



Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring*

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Sustainable use of tropical forest systems requires continuous monitoring of biological diversity and ecosystem functions. This can be efficiently done with 'early warning' (short-cycle) indicator groups of non-economical insects, whose population levels and resources are readily measured. Twenty-one groups of insects are evaluated as focal indicator taxa for rapid assessment of changes in Neotropical forest systems. Composite environmental indices for heterogeneity, richness, and natural disturbance are correlated positively with butterfly diversity in 56 Neotropical sites studied over many years. Various components of α , β and γ -diversity show typical responses to increased disturbance and different land-use regimes. Diversity often increases with disturbance near or below natural levels, but some sensitive species and genes are eliminated at very low levels of interference. Agricultural and silvicultural mosaics with over 30% conversion, including selective logging of three or more large trees per hectare, show shifts in species composition with irreversible loss of many components of the butterfly community, indicating non-sustainable land and resource use and reduction of future options. Monitoring of several insect indicator groups by local residents in a species-rich Brazilian Amazon extractive reserve has helped suggest guidelines for ecologically, economically, and socially sustainable zoning and use regimes.

Keywords: conservation monitoring; insect indicators; Neotropical forests; disturbance and biodiversity; sustainability.

Introduction: biological diversity and sustainable use of tropical forests

Most present models and methods for the use of tropical forest products, from conservation with rigorous protection of the systems, through commercial extractivism or fruit-gathering, selective logging, or agroforestry to clear-cutting, pose a primary management question that can be reduced to three words: 'Is it sustainable?' (Hartshorn, 1995). A 'yes' answer to this question, especially if demonstrated in ecological and social as well as economic aspects, would achieve the primary goal of wise use and conservation of natural resources, and thus receive widespread support from all sectors of society (Vane-Wright, 1996).

The evaluation of sustainability requires the understanding and monitoring of local ecosystem functions before, during and after the use of the forest or its renewable products. Biological diversity is a frequently used surrogate for ecosystem health and function (Schulze and Mooney, 1993). Genetic, specific, and system diversity, and their turnover rates through space and time, can be evaluated through indicator 'focal'

taxa of plants and animals (Noss, 1990; Kremen, 1992, 1994; Oliver and Beattie, 1993; Longino, 1994; Kremen *et al.*, 1994).

Arthropod assemblages have been used for conservation monitoring since early suggestions by Pyle *et al.* (1981) (Rosenberg *et al.*, 1986; Brown, 1991, 1996a; Pearson, 1992; Kremen *et al.*, 1993, 1994; Halfpeter and Favila, 1993; Sparrow *et al.*, 1994; Kremen, 1994). Most authors agree that no single group of organisms can be sufficient for adequate inventory and monitoring (Landres *et al.*, 1988), since each group subtends its own formulae for extrapolation from species-time accumulation curves or genetic diversity measurements to general richness or diversity values (Soberón and Llorente, 1993). The groups used should be common, biologically and taxonomically well understood, easily observed and identified in any site or season, widespread and comparable across sites, seasons, habitats and human use regimes, faithful and sensitive to given physical and biological factors and processes in their habitat, closely associated with other taxa, resources, and ecosystem characters, and show a predictable early

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reaction to any unsustainable resource use which could lead to local habitat degradation (Brown, 1991; Pearson and Cassola, 1992; Pearson, 1994). This paper will examine the application of these 'first principles' to conservation monitoring in Neotropical forests, with a summary of extensive data on environmental parameters and the effects of different kinds of land use on the diversity of butterfly communities in chosen sites throughout the region.

The choice of adequate indicators for monitoring sustainability of ecosystem use

Superficial analyses of sustainability in resource use are sometimes restricted to the actual species (usually large trees or vertebrate animals) providing the materials being produced (such as wood, meat, fruits, oils or latex). The use of such few and limited economic species, continually removed from the system (thus not independent variables), as surrogates for monitoring the system functions and biological diversity that permit their continued renewal, is fraught with danger (Landres *et al.*, 1988). Furthermore, such long-cycle organisms can give information on sustainability only after several generations, usually years to decades. The vast majority of the flow of matter and energy in tropical forest systems involves microorganisms and invertebrates at the soil-plant and plant-herbivore interfaces. These represent almost all the species in the system, as well as their most easily measurable variation in time and space (β -diversity) (Wilson, 1987). They also include essentially all the non-wood biomass, and direct the principal ecosystem functions, inevitably including those responsible for renewal and sustainability of the principal forest products at any scale (Hawksworth, 1991; Hammond, 1995).

The soil and litter nutrient-recycling biota has been called 'the other last biotic frontier' (André *et al.*, 1994). It includes an unfathomable diversity of microorganisms and fungi (Hawksworth and Colwell, 1992; Hammond, 1995), mostly still undescribed and possibly even exceeding the astronomical number of herbivorous and parasitic insects predicted to occur in tropical forest systems. Little can be said yet about the physical determinants, chemical preferences, specificity, dispersal, distribution, or functions of the soil and litter biota (Lavelle, 1986, 1996; Moldenke and Lattin, 1990). Accessible elements that might be useful indicators, at the present level of knowledge, include earthworms, termites, ants, some beetles, and Collembola (Greenslade, 1985; Lavelle, 1986, 1996; Brown, 1991; Lavelle *et al.*, 1993). Nepsted *et al.* (1994) have recently

shown that deep roots (to -18 m) are responsible for keeping leaves on the canopy trees of Amazonian upland seasonal forests during periods of soil water stress, and thereby preventing drying out of the litter and eventual disastrous fires. These findings conflict dramatically with reigning myths about tropical forest systems, and reflect our continued ignorance about their structure, function, diversity, nutrient cycling, equations, resilience, composition, recovery, and optimum sustainable use regimes. Recognition of this ignorance gives support for using these systems as gently as possible, close to natural disturbance regimes, until more can be said with confidence on these parameters, under different use regimes.

In contrast, many elements of the above-soil invertebrate (and especially insect) diversity are relatively well known. Although some groups are still little-studied (especially those living in the higher strata of the vegetation), others, including whole families and suborders important in system function, are taxonomically tractable, ecologically well understood, and easy to locate and inventory in most Neotropical sites (Table 1). All of these have been suggested, and some extensively used, as indicators for biological diversity and system function (including historical aspects on different scales) in Neotropical forests (see Brown, 1991, 1996a).

These small animals have two properties important for the monitoring of systems: short life-cycle and low resilience. Although these may give high turnover rates and complicate the establishment of a baseline for inventory (Brown and Hutchings, 1997) and the evaluation of economic sustainability of forest products and use regimes, they make these animals quickly sensitive to small changes in system parameters. They thus represent an efficient and easily observed early warning system for subtle changes in the whole system, or in the sustainability of its use. Phytophagous insects are especially tightly tied into light structure, humidity, nutrient availability, and specific plant growth cycles, chemical compounds, and taxonomy, and thus indicate fluctuations in all these elements in the system that supports them. Any change in their abundance will immediately imply an increase or decrease of their primary plant resources, their habitat, or their enemies. Understorey plants, equally sensitive to many of the same factors (as well as to their insect enemies), are often tied into 6–12 month generation times, beyond the patience of many managers who need more rapid evaluations of the effects of their actions on the systems.

Many other groups of plants and animals have been,



Table 1. Some insect groups identified as practical, informative and ecologically faithful indicators for monitoring environmental changes in the Brazilian Atlantic Forests^a

Order: Family	Approx. no. of species ^b	Habitat: import. factors ^c	Respon. Disturb. L M H ^d	Col & Lit	Distrib. map	Sedentary?	Easy to find?	Easy to ident?	Easy to eval?	Predict patterns?	Resource specialist	Ecol well stud.	Eco syst funct.	T O
Collembola	200	1,3,8	-X-	+	+	++	++	+	++	++	++	++	++	17
Odonata	200	3,4,8,9	+X0	++	+	++	++	++	+	++	++	++	++	18
Isoptera	300	1,2,8	+X0	++	+	++	++	+	++	++	++	++	++	18
Homoptera:														
Membracidae	200	5,6,10	++-	++	+	+	++	++	++	+	++	++	+	16
Hemiptera:														
Pentatomidae	200	4,5,6	++-	++	++	+	+	++	+	+	++	++	+	15
Ephem, Pleco, Trichoptera														
Trichoptera	600	3,4,6	-X-	++	+	+	++	++	+	+	+	++	++	15
Coleoptera:														
Elateridae	1000	1,6,8	++-	++	+	++	+	++	+	++	+	++	++	16
Cerambycidae	10000	1,5,6,8	++-	++	+	++	++	++	+	+	++	++	++	17
Cassidinae	500	5,6,8	++0	++	+	++	++	++	+	++	++	++	+	17
Diptera:														
Muscidae (pt)	100	1,8	++X	++	++	+	++	++	++	+	++	++	+	17
Tephritidae	200	5,6,7,8	++X	++	+	+	++	+	+	+	+	++	++	14
Phlebotominae	300	3,4,5,8	++X	++	++	+	++	++	+	++	+	++	+	16
Bibionidae (pt)	200	1,2,4,7	++0	++	++	+	+	++	+	++	++	+	+	15
Lepidoptera:														
Arctiidae (s.l.)	1300	5,6,7	+X-	++	+	++	++	++	++	+	++	++	+	17
Saturniidae + Sphingidae	400	5,6,7,8	+X0	++	+	+	++	++	++	+	+	++	+	15
Lycaenidae:														
Riodininae	700	5-10	+X-	+	+	++	++	++	+	++	++	++	++	17
Nymphalidae:														
Ith, Sat, Hel	200	5,6,7,8	++-	++	++	++	++	++	++	++	++	++	+	19
Other Nymph. + Papilio., Pier.	400	5,6,7,9	+X0	++	++	+	+	++	++	++	++	++	+	17
Hymenoptera:														
Formicidae	800	4-7,10	+X-	++	+	++	++	++	++	++	++	++	++	19
Meliponinae	200	5,6,7	-X-	++	++	++	++	++	++	++	++	++	+	19
Euglossinae	100	5-8,10	0--	++	++	+	++	++	++	+	++	++	++	18

^a List assembled by a group of Brazilian entomologists meeting under the auspices of the Fundação Biodiversitas and Conservation International in Campinas, SP, on 23-24 May, 1996 (Workshop on distribution patterns of biodiversity in the Atlantic forests of southeastern and southern Brazil). Also includes some groups and information from the corresponding tables in Brown (1991, 1996a).

^b Approximate number of Atlantic forest species in the respective group evaluated.

^c Main environmental factors to which these insects respond: 1 = Litter and detritus, 2 = Soil structure and heterogeneity, 3 = Water quality and variety, 4 = Prey items, 5 = Plant diversity, 6 = Plant chemistry, 7 = Nectar sources, 8 = Humidity, 9 = Light intensity, 10 = Mutualists.

^d Diversity response syndromes at low (L), moderate (M) and high (H) disturbance regimes, coded as: - = diversity reduced, 0 = little or no effect, + = diversity increased, X = some species lost, replaced by others (community exchange).



are being, or could be used as environmental 'early warning' indicators in the Neotropics. Table 1 includes a number of characters that may be applied in choosing an adequate group to rapidly detect system changes. It is unlikely that any group will be 'all ready to be used' in a previously little-studied or inventoried region – some preliminary information, field work, and choices adapted to the given time, space, and human dimensions will always be necessary, and it would be wise to have a number of options that can give independent and convergent (or divergent or complementary) information about the past, present, and likely future of the system and site under use and study. For further aspects and applications, see Wilcox *et al.* (1986), Noss (1990), Brown (1991, 1996a), Raguso and Llorente (1991), Kremen (1992), Kremen *et al.* (1993), Oliver and Beattie (1993), Tyler *et al.* (1994), Pearson (1994), and Longino (1994).

Methods: Neotropical sites studied for butterfly diversity responses

The data used to prepare the tables and figures have been collected on communities of butterflies (diurnal Lepidoptera: Hesperioidea and Papilionoidea) over varying time-periods between 1900 and 1996, in nearly 1000 study sites in Brazil and other parts of the Neotropical forests. Although some of the data are not rigorously comparable nor collected in fully standardized fashion, all since 1964 are based on written daily observation lists from which at least the following quantitative information can be extracted: exact location, area covered, vegetation type(s), weather conditions and their variation, all species observed and relative abundance, genetic variation, and sex ratio of each (including by subhabitat, often permitting β -diversity estimates on different scales), foodplants and microhabitats for many species, and total effort invested during the day (see Brown and Hutchings, 1997). These lists were made by the author and other trained observers, on extensive observation transects during entire days (Brown, 1972). Baits of pyrrolizidine alkaloids (for Danainae and Ithomiinae), fermented fruits or excrement (for Satyrines and many other Nymphalidae), flowers (for all nectarivorous species), and coloured cloths (for territorial individuals) helped in the counts. Most areas were repeatedly visited in different seasons and years. Reasonably complete baseline information has been accumulated for the 56 localities in the Appendix Table, over the periods and with the characteristics indicated. For these localities, a fairly good idea can be obtained about the species present,

with their total richness and the evenness of taxocenes, in each season or year, in accord with local patterns of land use, fragment sizes, topography, soils and vegetation. Deviations from this baseline, associated with changes in land use, are usually obvious in the whole community or various of the groups observed (especially the more common, forest-restricted aposematic species).

Results: response of Neotropical forest butterfly diversity to environmental factors

'First principles' were used to transform the raw data in the Appendix Table to numerical indices reflecting overall butterfly diversity (**BDiv**), environmental heterogeneity (**EHet**), resource richness (**RR**), and natural disturbance level (**NDis**) in each site (Table 2).

The values assigned to the diversity categories (D, T, G, and Q) were as follows: **D** (Daily list), A = 4, B = 3, C = 2, D = 1; **T** (Total list), A = 3, B = 2, C = 1; **G** (Genetic diversity), A = 2, B = 1, C = 0; **Q** (Quality of the community), A = 2, B or B' = 1, C = 0. Final diversity indices varied from 3 (Caraballeda, Manaus) to 11 (Rio Negro and Limoncocha) (Table 2). They were surprisingly little associated with sampling effort (A–C in Appendix Table = 2, 1, or 0) or with area covered (+ in Appendix Table = 1, or 0) at this level of study; of the 13 indices of 9 or higher, five were only moderately sampled (total 2) and three poorly (0); of the eight indices of 5 or lower, three were well sampled (total 3) and three moderately well (2 or 1).

The environmental indices were calculated with the following numbers added or subtracted from the base value of 5:

- Elevation:** for **EHet**, +1 if range > 1000 m or mostly between 300 and 1200 m; –1 if all below 300 m.
 RR, +1 if on steep, rolling terrain, –1 if total elevation range 200 m or less.
 NDis, +1 if elevation range 600 m or more or on rolling terrain, –1 if very flat.
- Rainfall:** for **EHet** and **RR**, +1 if between 2000 and 4000 mm, –1 if ≤ 1000 mm or ≥ 6000 mm.
 NDis, +1 if 3000 mm or more.
- Dry Season:** for **EHet** and **RR**, +1 if 2–4 months, –1 if can be 5 months or more.
 NDis, +1 if very variable (more than 3 months)



Table 2. Composite environmental and diversity indices for 56 Neotropical sites (see Appendix Table)

Site No.	Name	Effort	Div. Index	EHet variation						RR resource richness						NDIs disturbance					
				Elev	Rain	Dry	Soil	Veg	TOT	Elev	Rain	Dry	Soil	Veg	TOT	Elev	Rain	Dry	Soil	Veg	TOT
1	Teocelo	3	6	1	1	1	0	0	8	1	1	1	2	0	10	1	1	0	1	0	8
2	Tuxtla	3	6	1	1	0	1	1	9	1	1	0	2	2	11	1	1	0	0	1	8
3	Juárez	3	6	1	0	0	1	0	7	1	0	0	2	2	10	1	1	0	1	2	10
4	Atoyac	3	5	1	0	-1	1	0	6	1	0	-1	0	1	6	1	0	0	1	0	7
5	Chajul	1	6	-1	1	1	1	-1	6	-1	1	1	2	1	9	1	1	0	1	1	9
6	C. Cmpn	2	8	1	1	1	1	0	9	1	1	1	0	0	8	1	0	0	1	-1	6
7	Piña	2	6.5	-1	1	0	0	-1	4	-1	1	0	2	1	8	0	1	0	0	1	7
8	C. Pirre	2	7.5	1	1	0	1	0	8	1	1	0	0	2	9	1	1	0	1	2	10
9	Arima	3	6	1	1	1	1	-1	8	1	1	1	0	1	9	1	0	0	1	1	8
10	Caraball	0	3	0	-1	-1	1	-1	3	0	-1	-1	0	0	3	1	0	0	2	-1	7
11	Maraca	3	7	1	0	1	1	0	8	1	0	1	0	1	8	1	0	0	1	0	7
12	Naranjo	0	8	1	0	1	1	0	8	0	0	1	0	1	7	1	0	0	1	0	7
13	R. Frio	1	8	1	1	0	1	0	8	0	1	0	0	1	7	1	0	0	1	0	7
14	R. Negro	3	11	1	1	0	2	1	10	1	1	0	1	0	8	1	0	0	1	-1	6
15	Cartón	0	4	-1	-1	0	0	0	3	-1	-1	0	0	0	3	0	1	0	1	0	7
16	Tatabro	1	7.5	0	-1	0	0	0	4	0	-1	0	1	0	5	1	1	0	0	0	7
17	S. Anton	0	7	0	1	0	0	-1	5	0	1	0	2	1	9	1	1	0	1	1	9
18	Tinalnd	2	8	1	1	0	0	0	7	1	1	0	2	2	11	1	1	0	1	2	10
19	Limonc	3	11	-1	1	0	2	1	8	-1	1	0	1	1	7	-1	1	0	1	2	8
20	Topo	2	8	1	1	0	0	0	7	1	1	0	1	2	10	1	0	0	1	2	9
21	Pichita	3	7	1	1	0	1	0	8	1	1	0	1	2	10	1	0	0	1	2	9
22	Pakitza	2	9	1	1	1	1	1	10	-1	1	1	1	2	9	1	0	0	1	4	11
23	Tambop	2	9	1	1	1	1	1	10	-1	1	1	1	2	9	1	0	1	1	4	12
24	Utinga	3	4	-1	1	0	0	0	5	-1	1	0	1	0	6	-1	0	0	0	0	4
25	Manaus	3	3	-1	1	0	-1	-1	3	-1	1	0	0	-1	4	0	0	0	-1	-1	3
26	Carajás	2	8	1	0	1	3	1	11	1	0	1	0	1	8	1	0	0	0	1	7
27	Humaitá	0	7	-1	1	1	1	1	8	-1	1	1	-1	-1	4	-1	0	0	0	-1	3
28	A. Juruá	2	10.5	1	1	1	2	1	11	-1	1	1	2	2	10	1	0	1	2	4	13
29	Xapuri	1	8	0	1	1	1	1	9	-1	1	1	2	1	9	0	0	0	1	2	8
30	Cacauln	3	10	1	1	1	2	1	11	-1	1	1	2	0	8	1	0	1	1	1	9
31	Jaru	2	10	1	1	1	2	1	11	-1	1	1	2	1	9	1	0	1	1	2	10
32	R. zinho	0	9	0	1	1	1	1	9	-1	1	1	2	0	8	-1	0	1	1	0	6
33	Colorad	1	8	1	0	1	1	0	8	0	0	1	2	1	9	1	0	1	-1	0	6
34	S.Céu	0	9	1	0	1	0	0	7	-1	0	1	2	1	8	1	0	0	0	0	6
35	Bugres	0	9	-1	0	1	0	0	5	-1	-1	1	1	1	6	-1	0	0	0	0	4
36	Buriti	3	9	1	0	1	-1	0	6	0	0	1	0	-1	5	1	0	0	-2	-2	2
37	Vicente	0	8	1	0	1	0	0	7	-1	0	1	0	-1	4	1	0	0	0	-2	4
38	Buraq	2	4	-1	0	0	1	1	6	-1	0	0	0	-2	2	0	0	0	-1	-3	1
39	Tiúma	2	5	-1	1	0	1	0	6	-1	1	0	0	-1	4	0	0	0	-1	-2	2
40	Brasília	3	7	1	0	-1	0	0	5	0	0	-1	0	-1	3	0	0	0	0	-2	3
41	Paracatu	0	7	1	0	-1	0	0	5	0	0	-1	0	-1	3	1	0	0	0	-2	4
42	Camacã	0	7	0	0	0	1	0	6	0	0	0	2	0	7	1	0	0	0	0	6



Table 2. Continued

Site No.	Name	Effort	Div. Index	EHet variation						TOT	RR resource richness						TOT	NDis disturbance						TOT
				Elev	Rain	Dry	Soil	Veg	Elev		Rain	Dry	Soil	Veg	Elev	Rain		Dry	Soil	Veg				
43	Itamaraj	0	7	0	0	1	2	0	8	0	0	1	1	0	7	1	0	0	1	0	7			
44	Linhares	3	8	-1	0	0	1	1	6	-1	0	0	1	-1	4	-1	0	1	1	-3	3			
45	S. Teresa	3	9	1	1	0	0	1	8	0	1	0	0	-1	5	1	0	0	1	-3	4			
46	Paraopb	0	7	1	0	-1	1	0	6	-1	0	-1	0	-1	2	-1	0	0	-1	-2	1			
47	B. Horiz	2	9	1	0	1	2	1	10	0	0	1	0	0	6	1	0	0	1	-1	6			
48	Caldas	2	7	1	0	1	0	1	8	1	0	1	1	0	8	1	0	0	0	-1	5			
49	Campi	2	7	1	0	0	1	1	8	-1	0	0	0	0	4	-1	0	0	-1	-1	2			
50	Japi	3	7	1	0	0	1	1	8	0	0	0	0	0	5	1	0	0	2	-1	7			
51	Itatiaia	3	7	1	1	0	1	1	9	1	1	0	0	2	9	1	0	0	2	1	9			
52	Petrop	3	6	1	1	0	-1	0	6	0	1	0	0	0	6	1	0	0	1	0	7			
53	Xerém	1	7	0	1	0	0	0	6	0	1	0	0	0	6	0	0	0	0	0	5			
54	R. Janeir	3	6	1	0	0	0	1	7	1	0	0	1	-1	6	1	0	0	-1	-1	4			
55	BS. João	1	4	-1	0	0	-1	1	4	-1	0	0	0	-3	1	-1	0	0	-1	-3	0			
56	Joinville	3	7	0	0	0	1	0	6	0	0	0	0	0	5	1	0	0	-1	0	5			

Soils: for **EHet**, +1 if three or more major classes, also +1 for each of P and R; -1 if only one class, also -1 if t (lateritic).

RR, +2 if e (eutrophic), +1 if mixed e/d, 0 if d (dystrophic), -1 if t (lateritic).

NDis, +1 for each of A, C, or R; -1 for each of L or S.

Vegetation: for **EHet**, +1 if three or more classes, -1 if only one class.

RR, +1 for each of a, c, or r; -1 for each of d, m, o, or w.

NDis, +1 for each of a, b, c, f, or r; -1 for each of d, m, o, s, or w.

The final **EHet** indices varied from 3 (Caraballeda, Cartón) to 11 (Carajás, Alto Jurúa, Cacaúlândia, Jaru), the **RR** from 1 (Barra de São João) to 11 (Los Tuxtlas, Tinalandia), and the **NDis** from 0 (Barra de São João) to 13 (Alto Juruá) (Table 2).

Direct regression analysis confirmed a reasonable correlation ($R^2 = 0.469$) between butterfly diversity and environmental heterogeneity, not surprisingly (almost tautologically); a much less robust correlation ($R^2 = 0.109$) of diversity with resource richness, agreeing with most previous studies; and a similarly poor ($R^2 = 0.195$) though still positive ($b = 0.30$) correlation of diversity with the level of natural disturbance, with a strong suggestion of levelling off at 6 or above (mean **BDiv** for numbers from 6 to 12: 8.7, 6.5, 7.9, 7.5, 7.9, 9, 9). All strongly anomalous values of diversity, in rela-

tion to predictions from disturbance or other indices, represented either little-occupied sites with high levels of natural disturbance (**BDiv** much lower than predicted: sites 1, 2, 3, 5, 8, 18, 21, 22, 23, 26, and 28), or sites inventoried in the early stages of felling of virgin forest (**BDiv** above that predicted: sites 16, 19, 27, 35, 36, 37, 38, 40, 41, 44, 45, 46, and 55).

Disturbance and diversity in tropical forest butterflies: within-site comparisons

Drawing again upon 'first principles', the most accepted (but not the only) model suggests that highest diversity may appear at intermediate disturbance levels. Specifically for Neotropical butterflies, genetic diversity reaches a maximum in areas of mixture of races, between the endemic centres for subspecies, while species diversity peaks near the edges of these centres; peak endemism values occur in interior sites with lower diversity levels (Brown, 1979, 1982, 1984, 1987, 1991, 1996a; Otero and Brown, 1986; Brown and Brown, 1992). Correlation of high species-diversity sites with a palaeoecological-stability model ('forest refuges', well correlated with subspecies endemism) is negative. A present-day richness model does not overlap with some important high-diversity regions, while a heterogeneity model including unpredictable mild disturbance shows a positive correlation with diversity (Brown, 1982). Expansion of these relationships, with separation of the α , β , and γ -diversity components, leads to the relationships to disturbance shown in Fig.

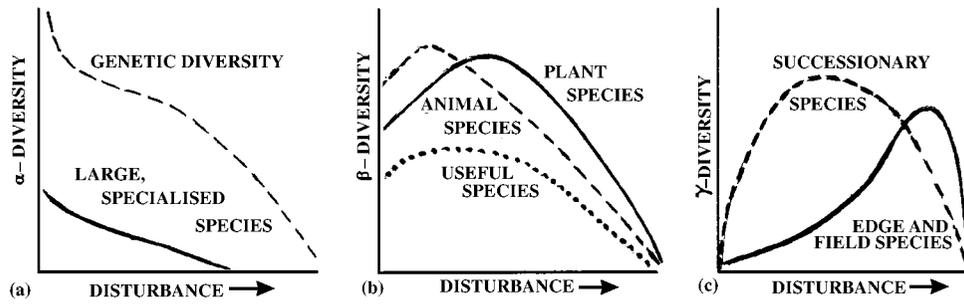


Figure 1. Patterns in disturbance/diversity relationships. (a) Variation in α -diversity of genes and microorganisms (upper curve) and large, specialized or top predator species in Neotropical forests (lower curve) versus disturbance. Note that both are decreased even by small disturbance in the system. (b) Variation in β -diversity of plant and animal species and of useful species to local human populations, in relation to disturbance in Neotropical forests. Note that the density of different habitat patches tends to increase with moderate disturbance, giving higher species diversity in smaller areas. (c) Variation in γ -diversity of successional patches and of edge and field species in relation to disturbance in Neotropical forests. Note that these show peaks at higher disturbance levels in the regional landscape.

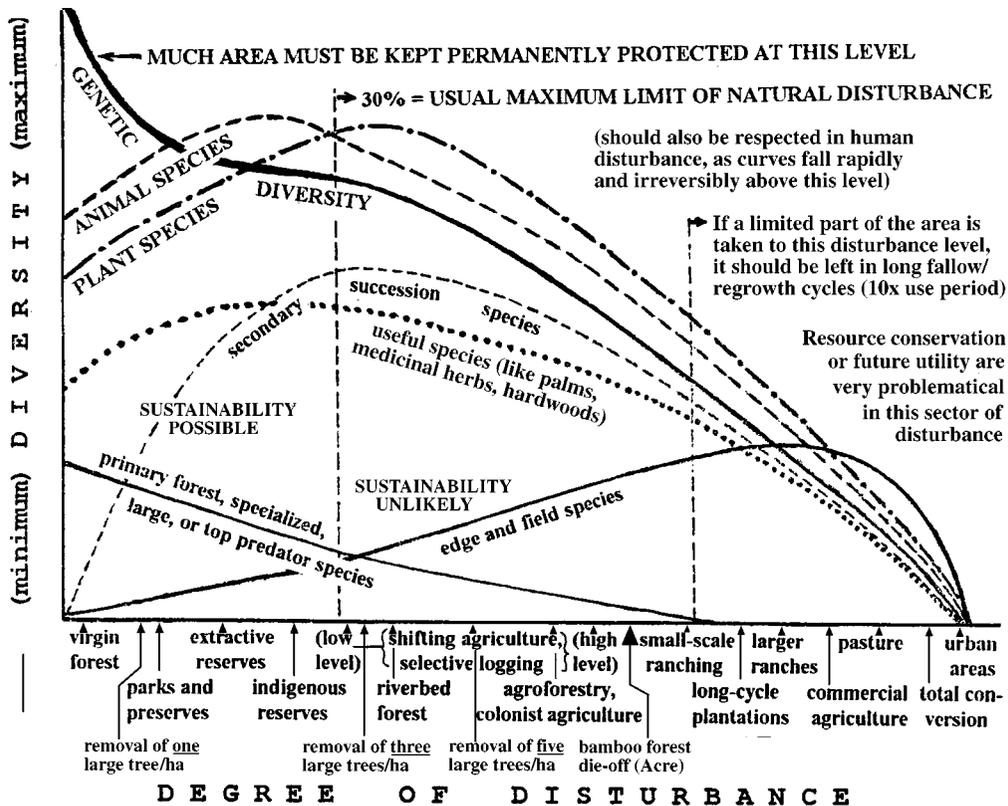


Figure 2. Combination of Figs 1a–c: diversity versus disturbance in Neotropical forests. Adapted from Brown (1996a, b).

1a–c and combined in Fig. 2 (Brown and Brown, 1992; Brown, 1996a,b). The points supporting the curves in Figs 1–2 come from sites in Table 2 that have been studied along disturbance gradients (x-axis) through time, space, and progressive human occupation (the 40 with asterisks in the Appendix Table).

Starting with different principles, many butterflies

need heat and light energy to fly and find their flower resources (which also multiply with light), and their larval food is usually understorey plants or new growth on trees, also responsive to light levels. Thus, when mild disturbance opens up light-gaps in the forest, mobile butterflies can increase there, both in density and diversity. However, when stronger sun-



light bakes the plants and lowers the humidity in the forest, many shade-adapted insects will not survive, reducing diversity. Low to moderate disturbance levels should produce maximum diversity in both forest plants and animals (Fig. 1b), also allowing some open-vegetation species to move in, and secondary succession to multiply plant diversity (Fig. 1c). Genetic diversity is initially reduced by elimination of local populations with their own adaptive alleles (left part of Fig. 1a), and later by species elimination in more altered systems (right part). Large, top-predator, or highly specialized species needing extensive areas to find their scarce resources will also be affected by any unnatural disturbance in the forest (Fig. 1a). All of these phenomena are very familiar to field workers on butterfly communities, and have also been recorded for many other groups of plants and animals in rich tropical systems: diversity is highly correlated with environmental heterogeneity, and is increased with mild disturbance and then reduced by higher levels, eventually leading to irreversible simplification of the system (Fig. 2) and reduction of options for further use (Brown, 1996a).

Quantitative data on Neotropical butterfly diversity versus disturbance may be found in 160 daily lists made in continuous forest (with or without natural clearings) and various isolated fragments of different sizes (1, 10, 100, and 1000 ha) in the Biological Dynamics of Forest Fragments project north of Manaus in the central Brazilian Amazon (site 25: Lovejoy *et al.*, 1986; Brown, 1991; Brown and Hutchings, 1997). The relatively flat, low-productivity, dense-canopy forest has a depauperate butterfly community (**BDiv** = 3) almost without HesperIIDae (from lack of flowers); unlike most other sites, it was first sampled when almost undisturbed (**NDiv** = 3, very low). Any breaks in the closed canopy (natural clearings or artificial edges) gave a great increase in understorey light, plant invasion and regrowth, and butterfly diversity, composed of true edge species rather than canopy obligates (Fig. 3). More severe disturbance, however, greatly reduced the community (lower regression in Fig. 3). Both these factors were much better predictors than area effects for the size of the community sampled in a day (Brown and Hutchings, 1997).

These mild-disturbance effects can be seen not only in poor systems like that of Manaus, but also in very rich systems in Central America (sites 1–3), the Andean foothills (sites 14, 18–23), and especially Rondônia and Acre in SW Brazil (sites 28–33), where natural heterogeneity and disturbance can also reach high levels, thus giving maximum genetic and species diversity in many

groups of organisms (Brown, 1984, 1996a,b; Dressler, 1985; Erwin, 1985, 1991; Fisher, 1985; Lamas, 1985; Paulson, 1985; Pearson, 1985; Wilkerson and Fairchild, 1985; Emmel and Austin, 1990; Woodman *et al.*, 1991; and Robbins *et al.*, 1997). In Mexico, Raguso and Llorente (1991) have commented on recent changes in the butterfly communities in Los Tuxtlas (site 2) after extensive deforestation, that also included understorey simplification after the hunting of small mammals, profoundly restructuring the whole system (Dirzo and Miranda, 1991). Edge effects are not always positive; in Campinas (site 49), a flowered reserve edge kept clear of grasses by horses greatly increased daily and total butterfly lists, but removal of these non-native herbivores led to a much poorer system, only partly reversed when pseudo-grazed by human weeders. In the Alto Juruá, Acre (site 28), large areas of bamboo forest that die out and collapse after flowering gave natural disturbance of over 50% (in area, but not biomass or species) (Fig. 2), which however, quickly regenerated a rich polysuccessional system when not 'cleaned up' or burned. Secondary succession proceeds differently, and leads to a 'recovered' system very different from the natural course, after human disturbance on poor soils in the Amazon (sites 24–35) or in hunted and logged seasonal forests (sites 4, 10, 30–37, 43–44, 46, 49). High rainfall in western Colombia (sites 15–16) can rapidly destroy exposed latosols and turn mildly logged patches (with severed trees gently pulled up to cables stretched between ridge roads) into systems that regenerate wood but remain very poor in insects, excellent indicators of the health of all such systems. Elimination of special cloud-forest microhabitats (biotopes), especially along creeks, in sites 3, 6, 8, 14, 17, 21, and 51 can wipe out whole communities of specialists (including insectivorous-understorey and frugivorous-canopy birds, also good indicator groups) without profoundly transforming the landscape (see Kattan *et al.*, 1994). Diversity in rich savanna-seasonal forest systems in central Brazil (sites 34–37, 40–41, 46) also collapses when microhabitats dependent on certain shrubs, fertility, or sinkholes are altered. Substitution of river-bottom, terrace, or ridgetop forests by tree crops in sites 12, 13, 20, 45, 47 and 53 likewise leads to the collapse of diversity, but hillside forests can be replaced by coffee crops with minimum species loss, especially if larval foodplants are permitted to regenerate on the slopes. This is somewhat ironic, since the Brazilian Forest Code protects steeper hillsides and gallery forests, to prevent soil and bank erosion, while valley, terrace and ridgetop areas are not specifically protected.

The extremely heterogeneous systems of the topo-

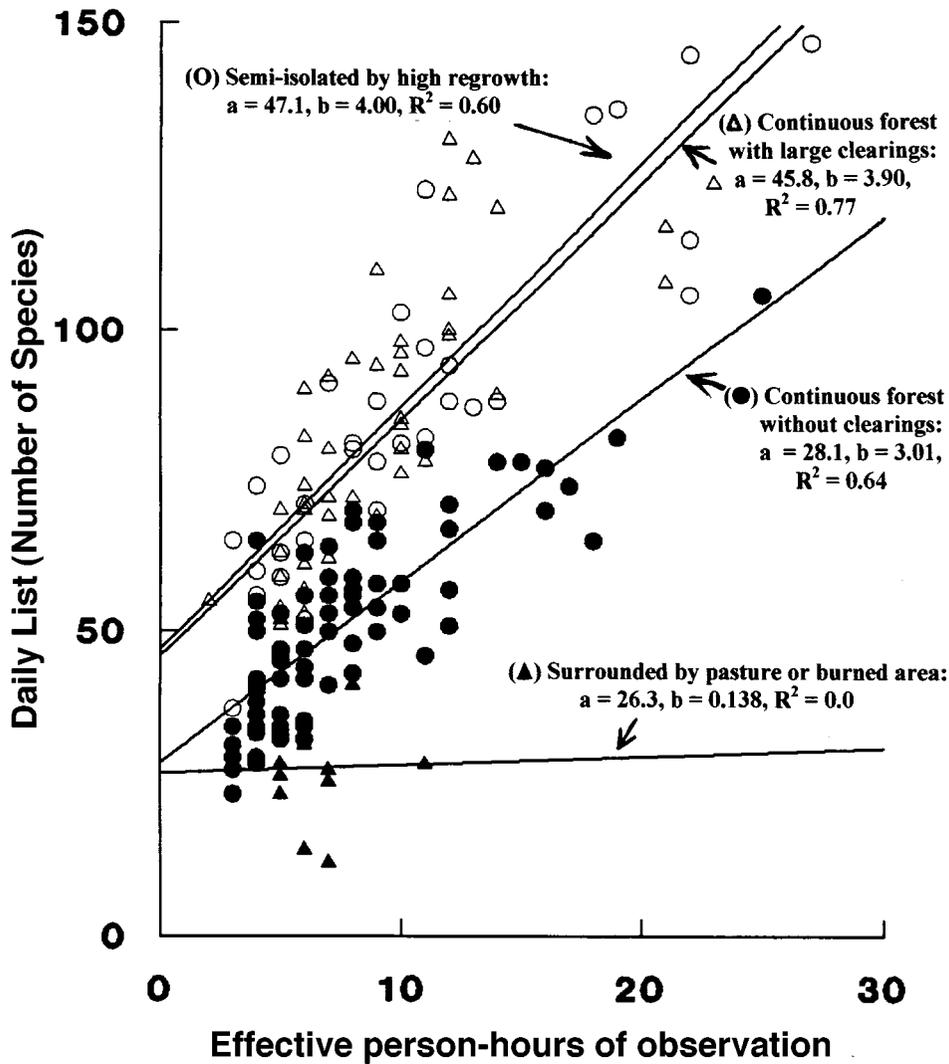


Figure 3. Daily list of butterflies versus effort (person-hours) in dense low-productivity forests north of Manaus, Amazonas, Brazil, in different categories of reserves of various sizes. Adapted from Brown (1991) and Brown and Hutchings (1997).

graphically diverse Atlantic forests in eastern Brazil show very high β and γ components, with the α -diversity depending upon history, microheterogeneity, and temperature/water availability cycles. Although 90% of these forests have been removed in the past 500 years, large areas are still intact, and most parts of the biota seem to be remarkably resistant to confinement in small fragments (perhaps because these elements always occupied small differentiated habitats; see Brown and Brown, 1992). Exceptions occur in the coastal plain forest on poor latosols (sites 38–39, 43–44, 53–55), where (like in Acre) deforestation leads to sterile systems that, unlike hillside or canyon biotas, generally do not return to the original state (see Otero and Brown, 1986). A long history of such processes, both

natural and (more recently) human-provoked, has left some amazing ‘pockets’ of rare and ancient plant and animal species in certain favoured hilly sites, designated ‘paleoenvironments’ (Brown, 1991). A number of these are described in the Appendix Table (marked with superscript-8), and more are continually being discovered. Though their presence today testifies to their resilience, ‘modern’ methods of intensive, mechanized, or homogeneous use (especially levelling, terracing, ploughing, soil compaction, and repeated burning) turn even these into sterile landscapes, in which the biota does not recover. Some small fragments (< 20 ha) in this landscape show not only a reduced fauna, but clear signs of nanism and sterility in various populations, suggesting inbreeding depression



and emphasizing the importance of gene flow between metapopulation subunits in the habitat islands of this forest matrix.

With so many nuances related to fine details of topography, soils and vegetation, it is not unexpected that 'general disturbance' (NDIs) and human intervention can have extremely variable effect on diversity. Nevertheless, the broad patterns shown in Figs. 1–2 have been widely confirmed in almost all the sites studied.

When the whole butterfly community is large, difficult to inventory, or shows complex multiple responses to disturbance, some of its speciose components can be effectively used as finer indicators (Table 3). A few are easy to monitor and show parallel responses in many systems. The easily sampled Ithomiinae (rightmost 2 columns) have been claimed to be among the most reli-

able and have even been proposed as surrogates for total butterfly diversity (a 'reasonably invariant' 4.3–4.6% of the total) and even for insect and invertebrate biodiversity (Beccaloni and Gaston, 1994). Their variable response to disturbance (Table 3) and much wider percentage variation in a more complete sample (Table 3; Brown, 1996b: Table 2), of less than 2% to nearly 8% of the total, leads to an unacceptable variation in the predicted total. This can be reduced by including in the surrogate group Heliconiinae, Brassoliniinae, Pieridae and/or Papilionidae (also reasonably rapidly sampled groups), whose total usually comes to about 12–16% of the fauna (Brown, unpublished). A better approach is to note that the proportion is usually low at the extremes of the tropics (Mexico, S Brazil), on islands, or in dryer landscapes or those on poor soils, and high in steeper humid areas with rich soils.

Table 3. Species richness of various butterfly groups in selected Neotropical sites with observed response to moderate disturbance in the system^a

Neotropical sites studied		Total species richness and response to moderate disturbance for:										
No.	Name (see Table 2)	Rhop. ^b	Thecl	Riodi	Pierid	Papili	Nymph ^c	Satyr ^d	Euryt ^e	Helic ^f	Ithom ^g	%
2	Los Tuxtlas, VC, México	719*	150+	53–	36+	23–	(170+)	25+	30–	36+	17–	2.4
22	Pakitza, M. Diós, Peru	1300	181+	246–	31+	25X	(396X)	134–	65X	37+	62–	4.8
23	Tambopata, MD, Peru	1234	170+	239–	26+	25X	(337X)	116–	54X	33+	42–	3.4
28	Alto Juruá, Acre, Brazil	1700*	180+	270–	36+	33X	(442+)	140–	90–	48+	80–	4.7
30	Cacaulândia, RO, Brazil	1575*	250X	261–	31+	27+	(415X)	132X	90–	47+	64–	4.1
31	Jaru, Rondônia, Brazil	1330*	87+	196–	26+	23X	(343+)	126X	52–	41+	57–	4.3
16	Serra dos Carajás, Pará	720*	44+	87X	23X	18–	(198+)	57+	34–	39+	33+	4.6
25	PDBFF, Manaus, AM	650*	94+	180–	8+	11+	(181+)	65–	25+	24+	20+	3.1
40	Brasília, DF, Brazil	761	130+	130+	27+	15+	(205+)	64+	37–	38+	22–	2.9
44	Linhares, Espírito Santo	819	79X	103–	24X	16+	(219+)	59–	42–	34+	32–	3.9
45	Santa Teresa, ES, Brazil	700*	30+	70–	35X	18+	(220+)	68+	34+	43+	34–	4.9
48	Poços de Caldas, MG	572	84+	47–	35X	16+	(164+)	46+	29+	35+	21X	3.7
50	Serra do Japi, São Paulo	750*	108+	52–	36X	19+	(195+)	46+	34+	43+	28X	3.7
51	Itatiaia, Rio de Janeiro	931	150+	119–	40X	21+	(223+)	73+	35+	44+	27X	2.9
49	Campinas, São Paulo	550*	35+	27+	27+	16+	(176+)	37+	36–	40+	21X	3.8
54	Rio de Janeiro, RJ	700*	100+	80–	36X	20X	(169+)	32X	27–	37+	29–	4.1

^a Responses are coded as + = richness increases after moderate disturbance, – = richness decreases, and X = little overall difference, but forest species are substituted in part by open-vegetation species.

^b Total numbers of butterflies recorded, unless marked with an asterisk (*), indicating an estimated number due to deficient recording of Hesperiiidae.

^c Total number of Nymphalidae recorded.

^d Includes Satyrinae, Brassoliniinae and Morphinae.

^e Eurytelinae, including most larger bait-attracted species, but not Limenitidinae (*Adelpha*), Cyrestidinae (*Marpesia*), Coloburinae, Apaturinae (*Doxocopa*), or Charaxinae.

^f Includes Heliconiini, Acraeini, Melitaeinae, and Nymphalinae (sensu strictu).

^g See text for a discussion of the use of Ithomiinae as a biodiversity indicator.



The variations in response of a single group among sites seem to be primarily related to the local climate and substrate and their effects on the adaptation of the local butterfly fauna to the structure, composition, and productivity of the native forest (see Table 2). Identifiable syndromes include cold-winter areas (2, 45, 48–51) that give unique patterns of response; open-canopy forests with high light levels and heterogeneous vegetation (2, 16, 22, 23, 28, 30, 31, 40, 44) show very different patterns from dark uniform closed-canopy sites (25). Steep terrain with high natural disturbance (45, 48, 50, 51, 54) differs from flat areas (22, 23, 25, 44). In an unsampled site, a preliminary rapid survey of satyrine and ithomiine butterflies with baits, across different disturbance levels, will help to define the most likely syndrome; environmental indices can also be calculated (Table 2).

Extrapolation of these results (Tables 2–3, Figs 1–3) to other insects should be done only with due consideration of possible differences in disturbance/diversity relationships, especially likely in non-herbivores (soil/litter decomposers (Didham, 1997), predators, or other ecological groups: see Table 1).

Discussion and conclusions: butterflies as indicators for conservation monitoring

These results tend to support the utility of insects in general and butterflies in particular for following changes in forest cover, structure, and composition. They indicate that in Neotropical forests, enrichment of plant species, selective logging of larger trees, soil exposure or compaction, shifting agriculture, agroforestry, formation of larger clearings, and introduction of economic plant species all have specific effects on the butterfly community, usually resulting in the loss of a part or all of the most fragile species, and the appearance of aggressive synanthropic elements that may displace still other native elements. Even though fragmentation of forests (up to about 30% destruction) can have a positive effect on butterfly β and γ -diversity due to immigration of edge species, many delicate species are lost. It also can lead to genetic impoverishment and reduction in viability of inbred individuals.

Agriculture or silviculture mosaics of about equal amounts of anthropic and natural habitat may provide some forest products with economic sustainability (including wood and fruits) but do not include important elements of the flora and fauna of less-disturbed systems. Thus, they are not ecologically sustainable and may never be able to return to the original system with its genetic and species diversity (see Kremen *et al.*,

1994). They thereby should be classified as forms of agriculture, not confused with sustainable use and conservation of the original system. Furthermore, some large areas in all regions must remain under total protection, with no disturbance above natural levels, if genetic diversity is to remain intact with its customary turnover rate, and the more delicate species are to persist.

Forest regeneration processes are linked to other fundamental system parameters and mechanisms, including the soil biota and the influence of herbivores on succession, which may easily be lost in intermediate-use regimes or even upon 'gentle' selective logging. Thus, a policy of maintenance of options must employ different intensities of use in different large plots, and always maintain much primary vegetation under minimum disturbance regimes or total protection, to compensate for irreversible mistakes in other areas or underestimations of system effects under different management schemes.

The link to practice: ecological, economic, and social sustainability

Sensitive butterfly indicators suggest that an 'optimum' level for tropical forest use is not an adequate management goal, since most parameters (like recycling efficiency of energy and nutrients, subsidies for system maintenance, and genetic conservation) are continually degraded at levels greater than natural disturbance (Figs 2 and 4). It would be wise to keep large areas under either strict protection (left margin of these figures) or sustainable use regimes (left quarter), reusing already degraded areas in the more problematical centre sectors (managed agriculture or forestry) rather than converting any new forest, and avoiding the general system degeneration characteristic of landscapes in the right-hand sectors of these graphs. There may be great delay or difficulty in the return from enriched, logged, or silvicultural systems to primitive forest. Such irreversibility in intermediate-use types seems to be empirically confirmed in the study of understory plants and herbivorous insects throughout the Neotropics, and should be accepted and taken into account by managers, avoiding conversion of new primitive or minimum-use systems to energetically more demanding and ecologically less sustainable systems, with fewer options for future use (Fig. 4), at least in the high-diversity Neotropical forests.

Because most forest products are just as tightly tied into the overall system function as are insect populations or soil organisms, the ecological and economic

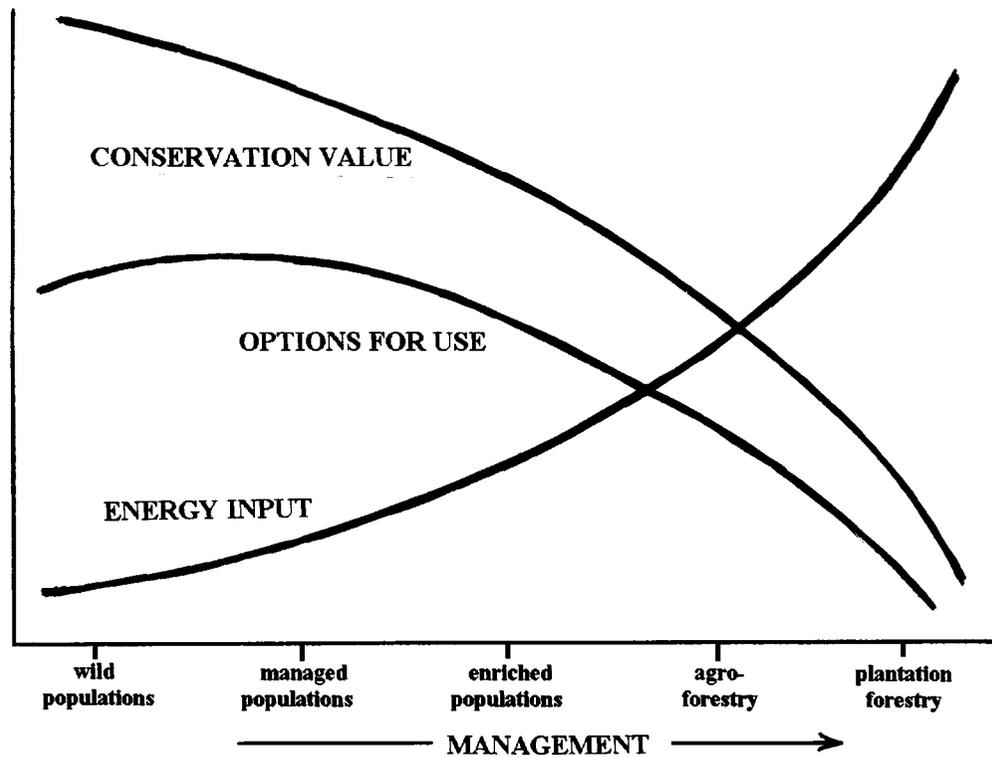


Figure 4. Conservation value (top), options for use (centre), and energy input (lower curve) versus forestry management structure in the Neotropics: the results of simplification. Adapted from Fig. 2 (centre curve) and a sketch by Virgilio Viana, IPEF-ESALQ, Universidade de São Paulo, Piracicaba.

aspects of sustainability run together, with the changes in indicator groups serving as an early warning for later changes in the economic potential of the system. Indeed, the utility of the forest system to humans is just one aspect of its overall complex functioning, just as likely to be modified by a change in forest structure (such as removal of large trees) as are the composition and richness of understorey vegetation, soil biota, and indicator insect communities. Because outside market pressure will tend to push forest product use regimes to and beyond the limits of sustainability, careful attention to early-warning indicators can help prevent irreversible changes in the systems that support the economic use of the forest (Fig. 2).

The social aspects of sustainability are even harder to define, since human culture and product valuation change very rapidly when forest systems are brought under market pressure from industrial or consumer economies. Under such conditions, in addition to continual monitoring of indicator groups, respect for some simple rules may help to maintain sustainable-use regimes for forest products, that are ecologically sound, economically viable, socially responsible, and politic-

ally acceptable (Hartshorn, 1995), even in the face of evolving local cultural and political scenes:

- (i) In the lack of firm data, the best policy for use is that which maintains intact the largest number of options for future use (Figs 2–4); most options will continue to be viable under time-tested, empirical methods of sustainable use of the systems, with total protection of traditionally preserved areas and both biological and social community structures.
- (ii) Local control of the land and its resources is more likely to maintain sustainable use regimes than imposition of ‘high-yield’ management regimes from outside. A local market cooperative, to interface with outside markets and help in the equitable distribution of benefits from the use of forest products, can help preserve the empirically sustainable methods of mobilization of the products. In addition, local value-added processing of the products should be a permanent objective for all types of use.
- (iii) Conservation of resources for the future should be a conscious and continual interest of the local com-



munities responsible for their use. Preservation of the local community and its methods of traditional resource use is most successful when it involves members of this community not only in inventory and monitoring of indicator groups and the environment, but also in strengthening programmes of health services, education, transport, social service, and political structures, using outside 'consultors' to help train and orient local residents, especially primary-school teachers and naturalists.

Over the past seven years, an interdisciplinary team from many Brazilian research groups, sponsored in 1993–1995 by a grant from the MacArthur Foundation, has tested and implemented these policies in the Upper Juruá Extractive Reserve (site 28), under coordination by the local Association of Rubber-Tappers and Farmers. Some important aspects such as new product development, contacts with markets, and thorough scientific inventory have gone relatively slowly, awaiting the strengthening of local community structures, adequate to discern ideal policies for the maintenance of sustainability in the traditional use regimes. The emphasis is on communication among persons and groups with different experiences. This programme uses non-economic, short-cycle animals including songbirds, frogs, dragonflies, and butterflies as early indicators of system degradation, monitored by local residents during their daily activities. If this structure for base conservation and diversity monitoring can be effectively carried out in this and other Neotropical forests, it may be possible to create virtual 'conservation landscapes' in which the primary natural processes and their results (diversity, endemism, and rarity in different taxa, and human cultural practices leading to sustainable resource use) can be effectively preserved for indefinite time.

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Appendix Table. Characteristics of Neotropical forest sites studied for butterfly diversity

Site ¹ No.	Name (General)	Coordinates ²	Effort ph ha ³	Study period	Environmental parameters					Vegetation	Butt. (%cnv) ⁶	Divers.				References ¹ Literature/Observers
					Elevation	Rain ⁴	Dry ⁴	Soils ⁵	D			T	G	Q ⁷		
Central America: Mexico																
1	Teocelo, Veracruz	19/97	A +	1974–94	600–1350	3000	2	Ce,Ve	cd	10–40	B	B	C	B'	Llorente <i>et al.</i> , 1986; KB	
2*	Los Tuxtlas, VC	18/95	A +	1962–90	200–1300	4000	0	Ve,Pe	crs	10–50	B	B	C	AC	Ross, 1975–7; Raguso & Llor., 1991	
3*	Sa. de Juárez, OAX ⁸	18/96	A +	1965–93	100–3100	5000	0–1	Ce,Pe	cr	0–20	B	B	C	BB'	Luiz-M. <i>et al.</i> , 1991; KB	
4	Sa. de Atoyac, GRO	17/100	A +	1975–92	300–2450	1500	6	Cd,Pd	cs	10–40	C	B	C	B'	Vargas <i>et al.</i> , 1991	
5	Chajul, Chiapas	16/91	B 0	1979–94	140–250	3000	2	Ae,Pe	r	10–20	B	B	C	B'	J. & R. de la Maza-E., 1985	
Panama																
6*	Cerro Campana ⁸	9/80	A 0	1960–86	400–1000	2000	4	Cd,Pd	cos	30–70	B	B	A	BC	Gordon Small; KB	
7*	Piña Forest	9/80	A 0	1960–86	10–150	3000	0	Pe	r	5–20	C	B	B	AB	Gordon Small; KB	
8	Cerro Pirre ⁸	8/78	A 0	1982–84	500–1550	3000	0	Cd,Pd	cr	0–10	C	B	A	AB	Gordon Small	
Andean region: Trinidad																
9*	Arima Valley	11/61	A +	1950–90	100–700	2500	2	Cd,Pd	r	10–40	C	C	B	A	Barcant, 1970; NYZS; KB, others	
Venezuela																
10	Caraballeda, DF	11/67	C 0	1965–90	100–500	1000	6	Cd,Rd	s	20–60	C	C	C	C	K. Negishi; KB, others	
11	Maracay, Aragua	10/68	A +	1950–93	200–1000	1500	4	Cd,Pd	cs	10–50	B	B	C	A	F. Fernández Yépez; KB, others	
12*	Los Naranjos, TA	8/72	C 0	1976–93	400–800	1500	2	Cd,Pd	cs	30–70	B	B	B	A	KB	
13*	Río Frío, Táchira ⁸	8/72	B 0	1975–94	400–800	2500	0	Cd,Pd	cs	10–30	A	B	B	B'	Manrique, F. Romero; KB, others	
Colombia																
14*	Río Negro, Meta ⁸	4/74	A +	1900–90	400–2000	2500	0	Ce,Pde	cos	10–30	A	A	A	A	Fassl, Schmidt-Mumm; KB, others	
15*	Cartón, Valle	4/77	C 0	1985–87	20–150	6000	0	Ld,Ad	dr	20–50	C	C	B	C	E. & L.M. Constantino; KB, others	
16*	Río Tatabro, Valle	4/77	B 0	1983–94	10–400	7500	0	Ce,Ld	dr	0–20	B	B	B	AB	Constantinos; KB, C. Callaghan	
17*	San Antonio, Valle	3/77	C 0	1911–92	1600–2100	4000	0	Re	c	10–30	B	B	B	B'	Kattan <i>et al.</i> , 1991; KB	
Ecuador																
18	Tinalandia, Pich.	0/79	A 0	1970–94	700–1500	4000	0	Ce,Ve	cr	20–40	A	B	C	A	Emmel & many others; KB, others	
19	Limoncocha, Napo	0/77	A +	1965–94	200–250	3500	0	Ae,Pde	adfr	10–20	A	A	A	A	Drummond, Emmel & others; KB	
20*	Topo/Zuñag, Tung. ⁸	1/78	A 0	1930–90	900–1500	2500	0	Cd,Ve	c	10–30	A	B	B	B'	Velástegui family; KB, T. Racheli	
Peru																
21*	Mina Pichita, Junin ⁸	11/75	A +	1900–90	700–2200	2500	0–2	Cd,Pe	cr	0–30	B	B	B	B	L. Harris, G. Lamas; KB	
22*	Pakitza, M. Diós	12/71	A 0	1975–93	350–500	2000	2–4	Ae,Pd	abfpr	0–10	B	A	B	A	Lamas; Erwin, 1991; Robbins <i>et al.</i>	
23*	Tambopata, M.D.	13/69	A 0	1979–93	300–400	2500	1–4	Ae,Pd	abfpr	0–10	B	A	B	A	Lamas, 1985; Robbins <i>et al.</i>	
Brazilian Amazonian forests																
24*	Utinga, Belém, PA	1/48	A +	1912–93	0–20	2750	0	Ld,Ae	ad	30–80	C	B	C	C	Moss, Kesselring; KB, others	
25*	PDBFF, Manaus	2/60	A +	1980–94	30–100	2250	0	Ld	d	0–10	D	C	B	B	Brown, 1991; Brown & Hutchings	
26*	Sa. do Carajás, Pará	6/50	B +	1978–91	50–800	1500	2–4	Ld,Pd,Rd	clopr	5–30	B	B	B	A	Gifford, Benson, Otero; KB, others	
27	Humaitá, Amazonas	8/63	C 0	1970–80	100–150	2500	2	Ad,Pd,Lt	adopr	10–30	B	B	C	A	D. Gifford; KB	
28*	Alto Juruá, Acre	9/72	B +	1930–95	250–400	2000	2–6	Ae,Ce,Pe	abfpr	0–20	A	A	A	AB	KB, André Victor Freitas	
29*	Xapuri, Acre	11/69	C +	1955–94	250–350	2000	2–4	Ae,Pe	abdr	10–30	B	B	B	A	J. Oiticica; KB, others	
30*	Cacaulândia, RO	10/63	A +	1985–95	200–400	2250	2–6	Pe,Re	bdpr	10–30	A	A	B	A	Emmel & Austin, 1990; others	
31*	Jaru, Rondônia ⁸	10/62	B +	1972–85	250–400	2250	2–6	Pe,Re	bpr	10–30	A	A	B	A	Brown, 1984; H. Ebert, others	
32*	Riozinho, RO	12/61	C 0	1966–92	250–300	2000	2–6	Ce,Pe	dpr	20–40	B	B	A	A	B. Steingruber, Mielke; KB	





Site ¹ No. Name (General)	Coordinates ²	Effort ph ha ³	Study period	Environmental parameters						Butt. Divers.				References ¹ Literature/Observers	
				Elevation	Rain ⁴	Dry ⁴	Soils ⁵	Vegetation	(%cnv) ⁶	D	T	G	Q ⁷		
33*	Colorado, RO ⁸	13/60	C +	1975–87	250–600	1750	2–6	Le,Pe	rs	10–40	B	B	B	A	KB, D. Gifford, others
34	Salto do Ceu, MT	15/58	C 0	1971–83	300–500	1500	4–6	Pe	as	10–40	A	B	B	A	KB, O. Mielke
35*	Barra dos Bugres	15/57	C 0	1971–83	200–250	1250	4	Ae,Ld	as	10–30	A	B	B	A	KB
36*	Buriti, MT ⁸	15/56	A +	1925–88	400–800	1500	4	Ld,Sd	os	40–80	A	B	B	A	Collenette & Talbot, 1928; KB
37	São Vicente, MT	16/55	C 0	1967–78	500–700	1500	4	Pd	os	20–40	B	B	B	A	KB
Brazilian Planalto and Atlantic forests															
38*	Buraquinho, PB	7/35	A 0	1950–94	0–30	1750	0–2	Pd,Sd	dms	5–30	C	C	C	C	Kesselring & Ebert, 1979; KB
39	Tiama, Pernamb.	8/35	A 0	1955–93	50–200	2000	0–2	Ld,Pd	ds	10–50	C	C	C	A	Ebert 1969, Kesselring; KB
40*	Brasília, DF	16/48	A +	1965–93	800–1300	1500	5	Cd,Ld	os	20–60	B	B	C	A	KB, O. Mielke, S. Nicolay, others
41	Paracatu, MG	17/47	C 0	1967–80	650–900	1250	5	Cd,Ld	os	10–30	B	B	C	A	KB, O. Mielke, S. Nicolay, others
42	Camacã, Bahia ⁸	15/39	C 0	1976–91	100–500	1500	0–2	Pe	dr	10–30	B	B	C	A	O. Mielke; KB
43*	Itamaraju, Bahia ⁸	17/40	C 0	1972–92	100–500	1500	2–4	Pd,Re	dr	20–50	B	B	C	A	C.Elias; KB
44*	Linhares, E. Santo ⁸	19/40	A +	1969–94	0–30	1250	3–6	Ae,Ce,Sd	cdso	30–50	B	B	B	A	C.Elias; KB
45*	Santa Teresa, ES ⁸	20/41	A +	1964–95	500–1000	2000	0–2	Cd,Ld	cdso	20–50	B	B	A	A	C. Elias, O. Mielke; KB, others
46	Paraopeba, MG	19/44	C 0	1965–75	700–750	1500	5	Ld,Pd	os	20–50	C	C	A	A	KB, O. Mielke
47*	Belo Horizonte	20/44	B +	1965–93	800–1300	1500	4	Cd,Ld,Rd	cos	10–40	A	B	A	B'	KB, O. Mielke, S. Nicolay, others
48*	Poços Caldas, MG	22/47	B +	1963–94	800–1500	1750	2	Cd,Le	cos	20–60	B	B	B	B'	Ebert, 1969; KB
49*	Campinas, SP	23/47	A 0	1973–95	600–800	1500	0–2	Ld,Pd	s	50–95	B	B	B	B'	KB
50*	Serra do Japi, SP ⁸	23/47	A +	1984–95	750–1250	1250	0–2	Cd,Rd	cos	10–50	B	B	B	B'	Brown, 1992 and others
51*	Itatiaia, R. Janeiro ⁸	22/45	A +	1930–93	400–2800	2000	0–2	Cd,Rd	crs	0–10	B	B	B	B'	Zikán, 1968; O. Mielke, others; KB
52*	Petrópolis, RJ	23/43	A +	1965–91	800–1300	2000	0	Cd	c	10–40	B	B	C	B'	L. Otero, C. Callaghan; KB, others
53	Xerém, R. Janeiro	23/43	B 0	1966–90	10–400	2500	0	Ld,Cd	dr	0–20	B	B	C	A	KB
54*	Rio de Janeiro, RJ	23/43	A +	1920–95	0–1250	1250	0	Ldt,Pe	cdmro	5–50	B	B	C	AC	L. Otero, O. Mielke; KB, others
55*	Barra S. João, RJ ⁸	23/42	B 0	1971–95	0–10	1250	0–2	Sd	dmo	10–50	C	C	C	C	Otero & Brown, 1986
56*	Joinville, S. Catar. ⁸	26/49	A +	1920–95	0–350	1250	0	Ld,Pd	dr	30–60	B	B	C	A	H. Miers, O. Mielke; KB, others

¹ All but seven sites (2, 4, 5, 8, 22, 23 and 30) have been worked by the author (KB). Most quantitative data come from different disturbance levels in the 40 sites marked with *.

² Coordinates given as closest intersect of degrees of latitude (sites 1–17 = North, 20–56 = South)/longitude West of Greenwich.

³ Total person-hours (ph) of observations in site: A => 1500, B = 500–1000, C =< 500; Total area in hectares (ha) effectively covered in surveys, + => 1000 ha, 0 = 100–1000 ha.

⁴ Average annual rainfall in region given in mm (to nearest 250), followed by the usual number of dry months per year (monthly rainfall in mm less than twice the average temperature in °C).

⁵ Soils coded as: A = Aluvial (fluvial) or Humic Grey (aquept, aquent); C = Cambisol (tropept); L = Latosol (orthox, humox); P = Podzolized soils (alfisols, ultisols); R = Rocky soils (orthent); S = Sandy soils and spodosols (psamment, aquod, humod); V = Volcanic soils (andept); and e = eutrophic, d = dystrophic, t = lateritic. In general, the biological diversity (alpha and beta) and the general richness of the system decrease from e > d > t, and P > L, C > A > R, V > S. Both t and S may retain water well during a short dry spell. Both topography and climate, as well as grain size and mixture of the soils, influence vegetation quality, reducing determinism in the system.

⁶ Original vegetation coded as: a = alluvial forest (often mixed dense and open canopy, with palms), b = open bamboo forest, c = cloud and other montane forests, d = lowland poor dense forest, or other low-productivity dense forests, f = floodable forest, l = open liana forest, m = mangroves, restinga, and other coastal formations, o = open vegetation systems, nonforest types, savanna, p = open palm forests, r = rich rainforest (dense and open) on rolling terrain, s = semideciduous or deciduous seasonal forests, w = white sand formations (campina and campinarana); (x-y) indicates the percentage of original vegetation converted to early secondary series, edges, agriculture or silviculture, or other purely anthropic systems, in any larger blocks (> 100 ha or 1 km²) being worked or surveyed.

In general, biological α -diversity and system richness decrease in the order $r > a > c > l, p, s > b, f > d > m, o, w$, with types b, c, m, p and w having many specialists restricted to them and not found in richer systems. Highest β -diversity (often called 'species richness' in tropical forest areas over 0.25 km², containing several different systems) is associated with microheterogeneous matrices including 3–5 of these types plus 10–30% younger successional vegetation series.

⁷ Characters noted for the butterfly community diversity in the site: D = average daily list with 8–10 hours of work: A => 180, B = 120–180, C = 60–120, D =< 60 species. T = Total number of butterfly species recorded for the site, including Hesperidae: A => 1000, B = 600–1000, C =< 600. G = Genetic mixture in butterfly species in site: A = great, B = moderate, C = small. O = General quality of butterfly fauna: A = Balanced community with [Nymphalidae + Pieridae + Papilionidae] about equal to or less than Lycaenidae or Hesperidae, with maximum diversity; B = Almost only dense-forest species, with few Hesperidae or other light-obligate species present; B' = same as A, but low in Lycaenidae; C = Mostly clearing and sun-loving species, including depauperate faunas with predominance of edge and field (non-forest) species.

⁸ Locality with concentration of primitive species, often considered as threatened with extinction (a 'palaeoenvironment' in the sense of Brown, 1991).