

Diversity and composition of fruit-feeding butterflies in tropical *Eucalyptus* plantations

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Abstract Production landscapes are rarely considered as priority areas for biodiversity conservation in the tropics. Tree plantations have the potential to provide a conservation service in much of the humid tropics since they are rapidly increasing in extent and present less of a structural contrast with native vegetation than many more intensive agricultural land-uses. We used hierarchical partitioning to examine the factors that influence the value of large-scale *Eucalyptus* plantations for tropical fruit-feeding butterflies (Lepidoptera: Nymphalidae) in the Brazilian Amazon. We focused on evaluating the importance of landscape versus stand-level factors in determining the diversity and composition of butterfly assemblages, and how butterfly-environment relationships vary within and between subfamilies of Nymphalidae. Native understorey vegetation richness had the strongest independent effect on the richness, abundance and composition of all fruit-feeding butterflies, as well as a subset of species that had been recorded in nearby primary forests. However, overall patterns were strongly influenced by the most abundant subfamily (Satyrinae), and vegetation richness was not related to the abundance of any other subfamily, or non-Satyrinae species, highlighting the importance of disaggregating the fruit-feeding Nymphalidae when examining butterfly-environment relationships. Our results suggest that plantations can help conserve a limited number of forest species, and serve to highlight the research that is necessary to understand better the relationship between fruit-feeding butterflies and environmental variables that are amenable to management.

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Introduction

Biodiversity conservation in production landscapes is becoming increasingly recognized as a major conservation priority worldwide (Daily 2001; Lindenmayer and Franklin 2002; Fischer et al. 2006). The inadequacy of the current protected areas network (Rodrigues et al. 2004) highlights the potential importance of production areas in providing a vital complementary conservation service (Lindenmayer and Franklin 2002; Fischer et al. 2006). Tree plantations have the potential to provide a valued conservation service in much of the humid tropics as they (1) are rapidly increasing in extent, and (2) present less of a structural contrast with native vegetation than many alternative yet more intensive agricultural land-uses that are biologically impoverished (e.g. cattle ranches, soybean, cotton croplands). The coverage of plantation forestry in the tropics increased from c.17.8 million hectares in 1980 to c.70 million in 2000 (Brown 2000; FAO 2005), while it is estimated that around 1 million hectares of tropical forest are converted to tree plantations each year (FAO 2005). This coverage is likely to increase further (especially in areas of tropical forest, e.g. Fearnside 1998), in part due to both private and national investment in carbon-sequestration projects (Yu 2004) and a growing interest in biofuels and timber products (Pacala and Socolow 2004). In their latest Global Forest Resource Assessment the Food and Agriculture Organization of the UN has predicted a 50% increase in the production of industrial wood from plantations in the next 40 years (FAO 2005).

Plantation forests may support biodiversity conservation by buffering fragments of native forest, facilitating the movement of animals across the landscape matrix, and providing suitable habitat for some forest dependent species (Lindenmayer and Franklin 2002; Carnus et al. 2006; Fisher et al. 2006; Lindenmayer et al. 2006). However, despite their potential importance, the conservation value of extensive monocultures are very poorly understood (Kanowski et al. 2005), with most of the work restricted to a few well-studied taxa (birds and mammals) in temperate and subtropical regions (see Hartley 2002; Lindenmayer and Hobbs 2004). Furthermore, management recommendations for many temperate plantations focus on maximizing the amount of young “non-woodland” habitat suitable for the open-habitat specialists of greatest conservation concern (e.g. Humphrey et al. 1999; Eycott et al. 2006), and are of limited relevance for the humid tropics where most species of conservation concern are forest species.

We examined fruit-feeding butterflies (Lepidoptera: Nymphalidae) in *Eucalyptus* plantations in the north-east Brazilian Amazon. *Eucalyptus* currently accounts for around 50% of all tropical tree plantations (Evans and Turnbull 2004). Butterflies have frequently been used as indicators of the conservation value of tropical habitats and the consequences of disturbance and land-use change (e.g. Brown 1997; Hamer and Hill 2000; Koh et al. 2007), and in a previous study undertaken at the same study site fruit-feeding butterflies explained almost 57% of the variance in the responses of 14 other taxa to land-use change (J.Barlow et al. unpubl. data). However, despite their popularity as ecological and biodiversity indicators, we are only aware of three studies that have explicitly examined the value of tropical plantations for butterflies (Ramos 2000; Stork et al. 2003; Barlow et al. 2007). Moreover, we are not aware of any study that has evaluated how stand-level and landscape-level features interact to determine the conservation value of plantations for

butterflies. We addressed this information deficit by examining how landscape configuration, and plantation age, productivity, and understorey structure and composition all combine to influence the species richness, diversity and composition of fruit-feeding butterflies. Observations of butterflies in plantations from five sites in the same region (Barlow et al. 2007) led us to hypothesize that (1) the presence of fruit feeding butterflies would be strongly linked to local patterns of richness and structure of the native of understorey vegetation in individual sites (and less so to landscape context), and (2) that butterfly-environment relationships would be highly specific to subfamilies.

Methods

Study site

The project was conducted within the 1.7 million hectare Jari landholding 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"–5°20'00" W). The area was purchased in 1968 for cellulose pulp production, and held c. 53,000 ha of *Eucalyptus* plantations at the time of study. These plantations are embedded in a largely undisturbed primary forest matrix (>1 million hectares). All sample sites had similar stocking densities (c. 900–1100 trees ha⁻¹) and no thinning had occurred. However, the understorey native vegetation is periodically suppressed, typically at 0, 1 and 3 years of age, either by labour-intensive manual removal or herbicidal treatment (Glyphosate and Isoxaflutole). The species composition of the native understorey was variable despite this clearing: Species-poor sites tended to contain only one or two species of annuals (typically from the families Asteraceae, Rubiaceae, Piperaceae, Poaceae or Cyperaceae), while species-rich sites contained many species of lianas (including *Davilla* spp., Dilleniaceae) and small pioneer trees such as *Vismia* spp. (Clusiaceae), *Cecropia* spp. (Cecropiaceae), *Mabea taquari* and *Aparisthium cordatum* (Euphorbiaceae). The plantations are managed in short-cycles and stands are clear-felled every 5–7 years.

Butterfly sampling

Fruit-feeding butterflies were trapped at 30 spatially independent *Eucalyptus* plantation sites) using cylindrical VanSomeren-Rydon traps (Rydon 1964; DeVries et al. 1997), baited with a standard mixture of mashed and fermented banana. The mosquito netting capture cylinder was 90 cm in height, minimising the risk of escape once butterflies had entered. Four traps were placed in the understorey of each site, spaced 100 m apart along a 300 m long transect. The baited trays were suspended 50 cm from the ground. Traps were placed in the forest in the morning (0900–1000 h) and checked the following day between 1500 and 1600 h. All sampling was undertaken during mostly-dry days in May 2005. Butterfly identification was carried out at the Museu Paraense Emílio Goeldi (MPEG) in Belém, Brazil, using reference collections and the plates and descriptions in D'Abrera (1988) and Neild (1996). Nomenclature follows Lamas (2004).

We classified butterflies as primary forest species if they had been recorded within five independent neighbouring primary forest sites spread out across the wider landscape. Each of these sites was sampled four times during the previous year, maximizing our knowledge of occupancy across the year (see Barlow et al. 2007). Each seasonal replicate ran eight

understorey and eight canopy traps for five days at each site, totaling 1600 traps days of effort. All traps were located >500 m from the forest edge.

Environmental data

The structure and species richness of the native understorey vegetation was quantified in 20 m diameter circular plots at each trap location ($n = 4$ per site) using six variables that were recorded concurrently with butterfly sampling. Values from the four replicate plots per site were averaged to create a single site score. The variables measured were the percentage of vegetation cover on the ground, the mean vegetation height, maximum vegetation height, a score of understorey structure complexity (from 0–5, zero being *Eucalyptus* only, five being a highly developed understorey), a score of liana load on trees (from 0–5, with 0 = no lianas, and five = all *Eucalyptus* stems had lianas up to the sub-canopy), and a score of understorey vegetation richness (0–5), with 0 representing just one species, and 5 representing >25 species. We analysed the landscape composition and configuration of the study area with a vegetation and land-cover classification developed from a combination of land-use data from the landholding company and a supervised classification of a 2003 LandSat 7 (30 m pixel) satellite image. We calculated the percentage of primary forest within 1 km and 3 km buffer using a GIS (Arc-Info, Environmental Research Systems 1998).

We used the dominant height (the average total height of the 100 largest diameter, non-deformed trees per hectare) as our measure of stand productivity. Measurements of dominant height were made by Jari Celulose S.A. in the last 5 years, and all measurements were for *Eucalyptus urograndis* stands aged between 4 and 7.5 years. The relationship between *Eucalyptus* age at time of measurement and dominant height was weak ($r = 0.3$, $P = 0.15$), and most of the variance in dominant height (range 17–35 m) can be assumed to reflect local productivity rather than stand age.

Data reduction

We used Principal Components Analysis (PCA) to compose two composite variables for highly collinear independent variables (see Table 1). First, we constructed a composite variable to describe understorey structural complexity, composed of mean vegetation height, maximum vegetation height and the score of habitat structure complexity. The PCA loadings on the first factor were high for all these variables (0.96, 0.96 and 0.94, respectively), and the first factor explained 90.4% of the total variance. Second, we used a PCA to combine the percentage of primary forest within 1 km and 3 km buffers to create a score that helps describes the landscape composition around each sample site. The first factor explained 90.8% of the variance. For the purposes of analyses, the PCA score of understorey structure (+2 to remove negative numbers) and the liana load scores were \log_{10} transformed to achieve approximate normality. Vegetation cover scores were Arcsine transformed.

Data analysis

All trap data was pooled within sites to maximize site-level representation. Species richness and the completeness of overall sampling were examined using sample-based

Table 1 Correlation matrix between environmental variables, with correlation coefficient (r_s) shown in bottom left, and P -values in top right. Variables used to create composite variables through PCA are shown by superscript characters

	Understorey Ht (Max) ^a	Understorey Ht (Ave) ^a	Habitat complexity ^a	Liana load	Vegetation cover (%)	Vegetation richness score	Stand age	Dominant height	Primary forest in 1 km ^b	Primary forest in 3 km ^b
Understorey Ht (Max) ^a		<0.00	<0.001	<0.001	0.003	<0.001	0.001	ns	ns	ns
Understorey Ht (Ave) ^a	0.92		<0.00	<0.001	0.001	<0.001	<0.001	ns	ns	ns
Habitat complexity ^a	0.93	0.88		<0.001	0.005	<0.001	<0.001	ns	ns	ns
Liana load	0.66	0.64	0.75		0.003	0.001	0.017	ns	ns	ns
Vegetation cover (%)	0.53	0.59	0.50	0.52		0.010	<0.001	ns	ns	ns
Vegetation richness score	0.72	0.75	0.81	0.59	0.46		0.005	ns	ns	ns
Stand age	0.65	0.59	0.60	0.43	0.78	0.50		ns	ns	ns
Dominant height	0.18	0.17	0.17	0.00	0.23	0.17	0.22		ns	ns
Primary forest in 1 km ^b	0.04	-0.05	0.07	0.01	0.06	0.26	0.10	0.25		<0.001
Primary forest in 3 km ^b	0.15	0.11	0.20	0.12	0.14	0.22	0.25	0.13	0.78	

^a Combined by PCA to create understorey structure variable

^b Combined by PCA to create a distance to primary forest variable

rarefaction curves constructed using EstimateS v.7 (Colwell 2004). Sample-based rarefaction curves were also repeated for the four most abundant subfamilies (Satyrinae, Biblidinae, Nymphinae and Charaxinae). Total estimated species richness was calculated for all sites together and for each individual site using the mean of the four commonly employed abundance-based estimators (ACE, Chao 1, Jack 1 & Bootstrap, see Colwell 2004). The mean of these estimators was used in order to minimize any bias from any particular estimator, the performance of which often varies according to differences in richness, sampling effort, and community evenness (O'Hara 2005). The similarity of butterfly species composition in a given stand in relation to that in neighbouring primary forest (using data from Barlow et al. 2007) was examined using the Jaccard similarity index to avoid the influence of sample effort in biasing species relative abundance distributions.

Like other faunal groups, the observed species richness of fruit-feeding butterflies is highly sensitive to sampling effort (e.g. DeVries et al. 1997, Molleman et al., 2006, Koh et al. 2007). We tested the validity of our results by using rarefaction to analyse data from 20 additional samples of butterfly fauna in *Eucalyptus* (4 seasonal replicates conducted at 5 sites) which had used 10 times the sample effort employed in the current study (40 trap days per sample; see Barlow et al. 2007). Although four trap days only captured 37% of the number of species sampled over a longer period, the results from four trap days were a very good predictor of the pattern of observed richness across sites when sampled with the full 40 trap days of effort ($F_{1,18} = 63$, $r^2 = 0.78$, $P < 0.001$). We are therefore confident that the results of this short-term study are a realistic representation of the patterns of fruit-feeding butterfly richness and composition within these plantations at the time of year we sampled.

Linking butterfly data with environmental variables

We were interested in revealing the most likely causal factors from within our candidate set of explanatory variables. Traditional model selection techniques often fail in this task due to high levels of multicollinearity among explanatory variables (Graham 2003), resulting in a spurious understanding of the nature of particular species-environment relationships (Mac Nally 2000). To minimize the influence of multi-collinearity among related explanatory variables we used hierarchical partitioning (Chevan and Sutherland 1991) to examine the independent effects of the seven key environmental variables (understorey vegetation richness, understorey vegetation structure, liana load on trees, vegetation cover on ground, landscape configuration, dominant height [plantation productivity], and *Eucalyptus* age) on six dependent variables of interest; observed butterfly richness, abundance, diversity (Simpson's diversity), the similarity of species composition to primary forest of all fruit-feeding butterflies (Jaccard's index), and the richness and abundance of known primary forest species. In addition, we examined the influence of the same explanatory variables on the abundance of the four dominant subfamilies, and the 13 most abundant species (i.e. all species with more captures than sample sites, $n = 30$). Hierarchical partitioning is a regression technique in which all possible linear models are jointly considered in an attempt to identify the most likely causal factors, providing a measure of the effect of each variable that is largely independent from that of other variables (Chevan and Sutherland 1991, Mac Nally 2000). Patterns of species abundance were modelled using Poisson errors and a goodness of fit based on r-square. The significance of independent effects was calculated using Mac Nally's (2002) randomization test

Fig. 1 (a) Sample-based rarefaction curves for fruit-feeding butterflies in *Eucalyptus* plantations (Black symbols). Dotted lines denote 95% confidence intervals. Clear symbols lines show the mean estimated richness from four different richness estimators (ACE, Chao 1, Jackknife & Bootstrap). (b) Sample-based rarefaction curves for the four most abundant subfamilies

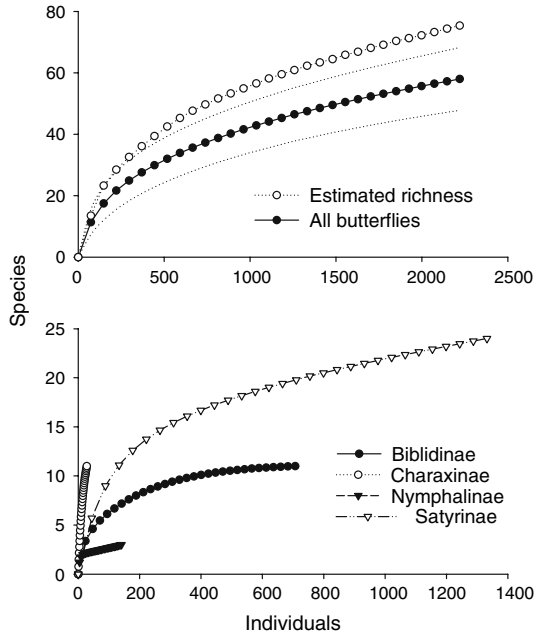


Table 2 Correlations between the abundance of the four most abundant butterfly subfamilies, with correlation coefficient (r_s) shown in bottom left, and P -values in top right. $n = 30$ for all correlations

	Biblidinae	Charaxinae	Nymphalinae	Satyrinae
Biblidinae		0.34	0.36	0.35
Charaxinae	-0.18		0.19	0.61
Nymphalinae	0.18	0.25		<0.001
Satyrinae	0.18	0.10	0.67	

with 1000 iterations. Hierarchical partitioning and associated randomization tests was implemented using the hier.part package freely available in the R statistical program (<http://www.r-project.org>). Finally, because hierarchical partitioning only partitions the variance explained by selected predictor variables, we also calculated a measure of overall model fit for each species, based on the explained deviance (R_{dev}^2) of a General Linear Model (Mac Nally 2002).

Results

We captured a total of 2200 butterflies and 56 species at the 30 sampled *Eucalyptus* plantation sites (Fig. 1). Capture success was highly variable across sites, ranging from as few as six to as many as 350 individual butterflies. Capture success was also unevenly distributed across species: the five and 10 most abundant species accounted for 62% and 85% of all captures respectively. *Hamadryas feronia* (Biblidinae) was the only species present at all sites and the second most abundant overall (14% of total captures). Sample rarefaction curves for individual subfamilies were highly variable, increasing very rapidly

for the Charaxinae, while the Biblidinae appeared to have reached their asymptote (Fig. 1). Of six pairwise correlations between the abundance of individual subfamilies, only that between the Nymphalinae and Satyrinae was significant ($P = 0.05$, Table 2).

Hierarchical partitioning revealed a strong independent effect of understorey vegetation richness on the abundance, richness and species composition of fruit-feeding butterflies captured in plantations, and on the richness and abundance of the primary forest species (Fig. 2). Liana load was the only other significant environmental variable (Fig. 2), and it had a significant effect on butterfly species richness. None of the environmental variables had a significant effect on species diversity. Analysing results separately by subfamily revealed that the results for all fruit-feeding butterflies were strongly influenced by the Satyrinae, which was the most abundant subfamily (Fig. 1) and the only subfamily that was significantly influenced by vegetation richness (Fig. 2). No other subfamily appeared to be significantly influenced by any of the environmental variables we recorded, and although the dominant height and the landscape configuration appeared to have much stronger effects on the abundance of the Charaxinae than the other variables, the overall model fit was rather low (Fig. 2).

The analysis of the 13 most abundant species (with >30 captures in total) revealed a fairly consistent influence of vegetation richness on species from within the Satyrinae (vegetation richness had a significant effect for six of the eight species; Table 3), although the percentage ground cover had a stronger effect than vegetation richness for *Ypthimoides renata*, plantation age and liana load had significant effects on *Cissia terrestris*, while none of the variables had significant effects on *Magneptychia libye* (Table 3). None of the measured environmental variables had a strong effect on the abundance of the three most abundant species of *Hamadryas* examined, reflecting the pattern for the Biblidinae as a whole. In addition, none of the measured variables had strong effects on the most abundant species of Nymphalinae (*Colobura dirce*), but plantation productivity (dominant height) had a strong and negative effect on the abundance of *Historis odius* (Nymphalinae).

Discussion

This short-term study of fruit-feeding butterflies in *Eucalyptus* plantations in the Brazilian Amazon supported our *a priori* hypotheses that (1) local stand-level vegetation structure and compositional factors would be more important than landscape context for fruit-feeding butterflies, and (2) butterfly–environment relationships would be highly specific to subfamilies. We examine the strength and validity of these butterfly–environment relationships focusing on vegetation richness, highlight future research priorities, and discuss the wider conservation implications of this study.

Butterfly–environment relationships

Overall, we found very few species–environment relationships that did not involve vegetation richness (Fig. 2, Table 3). Although butterfly species richness has been related to vegetation richness at large spatial scales (Thomas and Mallorie 1985; Kerr et al. 2001), more detailed statistical analyses suggest that such positive relationships may only be correlative, with both groups responding to similar environmental factors (Hawkins and Porter 2003). The link between vegetation richness and butterfly richness at local scales has stronger support: Gilbert and Smiley (1978) found a positive relationship between the

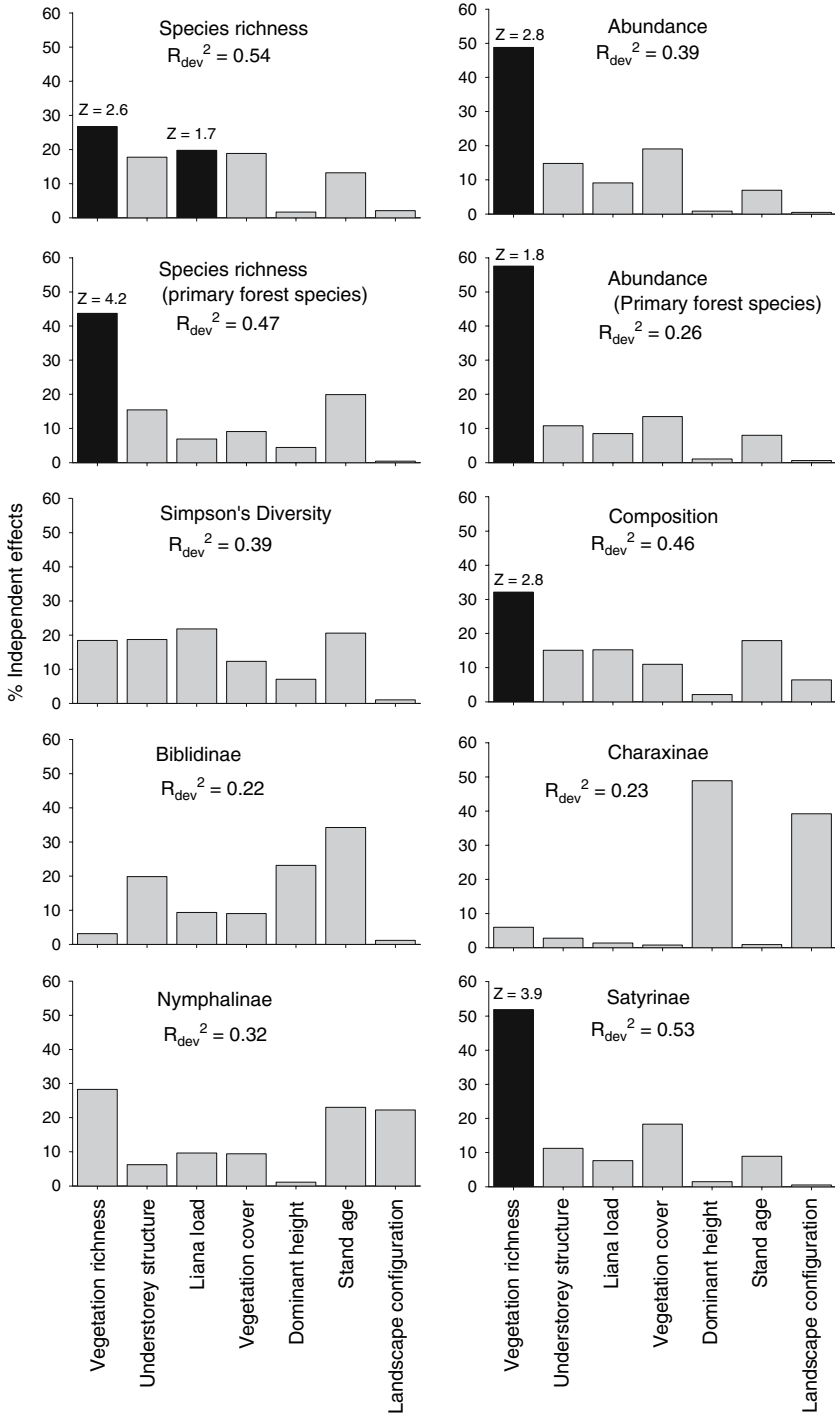


Fig. 2 Distribution of percentage independent effects of measured environmental variables on fruit-feeding butterflies in *Eucalyptus* plantation forests. Black bars represent significant effects ($P < 0.05$) as determined by randomization tests. All significant effects described positive relationships. R_{dev}^2 is the total deviance explained by a generalized linear model encompassing all measured variables

number of species of heliconid butterflies and their *Passiflora* host plants, and Steffan-Dewenter and Tschamtko (2000) report a close correlation between butterfly and vegetation richness in European grasslands. Furthermore, host-plant specificity is a key correlate of extinction risk in butterflies (Koh et al. 2004), and the presence or absence of a small number of specific host plants could have a large influence on butterfly diversity. However, these relationships are not ubiquitous, and Schulze et al. (2004) and Veddeler et al. (2005) failed to find a relationship between understorey richness and the richness of fruit-feeding butterfly in a study of land-use change in Indonesia, and Singer and Ehrlich (1991) found no evidence of a relationship between the richness of forest Satyrinae and their monocotyledonous host plants in Trinidad.

Although our results appear to lend strong support for the relationship between vegetation richness and butterfly richness at local scales, there are some reasons to interpret these butterfly-environment relationships with caution. The positive effect of vegetation richness was only found within the Satyrinae, which is a subfamily composed of generalists whose larvae are able to feed upon many different species of grasses, sedges and other monocotyledonous plants (DeVries 1997, Singer and Ehrlich 1991). For example, the larvae of three of the most abundant species in our study (*Cissia penelope*, *Ypthimoides renata* and *Hermeuptychia hermes*) have been observed feeding on up to eight species of grass or sedge in fragmented forests of Trinidad, and consumed all grass or sedge species offered to them in the laboratory (Singer and Ehrlich 1991). With such low levels of host specificity, it is unsurprising that the same study failed to find a relationship between Satyrinae richness and the number of species of available host plants, and it is difficult to envisage how our coarse scale observations of vegetation richness would have affected the richness and abundance of a group dominated by generalists. An alternative explanation could be that our estimates of vegetation richness were positively correlated with the abundance of grasses and sedges (that were common in the understorey in many sites, but not recorded specifically).

The lack of significant butterfly-environment relationships for the other subfamilies may also relate to our coarse measurement of environmental variables in general. For example, the most abundant genera of the Biblidinae (*Hamadryas*) are common in studies of *cerrado* vegetation (Pinheiro and Ortiz 1992) and disturbed tropical forests, where they track the abundance of their *Dalechampia* (Euphorbiaceae) hostplants (Shahabuddin and Ponte 2005; Uehara-Prado et al. 2007). Consequently species-environment relationships may well have been revealed if we had recorded the abundance of *Dalechampia* (which was present in at least some of the plots), and possibly some of the other species of Euphorbiaceae that were often abundant in the understorey (such as *Mabea taquari*, *Aparisthium cordatum*, and *Manihot* spp.).

The Nymphalinae were dominated by just two species (Appendix), both of which are known to feed upon the pioneer tree *Cecropia* spp. Although a previous study did not find a relationship between *Historis odius* and their *Cecropia* food plants (Shahabuddin and Ponte 2005), the strong negative effect of plantation productivity on *H. odius* suggests that the relationship between productivity and *Cecropia* abundance warrants further investigation.

Table 3 Distribution of percentage independent effects of measured environmental variables on patterns of abundance for 13 species of fruit-feeding butterflies in *Eucalyptus* plantation forests

Subfamily	Species	R ² _{dev}	Vegetation richness	Understorey structure	Liana load	Vegetation cover	Dominant height	Stand age	Landscape configuration
Satyrinae	<i>Cissia penelope</i>	0.46	37.0	11.0	14.4	17.6	1.7	17.9	0.4
Biblidinae	<i>Hamadryas feronia</i>	0.18	9.4	12.1	2.9	6.8	42.4	16.5	10.0
Satyrinae	<i>Paryphthimoides argulus</i>	0.38	61.1	7.1	10.4	12.6	1.8	4.8	2.1
Biblidinae	<i>Hamadryas februa</i>	0.30	2.8	21.9	4.8	10.9	16.0	37.8	5.8
Satyrinae	<i>Taygetis laches</i>	0.64	31.5	9.4	6.8	20.6	6.8	21.5	3.3
Biblidinae	<i>Hamadryas amphinome</i>	0.35	5.8	13.5	11.5	17.6	7.7	43.4	0.4
Satyrinae	<i>Paryphthimoides vestigata</i>	0.69	53.9	6.2	12.1	4.0	2.8	13.7	7.1
Nymphalinae	<i>Colobura dirce</i>	0.42	19.2	5.3	4.7	8.5	10.5	34.8	17.1
Satyrinae	<i>Ypthimoides renata</i>	0.73	25.1	13.1	12.6	31.7	3.0	11.3	3.2
Satyrinae	<i>Hermeuptychia hermes</i>	0.59	48.1	7.5	6.1	8.6	6.1	20.9	2.6
Satyrinae	<i>Cissia terrestris</i>	0.83	6.6	7.1	26.2	13.5	6.0	39.8	0.7
Nymphalinae	<i>Historis odius</i>	0.64	3.5	6.0	8.4	9.0	56.1(-)	14.8	2.2
Satyrinae	<i>Magneuptychia libye</i>	0.18	7.8	2.5	10.4	52.2	6.2	9.9	11.0

Values in bold represent significant effects ($P < 0.05$) determined by randomization tests. The only significant effect that depicts a negative relationship is shown in parentheses (*Historis odius*). R²_{dev} is the total deviance explained by a generalized linear model encompassing all variables

Finally, the ability of butterflies to utilize plantations may be linked to factors other than host-plant availability, include their flight morphology and ability to avoid avian predators (Chai and Srygley 1990). Our data provided limited support for the influence of landscape structure on the Charaxinae as the availability of primary forest in neighbouring buffer areas was strongly linked to their abundance (Fig. 2). The Charaxinae are typically composed of powerfully flying forest species (Neild 1996), and it is possible that sites closer to primary forest were more likely to capture transient butterflies moving across the matrix, or individuals that perceive plantation edges as natural forests gaps.

Disaggregating the responses of fruit-feeding Nymphalidae

Aggregating species' responses can mask patterns of change if groups or species respond in contrasting ways (Manning et al. 2004; Lindenmayer et al. 2005). Our results show that butterfly-environment relationships can be strongly affected by the aggregation of sub-families that may exhibit distinct ecological responses to patterns of habitat change, supporting previous assessments on responses of butterfly genera (Uehara-Prado et al. 2007) and studies of change across larger spatial scales (Brown and Freitas 2000). They also suggest that studies that failed to reveal any significant relationships between patterns of Nymphalidae richness and local vegetation (e.g. Schulze et al. 2004; Veddeler et al. 2005) may have analysed their data at an inappropriate taxonomic level.

Conservation implications

Although commercial plantations are in no way a replacement for native primary forests (e.g. Barlow et al. 2007), the *Eucalyptus* plantations that we examined were far from the “biological deserts” they are often portrayed as in the literature (see Kanowski et al. 2005). This study highlights the potential importance of the native understorey vegetation for the abundance, richness and diversity of some species of fruit-feeding butterflies, supporting similar findings from other taxa in tree plantations elsewhere in the world (e.g. Curry 1991; Chey et al. 1997; Humphrey et al. 1999; Lindenmayer and Hobbs 2004).

Whilst discussions about patterns of species richness within the wider countryside (Daily 2001) are of limited relevance for conservation unless the species are of conservation value (e.g. Petit and Petit 2003), we found similar results whether we consider all species, or only those known to occur in neighbouring areas of primary forest. We show that the conservation value of these forests for some subfamilies of fruit-feeding butterflies can be maximized if plantation managers tolerate a species-rich native understorey, but acknowledge that a comprehensive understanding of wider butterfly-environment relationships requires a more detailed examination of vegetation structure and composition as well as species richness. Finally, this short-term study provides just a snapshot of the patterns of butterfly diversity within plantations, and much longer-term work is required to examine different taxa, and across different seasons, years, and successive silvicultural rotations. The rapid loss of primary forest habitats and the growth of plantations in many areas of the world underline the urgency with which this work needs to be undertaken.

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Appendix

Summary of captures. Determination of primary forest species is based on independent data from Barlow et al. (2007). The subfamilies Coliadinae (Pieridae), Ithomiinae, and Limenitidinae (Nymphalidae) are not fruit-feeding

Subfamily	Species	Present in primary forest	Occupancy (out of 30 sites)	Abundance
Biblidinae	<i>Biblis hyperia</i>	No	3	3
Biblidinae	<i>Catonephele acontius</i>	Yes	9	10
Biblidinae	<i>Dynamine arene</i>	No	3	4
Biblidinae	<i>Ectima thecla</i>	Yes	1	1
Biblidinae	<i>Hamadryas amphinome</i>	Yes	18	133
Biblidinae	<i>Hamadryas arinome</i>	Yes	2	2
Biblidinae	<i>Hamadryas februa</i>	Yes	24	227
Biblidinae	<i>Hamadryas feronia</i>	Yes	30	310
Biblidinae	<i>Hamadryas iphthime</i>	No	3	13
Biblidinae	<i>Nessaea obrina</i>	Yes	3	4
Brassolinae	<i>Catoblepia generosa</i>	Yes	1	1
Brassolinae	<i>Eryphanis automedon</i>	Yes	1	1
Brassolinae	<i>Opsiphanes invirae</i>	Yes	2	2
Charaxinae	<i>Archaeoprepona demophon</i>	Yes	3	4
Charaxinae	<i>Archaeoprepona demophon</i>	Yes	2	2
Charaxinae	<i>Fountainea ryphaea</i>	Yes	3	3
Charaxinae	<i>Hypna clytemnestra</i>	Yes	1	1
Charaxinae	<i>Memphis acidalia</i>	Yes	5	6
Charaxinae	<i>Memphis moruus</i>	Yes	1	1
Charaxinae	<i>Memphis oenomais</i>	Yes	1	1
Charaxinae	<i>Memphis vicinia</i>	No	3	5
Charaxinae	<i>Memphis xenocles</i>	No	1	1
Charaxinae	<i>Siderone galanthis</i>	Yes	1	2
Charaxinae	<i>Zaretis itys</i>	Yes	2	2
Coliadinae	<i>Eurema albula</i>	No	1	2
Coliadinae	<i>Eurema nise</i>	No	1	1
Coliadinae	<i>Phoebis sennae</i>	No	1	1
Ithomiinae	<i>Hypothyris euclea</i>	No	1	1
Limenitidinae	<i>Adelpha pollina</i>	No	1	2
Morphinae	<i>Morpho helenor</i>	Yes	1	1
Nymphalinae	<i>Anartia jatrophae</i>	No	1	1
Nymphalinae	<i>Colobura dirce</i>	Yes	18	97

Appendix continued

Subfamily	Species	Present in primary forest	Occupancy (out of 30 sites)	Abundance
Nymphalinae	<i>Historis odius</i>	Yes	17	43
Satyrinae	<i>Caenopythchia bouletti</i>	Yes	1	1
Satyrinae	<i>Caeruleptychia scopulata</i>	No	1	1
Satyrinae	<i>Chloreuptychia agatha</i>	Yes	1	1
Satyrinae	<i>Cissia myncea</i>	Yes	5	8
Satyrinae	<i>Cissia penelope</i>	Yes	20	423
Satyrinae	<i>Cissia terrestris</i>	No	9	67
Satyrinae	<i>Erichthodes erichtho</i>	No	1	1
Satyrinae	<i>Hermeuptychia hermes</i>	Yes	17	91
Satyrinae	<i>Magneuptychia antonoe</i>	Yes	1	1
Satyrinae	<i>Magneuptychia libye</i>	Yes	14	36
Satyrinae	<i>Magneuptychia newtoni</i>	No	10	11
Satyrinae	<i>Magneuptychia tricolor</i>	Yes	1	1
Satyrinae	<i>Pareuptychia binocula</i>	Yes	1	1
Satyrinae	<i>Pareuptychia hesionides</i>	Yes	3	5
Satyrinae	<i>Paryphthimoides argulus</i>	No	12	288
Satyrinae	<i>Paryphthimoides numeria</i>	No	8	14
Satyrinae	<i>Paryphthimoides vestigiata</i>	Yes	10	102
Satyrinae	<i>Taygetis cleopatra</i>	Yes	3	11
Satyrinae	<i>Taygetis echo</i>	Yes	2	4
Satyrinae	<i>Taygetis kerea</i>	Yes	3	4
Satyrinae	<i>Taygetis laches</i>	Yes	21	140
Satyrinae	<i>Taygetis virgilia</i>	Yes	8	29
Satyrinae	<i>Yphthimoides renata</i>	Yes	18	92
Total				2200

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