

The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon

JOS BARLOW*† WILLIAM L. OVERAL*, IVANEI S. ARAUJO*,
TOBY A. GARDNER† and CARLOS A. PERES†

**Museu Paraense Emilio Goeldi (MPEG), Av. Magalhães Barata 376, Belém, Pará, 66040-170, Brazil; and*

†*Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK*

Summary

1. Secondary forests growing on cleared lands and tree plantations are becoming increasingly widespread land-uses in the tropics. Previous studies are divided on the conservation importance of these habitats for tropical forest butterflies.
2. We use a robust sampling design, accounting for both seasonality and vertical stratification, to examine fruit-feeding butterflies (Nymphalidae) in patches of secondary forest and *Eucalyptus* plantation 2–3 orders of magnitude larger than those previously sampled.
3. We recorded 10 587 butterflies and 128 species in 3200 trap-days. Species richness was highest in primary forest and lowest in plantations, while butterfly abundance showed the opposite response. All habitats were distinct in terms of community structure.
4. There was a significant interaction between habitat and season based on richness and abundance metrics, although not based on community structure. Secondary forest exhibited higher observed richness than primary forest in the peak of the dry-season, but not at other times of the year. This observation could explain the lack of consensus in previous studies, as those reporting higher richness in secondary forest only sampled during the dry-season.
5. In general, habitat quality appeared to be more important than the surrounding landscape in determining butterfly community structure. However, the community structure of the strong-flying Charaxinae was related to the amount of primary forest in surrounding landscape. There was very poor congruence between the response patterns of richness and abundance among different butterfly subfamilies.
6. Linear regressions between resource availability and butterfly abundance showed a strong influence of leaf phenology in both primary and secondary forest, but no influence of fruit phenology.
7. *Synthesis and applications:* A lack of seasonal replication and small sampling sizes may have led previous studies to over-emphasize the conservation importance of secondary forest and plantations for butterflies. We show that these habitats are significantly poorer than primary forest in terms of number of species, and hold distinct butterfly communities. Although quantifying the number of species restricted to primary forest remains difficult, these results cast doubt on the presumption that secondary habitats will provide refuge for many of the species being lost through deforestation. We therefore strongly urge measures that prioritize the conservation of remaining primary forests where they still exist.

Key-words: Nymphalidae, tropical forests, tree plantations, land-use change, forest biodiversity, Brazil.

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Introduction

Conservation biologists are divided over the extent to which extensive areas of regenerating and planted forests will be able to offset the loss of biodiversity from tropical deforestation (Daily 2001; Lindenmayer & Hobbs 2004; Brook *et al.* 2006; Wright & Muller-Landau 2006; Gardner *et al.* 2007). Secondary forests on cleared lands and commercial plantations are of particular relevance to the discussion on potential conservation benefits of human-dominated landscapes given their recent increase in coverage across the humid tropics. Globally, tropical secondary forests reclaimed one-sixth of all primary forests that were clear-cut in the 1990s (Wright 2005), and are likely to be a dominant feature of tropical forest landscapes in the future (Wright & Muller-Landau 2006). Additionally, tree plantations have become increasingly favoured in the tropics (Evans & Turnbull 2004), and their coverage in the tropics increased from ~17.8 Mha in 1980 to ~70 Mha in 2000 (Brown 2000; FAO 2001), 50% of which are *Eucalyptus* spp. (Evans & Turnbull 2004).

These global patterns are evident within the Brazilian Amazon. It is estimated that around 30% of the deforested area has subsequently been abandoned, resulting in the rapid proliferation of secondary forest (Houghton *et al.* 2000; Perz & Skole 2003; Smith *et al.* 2003). Plantations have increased rapidly within Brazil, and *Eucalyptus* planted for the pulpwood industry has shown a 17-fold increase in coverage since 1980 (SBS 2006). Furthermore, one of the key objectives of Brazil's National Forest Program (PFN 2000) is the expansion of the forest base on degraded lands through plantation forestry, with plans to cultivate 2.2 Mha of tree plantations on private properties and abandoned agricultural lands.

Despite their increased coverage and potential importance, the biodiversity conservation value of extensive monocultures and areas of native regeneration are poorly understood (e.g. Hartley 2002; Dunn 2004; Lindenmayer & Hobbs 2004; Gardner *et al.* 2007). As butterflies are conspicuous and relatively easy to sample and identify, they have been used frequently as indicators of the conservation value of tropical habitats and the consequences of land-use change. Furthermore, they demonstrate closely linked associations with the abundance of host plants, microclimate, and patterns of resource availability (e.g. Kremen 1992; Kuussaari, Nieminen & Hanski 1996). However, relatively few studies have examined butterflies in secondary forest following clear-felling, and these report both higher (Bowman *et al.* 1990; Lawton *et al.* 1998; Ramos 2000; Fermon *et al.* 2005; Bobo *et al.* 2006) and lower (Schulze *et al.* 2004; Veddeler *et al.* 2005) levels of species diversity and richness compared to native forest. Even less information is available for plantations – while some studies have examined moths (Chey, Holloway & Speight 1997; Zaniccio *et al.* 1998; Cunningham, Floyd & Weir 2005) and insects as a whole (Holloway, Kirkspriggs & Khen

1992), we are only aware of two studies that explicitly examined butterflies in plantations (Lawton *et al.* 1998; Ramos 2000).

The conclusions of these studies are weakened by various methodological shortcomings, which may explain the lack of consensus (Koh 2007). In particular, assessments of the effects of disturbance on butterfly communities can be strongly influenced by the spatial scale of the sampling (Hamer & Hill 2000), a lack of temporal replication across seasons (DeVries, Murray & Lande 1997; Hamer *et al.* 2005), and the failure to consider vertical stratification (Dumbrell & Hill 2005). All seven existing studies that we examined were conducted in very small plots (≤ 6 ha where information was made available), most were adjacent to nearby primary forest, only one (Fermon *et al.* 2005) sampled canopy butterflies in their control plots, and all but one (Schulze *et al.* 2004) sampled a narrow seasonal period (1–4 months). It is obviously difficult to extrapolate the contrasting results of such studies to predict the consequences of broad-scale reforestation of degraded tropical lands (e.g. Kanowski, Catterall & Wardell-Johnson 2005; Gardner *et al.* 2007).

The primary aim of this study was to add to our knowledge of the value of primary, secondary and plantation forests for fruit-feeding butterflies. We minimized edge effects by using plots > 3 orders of magnitude larger than those examined in previous studies, and implemented a replicated and robust experimental design that controlled for vertical stratification and seasonality. We examined fruit-feeding butterflies (Nymphalidae) as these are the easiest family of butterflies to sample using a standardized methodology (DeVries *et al.* 1997; DeVries, Walla & Greenway 1999; Brown & Freitas 2000). Specifically, we tested the following null hypotheses: that there is no (1) difference between the richness and abundance or composition of butterflies between primary, secondary and plantation forests, (2) interaction between habitat type and seasonality, (3) difference between the responses of different Nymphalidae subfamilies, (4) evidence of vertical stratification of butterflies within primary forest, and (5) relationship between the abundance of adult Nymphalidae butterflies and patterns of resource availability relevant to the larvae (i.e. young leaves) or adults (i.e. fruit availability).

Materials and methods

STUDY SITE

The project was conducted within a 1.7 Mha landholding, originally purchased in 1968 for cellulose pulp production and located on the border between the States of Pará and Amapá in north-eastern Brazilian Amazonia (00° 27' 00"–01° 30' 00" S, 51° 40' 00"–53° 20' 00" W). The Jari landholding currently contains 53 000 ha of *Eucalyptus* plantations and a similar quantity of regenerating native vegetation in areas where plantations

were once cut and subsequently abandoned (fallow land). The areas of plantation and fallow land we studied were embedded in a large and virtually undisturbed primary forest matrix (> 500 000 ha). Our results should be interpreted as a best-case scenario for primary forest butterflies, as other highly degraded regions are much farther from primary forest and sources of recolonization.

Fifteen transects were established, with five replicate sites in each of primary, secondary and plantation forests (see Barlow *et al.* 2007 for a map). The scale of the landscape enabled us to select study sites (the average size of *Eucalyptus* and secondary forest blocks are 17 km² and 27 km², respectively) that were spatially independent (average distances between replicate sites within primary, secondary and *Eucalyptus* were 30 km, 9 km, and 11 km, respectively). *Eucalyptus* and secondary forest sites were located at similar distances from the nearest areas of continuous primary forest (average distances were 1.1 km and 1.3 km, respectively).

The 1-ha tree plots in primary forest (25–30 m height) were dominated by Sapotaceae, Mimosaceae and Lauraceae, and had low levels of anthropogenic influence (although a few timber trees in the genera *Manilkara* and *Dimizia* had been felled 30–40 years ago for latex or wood). All secondary and plantation sites were cut, burned and bulldozed between 1970 and 1980. We selected second growth sites which were of similar age (14–19 year; 6–9 m average heights). These were characterized by arborescent palms, *Inga* spp. and other pioneer species. *Eucalyptus* transects were located in 4–5 years old plantations and were an average of 12–18 m in height (stands are harvested at ages 5–6 year). The plantation understorey consisted of annuals (including many Asteraceae, Rubiaceae, Piperaceae, Poaceae and Cyperaceae), lianas (e.g. *Davilla* spp., Dilleniaceae), and small trees such as *Vismia* spp. (Clusiaceae), *Mabea taquari* and *Aparisthium cordatum* (Euphorbiaceae).

BUTTERFLY SAMPLING

Fruit-feeding butterflies were trapped using cylindrical traps (VanSomeren-Rydon traps; Rydon 1964), baited with a standard mixture of mashed banana that had been fermenting in plastic buckets for 2 days. The trap net was 90 cm in height, minimizing the risk of escape once butterflies had entered. Eight traps were placed in the understorey in each site, spaced 100 m apart along each transect and with the baited trays suspended 50 cm from the ground. We placed an additional eight traps in the canopy of primary forest to sample the canopy fauna (Devries & Walla 2001; Fermon *et al.* 2005; Dumbrell & Hill 2005). Traps were suspended from canopy branches at ~25 m height, using a slingshot and weighted fishing line. We did not place canopy traps in secondary or plantation forests as understorey traps in these habitats were relatively close to the canopy and would attract species from all strata (Wood & Gillman 1998; Hill *et al.* 2001; Fermon *et al.* 2005).

We conducted four seasonal replicates, resampling the same sites every 3 months between May 2004 and February 2005. The four seasonal replicates coincided with the wet season (May), early dry season (August), dry season (November), and the early wet season (February). Rainfall during the survey year was 1880 mm, and monthly rainfall was highly correlated with the long-term (38 years) averages (2265 mm, $r = 0.93$, $n = 12$, $P < 0.001$).

Traps were operated for five full days (120 h) at each site during each seasonal replicate, equivalent to 800 trap-days of effort per habitat (and a further 800 trap-days of effort in the canopy of primary forest). Traps were checked between 09.00 and 15.00 hours, and we randomized the among-site visiting sequence to avoid any systematic bias (cf. Hughes, Daily & Ehrlich 1998). Bait was added on day 1 and day 3 of sampling, and the bait was stirred daily when traps were checked. Butterfly identification was carried out at the Museu Paraense Emilio Goeldi (MPEG) in Belém, Brazil, using reference collections and the plates and descriptions in D'Abrera (1987, 1988) and Neild (1996), and following the nomenclature of Lamas (2004).

ENVIRONMENTAL DATA

We measured 12 habitat structure variables with potential relevance for butterflies (see Table 4). Understorey density (USD) was measured by counting the number of 10 cm sections of a 2.5 m painted pole that were visible (0–25) from 15 m. Density of live saplings (LS) (taller than 1 m and < 10 cm d.b.h., diameter at breast height), and vines/lianas (VS) (< 5 cm d.b.h.) were determined by recording all stems within 2.5 × 2.5 m (6.25 m²) subplots placed every 50 m along, and 5 m from, each transect. Canopy height (CH) was estimated every 100 m at 23 sites per transect. Canopy openness (CO) was calculated using digital hemispherical photographs. Results are from the inner 0–30 degree ring of each photograph and were analysed using Gap Light Analyser vs. 2.0 (Frazer, Canham & Lertzman 1999). Vertical foliage density (VFD) was measured in six height intervals at 160 locations per site following Malcolm (1995), however, only the height class 2.2–5 m is used because of colinearity.

We measured all standing trees ≥ 10 cm d.b.h and lianas ≥ 5 cm d.b.h. in a 10 × 1000 m plot established at each of the 10 primary and secondary forest sites. Basal area in plantations was assessed in the same manner within 23 × 10 m radial plots per site (7226 m²) and converted to basal area density (m² ha⁻¹). We only recorded trees with more than half of their stem within each plot, and lianas that were rooted within each plot. Exotic stems were mostly *Eucalyptus urograndis* but included some regrowth of *Gmelina arborea* in secondary forest. We extracted the following variables from these data: basal area of lianas (BAL); basal area of live trees (BALT); basal area of arborescent palms (BAP); basal area of nonpalm trees (BANP), excluding all true palms (Arecaceae) and *Phenakospermum guyanense*

(Strelitzaceae); basal area of live native stems, excluding palms (BANS); and the basal area of exotic trees (BAEX).

We analysed the landcover of the study area within a GIS using vegetation and land-cover classification developed from a combination of land-use data obtained from the landholding company and a semi-supervised classification of a 2003 Landsat 7 (30-m pixel) satellite image. Within each buffer area we calculated the percentage of primary forest within a 1 km buffer (PFDI). Total fruit-fall per site (FR) was calculated as the sum of fallen fruit at each site over the 14-month sample period, standardized by trap effort (see resource data). Temperature (TE) was the mean midday temperature at each site, derived from data loggers placed in the understorey (at 70 cm height and under a shaded cap) at all sites over a 13-month period.

RESOURCE DATA (FRUIT AND LEAF FALL)

Twenty 50 × 50 cm (0.25 m²) litter-fall traps were placed 1 m above ground level and every 100 m along each transect ($N = 300$ in total). We placed traps perpendicularly 5 m from the transect, but avoided placing traps directly below obvious understorey obstructions. Trap contents at each site were collected on the same day every month for 14 months and oven-dried at 60 °C for 3 days before being separated into four constituent parts – fruits, flowers, branches, and leaves – and weighed to the nearest 0.1 g. Here we use the dry biomass of fruits and leaves per site per month, standardized by the number of traps to account for a few cases of damaged or stolen traps.

ANALYSIS

Data from replicate traps within sites were pooled to reduce variation caused by trap position and small sample sizes per trap (DeVries *et al.* 1999). Patterns of species richness between different forest types were compared using sample-based rarefaction curves constructed using EstimateS v.7 (Colwell 2004). Each seasonal replicate per site was defined as a sample ($n = 20$ per habitat). We re-ran the richness analysis both including and excluding canopy captures in primary forest. Patterns of species dominance were compared between habitats using species rank–abundance plots. Diversity was calculated at the habitat level using Simpson's diversity index (Magurran 2004). Estimated species richness was calculated for each habitat using EstimateS v.7, using the mean of the four commonly employed abundance-based estimators (ACE, CHAO1, JACK1 & BOOTSTRAP, see Colwell 2004).

All community structure analyses were undertaken using square-root transformed abundance data, site-standardized to reduce the influence of common species and differences in total site abundance in determining community patterns (Gotelli & Colwell 2001). Ordination analyses were undertaken in PC-ORD; McCune & Mefford 1999) using multidimensional scaling (MDS)

with the Bray-Curtis similarity index. Total abundance, observed richness and community structure at the 15 sites were compared across the four seasonal replicates using pair-wise correlations (r_s and rank-correlation RELATE tests in Primer v. 5). Repeated-measure ANOVAs were undertaken in SPSS v. 11.5. The preference of a species within primary forest was analysed using the IndVal procedure (Dufrene & Legendre 1997) to identify species that were consistent indicators of the canopy or understorey.

The coefficient of variance (CV) was used to assess the extent to which a species varied in abundance over the four temporal replicates. Only the most common species (≥ 10 captures in total) were used for each comparison. The CV scores of the most common species in each of the three habitats were then compared using Kruskal–Wallis tests. In addition, we used paired t -tests to compare the CV scores of species that were common in at least two habitats.

BIO-ENV analysis was conducted in Primer v. 5 to find the set of environmental variables that provided the best fit (or matching coefficient) with the butterfly community (Clarke & Warwick 2001). The environmental distance matrices were based on the normalized Euclidean distance. We examined the within-habitat influence of leaf-phenology and fruit-fall on butterfly abundance using linear regressions, comparing phenology data in the month during and prior to sampling with butterfly abundance across sites and seasonal replicates.

Results

We captured a total of 10 587 butterflies and 128 species in 3200 trap-days, with 1293, 1379 and 7915 in primary, secondary and plantation forests, respectively. Both observed and estimated species richness (mean \pm SE of 4 estimators) were higher in primary (108 and 135 ± 3.9) than in secondary (84 and 106 ± 3.6) or plantation forests (76 and 93 ± 2.6), and the accumulation curves in primary and secondary forests did not reach their asymptotes (Fig. 1). Species abundance ranged from 1225 individuals (11.6%) (*Paryphthimoides vestigiata*) to just one individual (for 19 species) (Appendix S1. See Supplementary material). *Eucalyptus* plantations were dominated by a few very abundant species (Fig. 2), and had the lowest diversity index (Simpson's = 11.1). Secondary forest exhibited the most even species–abundance distribution and had the highest diversity score (34.7), while the lower value recorded for primary forest diversity (28.8) was due to a higher level of dominance (Fig. 2). The community structure was different in each of the three habitats (Fig. 3, Table 1), and average dissimilarity was highest between primary and plantation forests, and lowest between primary and secondary forests (Table 1).

VERTICAL STRATIFICATION

Canopy traps in primary forest captured fewer individuals (303 against 990) and species (69 against 90) than

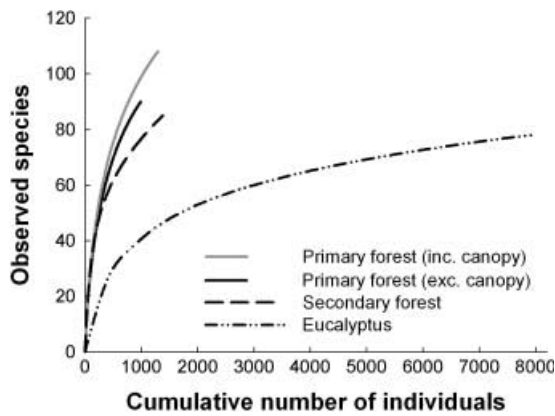


Fig. 1. Sample-based rarefaction curves for fruit-feeding butterflies in Amazonian primary forests (including and excluding captures from canopy traps), secondary forests and *Eucalyptus* plantations.

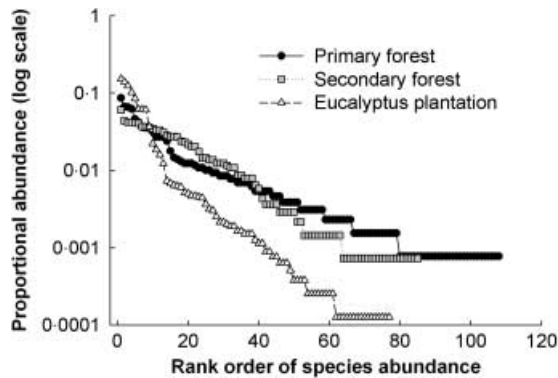


Fig. 2. Rank-abundance distribution of fruit-feeding butterflies species in primary, secondary and plantation forests in the Brazilian Amazon.

understorey traps. Thirty-nine species (36%) were only captured in the understorey, 51 (47%) were captured at both levels, and 18 species (17%) were only captured in the canopy. No species were significant indicators of the forest canopy using indicator species analysis, and only 10 species were significant indicators of the understorey (Appendix S1, see Supplementary material).

SEASONALITY

The CV scores of temporal variation of common species was not significantly different between habitats

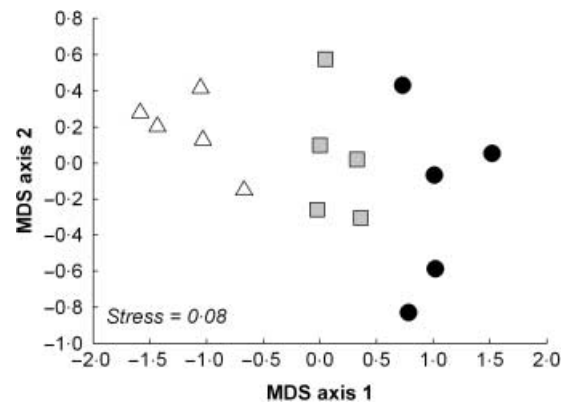


Fig. 3. Multi-Dimensional Scaling (MDS) ordination plot based on transformed and standardized abundance data (including canopy captures in primary forest). Symbols denote primary (filled circles), secondary (grey squares) and *Eucalyptus* forests (open triangles). There is a clear separation of community structure between the three habitats along axis 1, which explained 84% of the variation. Axis 2 explained just 7% of the variance.

(Kruskal–Wallis test, $\chi^2 = 1.1$, d.f. = 2, $P = 0.6$). Furthermore, there was no significant difference between the CV scores of the 16 species with 15 or more captures in both primary and secondary forests (Mean CV \pm SE in primary forest = 79 ± 9 ; secondary forest = 89 ± 13 ; paired t -test, $t = -6$, d.f. = 15, $P = 0.5$) or the 20 species with 15 or more captures in both secondary forest and plantations (Mean CV \pm SE in secondary forest = 92 ± 8 ; *Eucalyptus* = 77 ± 7 ; paired t -test, $t = 1.3$, d.f. = 19, $P = 0.2$). Too few species were common to both primary forest and *Eucalyptus* plantations to compare these habitats.

There were marked differences between the total abundance of fruit-feeding butterflies in different seasons, and interhabitat comparisons of abundance and richness were strongly influenced by the time of the year in which sampling was undertaken. The interaction terms were significant for all captures, and for three of the six subfamilies; Fig. 4, Table S1, see Supplementary material). Inter-season patterns of butterfly abundance were significantly correlated across sites in five of the six pairwise correlations. Observed richness was never correlated with richness in other seasons (Table 2). Inter-habitat comparisons of community structure were less affected by season, and all habitats were significantly different from each other in all seasons ($P < 0.01$ for all four ANOSIM tests), and the pattern of community

Table 1. Average Bray–Curtis dissimilarity scores (and ANOSIM P -values) for between habitat comparisons of the community structure of all fruit-feeding Nymphalidae butterflies and the six most abundant subfamilies. Significant interhabitat comparisons are marked with asterisks accordingly. * $P < 0.05$; ** $P < 0.01$

Taxonomic group	Primary – Secondary	Primary – <i>Eucalyptus</i>	Secondary – <i>Eucalyptus</i>	P
ALL	72**	54**	60**	0.001
Biblidinae	49	71**	59**	0.001
Brassoliniinae	50**	68**	51	0.001
Charaxinae	48**	56**	43*	0.001
Morphinae	36	59	42	0.03
Nymphalinae	43**	49**	30	0.001
Satyrinae	65**	73**	58**	0.001

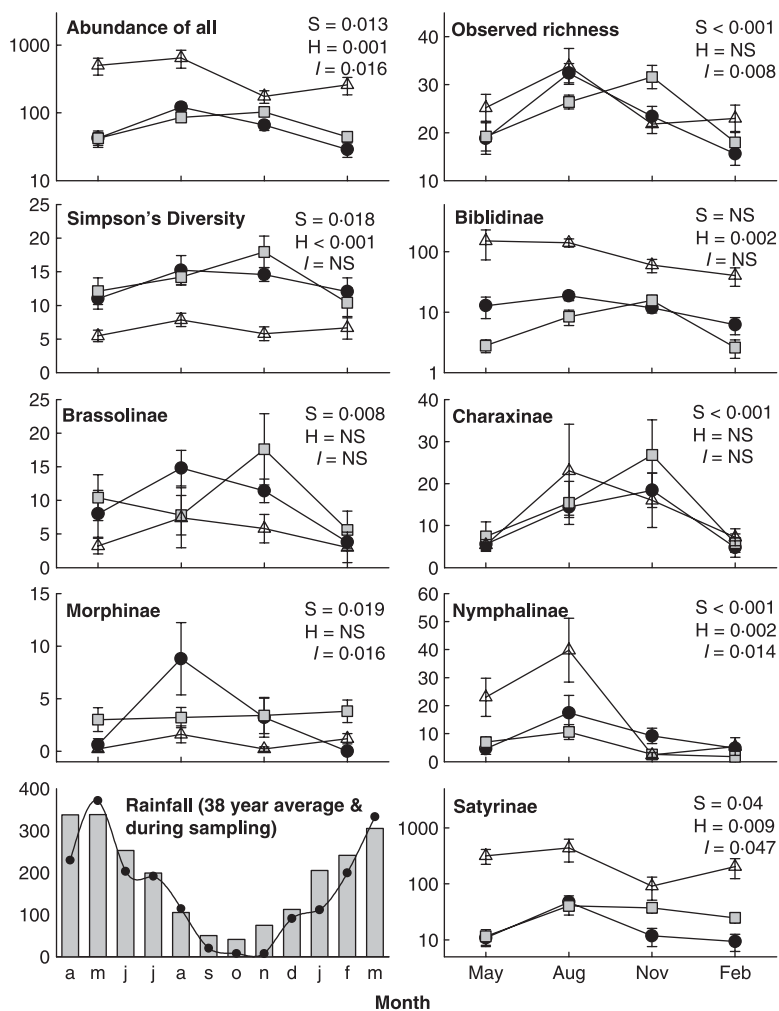


Fig. 4. Interhabitat comparisons of observed richness, abundance, and diversity of fruit-feeding Nymphalidae butterflies (and the abundance of the six most common subfamilies) were often dependent upon the timing of the seasonal replicate (wet, early dry, dry, early wet). Primary and secondary forests and *Eucalyptus* plantations are denoted by closed circles, grey squares and open triangles, respectively. *P*-values for two-way repeated measure ANOVAs are shown for season (S), habitat (H) and the interaction between them (I). Rainfall is shown for comparison (bars indicate the 38-year average, the line indicates rainfall during the sampling). Note log scale for Biblidinae and Satyrinae. Full ANOVA statistics are available in Table S1.

structure in any given season was always significantly correlated with the pattern in other seasons (Table 2).

CONGRUENCE OF SUBFAMILY RESPONSES

Taken as a whole, the Nymphalidae sampled by fruit-traps were effective indicators of land-use change regardless of whether the response metric used was species richness (Fig. 1), abundance (Fig. 4), or community structure (Fig. 3). Within subfamilies, the Satyrinae and Biblidinae became hyper-abundant in *Eucalyptus*, while the Brassolinae, Charaxinae, and Morphinae did not show significant differences between habitats in terms of abundance (Fig. 4). In terms of community structure, the Charaxinae and Satyrinae were the only subfamilies that significantly separated all habitat types, while the Morphinae were unable to statistically distinguish between any habitats (Table 1).

Table 2. Pairwise correlations across sites between the four seasonal replicates ($n = 15$), based on butterfly abundance (r_a), richness (r_s), and composition (Bray-Curtis index, Rho scores from RELATE tests). * $P < 0.05$, ** $P < 0.01$

Seasonal replicate	One	Two	Three
Abundance			
Two	0.73**		
Three	0.58*	0.5	
Four	0.68**	0.55*	0.61*
Richness			
Two	0.42		
Three	-0.71	-0.27	
Four	0.10	0.17	-0.30
Composition			
Two	0.36**		
Three	0.61**	0.59**	
Four	0.65**	0.48**	0.82**

There was little congruence between the response of subfamilies in terms of abundance or species richness. The abundance responses of the Charaxinae were positively correlated with those of the Brassolinae, but all other abundance results were insignificant or negatively correlated (Table 3). With observed species richness, there were only two significant correlations. Changes in community structure were much more consistent (Tables 1 and 3). There was no evidence that subfamilies were depleted by our trapping effort in any of the habitats (Fig. S1, see Supplementary material).

RELATIONSHIP WITH ENVIRONMENTAL FACTORS

Butterfly community structure was not influenced by the geographical distance between sites (Rho = -0.07, $P = 0.8$). Canopy openness (CO) was the best predictor of butterfly community structure for all butterflies and for two of the subfamilies across all 15 sites (Table 4). The basal area of native non-palm stems was also strongly correlated with the structure of most butterfly subfamilies. In contrast, the Charaxinae were best predicted by the percentage of primary forest in the surrounding landscape (PFDI). Comparisons made within-habitat revealed very high matching coefficients between the structure of the entire butterfly assemblage and canopy cover and basal area of lianas in primary forest, and with canopy cover and the percentage of primary forest in a 1 km buffer in *Eucalyptus*. Matching coefficients in secondary forest were considerably lower, although temperature and canopy height provided the best fit (Table 4).

RELATIONSHIPS WITH RESOURCE AVAILABILITY

Butterfly abundance in primary and secondary forests at each site in each seasonal replicate was positively

Table 3. Pairwise correlations between fruit-feeding butterfly subfamilies across sites, based on abundance (r_a), richness (r_r), and composition (Bray-Curtis index, Rho scores from RELATE tests). * $P < 0.05$, ** $P < 0.01$

Taxonomic group	Biblidinae	Brassolinae	Charaxinae	Morphinae	Nymphalinae
Abundance					
Brassolinae	-0.31				
Charaxinae	-0.10	0.64*			
Morphinae	-0.65**	0.36	0.27		
Nymphalinae	0.45	-0.37	0.14	-0.31	
Satyrinae	0.5	-0.61*	-0.39	-0.44	0.49
Richness					
Brassolinae	0.14				
Charaxinae	0.43	0.48			
Morphinae	0.21	0.58*	0.45		
Nymphalinae	0.70**	0.08	0.50	0.05	
Satyrinae	0.16	-0.07	0.10	-0.01	0.01
Composition					
Brassolinae	0.37**				
Charaxinae	0.27*	0.32**			
Morphinae†	0.01	0.12	0.26*		
Nymphalinae	0.30*	0.35**	0.35**	0.30*	
Satyrinae	0.32**	0.40**	0.31**	0.39**	0.50**

†Relate tests between Morphinae and other groups for 14 sites only (Morphinae were absent from one site).

Table 4. BIO-ENV analysis showing associations between 15 environmental variables† and butterfly community structure for all 15 sites, and separately for the 5 within-habitat comparisons

Taxa	Best	R	2nd best	R	Best combination	R
All – At 15 sites	CO	0.33	CH	0.30	USD,VS,BALT,BAP,TE	0.48
Biblidinae	BAEX	0.51	BANS	0.49	LS,CO,BAL,BANS,BAEX	0.60
Brassolinae	CO	0.51	BANS	0.43	LS,CO,BANS,BAEX,TE	0.54
Charaxinae	PFDI	0.48	TE	0.42	BANS,BAEX,TE,PFDI	0.53
Morphinae‡	BANS	0.17	PFDI	0.15	BANS,FR,PFDI	0.26
Nymphalinae	BANS	0.60	TE	0.53	BAL,BANS,TE	0.72
Satyrinae	CO	0.64	BANS	0.62	USD,BAL,BANS,TE,PFDI	0.74
All – Primary forest only	CO	0.77	BAL	0.70	CO, BAL, BAP, BANP, FR	0.96
All – Secondary forest only	TE	0.51	CH	0.44	CH, TE	0.52
All – <i>Eucalyptus</i> only	CO	0.90	PFDI	0.89	LS, CO, VFD, FR, PFDI	0.99

†USD Understorey density; LS Number of live saplings < 10 cm d.b.h.; VS Number of vines stems < 5 cm d.b.h.; CH Canopy Height; CO Canopy openness; VFD Vertical leaf density (2–5 m); BAL basal area lianas \geq 5 cm d.b.h.; BALT basal area live trees \geq 10 cm d.b.h.; BAP basal area palms \geq 10 cm d.b.h.; BANP nonpalm basal area \geq 10 cm d.b.h.; BANS basal area live native stems (excluding palms) \geq 10 cm d.b.h.; BAEX basal area exotic trees \geq 10 cm d.b.h.; TE Temperature; FR fruit fall; PFDI percentage of primary forest within 1 km.

‡For 14 sites only (Morphinae were absent from one *Eucalyptus* site).

related to leaf-fall during the month of sampling butterflies (Fig. 5). There was no significant relationship between leaf-fall and butterfly abundance in *Eucalyptus* plantations ($P > 0.2$ for all comparisons), or between abundance and fruit-fall in any of the three habitats ($P > 0.5$ for all comparisons).

Discussion

The hypothesis that primary, secondary, and *Eucalyptus* plantations would hold a similar species richness and community structure of fruit-feeding butterflies was rejected in this study. Further, species richness was consistently highest in primary forest, regardless of whether or not canopy traps were included (Fig. 1, cf. Dumbrell

& Hill 2005). The lower richness of butterflies in secondary forest was also found by Schulze *et al.* (2004) and Veddeler *et al.* (2005), but not by five other studies which report higher richness (Bowman *et al.* 1990; Lawton *et al.* 1998; Ramos 2000; Fermon *et al.* 2005; Bobo *et al.* 2006). Studies on plantations also yield mixed results: Ramos (2000) reports higher levels of species richness in *Eucalyptus* plantations than in primary forest; Lawton *et al.* (1998) reports similar richness in their plantations and their control sites, and Bobo *et al.* (2006) report slightly (but not significantly) higher species richness in agroforestry systems than in their least-disturbed native forest treatment. First we discuss how differences in sampling methodology and data analysis could explain these contrasting conclusions. We then

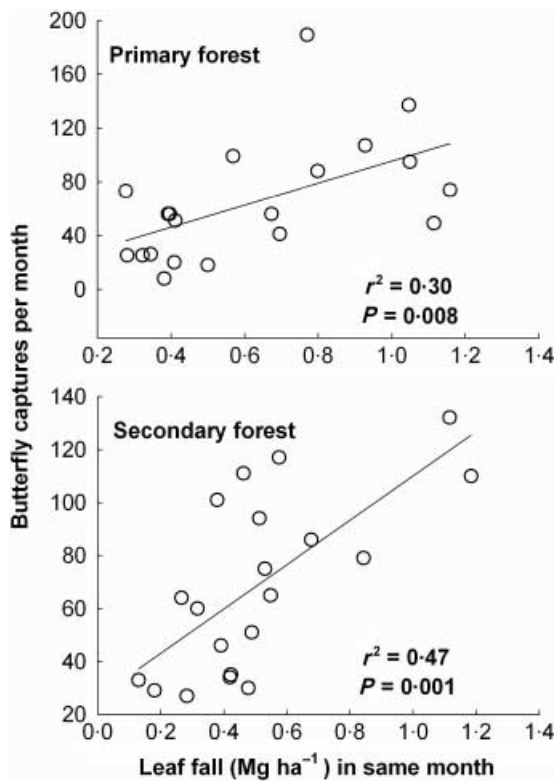


Fig. 5. The positive relationships between leaf-fall (dry weight in grams recorded in litter traps) and the abundance of fruit-feeding butterflies in primary and secondary forest. Each point represents a seasonal replicate of each of the within-habitat samples (pooled $n = 20$).

examine the role of resource availability and habitat and landscape factors in determining butterfly composition and abundance.

SPATIAL SCALE

The spatial scale of a study can affect its conclusions, with studies undertaken at small spatial scales failing to sample the increased heterogeneity evident at larger spatial scales in undisturbed forests (Hamer & Hill 2000). However, while the use of short transects could have contributed to their finding of lower richness in the least disturbed sites in one study (Bowman *et al.* 1990), it did not appear to do so in another (Schulze *et al.* 2004). Moreover, the five other pertinent studies are difficult to differentiate using the definition of scale used by Hamer & Hill (2000), as although all used traps baited with fruit, which sample over a large scale, they were also all undertaken in very small habitat patches (= 6 ha where reported).

SAMPLING EFFORT

Although species richness as estimated by rarefaction analyses was highest in primary and lowest in plantations (Fig. 1), there was no significant effect of habitat type on observed species richness at the site level among different seasons (Fig. 4), illustrating the unreliability

of observed richness and the problem of undersampling the most species rich habitats (cf. DeVries *et al.* 1999; Gotelli & Colwell 2001). By using a standardized index of sampling effort that takes into account differences in capture success (the number of individuals per species; cf. Gotelli & Colwell 2001), we note that studies based on baited fruit traps that reported an increased richness or diversity in secondary forest (compared to primary forest) had smaller sample sizes than those that reported a decrease (increased richness: 9.8, 19.4 and 39.4 individuals per species for Fermon *et al.* 2005; Bobo *et al.* 2006; Ramos 2000, respectively; decreased richness: 70.4 and 82.1 for Veddeler *et al.* 2005 and this study, respectively). Furthermore, all three studies reporting a decrease in richness or diversity in secondary forest controlled for differences in sampling effort by using species richness estimators or rarefaction (Schulze *et al.* 2004; Veddeler *et al.* 2005; this study), while only two of those reporting increased richness or diversity used either richness estimators and/or species accumulation curves (Fermon *et al.* 2005; Bobo *et al.* 2006).

TEMPORAL VARIATION

Temporal variability in tropical forest butterfly communities has been demonstrated many times (Larsen & Riley 1979; Raguso & Llorente-Bousquets 1990; Spitzer *et al.* 1993; DeVries *et al.* 1997, 1999; Shahabuddin & Terborgh 1999; Brown & Freitas 2000; Hamer *et al.* 2005; Molleman *et al.* 2006; Fig. 4). However, we also show that comparisons of abundance and species richness between habitats and across a disturbance gradient can give contrasting results in different seasons, supporting similar findings in relation to the effects of habitat fragmentation and selective logging (Shahabuddin & Terborgh 2000; Hamer *et al.* 2005). Moreover, the seasonal timing of sampling in existing studies of secondary forest closely matches the response trajectory of species richness. All of the five available studies that reported an increase in richness in secondary forest were undertaken during a limited period (1–4 months), and during the driest period of the year (Bowman *et al.* 1990; Lawton *et al.* 1998; Ramos 2000; Fermon *et al.* 2005; Bobo *et al.* 2006). In contrast, those reporting a decrease in richness were undertaken during the wet season (Veddeler *et al.* 2005) or throughout the year (Schulze *et al.* 2004; this study). This conclusion is further reinforced by the seasonal patterns found in our study, where secondary forest had higher observed species richness, abundance and diversity than primary forest during the peak dry season sampling period, but lower or equivalent at other times of the year (Fig. 4). Although butterfly sampling during the dry season can be logistically preferable to investigators, it should always be complemented by at least a further seasonal replicate in the wet season.

Hamer *et al.* (2005) found the diversity of selectively logged areas to be lowest in the dry season, and that disturbance led to lower temporal variation. We found

higher richness in the dry season in secondary forest, and no evidence to suggest that secondary forest or plantations were any more or less seasonal than primary forest. The reason for these differences are unclear, and the interaction between seasonality and habitat type could depend on many factors including which sub-families dominate the samples, the degree of seasonality in the region, and the characteristics of the habitats examined. Regardless of the causes, both this study and Hamer *et al.* (2005) clearly demonstrate the need for longer-term surveys of speciose taxa, such as lepidopterans, in tropical forests (cf. DeVries *et al.* 1999).

CONGRUENCE OF SUBFAMILY RESPONSES

Low levels of congruency have been found among the responses of higher taxonomic groups to habitat disturbance (Lawton *et al.* 1998; Ghazoul 2002; Kati *et al.* 2004; but see Schulze *et al.* 2004). Although higher levels of congruence have been found in more closely related butterfly taxa (Beccaloni & Gaston 1995; Cleary & Mooers 2004), we found very poor levels of congruence between Nymphalidae subfamilies attracted to rotten fruit using the commonly used metrics of species richness and abundance (Table 3).

Different subfamilies also varied in their ability to distinguish the three forest habitats (Table 1). The Satyrinae were the only taxon to successfully split all habitats both in terms of abundance and community structure, reflecting the variety of responses to disturbance within this subfamily, which includes both understorey forest specialists that avoid light (Brown & Freitas 2000; Ghazoul 2002) and species that become highly abundant following disturbance (e.g. Raguso & Llorente-Bousquets 1990; Daily & Ehrlich 1995; Shahabuddin & Terborgh 2000; Fermon *et al.* 2005).

RELATIONSHIPS WITH RESOURCE AVAILABILITY

Many phytophagous insects in tropical forests depend on the availability of young leaves (Wolda 1978) which have lower levels of plant defences and generally suffer the highest amount of damage (Coley & Barone 1996). Adult butterflies are no exception, and their abundance was strongly related to leaf fall (a surrogate of new leaf production) in primary and secondary forest (Fig. 5), presumably being driven by either community-wide larval feeding requirements (although not all species may prefer young leaves). This observation is further supported by changes in the abundance of subfamilies with specific host-plant preferences. For example, the degree of host-plant specificity is one of the key features influencing butterfly response to disturbance and fragmentation (Steffan-Dewenter & Tscharnkte 2000; Koh, Sodhi & Brook 2004), and many studies report an increase in the Satyrinae with increased forest disturbance (Fig. 4; Daily & Ehrlich 1995; Raguso & Llorente-Bousquets 1990; Shahabuddin & Terborgh 2000;

Fermon *et al.* 2005), related to the increase in the monocotyledonous annual plants on which their larva depend.

Although the abundance of butterflies has also been related to the availability of resources used by adults (such as nectar; Kuussaari *et al.* 1996; Haddad & Baum 1999), both this study and Hamer *et al.* (2005) failed to find any relationship between the capture success of adult fruit-feeding butterflies and fruit-fall. Fruit-fall was also a poor predictor of butterfly community structure (Table 4). However, any potential relationship may be masked by changes in trap efficiency and butterfly behaviour, as butterflies tend to forage farther in areas with less fruit (Fermon *et al.* 2005) and baited traps may become less attractive to butterflies during periods of high alternative fruit availability.

LANDSCAPE EFFECTS VS. HABITAT STRUCTURE

The composition of lepidopteran communities in disturbed or fragmented habitats can be affected by the composition of the surrounding habitat matrix (Zanuncio *et al.* 1998; Shahabuddin & Terborgh 2000; Horner-Devine *et al.* 2003; Hawes 2005), suggesting that the influence of transient species can confound assessments of habitat value (Ghazoul 2002). Although our experimental design was established to explicitly minimize the effect of surrounding landscapes, there is still some evidence that the dispersal ability of the strong-flying Charaxinae influenced their response. Butterflies in the genera *Prepona* and *Archaeoprepona* were occasionally seen flying down from the canopy of *Eucalyptus* to investigate our baited traps, and the Charaxinae were the only family to show a strong matching coefficient between their composition and the amount of primary forest surrounding each plot (Table 4). However, movement by butterflies is often less than their potential vagility (Fermon *et al.* 2005) and in most cases, at the scale we examined, habitat type and local vegetation structure were more important than the surrounding landscape (cf. Pinheiro & Ortiz 1992; Sparrow *et al.* 1994; Hill *et al.* 2001; Lewis 2001; Ghazoul 2002; Veddel *et al.* 2005; Bobo *et al.* 2006).

DEFINING SPECIES OF CONSERVATION CONCERN

Conservation strategies rely on identifying species of conservation concern, yet many of the life-history traits that define species vulnerability (see Koh *et al.* 2004) are poorly known for Amazonian butterflies (Brown 1996). A more practical approach would be to focus on species that are unable to persist outside of primary forest, especially as these are also the most likely to be endemic (e.g. Cleary & Mooers 2006). However, although our results reinforce the conservation concern regarding some of the most charismatic species (such as *Agrias* spp., cf. Brown 1996 and Appendix S1), they also point out some of the problems associated with accurately

quantifying the dependence of species on primary forest. For example, many vagile and transient individuals may be recorded infrequently outside primary forest, we have no knowledge regarding long-term population persistence in anthropogenic habitats, and it is very difficult to attain sample sizes of sufficient statistical power to examine the habitat preferences of the many rare species that are typical of primary habitats. As a result of these problems, only 22% of species were unique to primary forest, and only eight species were significant indicators of that habitat (Appendix S1) – numbers that we believe grossly underestimate the true level of primary forest dependence (cf. Gardner *et al.* 2007). Nevertheless, evaluating the conservation value of different habitats requires the development of simple and effective indices if ecologists are to understand the consequences of ongoing land-use change and habitat degradation. In this respect, our results suggest that patterns of community turnover in butterflies provide a more effective indicator of habitat change than either patterns of species richness or abundance (Table 3), or the abundance of specific species (cf. Su *et al.* 2004).

Conclusion

Our analysis of the importance of primary, secondary and plantation forests took into account potential sampling pitfalls, and show that although secondary forest and tree plantations held high numbers of fruit-feeding Nymphalidae butterflies, they have a significantly lower conservation value for these lepidopterans in terms of species richness and composition. Some previous studies may have over-emphasized the conservation importance of secondary forest and plantations by undersampling primary forest habitats, and restricting their sampling to a limited period of the year, particularly the dry season. These results cast doubt on the presumption that secondary habitats (Wright & Muller-Landau 2006) and the wider countryside (Daily 2001; Horner-Devine *et al.* 2002) will provide refuge for many of the species being lost through tropical deforestation, and we strongly urge measures that prioritize the conservation of primary forests where they still exist.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Species list from the three habitats examined, and indicator species analysis

Table S1. Statistics from repeated measures ANOVAS.

Fig. S1. Subfamily abundance by sample day in the three habitats.

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