinae: Acraeini	6	10–11	8–9	**0.74**	**0.89**	7	11	11	**0.78**	**1.00**
Heliconiinae: Heliconiini	8–9	8–10	7–9	0.90	0.94	9	10	9	0.95	0.95
Nymphalidae (total)	93–100	94–106	109–113	0.76	0.85	135	136	142	0.80	0.88
Nymph + Papil + Pieridae (= NPP)	117–126	121–134	138–144	0.77	0.86	170	173	180	0.82	0.88
Theclinae + Polyommatinae	17–26	18–26	16–21	0.54	0.61	44	43	42	0.71	0.71
Riodininae	9–18	12–18	12–14	**0.48**	**0.61**	26	26	24	**0.65**	**0.84**
Lycaenidae (total)	29–44	31–44	28–35	0.52	0.61	70	69	66	0.69	0.76
Pyrrhopyginae + Pyrginae-1	22–32	26–29	26–34	0.67	0.75	48	40	43	0.77	0.77
Pyrginae-2	41–44	48–52	46–50	**0.78**	**0.84**	61	62	59	**0.83**	**0.91**
Hesperiinae	45–57	45–55	45–63	0.68	0.71	98	87	110	0.71	0.72
Hesperiidae (total)	108–133	123–130	118–147	0.71	0.76	207	189	202	0.76	0.79
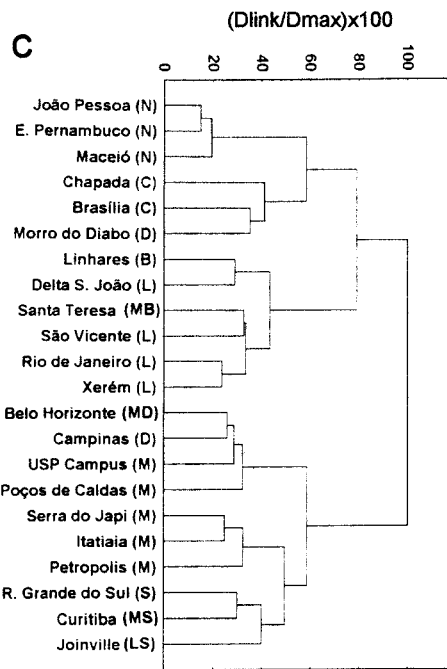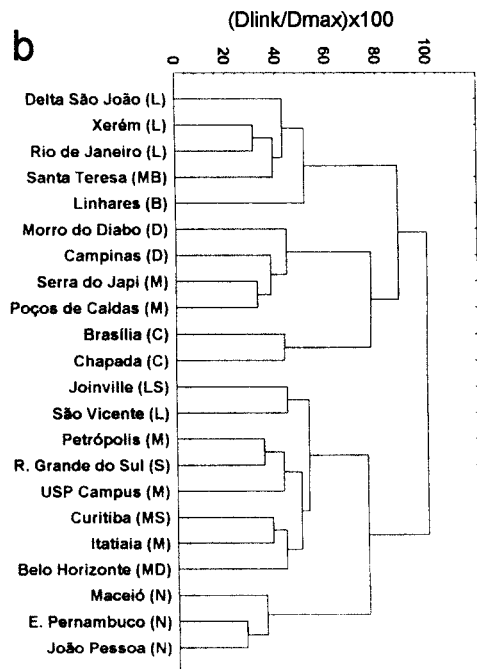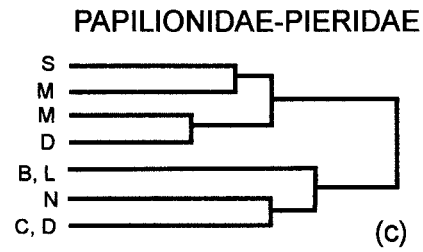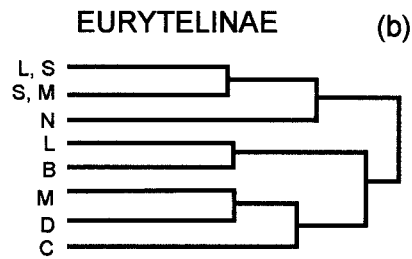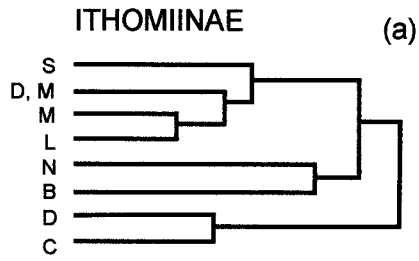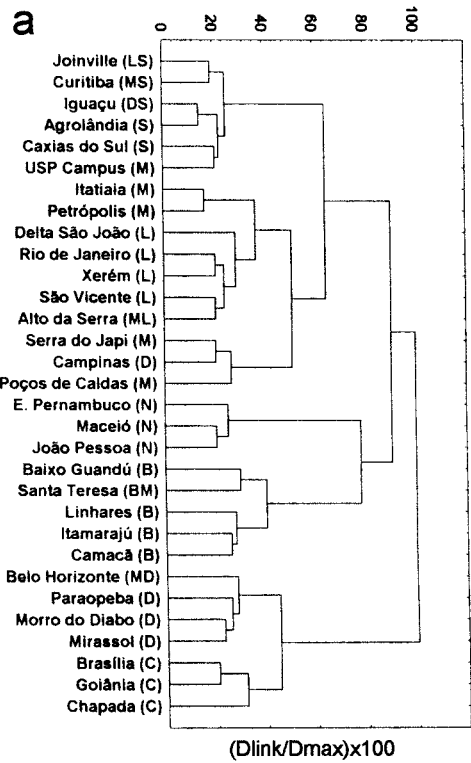
ary vegetation along axis 1, and connectivity, vegetation category, and bamboos along axis 2 (Table 7; Fig. 3b).

DISCUSSION

Sampling of atlantic forest butterfly communities.—For organisms to be useful in environmental monitoring, they need to be numerous, well known, easily identified, and rapidly sampled. They also should vary in presence and abundance among different environments and stages in landscape modification, and have clear preferences for certain habitats and resources.

Atlantic Forest butterfly communities are sufficiently rich and varied (Tables 1 and 5) to provide many options for monitoring through time, space, and disturbance transects. The two most rapidly inventoried families, Papilionidae and Pieridae (Table 3; Fig. 2c), are small, but include in any site 15–30 potentially informative species (Table 1; considering as useful all except widespread and migratory species). Nymphalidae are usually common and easy to recognize, and include 150–250 species in a single site (Table 1), of which well over half can be rapidly recorded (Tables 3 and 4). These three easily sampled families (NPP, Tables 4 and 5) make up about half of a weekly standard list (Table 4).

Highest standard weekly censuses, including up to half of the total long-term site list for many butterfly groups (Table 4), were heavily biased toward these more common species. Another weekly list would include most of these, but a different subset of the rarer species (mostly Lycaenidae and Hesperiidae). The great difficulty in sampling these small or rare species made their recording very sensitive to effort and recognition capacity of the observer. Even in full-effort censuses (> 10 hours), the least common species varied greatly from day to day, with "peaks" being easily recognized that corresponded to multispecies migratory swarms of Theclinae (Robbins & Small 1981) and to highly mobile Hesperiidae visiting bursts of flowers. This continual turnover of many species in the butterfly community is seen easily in similarity indices among site censuses separated by various periods (Brown & Hutchings 1997; Tables 3 and 4). The similarity among censuses of larger butterflies was always higher and less variable than that for the smaller species, even when extra efforts were made to recognize and record, especially on flowers, the species in these highly diversified groups (Lycaenidae and Hesperiidae, representing two-thirds of all butterflies in a well-sampled site; Table 1).

Biogeography of atlantic forest butterflies.—The geographical divisions of the butterfly fauna (Fig. 2) corresponded to well-known vegetation and climatic subunits of the region (Oliveira-Filho & Fontes 2000). As seen in vegetation analysis (Oliveira-Filho & Fontes 2000), the gallery and headwater forests in the Cerrado biome were closely associated with the Atlantic Forest biome, even though some Amazonian influence was seen in Brasília and more in the Chapada dos Guimarães (Table 1). These naturally isolated, moist forest inclusions shelter most of the butterfly diversity in the Central Brazil Plateau (Brown & Mielke 1967a, b; Brown 1987, 2000), and serve as a model for study in the presently fragmented anthropic landscapes nearer the coast.

The site groupings (Fig. 2) varied somewhat with the habitat preferences and biogeography of differentiation in the various butterfly groups analyzed. The basal division for Ithomiinae (Fig. 2a; migratory and sensitive to variations in temperature range, vegetation, and topography; Table 5) was between coastal/montane rain forest sites versus Planalto sites with semi-deciduous forest (C and D except Campinas, with much influence from nearby mountains), followed by separation of warmer sites into northeast (N) and Bahia (B), then extreme southern sites (S), and finally coastal (L) from montane (M). In Eurytelinae and related bait-attracted Nymphalidae (Table 5; Fig. 2b; sensitive to warmth and disturbance regimes), peripheral (N, S), montane (M), and two cold subcoastal sites

←

FIGURE 2. Natural divisions of butterfly faunas in the Atlantic Forest region; Ward's (1963) minimum variance clustering of similarities (species presence/absence) in 31 sites for 75 taxa of a) Ithomiinae, and 22 sites for 88 taxa of b) Eurytelinae/Apaturinae/Coloburini/Cyrestidini and 93 taxa of c) Papilionidae/Pierinae/Dismorphiinae. Reduced and simplified dendrograms for each group are in the upper right quadrant. All dendrograms suggest separate faunas centered in the northeast (code N), central (B), and southeastern coastal regions (L), southeastern mountainous areas (M), the central plateau (D in the south, C farther north), and frost-prone areas south of 24° (S); double letters indicate sites transitional between two biomes (site locations in Fig. 1).

TABLE 5. *Correlation values (τ) between environmental factors and species richness of butterflies in 21 Atlantic Forest sites. All significant values (P < 0.05) are included, with all values >0.65 in bold. Non-significant values between 0.35 and 0.43 also are included (in italics). Butterfly groups are coded by their first three to five letters. Additional codes are: 8GRP = eight groups (Fig. 1); HESN = Hesperiinae; HESD = Hesperiidae, and THRT = threatened species (Table 1).*

Environmental factors[a]	PAP	PIER	ITH	MOR	BRA	SAT	CHA	ALCC	EUR	NYM
Median altitude	—	0.64	—	—	—	—	—	—	—	0.53
Altitude range	—	**0.65**	—	0.44	0.43	*0.41*	—	—	—	—
Topography	*0.43*	**0.72**	0.53	0.58	—	—	—	—	—	0.45
Mean temperature	—	**−0.70**	—	−0.48	−0.43	—	—	—	—	**−0.71**
Temperature range	0.63	0.51	0.62	—	0.56	0.48	*0.40*	0.44	0.51	**0.74**
Dry months	—	−0.53	—	−0.55	—	—	—	—	—	−0.44
Permanent water	—	0.43	—	—	—	—	—	—	—	—
Soil category	0.44	—	—	—	—	—	—	—	—	—
Soil mosaic	—	—	—	—	—	0.49	0.54	—	0.47	—
Vegetation category	0.49	0.53	0.46	**0.66**	0.48	—	—	—	—	—
Vegetation mosaic	*0.42*	0.57	0.52	0.51	0.62	0.58	—	—	—	0.51
Abundance of vines	—	—	0.45	—	—	0.47	0.45	—	0.64	—
Bamboos	—	0.58	0.50	—	0.42	0.48	—	—	—	0.59
Disturbance	—	—	−0.59	—	−0.45	**−0.75**	−0.50	*−0.40*	−0.56	—
Pollution	−0.47	—	−0.46	—	−0.57	**−0.71**	−0.64	−0.51	−0.59	—
Secondary vegetation	−0.48	−0.51	−0.60	—	−0.44	−0.60	−0.51	−0.56	−0.62	*−0.41*
Connectivity	**0.71**	**0.70**	0.64	0.56	0.52	0.45	*0.43*	0.50	—	0.57
Distance from coast	—	—	—	—	—	0.57	—	—	0.57	—
Heterogeneity index	0.46	0.45	0.48	—	0.45	**0.69**	0.57	—	0.59	0.45
Natural disturbance	0.51	**0.65**	**0.68**	—	0.52	0.54	—	—	0.53	**0.68**
Anthropogenic disturbance	—	—	—	—	—	−0.49	−0.52	−0.48	—	—

[a] The environmental variables "annual rainfall" and "soil fertility" showed no significant correlations.

(L) were initially separated from central or warmer ones (B, C, D, L, and two Ms bordering the Planalto). Papilionidae and non-coliadine Pieridae (Fig. 2c; correlating strongly with temperature and connectivity) initially segregated between warmer (B, C, D, L, and N) and cooler (M including Campinas, S) sites.

Community structure and connectivity.—In the Atlantic Forests, seasonal movements of individual butterflies have been recorded over tens of kilometers (Papilionidae: Brown *et al.* 1981, Tyler *et al.* 1994; Nymphalidae: Brown & Vasconcellos-Neto 1976, Brown 1992: 145), and migrations of populations and communities may be inferred over many hundreds of kilometers (Lycaenidae, Pieridae, and Hesperiidae known only from distant regions) as species seek new leaves on larval food plants (especially in the early rainy season) or flower resources for adults (especially in the early dry season). Vertical movements also are seen frequently on the seaward slope of the coastal mountains, downward in late fall and winter, and upward in late spring and early summer, flowing into the interior during late summer to early fall (Brown & Mielke 1972, Brown 1992, Freitas 1993). Thus, a certain amount of turnover in the local community is in-

evitable, and needs to be factored out of inventories in order to see the signal for environmental change due only to changes in the resident community.

While it is expected that sites in more fragmented landscapes will show lower species turnover rates (Brown & Hutchings 1997: 100–101), species turnover is still prominent in an isolated forest surrounded by agriculture (Santa Genebra in Campinas). Strongly isolated urban fragments like João Pessoa, Maceió, and the USP campus (Tables 1 and 2), however, showed skewed small communities having structures that may be related to "hard" isolation (reduced vegetation) rather than to season, size, or ecological factors. The connectivity of the sites analyzed (Table 2) was strongly correlated with species richness of almost all butterfly groups (Table 5). It was also the third most important contributor to the first PCA axis defining sites and influencing the richness in most groups (Table 6); it also appeared as a significant component of the second axis in CANOCO analysis of the six larger groups (Fig. 3b), with a large influence (12%) on butterfly community structure (group proportions).

Metapopulation and metacommunity dynamics.—Although most "resident" butterfly groups

TABLE 5. *Extended.*

ACR	HEL	BAIT	MIM	8GRP	THEC	RIOD	LYC	PYR	HESN	HESD	TOTAL	THRT
0.66	—	—	0.47	*0.38*	—	—	—	—	—	—	—	—
0.66	—	—	0.52	0.49	0.59	—	0.51	—	*0.42*	*0.40*	0.48	0.49
0.58	—	—	0.64	0.53	—	—	—	—	—	—	—	—
−0.74	—	—	−0.58	−0.44	—	—	—	—	—	—	—	—
0.62	—	0.56	**0.71**	**0.68**	—	—	—	—	0.48	*0.43*	0.48	—
—	—	—	−0.49	—	—	—	—	—	—	—	—	—
—	—	—	—	—	*−0.42*	—	—	−0.55	—	−0.48	*−0.42*	−0.48
—	−0.50	—	—	—	—	—	—	—	—	—	—	—
—	0.45	0.48	—	—	0.56	0.63	0.63	0.51	0.45	0.49	0.55	—
0.42	0.55	—	0.57	0.50	—	—	—	—	—	—	—	0.48
0.46	*0.41*	0.54	0.60	0.60	—	0.46	0.43	0.50	0.59	0.57	0.58	0.55
—	—	0.50	—	—	—	—	—	0.48	—	—	*−0.39*	—
0.70	—	*0.41*	0.58	0.54	—	—	—	—	—	—	—	—
—	*−0.41*	**−0.66**	−0.46	−0.54	*−0.40*	−0.60	−0.53	−0.45	—	*−0.42*	−0.54	—
—	−0.44	**−0.72**	−0.46	−0.57	−0.49	**−0.67**	−0.61	−0.48	—	−0.43	−0.59	−0.53
−0.56	—	**−0.66**	−0.60	**−0.65**	−0.44	*−0.39*	−0.44	−0.48	−0.49	−0.50	−0.57	—
0.70	0.47	0.54	**0.80**	**0.74**	—	—	—	—	—	—	0.46	0.44
—	—	0.44	—	—	*0.39*	0.58	0.51	—	—	—	—	—
0.46	—	**0.66**	0.55	0.61	0.62	0.64	**0.67**	0.56	0.52	0.55	**0.66**	—
0.70	—	0.57	**0.74**	**0.71**	—	—	—	*0.40*	0.47	0.45	0.51	—
—	*−0.42*	−0.51	—	—	—	−0.61	−0.52	—	—	—	−0.45	*−0.42*

might be considered as unlikely to move about frequently between their metapopulation subunits in a fragmented or heterogeneous landscape, they fly (and are blown) far on cloudy or rainy days, or move in search of resources on cool humid mornings (Brown & Vasconcellos-Neto 1976). Numerous attempted colonizations by previously unrecorded species in all butterfly groups have been discovered early and followed in the best-studied sites, with their success (a viable second generation) partly predictable from the availability of known resources (Table 2 in Brown 2001). Thus, the presence of some butterfly species in a site may be a better indicator of adequate connectivity and ecological conditions, rather than of their historical origin or long-term residence there. Atlantic Forest butterfly communities seem to be open, fluid, and more influenced by ecological factors than by evolutionary constraints (Brown 2001). This is important for the interpretation of monitoring results. Although frequent colonizations may increase stochasticity in the local community, this is partly compensated by the increased number and variety of species present, each one indicating its specific resources and habitats.

Among major natural disturbance factors, bamboo patch die-offs (after flowering, 5- to 30-yr intervals) are especially interesting in local community dynamics because they result in the crash of all species dependent upon this resource (including many Morphinae, Brassolinae, Satyrinae, and Hesperiinae), especially in small forest fragments. In this situation, gradual recolonization occurs slowly, over a decade or more, as adequate amounts of the bamboos regrow. The cyclic bamboo association is a typical example of a metacommunity, a group of interacting plant and animal species associated with a patchily distributed and often unstable resource or habitat (Wiens 1997). Other interesting examples observed in Atlantic Forest insects include associations based on early succession plants, large forest clearings, windthrows and other treefalls, burns, river beaches and small swamps (all of which are used very frequently by butterflies), standing dead or dying trees (frequently colonized by beetles, ants, termites, and many other insects), rain puddles and uproot pondlets (especially for dragonflies and other aquatic species), large fecund trees (which attract all kinds of pollinators and frugivores), anthropic flower gardens (often among the richest habitats near forests), and any other special and temporary habitats lasting for 5 to 50 generations of the colonizing animals (Blau 1980). Insect species with short life cycles and responsive to such temporary habitats are especially useful in monitoring disturbance, although their presence or ab-

TABLE 6. *(a) Participation of 20 environmental variables in the first three axes of a PCA analysis for 21 Atlantic Forest sites, and (b) variation in richness of 16 butterfly groups and four combinations, explained by each of these axes.*

(a) Factors	Axis 1	Axis 2	Axis 3
Median altitude	−0.291	−0.085	0.371
Altitude range	−0.291	−0.016	0.051
Topography	−0.292	0.204	0.059
Mean temperature	0.295	−0.094	−0.242
Temperature range	−0.317	−0.093	−0.108
Annual rainfall	−0.129	0.254	−0.146
Dry months	0.145	−0.405	−0.031
Permanent water	0.079	0.078	−0.299
Soil category	0.009	−0.121	0.518
Soil fertility	0.189	−0.221	−0.064
Soil mosaic	−0.011	−0.221	−0.241
Vegetation category	−0.189	0.322	−0.251
Vegetation mosaic	−0.228	−0.026	−0.137
Abundance of vines	−0.121	−0.381	0.184
Bamboos	−0.322	−0.073	0.142
Disturbance	0.202	0.279	0.241
Pollution	0.166	0.255	0.333
Secondary vegetation	0.273	0.159	0.057
Connectivity	−0.308	0.082	−0.154
Distance from coast	−0.054	−0.395	−0.104

	R^2 = percent variance in group explained by:		
(b) Butterfly groups	Axis 1	Axis 2	Axis 3
Papilionidae	32	00	17
Pieridae	63	02	02
Ithomiinae	46	01	05
Morphinae	35	09	02
Brassolinae	38	00	08
Satyrinae	33	33	11
Charaxinae	13	17	25
ALCC	17	04	14
Eurytelinae	17	40	10
Nymphalinae	40	00	01
Acraeini	64	01	00
Heliconiini	07	00	41
Theclinae	17	23	01
Riodininae	11	30	22
Pyrginae–Pyrrhopyginae	26	06	03
Hesperiinae	30	19	07
Bait-attracted species	67	00	04
Models and mimics	58	02	07
Total butterflies	52	08	11

sence often may be due to natural rather than anthropogenic changes in the landscape and greatly influenced by connectivity.

ENVIRONMENTAL FACTORS AFFECTING BUTTERFLIES.—All analyses clearly showed climatic and disturbance factors as important in determining both richness and community structure of butterflies in Atlantic Forest sites, with major influence also from topography, vegetation, and soils. The combination of data from correlation, PCA, and canonical analyses indicated the utility of each butterfly group for following certain changes in the environment. This showed that Pieridae, Nymphalinae, and Acraeini were tightly associated with variable low temperatures (subtropical climate), and thus should disappear with warming in anthropogenic systems. Forest-inhabiting Ithomiinae, Satyrinae, Charaxinae, Eurytelinae, and Riodininae were shown to be very sensitive to disturbance and pollution, and their disappearance may be among the best indicators of these effects in natural systems. Papilionidae, Pieridae, Ithomiinae, and Acraeinae were strongly correlated with connectivity, Eurytelinae with vines,
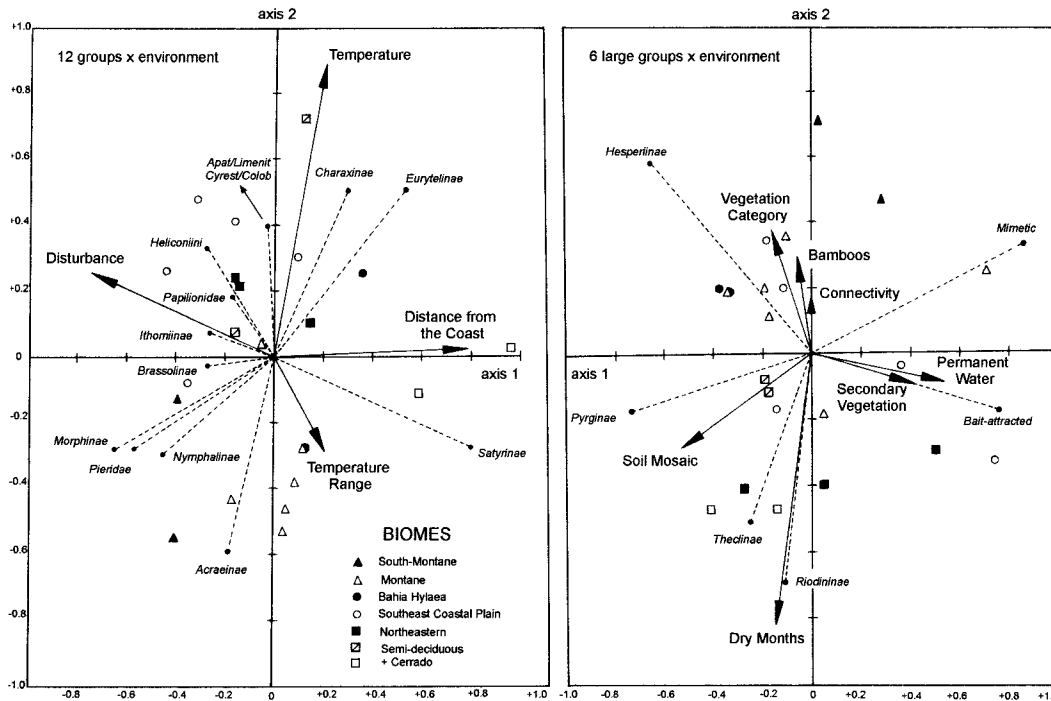
FIGURE 3.   (a) Redundancy analysis of proportions of 12 small butterfly groups (Papilionidae, Pieridae, and all Nymphalidae divided into 10 groups; Table 1, dashed vectors and heavy arrows represent the four significant environmental vectors [$F > 2$]) influencing the composition of the community in 21 Atlantic Forest sites. (b) Redundancy analysis for the same sites, using 6 larger butterfly groups that include the entire fauna, showing 7 significant environmental correlates that divide these into 3 pairs of most closely related butterflies. Statistical values and probabilities for the environmental vectors are in Table 7.

Brassolinae with vegetation mosaic, and Morphinae with vegetation category. Ithomiinae, Satyrinae, and Eurytelinae were confirmed as good indicators of intact heterogeneous forest systems (Tables 5–7; Fig. 3). The use of any of these groups in monitoring natural environments would provide rapid information on directional changes in key factors also affecting many other parts of the system, including vegetation.

In the RDA, the eigenvectors of several pairs of very closely related butterfly groups practically opposed each other in the triplot (Fig. 3a; Satyrinae vs. Brassolinae, Acraeini vs. Heliconiini, and Nymphalinae vs. Eurytelinae), implying a strong dissociation of habitat; indeed, the first member of each pair often inhabited open and cool areas and the second preferred warm forests. Substitutions of environmental vectors by others, sub-equivalent or opposed, in the RDAs had only minor effects on the eigenvectors of most butterfly groups (Table 7; Fig. 3), a measure of the robustness (and redundancy) of the analysis. Based on these analyses and

correlations, it is probable that for almost any type of habitat to be evaluated, some group of Nymphalidae can be found to monitor its quality and continuity (Table 6), provided it can be sampled easily in the site.

CONSERVATION OF BIOLOGICAL DIVERSITY IN A SITE: BUTTERFLY SURROGATE GROUPS—Rapid inventories of select species in threatened areas of the Neotropics are useful for evaluating the total fauna and importance of a given biome or landscape. For this purpose, surrogates for total butterfly richness are needed to obtain comparable species lists in a period of few months or even days (Beccaloni & Gaston 1995). The Nymphalidae make up *ca* 25–29 percent of the total butterfly community in a thoroughly sampled site. The resulting predictor of total butterfly species, *ca* 3.7 ± 0.23 times total Nymphalidae species number (Table 1), holds in many parts of the Neotropics (Table 3 in Brown 1997a). The Ithomiinae, often *ca* 15 percent of the Nymphalidae (Table 1) can be sampled rapidly and

TABLE 7. *Statistics of the principal vectors obtained in the RDA between environmental factors and proportions of butterfly groups in the community at 21 Atlantic Forest sites.*

Factors	F	P	%
12 groups			
Distance from coast	4.72	0.001	20
Disturbance	3.16	0.001	12
Mean temperature	3.64	0.03	12
Temperature range	3.45	0.01	10
Vegetation category	1.73 (n.s.)	0.068	5
12 groups (removing distance from coast)			
Disturbance	4.51	0.001	19
Dry months	4.00	0.001	15
Mean temperature	2.67	0.009	9
Temperature range	2.58	0.018	8
Vegetation category	2.30	0.017	7
12 groups (removing disturbance)			
Pollution	4.35	0.001	19
Dry months	3.81	0.002	14
Mean temperature	2.89	0.012	10
Temperature range	2.32	0.022	10
6 groups			
Soil mosaic	3.62	0.002	16
Dry months	3.16	0.04	13
Permanent water	3.93	0.018	13
Secondary vegetation	2.66	0.054	8
Connectivity	4.80	0.002	12
Vegetation category	3.18	0.025	7
Bamboos	2.66	0.039	5

easily on certain pyrrolizidine-alkaloid-containing baits or flowers (Beebe 1955, Brown 1985), and have been proposed as a general surrogate for calculation of butterfly species richness at a reasonably invariant 4.3–4.6 percent of the total (Beccaloni & Gaston 1995). In fact, Ithomiinae varied in well-sampled Atlantic Forest sites from two (Joinville) to six percent (Xerém) of the fauna (Table 1); extremes of less than two (peripheral, colder, or dryer sites) to eight percent (eastern Andean slopes) are known also in other regions (Brown 1996b, 1997a, b), giving a wide variance (0.5–2.0 x) in the calculated total butterfly fauna (Table 1). The local Ithomiinae fauna also varied greatly with season, and was invaded frequently by mobile swarms of nonresident species or subspecies seeking humidity, flower nectar, and available host plants. The apparent early asymptote of Ithomiinae species richness is thus deceptive (Table 3), further reducing its value as a species richness surrogate (Brown 1997a). Nevertheless, predicted total site lists based on Ithomiinae (4.0%) and Nymphalidae (27%) were significantly correlated with the observed values of the total fauna for the 21 sites in Table 1

($R^2 = 0.33$ and $P = 0.006$ for the first, $R^2 = 0.68$ and $P < 0.0001$ for the second).

The best predictors of the total faunal richness were its largest components, the two divisions each of Lycaenidae and Hesperiidae. Unfortunately, these groups were also the hardest to inventory and sample to a reasonable proportion of the species present (Tables 3 and 4). In their place, various small groups of Nymphalidae were easy to sample and still practical for prediction; the highest correlation of small groups with total fauna was shown by the bait-attracted groups, combined ($r = 0.92$) or separately (*e.g.*, Satyrinae, 0.83; Charaxinae, 0.82; and Eurytelinae, usually easy to inventory, 0.80).

CONSERVATION OF ATLANTIC FOREST LANDSCAPES IN PRACTICE.—The presence of certain rare butterfly species can indicate habitats that are most likely to contain the greatest richness, as well as concentrations of threatened species in many groups. In the Atlantic Forests, 65 butterfly species have been designated as threatened in state, national, or other official lists (Bernardes *et al.* 1990; Brown 1991, 1993a–c, 1996b, c; Casagrande & Mielke 1993; Brown *et al.* 1998; Casagrande *et al.* 1998; Otero *et al.* 2000). These species merit special attention for their extreme geographical restriction, diminishing population levels, vanishing habitat, reduced adaptability, or apparent disappearance. Because most are very rarely observed in any site, their accumulation on a list is principally a function of total inventory effort, rather than any easily identifiable ecological factor; indeed, they show little correlation with the environmental factors analyzed (Table 5, at right). Nevertheless, in some sites, these rare species turn up very early in the inventory process (within the first few days). Such sites with concentrations of rare butterflies usually also include threatened species of other insects, frogs, birds, mammals, and plants, and have been called "paleoenvironments" (Brown 1991). This term does not refer to their great age or stability, but to the ancient, morphologically "primitive", and often behaviorally specialized and very rarely encountered species found there which are absent from most other sites or anthropic systems. They are discovered typically in medium-elevation, strongly dissected, always-humid regions, on deep fertile soils in secluded valleys in the Atlantic Forests; they are often in marginal areas near major environmental discontinuities that are subject to high levels of natural disturbance. These places seem to function as "hideaways" or sites where physical complexity

leads to highly variable vegetation in small patches, making more probable the successful persistence of ancient species, probably competitively inferior to their descendents under today's conditions (see discussion of *Heliconius nattereri* in Brown 1972b).

As efficient indicators of landscape diversity and integrity (Halffter 1998), butterflies and other insects can participate and be useful in many aspects of the ongoing conservation of the unique Atlantic Forest biota as a MAB-UNESCO Biosphere Reserve. In nuclear (core) areas of permanent preservation, baselines for optimum levels of protection, heterogeneity, and natural succession can be established by focusing on rare or threatened species present, and studying levels and mechanisms of metapopulation and metacommunity integrity over long periods. These studies will be necessary for the management not only of these areas but also of the surrounding landscapes. In buffer zones where sustainable resource-use practices must be maintained, routine monitoring of diversity and continuity of butterfly focal groups not only will help to maintain sustainability (giving early warning for possibly irreversible landscape degeneration), but also test the predictions and conclusions about disturbance/diversity relationships (Brown 1996a, b, 1997a) derived from observations in the core areas. In the remaining intensive use zones, monitoring of butterflies can help detect possible long-term environmental effects of vegetation removal or atmospheric and water pollution, as well as verify the health and optimum size of remaining fragments of natural systems, through observing changes in composition and diversity of the remnant communities in these regions. Target butterfly species also can be maintained by selection and cultivation of plants useful as resources for larvae and adults, especially strains resistant to the modified environments in these zones (see Otero & Brown 1986 for a case of a threatened species, *Parides ascanius*, in a disappearing habitat of the Atlantic Forests).

As well known and much appreciated popular symbols of natural harmony, beauty, and renewal, butterflies (along with birds and large mammals) have a special place in peoples' views about, and enjoyment of, natural systems. The combination of these attitudes with the use of butterflies as indicators in landscape ecology should help in both popular and scientific actions favoring the conservation of the remaining Atlantic Forest systems, now and in the future.

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