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ORIGINAL PAPER

The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil

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Abstract The Amazon region represents more than a half of all tropical forests in the world, and has been threatened by many anthropogenic activities, including several kinds of timber harvesting. The reduced-impact logging (RIL) is considered a less destructive method of timber harvesting, but there is a general lack of information about the effects on Amazonian invertebrates, including butterflies. We investigated the effect of RIL on fruit-feeding butterflies by comparing canopy and understory between an area under RIL and a control area without RIL. The canopy fauna is different and significantly richer than the understory fauna, showing that sampling only the lower strata underestimates the diversity of fruit-feeding butterflies. The effects of RIL were mainly detected in the understory butterfly assemblage, as significant differences were observed in species composition within this stratum. Effects of the RIL regime, which include tree cutting, skid trails and roads openings, are stronger in the understory than in the canopy, explaining the reported differences. Despite the detectable effects of RIL on the composition of fruit-feeding butterfly assemblages, the overall diversity was not affected. A similar pattern has been detected in many other groups, indicating that a noticeable part of the diversity of many taxa could be preserved in areas under RIL management. Therefore, in view of the problems of creating protected areas in the Amazon, RIL is a good alternative to preserve fruit-feeding butterflies and surely many other taxa, and it might be a desirable economic alternative for the region.

Keywords Canopy · Ecological indicators · Forest degradation · Nymphalidae · Tropical · Understory

Introduction

The Amazon region represents 60% of all tropical forest areas in the world (Lovejoy 1999). A total of 6,451 km^2 was cleared, and additional 13,301 km^2 suffered logging activities of different intensities from August 2009 to August 2010 (INPE 2010; Sist 2000).

The major causes of forest degradation in the Amazon are the understory fires and timber extraction (INPE 2010). Timber extraction can be done, without clear cutting, in two basically different ways: (1) conventional logging, where most individuals of the species of high economic value are removed, without previous planning, and (2) reduced-impact logging (RIL) were only few individuals are removed per hectare using techniques to reduce the impact of timber extraction in the remaining vegetation (Sist 2000; Laurance et al. 2005).

Most of the logging activities in the tropics are conducted by untrained and unsupervised crews without previous planning, and this implies in several impacts in the remaining vegetation and high levels of injuries to the workers (Putz 2008). Traditional selective logging affects several different groups of organisms (Johns 1985; Azevedo-Ramos et al. 2006; DeVries et al. 1997; Devy and Davidar 2001; Dumbrell and Hill 2005) and heavily changes the structure of the remaining forest (Gerwing 2002). This also causes changes in the physical environment, including soil compaction, and light incidence in the

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understory (Rab 1994; Whitman et al. 1997), leading to an increase in erosion and sediment deposition in the soil (Megahan and Kidd 1972). Additionally, the process can affect the forest streams by increasing temperature and causing silting (Holtby 1988). Other detected effect of conventional selective logging is the increased chances of forest fires due to the increased amounts of coarse woody debris and dryness caused by the greatly reduced canopy cover (Gerwing 2002). All the above factors can change the forest structure (Johns et al. 1996; Aström et al. 2005), the recruitment rates of forest trees, the seedling survival (Whitman et al. 1997) and gene flow among tree populations (Murawski et al. 1994).

The RIL is an alternative to conventional timber harvest that aim to reduce the risks to the workers and the environmental impacts in the stand vegetation. The RIL can be defined as an intensively planned and carefully controlled timber harvesting conducted by trained workers in ways that minimize the deleterious impacts of logging (Putz and Pinard 1993). In Brazil these practice involves a series of recommendations of how to plan and execute the timber extraction avoiding unnecessary damage to non-extracted trees, and monitoring the forest after timber harvest (Sabogal et al. 2000). Those recommendations results in less skid trails opened, the extraction of a controlled number of individuals and wood volume (up to 40 m^3/ha), a minimal recovery time (20–30 years) between each harvest, and several other activities aiming to reduce the environmental damage caused by logging activities (Sabogal et al. 2000).

Despite all benefits of RIL in Amazon, previous studies have demonstrated that this activity can affect some groups of animals (Castro-Arellano et al. 2007; Dias et al. 2010; Felton et al. 2008). However those studies often target vertebrates species with few exceptions (e.g. Azevedo-Ramos et al. 2006), and little attention has been given to insect communities. Considering that insects comprising 77% of knew animal species on earth (Grimaldi and Engel 2005) it is important to know how RIL affect species in this group.

Among insects, butterflies can be considered one of the best groups to study RIL effects. Butterflies combine a series of characteristics such as relatively large size, high conspicuousness, ease of sampling and a relatively well-known taxonomy (Brown 1991, 1992; DeVries et al. 1997; Veddeler et al. 2005). This combination of factors in such a well-known group of insects suggests an great potential for their use as ecological models for conservation studies of species and habitats (Brown 1991; New 1991; Steffan-Dewenter and Tscharntke 1997; Brown and Freitas 2000; Schulze et al. 2001; Barlow et al. 2007a; Ghazoul 2002). Adult butterflies are normally divided into two major guilds: nectar-feeding and fruit-feeding (DeVries 1987). Fruit-feeding butterflies gain most of their nutritional requirements from rotting fruits, plant sap and decaying material, and they are represented mainly by Nymphalidae subfamilies Satyrinae, Biblidinae, Charaxinae and the tribe Coeini (Nymphalinae) (Wahlberg et al. 2009), comprising 50–75% of all neotropical Nymphalidae (Brown 2005). Species in this guild can be easily sampled with traps baited with rotting fruits, which allow simultaneous sampling in several areas with similar effort. Additionally, local richness and diversity in this group are correlated with total butterfly and bird diversity (Brown and Freitas 2000; Schulze et al. 2001; Horner-Devine et al. 2003), and they are good predictors of the community responses of several arthropod groups, vertebrates, trees and lianas (Gardner et al. 2007; Barlow et al. 2007b).

Several studies have shown that logging activities can affect the richness, diversity, composition, and vertical stratification of the fruit-feeding butterflies, but there is still no consensus about this effects (Koh 2007; Dumbrell and Hill 2005). Additionally, most of the published studies took place in tropical Asia, West Amazonia and Central America (DeVries et al. 1997; Devy and Davidar 2001; Lewis 2001; Dumbrell and Hill 2005), and only one of them was conducted in an area under of experimental RIL regime (Lewis 2001). The present paper is the first one conducted in an area under a commercial regime of RIL, to test the effects of RIL on butterflies, and the first to study effects of logging sensu lato in fruit-feeding butterflies in the Brazilian Amazon.

We aimed to test whether fruit-feeding butterfly assemblages differ among areas with and without RIL regimes by answering two main questions:

1. Are there differences in the community parameters (diversity, abundance and species composition) of fruit-feeding butterfly assemblages between the RIL and the unlogged areas?
2. Does the RIL regime affect the vertical stratification of fruit-feeding butterflies?

Materials and methods

Study site

The study site is located in the Amazon River Basin, Itacoatiara Municipality, Amazon State, Brazil, and is property of the “Precious Woods Amazon” (centred in 2°53′39″ S and 58°42′58″ W) (Fig. 1a). The altitude is ca. 18 m above sea level, and the climate is hot, rainy and humid, without dry season, with mean temperature of 26°C and average annual rainfall of about 2,250 mm (MME 1983). In the present study, we compared the fruit-feeding butterfly assemblage of an area of primary forest with a 3-year-old RIL (8,100 ha) area (hereafter called unlogged forest and RIL forest

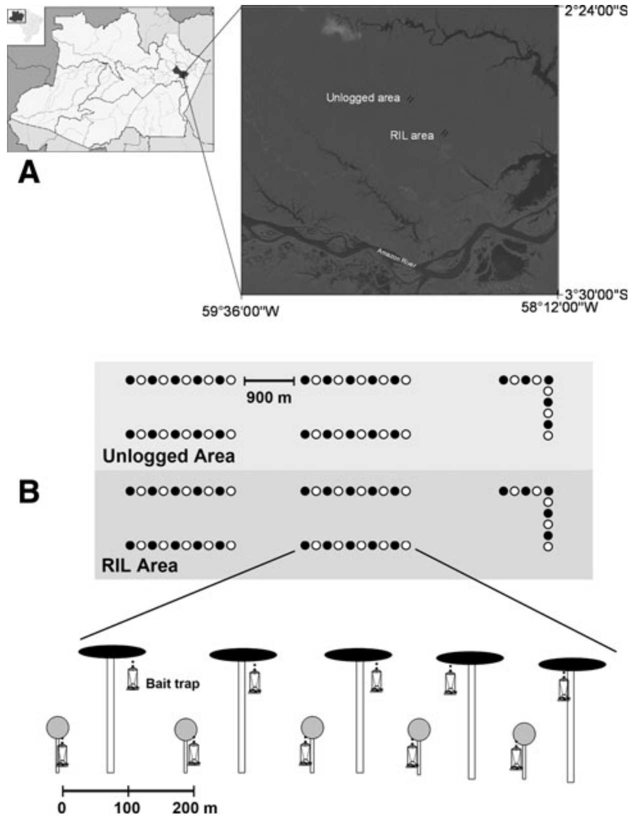

Fig. 1 **a** Localization of the study area, Itacoatiara Municipality, Amazon State, Brazil (2°53′39″ S and 58°42′58″ W); the *two parallel black lines* represent the positions of the sampling transects (as follows). **b** Layout of the sampling design. The *lines of small circles* represent the ten sampling unities of 10 traps each in both areas (RIL and unlogged; see text for further details). *Solid circles* represent understory traps; *open circles* represent canopy traps

respectively). The two areas are ca. 25 km apart, and are within a continuum of forest of ca. 6 million km^2. The main differences between the forest structure in both areas is that the canopy cover (measured 0.4 m above the ground) is greater in the unlogged forest, probably due to an increase of understory plants in the RIL forest, and the trees had a wider basal area and a taller height in unlogged forest. Another noticeable difference is the number of seedlings and saplings, which are significantly bigger in the logged forest (D. B. R. and L. C.Garcia, unpublished data).

Management system

The company owns several areas of wood extraction based on the Celos Management System described by De Graaf and Poels (1990) and has an unlogged forest of 7,500 ha with no extraction. The low-impact standard operation is based on an inventory that selects trees with more than 50 cm DBH (Diameter at Breast Height) from among 70 valuable species. A system of roads and skill trails is implemented, and trees are cut using directional felling practices. Around 15–20 m^3 of roundwood were extracted per hectare (with a maximum of six trees extracted per hectare) during the first rotation cycle, which lasted 30 years. The cuted trees are then locally processed providing employment opportunities and other services to the local community, and the products are sold to the US, Europe and Asia.

This study was conducted in an upland forest, which is commonly more open than other Amazon vegetations, with greater spacing among trees and not subject to flooding. There are many rare plant species and no clear dominance of any single species (Rizzini et al. 1988).

Butterfly sampling

The sampling protocol was adapted from Ribeiro et al. (2008, 2010). Fifty traps were placed in each area in two heights: 25 in the understory (1.5 m above the ground) and 25 in the canopy (ca. 20 m above the ground inside the tree crowns). The canopy traps were installed using a catapult to get a line over a limb then hauled up to the appropriate height. Traps were installed in groups of ten in alternating heights to avoid the interference of canopy traps in the understory traps (see Fig. 1b for a detailed description of the sampling layout). Based on previous studies (Pinheiro and Ortiz 1992; Hill et al. 2001; Hamer et al. 2003), all traps were disposed at a distance of 100 m from each other to reduce the interference among traps. Additionally, Ribeiro et al. (2012) showed that fruit-feeding butterfly assemblages are significantly affected by the vegetation structure in the nearest 100–200 m radius around each trap. The groups of 10 traps were disposed 900 m apart from each other. The traps were disposed in a 10 km "U" transect, ignoring topography, and comprising a representative range of variation in forest structure within each habitat (Fig. 1b). The butterflies were sampled monthly from July to November 2007 during the dry season, to maximize butterfly sampling (Ebert 1969; Checa et al. 2009; K. S. Brown personal communication) traps remained open for 14 days, and were visited at 48 h intervals (adapted from Ribeiro et al. 2008, 2010) totaling 4,800 trap days. During each visit the bait was replaced, and all captured individuals were collected.

Data analysis

To verify whether RIL management reduce/increase the number of species in the butterfly assemblage we calculate indices of diversity, Shannon (H′), Simpson (1 − D) and Fisher's Alpha (α), for each management system and height: unlogged understory (UU), unlogged canopy (UC), RIL understory (RU), and RIL canopy (RU).

Rarefaction curves were produced to eliminate the influence of sample size when comparing richness. These curves calculate the expected species richness with the use of random sub-samples of individuals (Gotelli and Graves 1996), making it possible to compare the richness among different sized samples.

We used Fisher's Alpha as the diversity index (Fisher et al. 1943) because it is a robust, trustworthy index, little affected by the sample size and broadly used in biodiversity studies (Magurran 2004). We also used Simpson (1-D) and Shannon (H′) indices for comparative purposes with other studies. The diversity indices (Fisher's Alpha, Shannon and Simpson) were compared with the bootstrap procedure, with confidence intervals of the indices calculated and compared using the software PAST® (Hammer et al. 2001). The critical values of α were corrected with the FDR procedure (False Discovery Rate), in order to minimize the incidence of type I errors (i.e., to reject the null hypothesis when it is true). This kind of correction (FDR) is more powerful than FWER (Family Wise Error Rate) procedures (e.g. Bonferroni, Hochberg), and, therefore, it is more appropriate for multiple comparisons (Benjamini and Hochberg 1995).

The richness estimates (Chao2 and Jacknife 1) were calculated with the software Estimates 7.5 (Colwell 2005) to evaluate the representation of each sample according to the total community. We choose these estimators because they provides the least biased estimates of species richness for small numbers of samples, and allow detectability to vary across species (Burnham and Overton 1978; Colwell and Coddington 1994).

To compare whether was feasible to detect differences between butterfly assemblages using high taxonomic levels we calculate the differences in butterfly abundance and subfamilies proportion in each combination of management and height (UU, UC, RU, RC). These differences were tested with analyses of variance (ANOVA). For comparative purposes with other studies we followed (Freitas and Brown 2004) division of subfamilies modified after (Wahlberg et al. 2009) (Biblidinae, Charaxinae, Satyrinae: tribes Morphini, Brassolini and Satyrini, and the Nymphalinae: tribe Coeini). Two additional analyses were performed to verify the difference among butterfly assemblage composition, Cluster analysis and Principal Coordinates Analyses. A cluster analysis using Bray–Curtis distance was used to verify if traps were grouped by management system and/or heights (UU, UC, RU, RC). To verify the influence of the composition of fruit-feeding butterflies in the distribution of the samples in the ordination space, we performed Principal Coordinates Analyses (PCO). In this analysis, we used the Morisita–Horn similarity index as it measures the beta diversity independent of the alpha (Jost 2007). The PCO was performed with understory and canopy samples separately, to test the effect of RIL in each height. Anosim analyses were conducted to compare assemblage composition between RIL and Unlogged areas in each trapping height. We used a transformed ($\log_{10}$ x + 1) matrix to avoid the over-influence of abundance in the results. PCO, Anosim and cluster analyses were carried with Fitopac 2.0 (Shepherd 2009). Additionally, we perform an Mann–Whitney test between the abundance of species with more than 14 individuals and noticeable differences between RIL and Unlogged areas.

Additive partitioning of diversity was also done to test how diversity is distributed vertically (understory and canopy) and horizontally (among sampling points). The analyses were performed with Partition@ 3.0 Software (Veech and Crist 2009). Additive richness and Shannon index were used as diversity measures; using the trap average diversity as α diversity, the β diversity was measured in tree levels: $\beta1$—among traps in the same group and height, $\beta2$—among groups in the same height, $\beta3$—among height in the same treatment. We used individual-based procedure to calculate the α and $\beta1$; for the other measurements we used a sample-based procedure. We weighted the partitioning by abundance and used the pooled data of all sampling months aggregated by trap, group, height and treatment resulting in hierarchy of 100, 20 and 4 units. The randomization process was repeated 1,000 times to obtain null distributions of the beta diversity estimates at each hierarchical level (Crist et al. 2003).

Results

We collected 1,091 individuals of 68 species belonging to all fruit-feeding Nymphalidae clades (Biblidinae, Charaxinae, Nymphalinae: Coeini, Satyrinae: Morphini, Brassolini and Satyrini), with 22 species collected only in the canopy, 21 only in the understory, and 25 in both strata (Appendix). The richness and diversity (H′, 1 − D, Fisher's α) were significantly different between layers but not between management systems (Table 1), with the canopy richer than the understory (Fig. 2). The richness estimators showed that we sampled about 67–77% of the total richness, which can be considered a good representation of the actual assemblage.

The abundance of fruit-feeding butterflies was significantly different between layers (F = 15.59; $p = 0.00015$) and management systems (F = 52.74; $p < 0.0001$) and there was no interaction between factors (F = 0.500; $p = 0.48$). The proportion of subfamilies was significantly different between heights (F = 45.75; $p < 0.0001$) and marginally significantly between management systems (F = 9.49; $p = 0.056$).

Table 1 Diversity, richness and abundance of the fruit-feeding butterflies in Central Amazon, Brazil

Management	Richness	Abundance	Diversity			Richness estimators			
			H'	$(1 - D)$	α	Chao 1	SD	Jack 2	SD
RIL									
Undestory	40	440	2.71	0.886	10.69[a]	45.6	4.8	53.6	2.7
Canopy	41	204	3.35	0.956	15.45b	46.9	5.6	57.4	3.7
Total	62	644	3.28	0.943	16.91	79.1	11.5	84.6	2.4
Unlogged									
Undestory	34	291	2.58	0.888	9.98a	58.0	16.4	59.7	3.7
Canopy	38	156	3.31	0.954	16b	45.9	6.3	52.5	2.2
Total	54	447	3.31	0.943	15.07	71.5	12.1	78.4	2.2
Total	68	1091	3.38	0.943	16.06	89.0	14.7	93.7	1.0

The diversity indices represented in the table are: Fisher's Alpha—α; Shannon—H' and Simpson—$(1 - D)$. Different letters in front of diversity measures indicate the significantly differences ($p < 0.01$) in bootstrap (10,000 runs) test

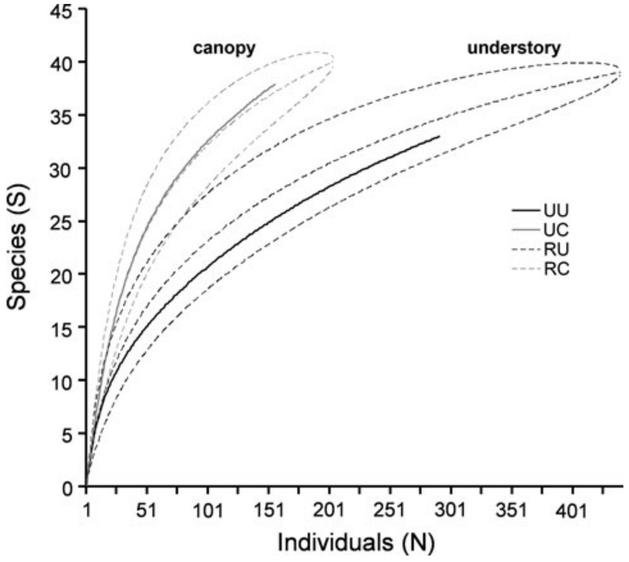

Fig. 2 Rarefaction analyses of the fruit-feeding butterflies assemblage in Central Amazon, Brazil. RU, samples in Understory of RIL management areas; RC, samples in canopy of RIL management areas; UU, samples in understory of unlogged areas; UC, samples in canopy of unlogged areas

The samples were grouped by height in cluster analysis (UPGMA/Bray-Curtis) but not by management system (Fig. 3). In the Principal Coordinates Analyses (PCO) we found segregation by management system in the understory samples ($R = 0.241$; $p < 0.0001$) (Fig. 4b) but not in the canopy samples ($R = 0.042$; $p = 0.08$) (Fig. 4a). *Catonephele acontius* ($U = 235.5$; $p = 0.03$) and *Hamadryas arinome* ($U = 237.5$; $p = 0.01$) had significant differences in the abundance in the canopy between RIL and Unlogged areas. The main species leading to the pattern found in understory samples were *C. acontius*, *H. arinome*, *Memphis vicinia* and *Tigridia acesta* that increased their abundance in the RIL, while *Catoblepia xanthus* and *Morpho helenor* were less abundant in the RIL area (Appendix). Despite the increase in abundance, significant differences between the understory abundances in RIL and unlogged areas were found just in *C. acontius* ($U = 57.5$; $p < 0.001$) and *M. vicinia* ($U = 209.5$; $p = 0.004$).

The additive partitioning of the butterfly diversity indicated that the additive richness and diversity (Shannon H') in each trap (α) and among traps in the same group and layer ($\beta 1$) are not higher than that expected by chance (Table 2). The richness among groups in the same layer ($\beta 2$) was not different from that expected by chance, but the Shannon diversity was higher than that expected by chance (Table 2). The diversity (Richness and Shannon Index) between heights in the same management system was significantly higher than that expected by chance ($\beta 3$) (Table 2).

Discussion

Methodological implications

Fruit-feeding butterflies have often been used in ecological studies (Horner-Devine et al. 2003; Veddeler et al. 2005; Ribeiro and Freitas 2010; Barlow et al. 2007b; Shahabuddin and Ponte 2005) and our results could be useful to avoid some methodological caveats.

As found by DeVries et al. (1997) and Devries and Walla (2001) in Ecuador, the effects of RIL in fruit-feeding butterfly assemblages in the present study are much greater in the understory than in the canopy (Fig. 4a, b). This suggests that RIL has a relatively low impact in the canopy structure; on the other hand, the vegetation structure in the understory changes very much, probably because of the trails opened for timber removal. If the objective is to monitor logging effects in tropical forests, we suggest that

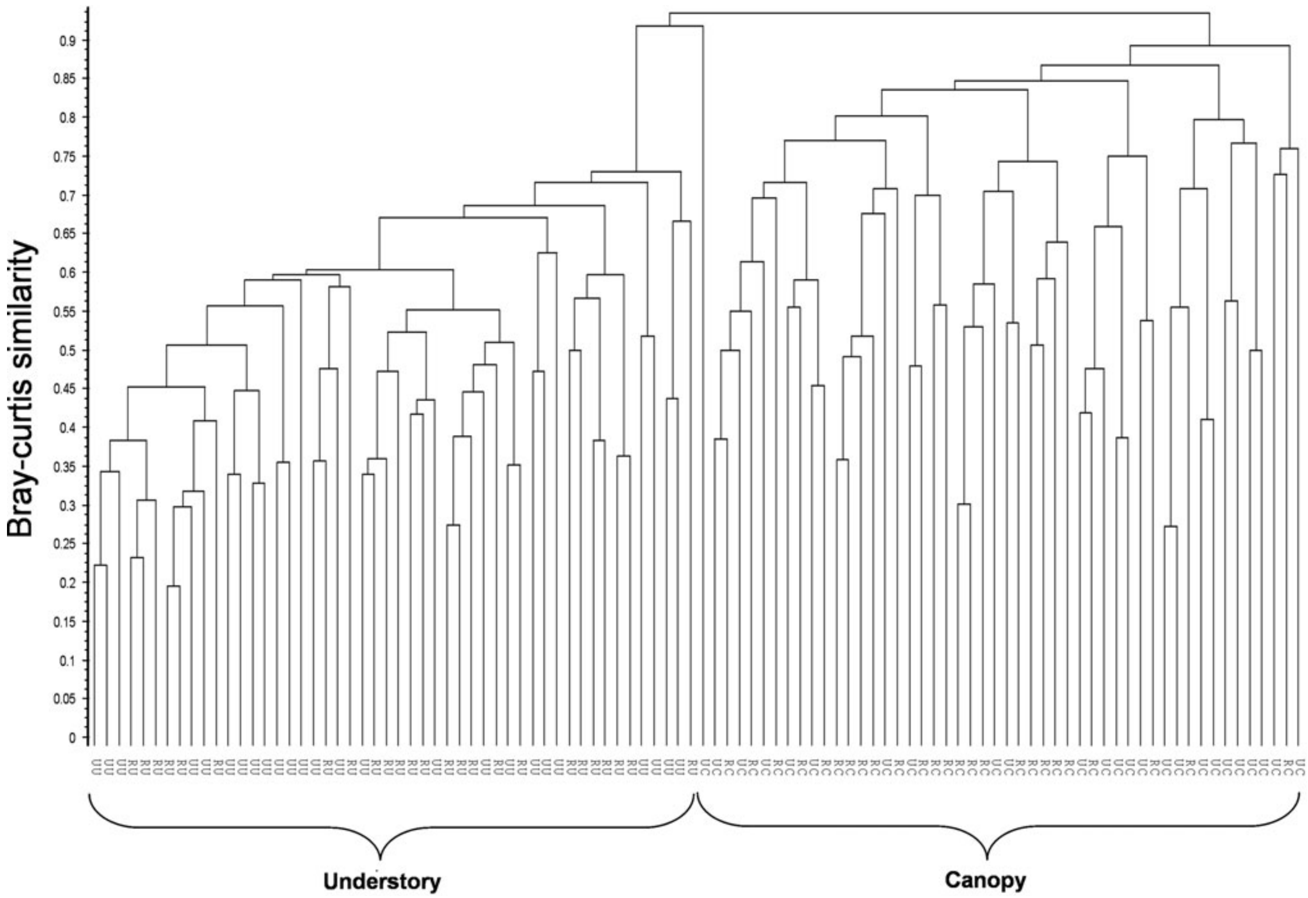

Fig. 3 Cluster analyses of the fruit-feeding butterflies assemblage in Central Amazon, Brazil. The cluster method used was UPGMA with Bray–Curtis similarity, Cofenetic correlation = 0.8137. RU, samples in understory of RIL management areas; RC, samples in canopy of RIL management areas; UU, samples in understory of unlogged areas; UC, samples in canopy of unlogged areas

sampling only the understory is enough to detect the ecological impacts that affect the forest structure.

Besides that, using the proportion of subfamilies instead of species could be a reasonable solution to overcome limitations in butterfly identification in very rich communities in Neotropical habitats. However, the above procedure can mask some small changes that are detectable when species composition is used. Accordingly, in the present study we found marginally significant differences between managements when using subfamily composition ($F = 9.49$; $p = 0.056$), despite the noticeable difference between species composition (Fig. 4b). The subfamily level has been investigated in other studies with relative success; DeVries et al. (1997) detected great beta diversity in subfamilies among habitats, and Schulze et al. (2001) found differences between forest strata. Therefore, we will recommend the use of subfamily level analyses only if species identification is an impediment.

The canopy assemblage comprised about 31% of the observed richness in our samples (Table 1), being richer (Fig. 1) and more diverse than the understory (Table 1). In the Amazon forest, exclusive canopy species comprised 17% (Barlow et al. 2007b) to 31% (DeVries et al. 1999) of the fruit-feeding butterfly assemblage, showing that sampling this stratum is essential for butterfly inventories in any forest with high canopies. The additive partitioning of butterfly diversity showed that the increment in richness and diversity ($\beta 3$) when canopy traps are included (Table 2) is higher than the expected by the increment in sampling effort, corroborating our previous statement, and also the findings of DeVries et al. (1997, 1999).

The additive partitioning of butterfly diversity demonstrates that the increments in richness in “among traps” in the same group and layer ($\beta 1$) is a consequence of the increase in sampling effort. The butterfly density in the present study (ca. 0.2 butterfly/trap/day) was much smaller than observed by other authors in the Amazon Forest (ca. 0.8 butterfly/trap/day—DeVries and Walla 2001; Barlow et al. 2007b) for this reason we recommend the use of sampling units combining at least 20 traps for each layer and habitat in forests with similar butterfly densities such as the Central Amazon. The present study is the first to decouple canopy and understory traps by placing them 100 m apart from each other. We strongly suggest that

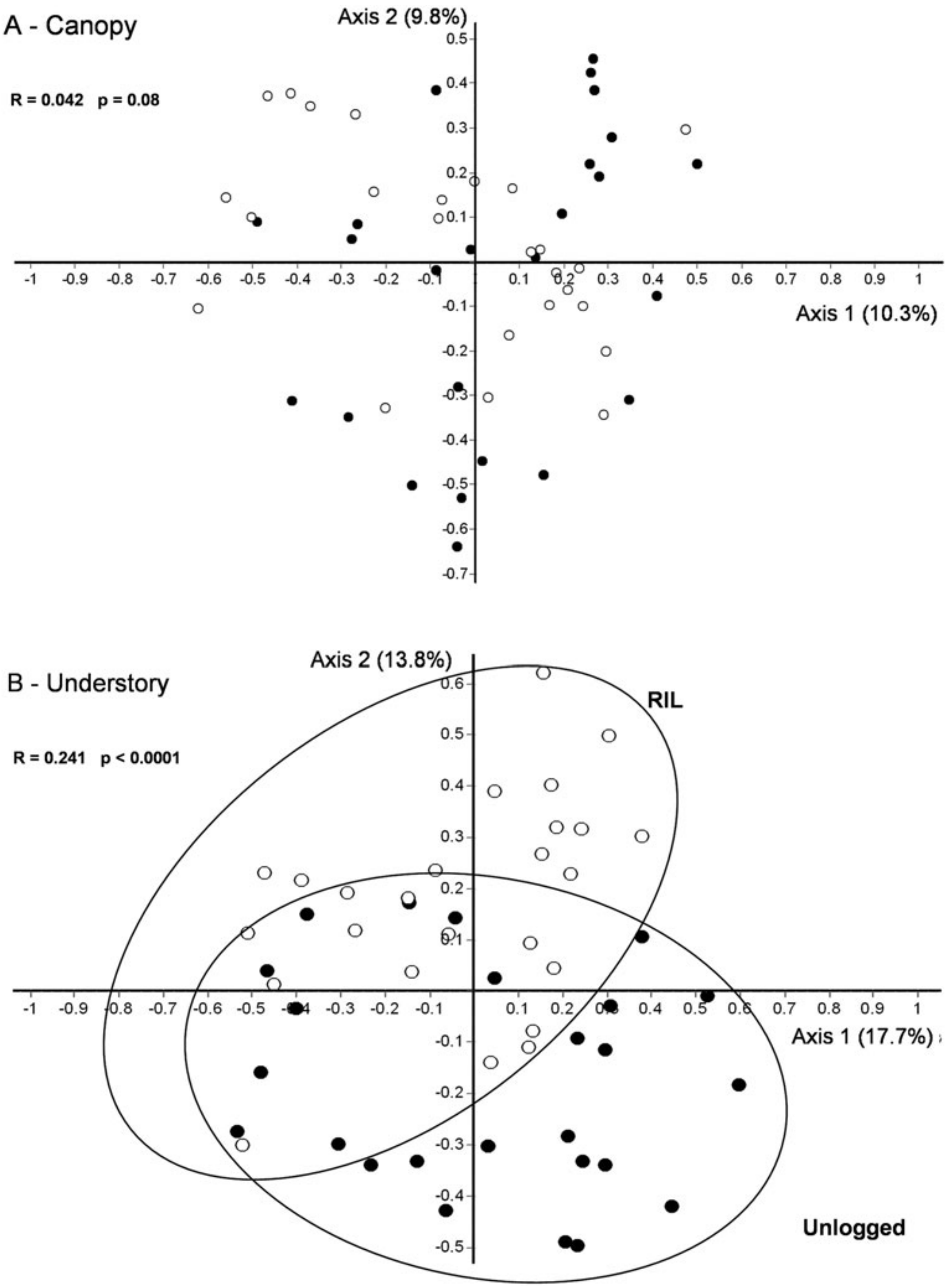

Fig. 4 Principal components analysis of fruit-feeding butterflies in Central Amazon, Brazil. We used Morisita–Horn as similarity measure. The *filled dots* represent samples of unlogged areas and the *empty dots* represent samples in areas under RIL management. **a** Canopy samples, **b** understory samples. The *R* and *p* showed in the plots concern to Anosim analyses performed with Morisita–Horn distance

future studies use this protocol to maintain the independence among sampling points and to avoid the interference of one trap to another, which is especially important in studies comparing different forest layers.

Biological implications

The present study demonstrates that the canopy assemblage is significantly richer and has fewer individuals than the understory, a pattern similar to that found by Schulze et al. (2001) and Dumbrell and Hill (2005) in Malaysia. Barlow et al. (2007b), however, found a lower abundance in the canopy, and no detectable differences in richness, working in Pará (Brazilian Amazon), and DeVries et al. (1999) and DeVries and Walla (2001) found no differences in both richness and abundance in Ecuadorian Amazon. These divergent responses could be attributed to the interference of the understory traps with the canopy traps, as the above studies installed both traps in the same point. We also note that disturbance levels and recovery periods are variable in the above studies. Anyway, the high diversity in the canopy appears to be a common pattern in tropical forests, but we still have no evidence about the reasons that explain such pattern.

Table 2 Spatial partitioning of species diversity of the assemblage of fruit-feeding Nymphalidae in Central Amazon, Brazil

Diversity		Observed	(%)	Expected	(%)	*p*
S[a]						
α	Withtin trap	7.92	11.6	10.4	14.9	NS
$\beta1$	Among traps	11.75	17.3	16.01	23.0	NS
$\beta2$	Among groups	18.63	27.4	18.34	26.4	NS
$\beta3$	Between layers	**20.42**	30.0	**11.4**	16.4	**<0.001**
$\beta4$	Between managements	9.28	13.6	13.45	19.3	
γ	Total	68		69.6		
H′[b]						
α	Withtin trap	6.2	50.7	8.58	59.2	NS
$\beta1$	Among traps	2.02	16.5	2.18	15.0	NS
$\beta2$	Among groups	**1.42**	11.6	**1.41**	9.7	**0.009**
$\beta3$	Between layers	**1.51**	12.3	**1.12**	7.7	**<0.001**
$\beta4$	Between managements	1.09	8.9	1.21	8.3	
γ	Total	12.24		14.5		

Results in bold type indicate that the observed diversity is significantly different from that expected in a random distribution

NS non significant

[a] Additive species richness

[b] Shannon diversity Index

Several studies showed that forest disturbance disrupt the vertical stratification of butterfly assemblages in forests (DeVries 1988; Schulze et al. 2001; Fermon et al. 2005). In the present study, we noticed this process only in *M. vicinia*; this specie was more common in the canopy of unlogged area, and was evenly distributed in both strata of the RIL area (Appendix), showing that this change in vertical stratification could be species dependent.

Thus, detectable effects of RIL were observed only in understory assemblages, which differed between treatments (Fig. 4a), while canopy assemblages maintained the same structure (Fig. 4b). Canopy assemblages are probably more tolerant to high levels of light and temperature and low humidity than understory butterflies, whose assemblages are structured under the forest shade. However, even if RIL does not change significantly the canopy structure, it has a noticeable effect in the forest understory by opening trails for timber removal (D. B. R. and L. C. Garcia, unpublished data), and benefiting some sun-loving species, displacing several typical understory butterfly species. The changes in vegetation structure could also increase the growth of pioneer plant species and decrease the populations of some shadowy plants (Silva et al. 1995), consequently changing the butterfly assemblages that depend on these resources. Other biological aspects such as microhabitat and forest specialization could also determine the final species pool that will persist after the logging (Koh 2007), but these data are still not available for most Neotropical butterfly species. In the present study differences in understory assemblages between RIL and unlogged areas were found mainly due to the increase in Biblidinae and Charaxinae and the decrease of Brassolini and Morphini in the RIL area (Appendix). Our results were similar to the results found by Hamer et al. (2003) in Borneo, showing that logging activities can affect in the same way related tribes and subfamilies of butterflies in tropical forests even in places as far as Borneo and Brazil.

In the present study, we found no differences in both richness and diversity when comparing RIL and unlogged areas (Fig. 2). This shows that the differences found between butterflies assemblages in understory were caused by species replacement and differences in abundance, and not by species extinction. Two species had a significant increase in abundance in RIL area: *C. acontius* and *M. vicinia*. Even though, in these two species, different processes explain the reported results. While in *M. vicinia* this pattern appears to be driven by a change in its behavior (see above), in *C. acontius* it was clearly a result of a real increase in abundance, probably related to the increase in its host-plant availability caused by RIL (the Euphorbiaceae *Alchornea* spp.).

The median term (2–8 years after logging) effects of RIL in assemblages of different groups of animals (ground foraging ants, birds, small mammals, bats and fishes) were similar to those reported in our study, showing that RIL promotes changes in abundance of some species and changes in species composition without, however, changing the overall diversity (Castro-Arellano et al. 2007; Presley et al. 2008; Lambert et al. 2005; Kalif et al. 2001; Wunderle et al. 2006). Changes in diversity were usually associated with other silvicultural treatments (e.g. enrichment strips) that were often absent in RIL areas or higher volumes of timber extraction (more than 80 m^3/ha) (Mason 1996; Davies 2000). The RIL regime proposed to Brazilian Amazon (Sabogal et al. 2000) do not impose intensive silvicultural practices or high volumes of timber extraction.

Obviously, pristine forests are the best way to preserve the biodivsersity in the Amazon (Gibson et al. 2011). Therefore, considering the needs of a growing planet with high requirements of natural resources, the RIL could be considered a good alternative to preserve fruit-feeding butterflies and many other taxa in places where it is not possible to implement protected areas, and is also an economically viable option for local populations.

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Appendix

See Table 3.

Table 3 Occurrence of the fruit-feeding butterflies species in Itacoatiara, Central Amazon, Brazil

Species	Unlogged		RIL		Total
	Understory	Canopy	Understory	Canopy	
Biblidinae					
Callicore excelsior (Hewitson, [1858])	0	2	0	5	7
Callicore pygas (Godart, [1824])	0	4	0	3	7
Catonephele acontius (L., 1771)	24	2	114	10	150
Catonephele numilia (Cramer, 1771)	0	5	1	2	8
Ectima iona Doubleday, [1848]	0	0	1	0	1
Eunica bechina bechina (Hewitson, 1852)	0	0	0	1	1
Eunica orphise (Cramer, 1775)	0	1	0	2	3
Hamadryas arinome (Lucas, 1853*)*	1	0	14	8	23
Myscelia capenas (Hewitson, [1857])	0	0	1	0	1
Nessaea obrinus (L., 1758)	56	1	56	1	114
Temenis laothoe (Cramer, 1777)	0	9	0	7	16
Total	81	24	187	39	331
Charaxinae					
Agrias amydon Hewtison, [1854]	1	0	0	1	2
Agrias claudina (Godart, [1824])	2	10	4	16	32
Agrias narcissus Staundinger, [1885]	1	3	2	1	7
Archaeoprepona amphimachus (Fabricius, 1775)	1	0	1	0	2
Archaeoprepona demophon (L., 1758)	23	2	22	2	49
Archaeoprepona demophoon (Hübner, [1814])	1	4	3	7	15
Archaeoprepona licomedes (Cramer, 1777)	0	0	1	0	1
Archaeoprepona meander (Cramer, 1775)	3	1	1	0	5
Memphis acidalia (Hübner, [1819])	1	3	2	2	8
Memphis basilia (Stoll, 1780)	0	0	0	2	2
Memphis glauce (Felder & Felder, 1862)	0	5	0	9	14
Memphis laertes (Cramer, 1775)	1	2	1	2	6
Memphis leonida (Stoll, 1782)	0	0	0	1	1
Memphis moruus (Fabricius, 1775)	0	1	4	3	8
Memphis oenomais (Boisduval, 1870)	0	3	0	3	6
Memphis phantes (Hopffer, 1874)	1	10	23	16	50
Memphis philumena (Doubleday, [1849])	0	5	0	6	11
Memphis polycarmes (Fabricius, 1775)	0	0	4	8	12
Polygrapha xenocrates (Westwood, 1850)	0	5	0	5	10
Prepona dexamenus Hopffer, 1874	1	5	0	1	7
Prepona eugenes Bates, 1865	0	1	0	0	1
Prepona laertes (Hübner [1811])	1	10	1	7	19
Prepona pheridamas (Cramer, 1777)	10	0	14	0	24
Prepona philipponi Le Moult, 1932	0	2	5	3	10

Table 3 continued

Species	Unlogged		RIL		Total
	Understory	Canopy	Understory	Canopy	
Prepona pseudomphale Le Moult, 1932	0	2	0	6	8
Prepona rothschildi Moult, 1932	0	1	0	0	1
Siderone galanthis (Cramer, 1775)	0	0	0	1	1
Zaretis itys (Cramer, 1777)	4	4	6	8	34
Zaretis isidora (Cramer, 1779)	0	4	0	8	12
Total	51	83	94	118	346
Nymphalinae: Coeini					
Baeotus aeilus (Stoll, 1780)	0	15	2	12	29
Baeotus deucalion (Felder & Felder, 1860)	0	1	0	1	2
Baeotus japetus (Staudinger, [1885])	1	0	0	0	1
Colobura dirce (L., 1758)	0	0	4	0	4
Historis acheronta (Fabricius, 1775)	2	12	0	7	21
Historis odius (Fabricius, 1775)	0	0	0	1	1
Tigridia acesta (L.,1758)	21	1	31	0	53
Total	24	29	37	21	111
Satyrinae: Satyrini					
Cepheuptychia cephus (Fabricius, 1775)	0	0	1	0	1
Chloreuptychia herseis (Godart, [1824])	0	0	4	0	4
Cissia myncea (Cramer, 1780)	0	1	0	0	1
Magneuptychia ca. analis (Godman, 1905)	0	3	0	4	7
Magneuptychia libie (L., 1767)	0	0	0	1	1
Megeuptychia antonoe (Cramer, 1775)	0	6	0	1	7
Pareuptychia lydia (Cramer, 1777)	1	0	0	0	1
Taygetis ca. cleopatra Felder & Felder, 1867	1	0	3	0	4
Taygetis echo (Cramer, 1775)	2	0	3	0	5
Taygetis laches (Fabricius, 1793)	2	0	5	0	7
Taygetis sosis Hopffer, 1874	4	0	2	0	6
Taygetis sp1	3	0	0	0	3
Taygetis sp2	1	0	2	0	3
Total	14	10	20	6	50
Satyrinae: Brassolini					
Bia actorion (L., 1763)	51	1	49	0	101
Catoblepia berecynthia (Cramer, 1777)	12	0	17	0	29
Catoblepia xanthus (L., 1758)	42	1	25	2	70
Opsiphanes cassiae (L., 1758)	0	0	1	0	1
Opsiphanes invirae (Hübner, [1808])	3	8	3	18	32
Opsiphanes quiteria (Stoll, 1780)	1	0	2	0	3
Selenophanes cassiope (Cramer, 1775)	1	0	2	0	3
Total	110	10	99	20	239
Satyrinae: Morphiini					
Morpho helenor (Cramer, 1776)	11	0	3	0	14
Total abundance	291	156	440	204	1,091

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