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Effect of Tree-Fall Gaps on Fruit-Feeding Nymphalid Butterfly Assemblages in a Peruvian Rain Forest

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ABSTRACT

One of the main natural disturbances that affects the structure of rain forests are tree falls, frequently resulting in gaps. Treefall gaps can bring drastic changes in environmental conditions compared to the undisturbed understory. We investigated the effect of treefall gaps on fruit-feeding butterfly (Nymphalidae) species assemblages in an undisturbed lowland rain forest in southeastern Peru. We used fruit-baited traps suspended 2 m above ground in 15 treefall gaps ranging in area from 100 to 1000 m² and in adjacent undisturbed understory. Our data support the hypothesis that treefall gap and understory habitats are utilized by different butterfly species assemblages. There were morphological differences between gap and understory species, where the understory species had a larger wing area to thoracic volume. Vegetation structure and composition were important factors affecting the butterfly assemblages. Most of the butterfly species showed an avoidance of vines and a strong association with the presence of trees and shrubs in gaps. There were also differences among gap assemblages that increased with gap size. Some of the species that were associated with gaps have been considered as canopy species. Other gap species in the present study, however, are known to feed on fruits and/or use host plants mainly, or only, occurring in gaps, implicating that the gap assemblage is a mix of canopy species and those unique to gaps. This indicates that, in an undisturbed Amazon forest, treefall gaps may contribute to maintain species diversity by creating a mosaic of specific habitats and resources that favors different butterfly assemblages.

RESUMO

Una de las principales perturbaciones naturales que afectan a la estructura de los bosques es la caída de árboles y la creación de claros. Estos nuevos espacios pueden conllevar cambios

drásticos en las condiciones ambientales de los claros en comparación con el sotobosque original. En nuestro estudio investigamos el efecto de la caída de árboles en la diversidad de especies de mariposas frutívoras (Nymphalidae) en un bosque tropical no perturbado de tierras bajas en el sureste de Perú. Utilizamos trampas con cebo (fruta) suspendidas a 2 metros de altura en 15 claros producidos por la caída de árboles con áreas variables desde 100 a 1.000 m² y en áreas adyacentes del bosque no perturbado. Nuestros resultados concuerdan con la hipótesis de que los claros son utilizados por distintos ensambles de mariposas. Encontramos diferencias morfológicas entre especies de claro y especies de sotobosque, las especies de sotobosque tenían una mayor área alar en relación con su volumen torácico. La estructura y la composición de la vegetación son factores importantes para los ensambles de mariposas. La mayoría de las especies de mariposas evitaban las lianas y mostraban una fuerte asociación con la presencia de árboles y arbustos en los claros. También se observaron diferencias en los ensambles al aumentar el área de los claros. Algunas de las especies asociadas a los claros son consideradas especies del dosel. Sin embargo, otras especies de claros identificadas en nuestro estudio se alimentan de fruta y/o utilizan plantas que de manera preferencial o exclusiva se localizan en claros. Esto implica que el ensamble de claro es una mezcla de especies del dosel y de especies exclusivas de claros. En consecuencia, en un bosque amazónico no perturbado, claros en el bosque causados por la caída natural de árboles puede contribuir a mantener la diversidad de las especies mediante la creación de un mosaico de hábitats específicos y recursos que favorecen diferentes ensambles de mariposas.

Key words: Amazonia; gap dynamics; intermediate disturbances; Lepidoptera; Manu National Park; Neotropics; vine.

THE PRINCIPAL NATURAL DISTURBANCE AFFECTING THE STRUCTURE OF RAIN FORESTS ARE TREE FALLS that create gaps within which succession is triggered by increased light reaching the understory (Connell 1978, Whitmore 1978). Gap size can affect the environmental conditions and thereby the resulting plant community composition (Molino & Sabatier 2001, Schnitzer & Carson 2001, Pearson *et al.* 2003). A consequence of tree falls is that the tropical rain forest can be considered as a mosaic of micro-successional patches, with few areas having a species composition near equilibrium (Terborgh 1992). This mosaic has been suggested as one of the most important factors that may maintain high species diversity in tropical rain forests.

Studies on the effect of treefall gaps on animals include birds (Levey 1988) and mammals (Beck *et al.* 2004, Beck 2008). Insects have received less attention (Richard & Windsor 2007), but include ants (Feener & Schupp 1998), day-flying insects (Shelly 1988, Richard & Windsor 2007), and butterflies (Hill *et al.* 2001). A number of studies have compared butterfly assemblages in unlogged forests with forest gaps created by selective logging (Willott *et al.* 2000, Hill & Hamer 2004, Hamer *et al.* 2003, Fermon *et al.* 2005, Cleary *et al.* 2009). Forest gaps created by selective logging differ from natural gaps in that they are more frequent and larger in size (Cleary *et al.* 2009) and so the response of butterflies to logging gaps might not be directly applicable to natural treefall gaps. The effect of natural treefall gaps on butterfly assemblages has been studied in Asian rain forests (Hill *et al.* 2001) but rarely elsewhere.

Here, we compared the species assemblages of Neotropical Nymphalidae found in naturally occurring treefall gaps with paired undisturbed understory sites. We hypothesized that different species assemblages would occur in treefall gaps compared to the undisturbed understory and that the differences would increase with increasing gap size. Furthermore, we

quantified the effect of sun exposure, vegetation structure, and the number of flowering and fruiting plants on the butterfly assemblages between gap and understory habitats.

METHODS

STUDY AREA.—The study was conducted in southeastern Peru, at the Cocha Cashu Biological Station (EBCC) located within the Manu National Park (11°51'23"S 71°43'17"W). With over two million hectare, Manu is one of few remaining pristine regions with an undisturbed but diverse biota. The average annual rainfall is about 2300 mm and a mean annual temperature of around 24°C. EBCC encompasses over 16 km² of lowland rain forest, served by around 60 km of trails.

SAMPLING DESIGN AND MEASUREMENT OF VARIABLES.—We randomly selected 15 treefall gaps, 5–10 yr old, ranging in area from approximately 100 m² to 1000 m². Gap areas were estimated following Brokaw's (1982) method. To reduce potential spatial autocorrelation, all gaps were separated by at least 100 m (the maximum distance was over 3 km). For each treefall gap one paired undisturbed understory control site was chosen by selecting a random compass direction and distance (between 50 m to 200 m) from the center of each gap (Fig. S1). If a control site overlapped with a treefall gap, a new random direction was chosen.

We used an incident light meter (Mastech, LX 1010B digital lux meter) to quantify the amount of incoming sunlight in gaps and understory controls. During days without cloud cover, we measured the sunlight at five locations (three along the length and two along the width) within each habitat, between 1100 to 1400 h and the mean sunlight were calculated and used in subsequent analyses.

For each gap and their understory control we randomly selected ten 1 m² plots and recorded the number, height, and diameter of all vines, herbaceous, and woody plants. In addition, we weekly quantified the number of flowering and fruiting plants in ten randomly selected 1 m² plots within all gaps and understories. All plants were identified to family level.

BUTTERFLY TRAPPING.—Butterflies were caught in traps consisting of a 65 cm long cylinder of black nylon mesh with a diameter of 30 cm (DeVries 1987; Sutherland 2006). A 35 cm plastic plate was attached 3 cm below the cylinder and used for baiting. Because gaps were elliptic in shape, two traps were placed equally spaced along the major axis, at one third and two thirds of its length. Thus a total of 60 traps, two traps within each treefall gap and two in understory controls were used. The traps were attached to branches, approximately 2 m above the ground level. The trapping period started at the beginning of July and ended in October 2009, covering 13 weeks, with five consecutive trapping days per week resulting in a total of 1950 trap days.

Each trap was baited with one ripe banana and some drops of vanilla extract. The bait was enclosed within a metal mesh to reduce consumption by other species while still allowing free access for the butterfly's proboscis. Each trap was re-baited every second day, and the old bait was left in the trap to ensure a mixture of ripe to over-ripe bait. All captured butterflies were photographed and individually marked by writing a number on the wing. Individuals were identified to species, following the nomenclature and classification of Lamas (2004).

Photographs and voucher specimens were also sent to specialists for identification and species verifications. Of a total of 1531 trapped individuals, 2.7 percent remained unidentified (primarily because they either escaped during handling, or had damaged wings) and were excluded from statistical analyses. Morphology on all captured butterflies was measured: body length, forewing

breadth (minimum distance between tornus and costa) and length, abdomen width and length, thorax width and length, all accurate to 1 mm. Thorax volume was calculated as $\text{length} \times \text{width}^2$. The distribution for each species was estimated in four classes from widespread in the Neotropical region to restricted to a single or a few countries based on Neild (1996, 2008).

STATISTICAL ANALYSES.—Species accumulation curves based on gap and understory traps were compiled using EstimateS v. 7.51 (Colwell 2011) and the MaoTau index (the number of species observed) per habitat. Species accumulation curves were also calculated by weeks to estimate potential effects of seasonality. Differences in species number and number of individuals (square-root transformed) was assessed in a mixed-model ANOVA using STATISTICA 12 (Statsoft Inc.), after merging data from the two traps per gap and corresponding understory. Hence, each gap contributed one data point, and gap/understory pair identity was used as a random factor.

Differences in species assemblages between gap and understory habitats, among gaps and individual species associations to environmental variables and habitats were analyzed by ordination using the CANOCO 4.5 software and Principal Component Analysis (PCA) (ter Braak & Smilauer 2002). The first PCA compared the butterfly species assemblages between gap and understory habitats and were used to display the individual species associations with vegetation structure (density, height, and diameter of vines, herbaceous and woody plants), number of flowering and fruiting plants from different families and light availability. All species data were transformed ($\log_{10}(x+1)$) in order to minimize the impact of a few very abundant species. Variables describing vegetation structure, flowering and fruiting plants and light were

passive variables in the analysis. The second PCA was conducted using only data from the gaps, involving the same variables but also including gap size as a passive variable.

We hypothesized that the species composition of understory and gap would become increasingly different with increasing gap size. We tested this by calculating χ^2 -distances, within each pair gap-understory pair, based on number of individuals from different species. A linear regression then related χ^2 -distances to gap size. The χ^2 -distances were based on transformed species data and gap sizes were square-root transformed.

To further explore the degree of species' association with gap versus understory habitats, a partial redundancy analysis (pRDA) was conducted. This involved gap/understory as the only (categorical) environmental variable and gap-understory -pair identity as a number of categorical covariables (thereby eliminating some of the spatial variation in the data). The statistical significance of the model was assessed in a Monte Carlo permutation test (9999 permutations). To further interpret the results, data on host plant associations were collected from DeVries (1987), Beccaloni *et al.* (2008) and Robinson *et al.* (2012) to identify possible mechanisms causing the patterns among butterfly assemblages.

RESULTS

BUTTERFLY ASSEMBLAGES IN GAPS AND UNDERSTORY.— A total of 1531 individuals belonging to 82 Nymphalid species were captured (42 individuals could not be identified). Of these, 775 were captured in the understory and 756 in gaps. We trapped significantly ($F_{1,14}=14.42$; $P=0.00196$) higher mean number of species in gaps (10.0 ± 4.1 SD, range 5–22) than in the corresponding understory sites (7.0 ± 2.9 , range 3–13; Fig. S2). There was no difference ($F_{1,14}=0.018$;

$P=0.894$), however, in mean number of individuals in the gaps (26.4 ± 13.3 , range 7–65) compared to the understory (26.9 ± 13.6 , range 11–57). *Panacea prola* was the most occurring species, representing 60.7 percent of the total number of individuals, both in gaps (52.3%) and understory habitats (68.9%). Overall, 71 species were found in gaps and 50 species in the understory (Fig. 1A). The time-based accumulation curves showed a relatively steep increase in number of species with time (Fig. 1B).

In general, there were larger between-site differences of butterfly assemblages in gaps than between assemblages in the understory (Fig. 2). Furthermore, the dissimilarity in butterfly assemblages compared to understory controls increased with gap size (Fig. 3).

PCA analyses across habitats and vegetation variables indicated that species associations were strongest affected by gap and understory habitats as indicated by the position of the centroids (Fig. 4A). If gap versus understory had been the overall dominating factor, their centroids should have been positioned along the first axis. The fact that this was not the case indicated that other factors were also important, most notably vine and herb densities, with arrows pointing perpendicular to gap and understory centroids (Fig. 4B). Light level was also a contributing factor but, as expected, it was highly associated with gaps. Overall, there were no clear associations of butterfly assemblages with most of the flowering and fruiting plant families (Fig 4C). Butterflies primarily encountered in the understory, for instance, *Tigridia acesta* and *Nessaea obrinius*, however, were associated with Malvaceae and Violaceae, whereas gap species such as *Zaretis isidora* and *Pyrrhogyra amphiro* showed a high association with Annonaceae. *Taygetis angulosa* was associated with several vines belonging to Siparunaceae and Verbenaceae (Fig. 4C).

The pRDA, performed to investigate the degree of species' association within gaps versus understory (after accounting for spatial patterns), indicated that the group associated with the understory contained relatively few species, including *T. acesta*, *Catoblepia berecynthia*, *C. xanthus*, and *N. obrinius* (Table 1, Table S1). The gap associated species were more numerous with *Pyrrhogyra crameri*, *Temenis laothoe*, *Archeoprepona demophon* and *Morpho helenor*, as the most distinct ones (Table 1, Table S1). We could also distinguish non-specialists, those with pRDA scores close to zero, *e.g.*, *Pseudobedis valentina*. There were a significant negative correlation between pRDA scores and wing area to thoracic volume ratio and abdomen length *i.e.*, species associated with understory had significantly higher wing area to thoracic volume (Table 2). There were no significant differences in pRDA scores between species with regard to distribution classes (one-way ANOVA: $F_{3,77}=1.014$, $P=0.39$).

COMPARISON OF BUTTERFLY ASSEMBLAGES AMONG GAPS.—When considering assemblages only in gaps, there were clear patterns of associations with vegetation structure (Fig. 5). The majority of the species avoided gaps with high vine densities, and were associated with higher light levels and a high density of plants other than vines. Only few species such as *Taygetis angulosa*, *T. sosis*, and *T. laches*, were associated with high vine density. Interestingly, several species, including *Nessaea obrinius* and *Pyrrhogyra crameri*, were associated with small gaps, whereas *Zaretis isidora*, *Adelpha jordani*, and *Memphis glauca* were associated with large gaps and a high amount of sunlight. There were no overall associations of butterfly assemblages with flowering and fruiting plant families in gaps (Fig. 5C). Most butterfly species, however, except *Taygetis* spp., avoided vines belonging to Siparunaceae, Verbenaceae, and Sapindaceae. *Pyrrhogyra crameri*, *Panacea prola*, and *P. regina* were associated with woody plants of the

family Solanaceae. Many butterfly species, *e.g.*, *A. jordani*, *Temenis laothoe*, and *M. glauce*, were associated with Costaceae and Annonaceae.

DISCUSSION

BUTTERFLY ASSEMBLAGES IN GAPS AND UNDERSTORY.—Our results support the hypothesis that natural disturbances can increase butterfly species diversity. Treefalls create gaps of varying size and vegetation structure which are utilized by different butterfly assemblages of fruit-feeding nymphalids than in the understory habitat. Some species showed strong associations with gaps (*i.e.*, *Pyrrhogyra amphiro* and *Temenis laothoe*) whereas other species clearly preferred the undisturbed understory (*i.e.*, *Tigridia acesta* and *Nessaea obrinius*). Whether this pattern holds for other butterfly groups or families remains to be established, as this study focuses only on fruit-feeding nymphalids.

The species associated with understory in this study had significantly higher wing area to thoracic volume and longer abdomens. Field observations by Hall and Willmott (2000) suggest that species with high wing area to thoracic volume often tend to be slow flying, with relatively low wing beat frequencies. Other studies have shown that species associated with rain forest canopy and gaps have a morphology indicating faster flight (Hill *et al.* 2001, DeVries *et al.* 2010) than species living in the understory. The reason for the differences between the species groups might be that species living in gaps utilize a habitat with high temperatures enabling fast flight (Hall & Willmott 2000) with a higher predation pressure. Chai and Srygley (1990) showed that butterflies with smaller wing areas and shorter and stouter bodies had a faster and more irregular flight and escape more frequently from predator attacks than butterflies with slender bodies and larger wing areas. Gap species has been shown to have better dispersal ability (Hill *et*

al. 2001) and that might be another reason for the morphology differences as gaps are a temporary habitat. Of the 82 species captured, 39 percent were only found in gaps, whereas 13 percent were restricted to the understory. Levey (1988) reported similar results from a Costa Rican wet forest where 40 percent of the birds species were found significantly more often in the gaps than in understory. Only 5 percent of the birds were found more often in the understory. Studies on insects reported mixed results. For example, a higher number of butterfly species in gaps were found in a Vietnamese montane rain forest (Spitzer *et al.* 1997), but in Bornean rain forests there was no difference in the number of species between gap and understory habitats (Hill & Hamer 2004; Hamer *et al.* 2003). In a study that sampled diurnal insects in a Panamanian lowland forest, significant lower abundances (indicating lower species richness) for Formicidae, Coleoptera, and Psocoptera were found in gaps than understory sites (Shelly 1988). In contrast, Feener and Schupp (1998) found no effect on ant assemblages in treefall gaps compared to understory in a lowland forest in Panama.

The number of species increased quickly during the first sampling weeks, and leveled off as sampling progressed. The species accumulation curve did not reach an asymptote, indicating that more species would have been found with an increased sampling period. Many species are seasonal (DeVries *et al.* 1999, DeVries & Walla 2001, Checa *et al.* 2009) and show a peak of abundance during a specific period only. For example, *Panacea prola* appeared first at week seven, and was the predominant species in both habitats (52% of the individuals in gaps and 69% in understory) from week 11 until the end of the study. A study covering ten years sampling in Ecuadorian Amazon showed that seasonal cycles of rainfall are the main drivers of seasonality of butterflies (Grøtan *et al.* 2012).

Another point worth noting is that our traps were close to the ground level as the majority of the frugivorous species are likely to be found at ground level where fallen ripe fruits occur (Hill *et al.* 2001, Tangah *et al.* 2004). Nevertheless, vertical stratification of frugivorous Neotropical butterflies in intact forest has been previously noted (DeVries *et al.* 1997, DeVries & Walla 2001) and additional traps at the canopy level in our own study might have resulted in higher species richness.

COMPARISON OF BUTTERFLY ASSEMBLAGES AMONG GAPS.—As hypothesized, the dissimilarity in butterfly assemblages increased with gap size, with assemblages in small gaps being more similar to those in nearby undisturbed understory. Gap size has been shown to affect temperature and humidity (Fetcher *et al.* 1985), vegetation structure (Denslow 1987) and densities of fruiting plants (Levey 1988). Somewhat unexpectedly, however, butterfly assemblages also seemed to be affected by the amount of vines with most of the butterfly species displaying an avoidance to vines. Instead, many species were associated with the presence of woody plants in gaps (high numbers here representing regeneration of woody species). There were also higher light levels in gaps with a large amount of woody plants. The amount of light has been shown to be an important component of the structure of tropical forests, affecting butterfly assemblages (Sparrow *et al.* 1994). The amount of sunlight reaching the ground is also a critical factor for plant growth (Terborgh 1992), and thus might indirectly effect the quality of butterfly host plants (Blau 1980, Richards & Coley 2008). The largest and most open gaps had the highest butterfly species diversity. Most vines are fast-growing species, covering gaps quickly, resulting in denser patches than woody plants. Thus the initial presence of vines might greatly influence the

vegetation succession and development in gaps (Schnitzer *et al.* 2000) and hence their butterfly assemblages.

IMPORTANCE OF HETEROGENEITY.—Different nymphalid species were associated with gaps of different characteristics. For example, we encountered *Pseudobedis valentina* and *Nessaea obrinius* mainly in small shaded gaps while *Adelpha jordani*, *Memphis glauce*, *Ypthimoides poltys*, *Temenis laothoe*, *Bia actorion*, and *Zaretis isidora* occurred mainly in large open gaps. Several species of the genus *Taygetis* (*T. angulosa*, *T. laches*, and *T. sosis*), were found primarily in large gaps with dense vine cover. The association with different habitats and vegetation characteristics is probably due to the distribution of suitable host plants and adult resources. For example *Temenis laothoe* occur in the canopy but females use Sapindaceae vines at ground level in gaps as host plants and they frequently descend to the ground for fermenting fruits (Muyshondt 1973). The species most associated with gaps in our study, *Pyrrhogyra crameri*, is known to oviposit on *Paullinea* sp. (Sapindaceae) in tree fall gaps (DeVries 1987). The *Taygetis* spp. all use grasses as host plants (DeVries 1987) and grasses were mainly found in large gaps in our study. Their preference for vines may be due to their preference for shadier conditions even though they use grasses as host plants. The species associated with small gaps, *Nessaea* spp., use seedlings of *Alchornea* spp. (Euphorbiaceae) (DeVries 1987) that grow in gaps. The species most associated with the understory was *Tigridia acesta*, which use the pioneer species *Cecropia* spp. and *Pourouma* spp. as host plants. Basset *et al.* (2003), however, report that the larvae have only been collected from small and shaded saplings of understory host plants suggesting that the butterfly is an understory specialist. Three other species strongly associated with the understory were *Catoblepia berecynthia*, *C. xanthus* and *Bia actorion*. These are encountered in deep shade

in the forest and all use palms as host plants, probably also in the shady understory. The butterflies classified as understory species in our study were also classified as understory species by DeVries and Walla (2001) in a study contrasting understory and canopy. Furthermore, several of the species associated with gaps in our study were classified as canopy species. It is likely that these species use both open gaps and canopy for feeding and for larval host plants.

Our results indicate considerable small-scale variation in butterfly species composition. Large differences in butterfly assemblages were found even between traps placed in the understory where variation in light and vegetation structure is limited. Similar variation between traps only 50–100 m apart has been found in central Brazil (Pinheiro & Ortiz 1992) and in Borneo (Hill *et al.* 2001). The variation in butterfly assemblages among the gap traps was even greater than in the understory. To what extent this variation is due to the existence of critical resources in gaps of different sizes and vegetation structure or simply a result of canopy specialists infrequently descending to the ground remains to be elucidated.

Our results suggest that heterogeneity within a rain forest consisting of gaps at different successional stages within the undisturbed understory matrix, might be a critical factor in maintaining high butterfly species diversity. The availability of different habitats, following a gradient from an undisturbed understory matrix to large newly formed open gaps, to smaller and denser gaps, could be an important requirement for the coexistence of the species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

TABLE S1. *Ordination scores of Nymphalidae species sampled in traps and analyzed within a pRDA using habitat (gap vs. understory) as explanatory variable and the pairs of traps as covariables.*

FIGURE S1. Spatial distribution of 15 gaps and their understory control sites, at Cocha Cashu Biological Station, within Manu National Park, Peru.

FIGURE S2. Number of species recorded in gaps and corresponding understory.

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TABLE 1. Results from a *pRDA* with habitat (gap vs. understory) as an explanatory variable and the pairs of traps as covariable. Only the twelve species with the highest scores and more than five individuals are shown here. P-value for the model was 0.0001 (Monte-Carlo permutation tests with 9999 permutations, Trace = 0.048).

	RDA scores	Frequency of individuals in understory	Frequency of individuals in gaps
<i>Tigridia acesta</i>	-0.4347	15	1
<i>Catoblepia berecynthia</i>	-0.3386	14	4
<i>Catoblepia xanthus</i>	-0.2737	12	3
<i>Bia actorion</i>	-0.2596	6	1
<i>Panacea prola</i>	-0.2102	555	414
<i>Nessaea obrinus</i>	-0.1717	29	19
<i>Adelpha iphiclus</i>	0.3025	1	10
<i>Zaretis isidora</i>	0.3239	0	8
<i>Morpho helenor</i>	0.3442	2	13
<i>Temenis laothoe</i>	0.3537	2	16
<i>Pyrrhogyra amphiro</i>	0.3563	0	8
<i>Pyrrhogyra crameri</i>	0.3912	2	18

TABLE 2. *Correlation coefficients between species (N=81) pRDA scores and morphological variables.*

Morphological variable	Transformation	R	P
Body length		-0.165	0.142
Forewing breadth		-0.0298	0.792
Forewing length		-0.0454	0.687
Abdomen width		-0.0571	0.612
Abdomen length	Square-root	-0.320	0.00360
Thorax width		+0.123	0.275
Thorax length		+0.0733	0.515
Thorax volume (TV)	Logarithmic	+0.129	0.253
Wing area (WA)	Logarithmic	-0.0452	0.689
Wing shape		-0.0341	0.763
WA/TV	Logarithmic	-0.269	0.0154

Figure legends

FIGURE 1. Butterfly species accumulation curves by traps (A) in a total of 30 traps, and by weeks (B) during 13 weeks, in gap and understory habitats. Each curve is presented with a 95% confidence interval. See Table S1 for species names.

FIGURE 2. PCA ordination diagram of butterfly assemblages from traps in gaps (A), divided in small ($< 300 \text{ m}^2$) and large gaps ($> 300 \text{ m}^2$), and understory (B). Lines link the two traps at a site. Eigenvalues of PC1 and PC2 were 17.5 and 10.7.

FIGURE 3. Dissimilarity (χ^2 -distances) between butterfly assemblages of Nymphalidae in pairs of gap and understory traps as a function of gap size. χ^2 -distances were calculated for the gap trap and understory trap that were located closest to each other, then averaged per gap. ($y = 2.22 + 0.0653x$; $r = 0.61$, $P = 0.0153$; $R^2 = 0.37$).

FIGURE 4. PCA ordination diagram of butterfly assemblages (A), environmental variables (B) and flowering and fruiting plant families (C). Only the 22 butterfly species that contribute most to the model are shown with species names. Eigenvalues of PC1 and PC2 were 17.5 and 10.7.

FIGURE 5. PCA ordination diagram of butterfly communities (A) environmental variables (B) and nectar and fruiting plant families (C) in 15 treefall gaps in Manu National Park, Peru. Only the 29 species that contribute most to the model are shown. Eigenvalues of PC1 (x axis) and PC2 (y axis) were 22.0 and 11.3.

TABLE S1. Ordination scores of Nymphalidae species sampled in traps and analyzed within a pRDA using habitat (gap vs. understory) as explanatory variable and the pairs of traps as covariables. The order of the species indicates their habitat preferences, starting from the species mostly associated with the understory to the species mostly associated with gaps. P-value for the model was 0.0001 (Monte-Carlo permutation tests with 9999 permutations, Trace = 0.048). Negative and positive pRDA value means association with understory and gap, respectively. Data on host plants associations were collected from DeVries (1987); Beccaloni et al. (2008) and Robinson et al. (2012). A question mark after the host plant family means that species-wise information are lacking but that the suggested host plant family is probable, due to general knowledge about the group or related species.

Habitat	Species	RDA	Understory			Gap			Host plant	Host plant family
			Frequency	No. of ind.	Trap records	Frequency	No. of ind.	Trap records		
Understory species	Tigridia acesta	-0.4347	15	15	12	1	1	1	Cecropia sp., Pourouma bicolor, Coussapoa nymphaeifolia, Ficus sp., Theobroma sp.	Urticaceae, Moraceae, Sterculiaceae
	Catoblepia berecynthia	-0.3386	14	11	13	4	4	4		Arecaceae
	Catoblepia xanthus	-0.2737	12	12	9	3	3	3		Arecaceae
	Bia actorion	-0.2596	6	6	6	1	1	1		Arecaceae
	Panacea prola	-0.2102	555	554	30	414	400	30	Caryodendron orinicense	Euphorbiaceae
	Hamadryas arinome	-0.1857	2	2	2	0	0	0	Dalechampia sp.	Euphorbiaceae
	Manataria hercyna	-0.1857	2	2	2	0	0	0	Bambusa sp.	Poaceae
	Nessaea obrinus	-0.1717	29	16	16	19	15	11	Alchornea sp.	Euphorbiaceae
	Chloreuptychia herseis	-0.1558	5	4	5	2	2	2		Poaceae
	Amphidecta calliomma	-0.1302	1	1	1	0	0	0		Poaceae?
	Amphidecta pignerator	-0.1302	1	1	1	0	0	0		Poaceae?

Batesia hypochlora	-0.1302	1	1	1	0	0	0	Caryodendron orinicense	Euphorbiaceae
Cissia sp.	-0.1302	1	1	1	0	0	0	Oryza latifolia	Marantaceae, Arecaceae, Poaceae
Epiphile lampethusa	-0.1302	1	1	1	0	0	0		Sapindaceae
Eryphanis automedon	-0.1302	1	1	1	0	0	0	Bambusa sp., Pennisetum polystachyon, Saccharum spontaneum	Poaceae
Historis odius	-0.1302	1	1	1	0	0	0	Cecropia sp., Celtis tala, Inga vera, Tabebuia sp., Trema micranthum, Urtica spathulata	Cecropiaceae, Ulmaceae, Fabaceae, Bignoniaceae, Urticaceae
Napeogenes inachia	-0.1302	1	1	1	0	0	0	Lycianthes sp.	Solanaceae
Taygetis inambari	-0.1302	1	1	1	0	0	0		Poaceae?
Heliconius numata	-0.0987	3	2	2	1	1	1	Passiflora sp., Dilkea sp. Tetrastylis ovalis	Passifloraceae
Memphis moruus	-0.0765	2	2	2	1	1	1	Camphorosma sp, Croton sp., Aniba citrifolia, Cinnamomum triplinerve, Endlicheria paniculata, Nectandra sp., Ocotea sp., Persea sp., Meliosma sp., Piper sp.	Chenopodiaceae, Euphorbiaceae, Lauraceae, Meliosmaceae, Piperaceae
Zaretis itys	-0.0765	2	2	2	1	1	1	Casearia sp., Ryanea sp., Laetia sp., Piper trigonum	Flacourtiaceae, Piperaceae

Pseudodebis valentina	-0.0453	27	21	12	22	18	13	Vitex sp., Piper arieianum	Poaceae
Adelpha heraclea	0	1	1	1	1	1	1		Verbenaceae, Piperaceae, Rubiaceae
Eunica sophonisba	0	1	1	1	1	1	1	Mabea sp.	Euphorbiaceae,
Morpho deidamia	0	1	1	1	1	1	1	Inga sp., Zygia latifolia, Iriarteia deltoidea	Fabaceae, Arecaceae
Oleria onega	0	1	1	1	1	1	1	Lycianthes sp., Solanum sp.	Solanaceae
Pyrrhogyra otolais	0	3	3	3	3	3	3	Paullinia pinnata, Serjania sp.	Sapindaceae
Taygetis mermeria	0	5	5	5	5	5	5	Bambusa sp., Dichorisandra amabilis, Olyra sp.	Poaceae
Taygetis virgilia	0.0195	4	4	3	4	4	4		Poaceae, Commelinaceae
Memphis offa	0.0431	5	5	5	6	5	6		Piperaceae, Euphorbiaceae, Lauraceae, Monimaceae, Annonaceae
Memphis polycarmes	0.0519	3	3	3	4	4	4		Piperaceae, Euphorbiaceae, Lauraceae, Monimaceae, Annonaceae
Taygetis laches	0.0613	11	9	9	13	13	11	Acroceras zizanioides, Olyra latifolia, Oryza latifolia, Panicum sp., Saccarum officinarum, setaria sp.	Poaceae, Arecaceae
Caligo idomeneus	0.0765	1	1	1	2	2	2	Musa acuminate, Palmeria sp.	Marantaceae, Musaceae, Monimiaceae
Hypna clytemnestra	0.0765	1	1	1	2	2	2	Croton sp.	Euphorbiaceae

Memphis acidalia	0.0765	1	1	1	2	2	2	Piper sp.	Piperaceae, Euphorbiaceae, Lauraceae, Monimaceae, Annonaceae
Taygetis angulosa	0.0765	1	1	1	2	2	2		Poaceae?
Panacea regina	0.105	17	17	10	22	22	13		
Colobura dirce	0.1236	16	15	11	22	19	16	Cecropia sp., Cassia sp., Inga sp., Cabralea canjerana, Eucalyptus sp., Urera baccifera	Urticaceae, Fabaceae, Meliceae
Adelpha thesprotia	0.1302	0	0	0	1	1	1	Pseudobombax munguba, Cecropia sp., Pourouma sp., Chodanthus splendens	Bombaceae, Urticaceae, Rubiaceae, Bignoniaceae
Adelpha viola	0.1302	0	0	0	1	1	1	Sabicea aspera	Rubiaceae
Archaeoprepona demophoon	0.1302	0	0	0	2	1	1	Persea americana, Nectandra sp., Ocotea sp.	Lauraceae
Archaeoprepona amphimachus	0,1302	0	0	0	1	1	1		Annonaceae, Malpigiaceae
Callicore eunomia	0.1302	0	0	0	1	1	1		Sapindaceae
Catoblepia xanthicles	0.1302	0	0	0	1	1	1		
Hamadryas feronia	0.1302	0	0	0	1	1	1	Dalechampia sp., Euphorbia pulcherrima, Zea mays, Inga sp., Syagrus romanzoffiana	Araraceae Euphorbiaceae, Poaceae, Fabaceae, Araraceae
Harjesia griseola	0.1302	0	0	0	1	1	1		
Harjesia obscura	0.1302	0	0	0	1	1	1		
Heliconius erato	0.1302	0	0	0	1	1	1	Passiflora sp., Dilkea sp., Tetrastylis ovalis	Passifloraceae

Marpesia chiron	0.1302	0	0	0	1	1	1	Artocarpus sp., Brosimum sp., Ficus sp., Maclura sp., Zanthoxylum sp, Hedera helix. Morus sp.	Moraceae, Araliaceae, Rutaceae
Memphis philumena	0.1302	0	0	0	1	1	1	Cinnamomum cinnamomifolium, Nectandra sp., Ocotea veraguensis	Lauraceae
Memphis pithyusa	0.1302	0	0	0	1	1	1	Croton sp., Piper sp.	Euphorbiaceae, Piperaceae
Memphis praxias	0.1302	0	0	0	1	1	1		
Nessaea hewitsonii	0.1302	0	0	0	1	1	1		
Opsiphanes invirae	0.1302	0	0	0	1	1	1	Heliconia sp., Musa sp., Archonophoenix cunninghamiana, Bactris sp., Butia sp., Cocos sp., Copernicia prunifera, Elaeis sp., Geonoma sp., Livistona sp., Phoenix sp., Prestoea sp., Cycas circinalis, Phoenix sp., Raphia sp., Phapis sp., Roystonea sp., Syagrus romanzoffiana	Arecaceae, Musaceae, Cycadaceae, Heliconiaceae
Paryphthimoides melobosis	0.1302	0	0	0	1	1	1		Poaceae?
Postaygetis penelea	0.1302	0	0	0	1	1	1		Poaceae?
Taygetis kerea	0.1302	0	0	0	1	1	1	Rhipidocladum racemiflorum	Poaceae
Taygetis sosis	0.1302	0	0	0	1	1	1		Poaceae
Taygetis sylvia	0.1302	0	0	0	1	1	1		Poaceae?
Yphthimoides maepius	0.1302	0	0	0	1	1	1		Poaceae
Adelpha plesaure	0.1558	2	2	2	5	5	5	Bathysa sp., Alibertia edulis, Amaioua corymbosa, Bathysa sp., Bertiera guianensis, Chimarrhis cymosa	Rubiaceae
Catonephele orites	0.1857	0	0	0	2	2	2	Alchornea sp.	Euphorbiaceae

Fountainea ryphea	0.1857	0	0	0	2	2	2	Croton sp., Ocotea acutifolia	Euphorbiaceae
Pareuptychia metaleuca	0.1857	0	0	0	2	2	2	Urera sp., Jacaranda mimosifolia, Laportea mexicana, Myriocarpa sp., Urtica chamaedryoides	Poaceaea
Smyrna blomfildia	0.1857	0	0	0	2	2	2		Bignoniaceae, Urticaceae
Paryphthimoides poltys	0.1857	0	0	0	2	1	2		Poaceae
Adelpha capucinus	0.1891	1	1	1	5	5	4	Mansoa difficilis, Bombax sp., Pachira aquatica, Cecropia sp.,	Bignoniaceae, Bombaceae, Urticaceae
Morpho achilles	0.1961	2	2	2	6	5	6	Paragonia pyramidata, Erythroxylum sp., Heliconia bihai, Gleditsia sp., Pithecellobium sp., Andira enermis, Arachis hypogaea, Dahlstedtia pinnata, Dalbergia sp., Dioclea sp., Erythrina sp., Lonchocarpus sp., Inga sp., Machaerium sp., Mucuna sp., Myrocarpus sp, Platymiscium sp., Pterocarpus sp., Rhyncosia edulis, Robinia sp., Swartzia sp., Heteropterys laurifolia, Musa sp., Ouratea lucens, Genipa americana, Pallinea pinnata	Bignoniaceae, Fabaceae, Erythroxylaceae, Heliconiaceae, Malpighiaceae, Musaceae, Ochnaceae, Rubiaceae, Sapindaceae
Consul fabius	0.2222	1	1	1	5	5	5	Casearia sp., Piper sp.,	Flacourtiaceae, Piperaceae
Adelpha jordani	0.2228	29	29	12	61	60	19	Vitex trifolia	Verbenaceae
Memphis xenocles	0.2232	0	0	0	4	4	3	Croton sp.	Euphorbiaceae,
Nica flavilla	0.2294	0	0	0	3	3	3	Cardiospermum sp., Serjania sp., Paullinia sp.	Sapindaceae

Prepona laertes	0.2294	0	0	0	3	3	3	Chrysobalanus icaco, Hirtella racemosa, Licania arborea, Inga sp., Zygia longifolia, Andira inermis, Psidium sp., Coffea arabica, Melicoccus bijugatus	Chrysobalanaceae, Fabaceae, Myrtaceae, Rubiaceae, Sapindaceae
Memphis glauce	0.2406	1	1	1	8	8	5		Piperaceae, Euphorbiaceae, Lauraceae, Monimaceae, Annonaceae?
Archaeoprepona demophon	0.2677	7	4	5	19	17	14	Anaxagorea crassipetala, Annona sp., Rourea glabra, Maripa panamanensis, Lacistema aggregatum, Nectandra purpurea, Ocotea sp., Persea americana, Malpighia glabra, Guarea sp., Mollinedia sp., Siparuna sp., Brosimum gaudichaudi, Triplaris sp., Theobroma cacao, Hybanthus sp.	Annonaceae, Connaraceae, Convulvaceae, Lacistematataceae, Lauraceae, Malpighiaceae, Meliaceae, Monimiaceae, Moraceae, Polygonaceae, Sterculiaceae, Violaceae
Memphis basilia	0.2954	1	1	1	8	8	7		
Adelpha iphiclus	0.3025	1	1	1	10	10	7	Alseis blackiana, Antirhea trichantha, Bathysa sp, Calycophyllum sp, Isertia haenkeana, Rondeletia panamensis, Sipanea sp, Uncaraia sp.	Rubiaceae
Zaretis isidora	0.3239	0	0	0	8	8	6	Casearia sp., Colubrina sp.	Flacourtiaceae, Rhamnaceae

Morpho helenor	0.3442	2	2	2	13	10	10	Machaerium sp., Pterocarpus sp., Lonchocarpus sp., Platymiscium sp, Swartzia sp., Mucuna sp., Myrocarpus sp, Erythrina sp., Inga sp., Dahlstedtia sp.	Fabaceae, Mimosaceae
Temenis laothoe	0.3537	2	2	2	16	16	10	Stigmaphyllon sp., Allophylus edulis, Cardiospermum sp, Paullinia sp., Serjania sp., Urvillea sp.	Malpighiaceae, Sapindaceae
Pyrrhogyra amphiro	0.3563	0	0	0	8	7	7		Sapindaceae?
Pyrrhogyra crameri	0.3912	2	2	2	18	18	12	Paullinia sp., Serjania mexicana	Sapindaceae