

Butterfly diversity of the Piedras Blancas National Park and its vicinity – a preliminary assessment (Lepidoptera: Papilionoidea & Hesperioidea)

Diversidad de mariposas del Parque Nacional Piedras Blancas y zonas cercanas – una evaluación preliminar (Lepidoptera: Papilionoidea & Hesperioidea)

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Abstract: Two short-term surveys were carried out in 2006 and 2007 to study butterfly diversity in different habitats around the Tropical Field Station La Gamba, adjacent to Piedras Blancas National Park. Three different land use types were examined: cultivated land (oil palm plantations, pastures, garden and roadside verges), secondary forest (regeneration forest and gallery woodland), and primary forest (near-natural ridge and riverine forest). As expected, species richness was lowest in habitats with intensive land use. Forests are more species-rich than habitats more affected by human interventions, but secondary forests are surprisingly similar in butterfly species composition to cultivated land, due to the dominance of some widespread and abundant species of the open countryside. Butterfly assemblages of primary forests are significantly different from, and more heterogeneous than, those of disturbed habitats. Differences in butterfly community composition appear to be due mainly to larval host plant affiliations and are less strongly governed by bionomic traits related to adult resource use. Despite their limited extent, short-term assessments of adult butterflies appear to be suitable for inferring habitat quality for butterfly species and communities. True forest butterflies were rarely observed in secondary or gallery forests. It is therefore recommended that in order to facilitate the exchange of individuals at the landscape scale, forest corridor plantations should be broad enough and contain a high variety of tree species.

Key words: butterfly diversity, species richness, land use systems, primary rainforest, life history traits.

Resumen: Se llevaron a cabo dos investigaciones de corto plazo durante los años 2006 y 2007 para estudiar la diversidad de mariposas en diferente hábitat alrededor de la Estación Tropical La Gamba, adyacente al Parque Nacional Piedras Blancas. Tres diferentes tipos de uso de suelo fueron examinados: suelos cultivados (plantaciones de palmas para aceite, pastizales, jardines y bordes de camino), bosque secundario (bosque de regeneración y bosque galería), y bosque primario (cumbre casi-natural y bosque ribereño). Como esperábamos, la riqueza de especies fue menor en hábitat con un uso intensivo del suelo. Los bosques son más ricos en especies que los hábitat más afectados por la intervención humana, pero los bosques secundarios en la composición de especies de mariposas, son sorprendentemente similares a las tierras de cultivo, debido a la dominancia de algunas especies de amplia distribución y abundancia de especies en las zonas rurales abiertas. Grupos de mariposas de los bosques primarios son significativamente diferentes, y más heterogéneos que aquellas de hábitat perturbados. Las diferencias en la composición de mariposas de la comunidad se deben principalmente a la afiliación de larvas a plantas hospedadoras, y en menor grado son gobernadas por rasgos bionómicos relacionados al uso de los recursos por los adultos. A pesar de su limitada extensión, evaluaciones a corto plazo de las mariposas adultas parecen adecuadas para inferir calidad del hábitat para las especies de mariposas y comunidades. Las verdaderas mariposas de bosques fueron raramente observadas en bosques secundarios o de galería. De esta forma se recomienda que en orden a un mejor intercambio de individuos en el paisaje, los corredores boscosos debieran ser lo suficientemente amplios y contener una elevada variedad de especies arbóreas.

Palabras clave: diversidad de mariposas, riqueza de especies, sistema de uso del suelo, bosque lluvioso primario, rasgos de historia de vida.

Introduction

Butterflies (20.000 recognised species) are a relatively small subgroup of the Lepidoptera, the second largest insect order with more than 160.000 described (and probably some 500.000 extant) species world-wide (KRISTENSEN et al. 2007). Costa Rica is home to more than 1000 butterfly species which constitutes 5% of the world total, even though Costa Rica's share of the world's land area is only 0.034%. The Golfo Dulce region belongs to the Pacific Lowland Evergreen Forest zone which extends from the Rio Grande de Tarcoles near San Mateo southward to Panama. This area alone harbours about half of Costa Rica's butterfly species, which is more than are known from all of Europe.

Although the butterflies of Costa Rica are relatively well known compared to other tropical countries, taxonomic, distributional and ecological information remains particularly scant for two large families, the skippers (Hesperiidae) and the blues (Lycaenidae). The remaining four families are covered by two excellent field guides by DEVRIES (1987, 1997). The latter book covers the Riodinidae (metalmarks), a puzzling family with maximum divergence in the Neotropical region. Riodinids include an amazing variety of phenotypes, many of them mimics of members from different other Lepidoptera families.

For the Golfo Dulce region, older and incomplete species inventories exist only for Corcovado National Park on the Osa Peninsula (DEVRIES 1978). The study of the butterfly fauna of the Piedras Blancas National Park, however, is still in its infancy. The unpublished diploma thesis by KEBER (1997) focused on flower preferences of butterflies in secondary forest near the tropical field station La Gamba on the eastern edge of the Piedras Blancas National Park. Unfortunately, many identifications are questionable because most were done in the field without collecting voucher specimens. Those specimens which had been collected were later accidentally destroyed with only a few exceptions. KEBER's species list is not therefore a reliable source of information for an inventory of the area.

Against this background, the first goal of our studies was to start an inventory of butterflies for the Esquinas rainforest which is part of the Piedras Blancas National Park. A second aim was to compare the diversity and species composition of butterfly communities between the different land use systems and forest types found in the area. While it is well known that deforestation is threatening biodiversity in tropical countries (BROOKS et al. 2002), the role of secondary forests for maintaining biodiversity is less well understood (BROWN & LUGO 1990; KOH 2007). Although Costa Rica has also been a

victim of intensive deforestation, this trend has been stopped in recent decades, and efforts are being undertaken to re-connect isolated forest fragments by planting tree corridors (HUBER et al. 2007). The urgent question is whether, and to what extent, species from primary forest are able to colonise such secondary habitats or may at least use them e.g. in order to move between forest fragments (cf. TEWKSBURY et al. 2002, HADDAD et al. 2003). The La Gamba field station appears to be at an ideal position for such studies, because it is situated at the intersection of unlogged primary forest and intensively manipulated agricultural land, and patches as well as linear elements of secondary forest exist in close proximity to each other (WEISSENHOFER 2005).

Butterflies are almost exclusively herbivores during their larval stage, most tropical species exhibit high host plant specificity (DYER et al. 2007) and individuals usually have limited home ranges (e.g. compared to birds). On the other hand, adult butterflies are mobile enough to colonise new habitats within a radius of a few kilometres in short periods of time (for temperate zone species see SHREEVE 1994) and often form metapopulations with extensive gene exchange on a landscape scale (HANSKI & GAGGIOTTI 2004). Thus, they appear to be suitable model organisms to study such questions.

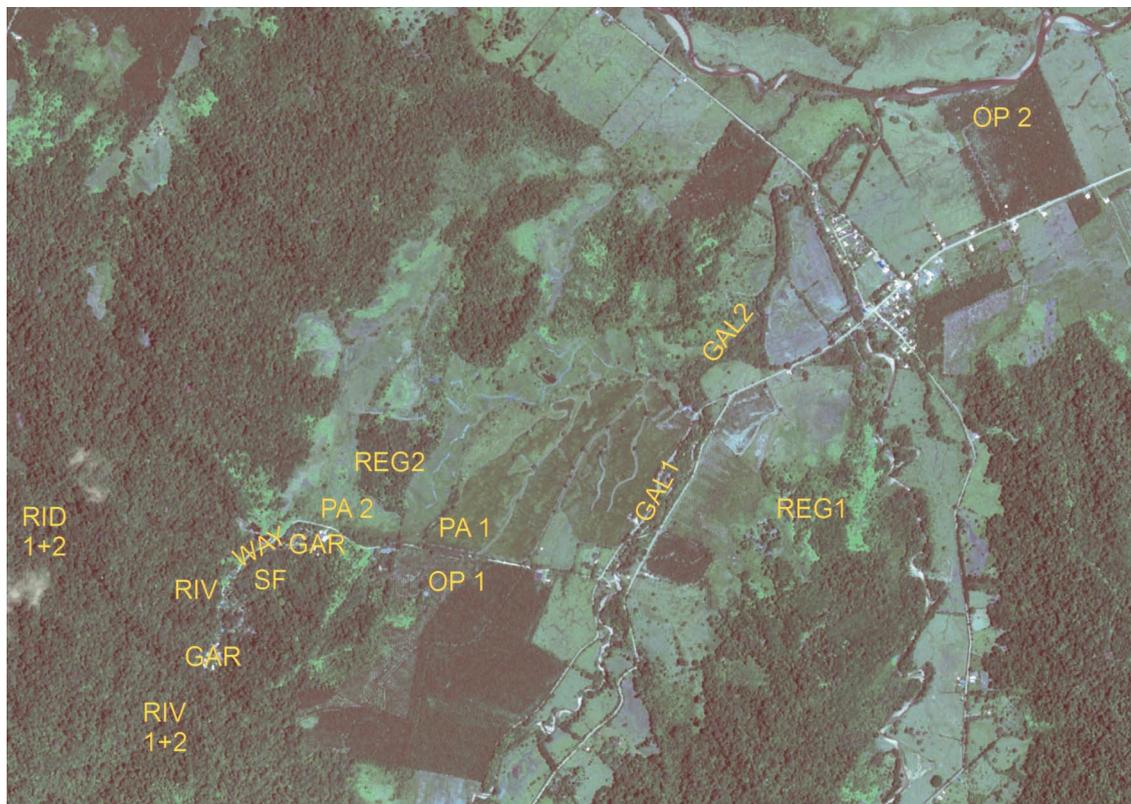
In particular, we address the following questions:

- How does the diversity of butterflies around La Gamba compare with published figures from Pacific evergreen forests in Costa Rica?
- How does the butterfly richness and diversity of secondary forests compare with intensively used land as well as with primary forest?
- Are there characteristic butterfly species for each of the three land use systems (intensive land use, disturbed forest, and natural forest)?
- Do assemblages of adult butterflies reflect resource requirements of the adult stage, or are these communities more strongly modulated by larval hostplant affiliations?
- What recommendations can be drawn from those preliminary results for conservation and management, e.g. with regard to the implementation of forest corridors to connect fragmented primary forests?

Material and methods

Field methods

The short surveys were carried out near La Gamba in two consecutive years during the dry season (6-11 February, 2006 and 28 January-2 February, 2007). Most field sites were located in the vicinity of the tropical field station La Gamba and the nearby Esquinas Lodge, and some sites were located towards or within the vil-



Map of the survey area near La Gamba (Costa Rica) with an indication of survey sites in 2006 and some major further sites used for transects in 2007 (abbreviations according to Table 1). Plots surveyed in 2006 were also included in the 2007 transects, with the exception of REG 1+2, OP 2 and PA 1+2. Map is based on QuickBird scene 0520173300 10_01_P001, 6/12/2007 © Digital Globe (2008), Distributed by Euroimage, Reprinted with permission.

lage of La Gamba (map). While cultivated land and remnants of secondary forest dominate the area around the village of La Gamba, the Esquinas Lodge is surrounded by primary rainforest. The tropical field station is situated at the interface of both land use types and is surrounded by a mosaic of different habitats with different land use intensity.

Two different methods were employed to sample the butterfly fauna of the area.

In 2006, 12 field sites were chosen to represent the three main land use systems in the area, viz. primary forest, secondary forest, and cultivated land. Within each land use system, two different habitat types were chosen, each represented by two sites (Table 1). In the primary forest, these were gaps in the ridge forest along the Fila Trail and in the riverine forest along the Waterfall Trail. The secondary forest type was represented by two patches of (dense and light) regeneration forest and by two segments of gallery forest along the La Gamba river. The dense regeneration forest was situated on a hillside and dominated by the tree species *Vochysia ferruginea* (Vochysiaceae), while the light regeneration forest was a (partly swampy) plantation of *Gmelina arborea* (Verbenaceae). The cultivated land consisted of two oil palm plantations (one near the field station, the other in the village La Gamba) and two patches of pasture.

Each site was sampled by a team of three students for a whole day (approximately 6 hours from 9:00 am to

3:00 pm) under weather conditions perfect for butterfly observations (sunny and dry with clouds only sometimes appearing in the late afternoon). The abundance of each observed butterfly species was recorded according to the following categories:

- (1): one specimen
- (2): 2-9 specimens
- (10): 10-50 specimens

Table 1: Survey sites around La Gamba with dates of survey and numbers of observation units

Habitat type	Abbreviation	Land use system	Date	Units	Int.*
Ridge forest 1 & 2	RID 1 & 2	Primary forest	07.-08.02.06	4	
Riverine forest 1 & 2	RIV 1 & 2	Primary forest	07.-08.02.06	4	
Regeneration forest 1 & 2	REG 1 & 2	Secondary forest	09.-10.02.06	4	
Gallery forest 1 & 2	GAL 1 & 2	Secondary forest	09.-10.02.06	4	
Oil palm plantation 1 & 2	OP 1 & 2	Cultivated land	06.&11.02.06	4	
Pasture 1 & 2	PA 1 & 2	Cultivated land	06.&11.02.06	4	
Ridge forest	RID	Primary forest	31.01.-01.02.07	4	25
Riverine forest	RIV	Primary forest	28.01.-02.02.07	11	30
Secondary forest	SF	Secondary forest	29.01.-02.02.07	5	18
Gallery forest	GAL	Secondary forest	30.01.07	2	18
Garden	GAR	Cultivated land	28.-02.02.07	6	12
Oil palm plantation	OP	Cultivated land	29.01.07	2	8
Wayside verges	WAY	Cultivated land	29.01.-02.02.07	5	8

* 15-minute-intervals (with data)

Table 2: Species numbers (observed and estimated) per butterfly family in La Gamba in comparison with published data from Corcovado National Park and the Pacific Evergreen Forest Zone.

	Papilionidae	Pieridae	Nymphalidae	Riodinidae	Lycaenidae	TOTAL
S_{obs}	3	10	66	24	15	118
ICE	6.9	10.3	88.2	57.9	33.0	179.6
S/ICE (%)	43	97	75	41	45	66
Chao2	3.8	10.2	83.3	152	35.2	180.5
- SD	1.8	0.5	9.6	143.6	20.2	23.9
Corcovado*	9	10	104	?	?	
PE**	17	26	174	79	?	

S_{obs} = observed number of species; ICE = incidence-based coverage estimator of species richness; S/ICE = proportion of observed species relative to ICE; Chao2 = Chao's incidence-based coverage estimator; SD = standard deviation of Chao2

* Corcovado = Observed number of species in Corcovado National Park (DEVRIES 1978)
 ** PE = Number of species in the Pacific Evergreen Forest of Costa Rica (DEVRIES 1997)

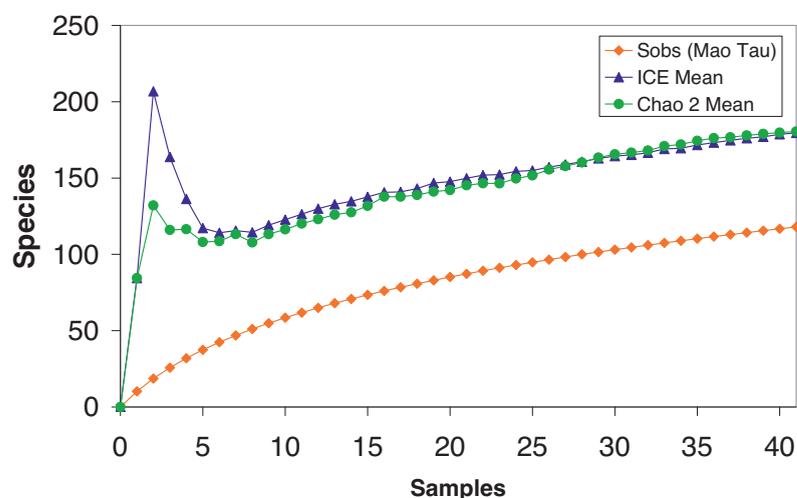


Fig. 1: Species accumulation curves for the entire study area, collated over samples from two years. The randomised accumulation of observed species (Sobs = Mao Tau), and the values of two incidence-based richness estimators (Chao2, ICE) as a function of sampling units are shown.

In 2007, a different survey system was used. Instead of fixed sample sites, transect counts were employed to represent the three land use systems. In this way, a larger array of habitats could be sampled. In the primary forest, sections of ridge forest (along the Fila Trail) as well as riverine forest (mainly along the Waterfall and Riverbed Trails) were sampled. The secondary forest was

situated around the field station (mainly along the Bird Trail adjacent to primary forest) and the gallery forest of the La Gamba river. The cultivated land was represented by oil palm plantations and gardens as well as roadside verges. The latter were mostly surrounded by pastures and rice fields. Presence-absence data were collected in 15-minute intervals during transect walks which were conducted during sunny weather conditions by groups of 2-3 observers. While the total effort remained similar in 2007 (six days with two groups of students), this time and in contrast to 2006, the efforts were not evenly distributed among land use systems. Because preliminary species accumulation curves showed a high sampling efficiency in cultivated land, but a low efficiency in primary forest, efforts were concentrated in primary forest at the cost of efforts in cultivated lands. The number of time units with data (i.e. at least one recorded individual) are shown in Table 1. Time units without data are mostly confined to dense tracts of forest without gaps which are especially common in the primary forest.

Butterflies were identified using the guides by DEVRIES (1987, 1997), and D'ABRERA (1995). Vouchers of each recorded species were kept or photographed for verification of the taxonomic identification. Where appropriate, taxonomic names were updated using the catalogue by LAMAS (2004). Survey data were then collated into species ↔ site matrices and used to measure butterfly diversity on three different scales (alpha-, beta- and gamma diversity; WHITTAKER 1972).

Alpha- & gamma diversity

Due to time constraints, recorded species numbers will usually only represent an unknown fraction of the real number of butterfly species in a given habitat (or area; GOTELLI & COLWELL 2001), the rate of which may differ between habitats. Even if methods are standardised, habitat differences can result in strongly different capture rates between habitats, e.g. because population densities differ or because sampling is easier in open habitat than in rainforests where many butterflies fly in the canopy. If species numbers are to be compared be-

Table 3: Observed and estimated butterfly species numbers in the area of La Gamba for the different land use systems based on daily intervals.

	Intensive land use			Disturbed forest			Natural forest			Total (La Gamba)		
	2006	2007	06+07	2006	2007	06+07	2006	2007	06+07	2006	2007	06+07
S_{obs}	29	33	47	47	35	59	42	48	70	83	83	118
ICE	39.4	60.4	73.7	83.6	101.1	115.9	91.0	73.4	121.1	124.3	143.1	179.6
S/ICE (%)	74	55	64	56	35	51	46	65	57.8	67	58	66
Chao2	36.6	54.3	69.2	77.7	76.1	149.7	75.1	78.7	130.2	113.6	179.8	180.5
- SD	6.0	14.5	13.3	16.2	23.8	49.6	17.2	16.2	27.3	13.6	43.4	23.9

S_{obs} = observed number of species; ICE = incidence-based coverage estimator of species richness; S/ICE = proportion of observed species relative to ICE; Chao2 = Chao's incidence-based coverage estimator; SD = standard deviation of Chao2

tween different habitat types, it is therefore important to account for these various types of sampling effects. For this reason, species accumulation curves and several incidence-based or abundance-based non-parametric species richness estimators were computed from the data with the software EstimateS (COLWELL 2005) using the classic Chao formula and 100 randomisations. This was generally done on the basis of sampling days (per observation group), but in 2007, 15-minute intervals were also used as time units. Species richness estimators were also calculated for the complete data set in order to estimate the total species richness (i.e. gamma diversity) for the area of La Gamba with the Esquinas rainforest.

Beta diversity

In order to compare species composition between habitats and land use types, a standardised Bray-Curtis similarity matrix was calculated using the programme PRIMER (version 5.2.9; CLARKE & GORLEY 2001) and a non-metric multidimensional scaling (NMDS) ordination was then carried out with Statistica (STATSOFT 2005). NMDS has been shown to be a particularly robust ordination method for incomplete samples from rich tropical insect faunas (BREHM & FIEDLER 2004). To test for the significance of differences in butterfly community composition between the habitat types, analyses of similarity (ANOSIM) were conducted. To identify those species which characterise distinct habitat types, species contributions to similarity percentages were also calculated using PRIMER with the help of the SIMPER algorithm.

Microdistribution in relation to life history traits

We also used our data to test whether the microdistribution of adult butterflies can be related to affiliations with larval host plants, or is more strongly governed by adult resource use. For this purpose, larval hostplants and adult resources were classified into functional groups as follows:

Larval hostplant group:

- woody (tree or shrub)
- vine or liana
- herb monocot
- herb dicot
- grasses
- others

Adult resources

- flowers
- flowers and pollen
- fruit and/or carrion

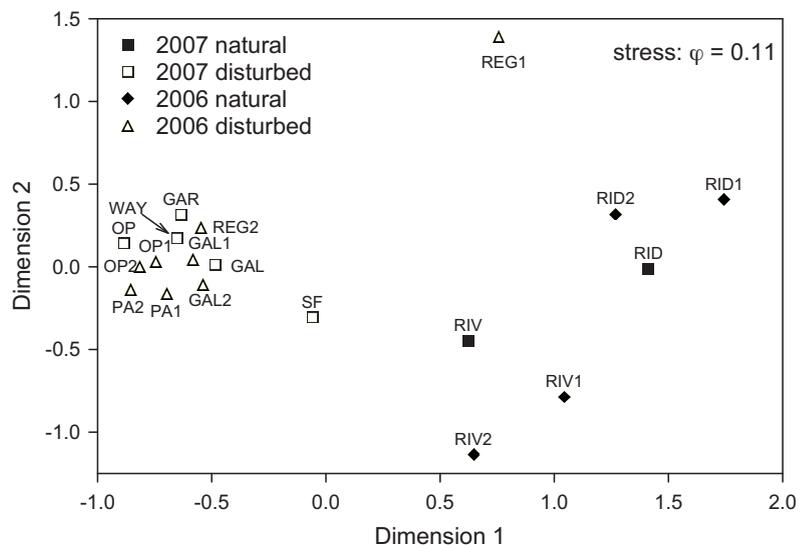


Fig. 2: NMDS ordination plot (based on Bray-Curtis similarities) of butterfly surveys from 2006 & 2007 for individual habitats. For explanation of abbreviations, see Table 1. The moderate stress value (a measure of poorness of fit between the original similarity matrix and its low-dimensional representation) indicates that the ordination reflects faunal differences reasonably well.

Life history traits of observed species were retrieved from DEVRIES (1987, 1997; supplemented where needed from other sources), and the proportional representation of each resource use type per site was calculated both on the basis of butterfly species as well as individuals. An analysis of variance (ANOVA) was conducted to test for differences across habitat types in the contribution of each functional group to the local butterfly fauna. Data were arcsine-square root transformed to match ANOVA requirements.

Results

Gamma diversity

A total of 118 species of butterflies (Papilionoidea only) was recorded during the short-term surveys in both years, of which 48 species (41%) were found both in 2006 and 2007. Table 2 shows observed and estimated species numbers according to two incidence-based methods (ICE, Chao2) for each butterfly family. As expected, the surveys were clearly incomplete. Various extrapolation estimators indicate that the true butterfly species richness of the area and during the study periods was in the range of 150-200 species of Papilionoidea. These estimates compare well with the long-term data collated by DEVRIES (1997, see Table 2). There is also obvious variation in the completeness of inventories across families. The larger-sized and more conspicuous families Pieridae and Nymphalidae were apparently better covered by our short-term surveys than small-sized and difficult to observe lycaenids and riodinids.

Table 4: Species contributions to similarity percentages for disturbed habitats (cut-off for low contributions: 90%)

Species	Average abundance	Average similarity	Similarity /SD	Contribution [%]	Cumulative contribution [%]
<i>Hermeuptychia hermes</i>	2.77	6.74	2.11	15.75	15.75
<i>Anartia jatrophae</i>	2.39	5.62	1.92	13.13	28.88
<i>Anartia fatima</i>	2.22	4.71	1.47	11.00	39.88
<i>Pyrisitia nise</i>	2.02	4.41	1.89	10.30	50.18
<i>Pareuptychia ocirrhoe</i>	1.86	3.94	1.41	9.21	59.39
<i>Eurema daira</i>	1.85	3.65	1.40	8.52	67.91
<i>Adelpha cytherea</i>	1.70	3.37	1.38	7.87	75.78
<i>Mechanitis polymnia</i>	1.22	2.07	0.86	4.84	80.62
<i>Anthanassa frisia</i>	1.09	1.47	0.71	3.44	84.05
<i>Magneuptychia libye</i>	0.77	0.94	0.59	2.20	86.25
<i>Everes comyntas</i>	0.69	0.72	0.56	1.68	87.93
<i>Hemiargus hanno</i>	0.72	0.66	0.45	1.55	89.48
<i>Arawacus togarna</i>	0.67	0.65	0.48	1.52	91.00
Average similarity: 42.80					

Table 5: Species contributions to similarity percentages for natural forests (cut-off for low contributions: 90%)

Species	Average abundance	Average similarity	Similarity /SD	Contribution [%]	Cumulative contribution [%]
<i>Philaethria dido</i>	1.24	3.75	2.98	15.82	15.82
<i>Heliconius sapho</i>	1.29	2.81	1.16	11.85	27.67
<i>Eueides lybia</i>	0.90	2.27	1.27	9.55	37.22
<i>Heliconius cydno</i>	1.28	2.24	0.70	9.44	46.66
<i>Arumecla galliena</i>	1.11	1.97	0.67	8.29	54.94
<i>Hermeuptychia hermes</i>	0.90	1.38	0.76	5.84	60.78
<i>Morpho menelaus</i>	0.67	1.32	0.75	5.57	66.35
<i>Chloreuptychia arnaca</i>	0.77	1.14	0.47	4.82	71.16
<i>Euptychia jesia</i>	0.96	1.13	0.47	4.78	75.94
<i>Archonias brassolis</i>	0.83	0.82	0.42	3.44	79.39
<i>Pierella helvina</i>	0.57	0.61	0.47	2.57	81.96
<i>Eueides lineata</i>	0.67	0.48	0.26	2.01	83.96
<i>Nessaea aglaura</i>	0.33	0.33	0.26	1.41	85.37
<i>Eresia ithomioides</i>	0.33	0.33	0.26	1.41	86.77
<i>Aeria eurimedia</i>	0.33	0.33	0.26	1.41	88.18
<i>Parides childrenae</i>	0.46	0.29	0.26	1.24	89.42
<i>Hyposcada virginiana</i>	0.46	0.29	0.26	1.24	90.67
Average similarity: 23.72					

Table 6: Species contributions to similarity percentages for ridge forests (cut-off for low contributions: 90%)

Species	Average abundance	Average similarity	Similarity /SD	Contribution [%]	Cumulative contribution [%]
<i>Heliconius cydno</i>	2.08	7.58	3.61	21.79	21.79
<i>Arumecla galliena</i>	1.88	7.27	32.12	20.91	42.71
<i>Chloreuptychia arnaca</i>	1.55	5.71	4.62	16.43	59.14
<i>Philaethria dido</i>	1.47	5.07	2.82	14.57	73.70
<i>Nessaea aglaura</i>	0.67	1.67	0.58	4.79	78.50
<i>Heliconius sapho</i>	0.91	1.64	0.58	4.73	83.22
<i>Euptychia jesia</i>	1.24	1.64	0.58	4.73	87.95
<i>Eueides lybia</i>	0.80	1.34	0.58	3.86	91.81
Average similarity: 34.78					

A preliminary checklist of all species observed thus far around La Gamba is given in the appendix. This checklist includes 11 more species of Papilionoidea which were found outside the survey periods and 14 species of skippers (Hesperiidae; Hesperioidea).

Alpha diversity

Local species richness figures for the different land use systems are listed in Table 3. Estimates based on 15-minute intervals (instead of dates) gave slightly more accurate results (i.e. lower standard deviation of Chao2) only for the intensive land use habitat type, while those estimates were grossly inaccurate for both forest types. Observed species totals rank the habitat types in the expected order (natural forest: 70; secondary forest: 59; open land: 47). The extrapolation analyses, however, suggest that total species richness is rather similar in both classes of forest habitats (Chao2: 130-150 spp.; ICE: 116-121 spp.), but much lower (69-74 spp.) in habitats representing intensive land use.

Beta diversity, species composition and characteristic species

Fig. 2 shows the NMDS plot for butterfly surveys from all habitats and combined for both sampling years. With the exception of one outlier (regeneration forest 1), all disturbed habitats (including various types of disturbed forest) cluster closely together and thus appear to have a similar butterfly species composition, while natural forests have a distinct species composition. This segregation was statistically highly significant (ANOSIM, Global R = 0.81, p = 0.001). Only the secondary forest sampled in 2007 showed up in an intermediate position between the cluster of disturbed habitats and riverine primary forests. Natural forest sites appear to be more dissimilar to each other than disturbed sites. Especially there was some segregation between butterfly communities of riverine and ridge forest, respectively. No significant difference was found between years of sampling (Global R = -0.11, p = 0.96; the negative value of which indicates that samples within years are even slightly more dissimilar than between years). Therefore samples from different years can be pooled for further analysis.

The analysis of similarity percentages (SIMPER) revealed that only four species account for more than 50% cumulative similarity among communities from disturbed habitats: *Hermeuptychia hermes* FABRICIUS, *Anartia jatrophae* LINNAEUS, *Anartia fatima* FABRICIUS and *Pyrisitia nise* CRAMER (Table 4). In contrast, the following five species made up for more than 50% similarity between natural forests: *Philaethria dido* LINNAEUS, *Heliconius sapho* DRURY, *Eueides lybia* FABRICIUS, *Heliconius*

cydno DOUBLEDAY and *Arumecla galliena* HEWITSON (Table 5). While the latter two species best characterise the ridge forest (with a cumulative contribution of 43%, Table 6), *Heliconius sapho* is more specific to riverine forest. Like *Archonias brassolis* FABRICIUS it contributes to 15% of similarity between riverine forest sites (Table 7). Overall, there was a very clear segregation between species that occur regularly in natural forest, as opposed to those in disturbed habitats (including secondary forest).

Microdistribution in relation to life history traits

The ANOVAs for species traits with regard to larval (Table 8) and adult resource use (Table 9) revealed significant differences between habitat types for a number of groups. Hence, larval as well as adult traits had strong influence on the species composition of butterflies around La Gamba, but overall, larval traits more often reflected differences in community composition. Butterflies with larvae feeding on dicot herbs were more prevalent in cultivated land, rarer in primary forest, and intermediate in secondary forest (Fig. 3). Butterflies with larvae feeding on climbing plants (Fig. 4) as well as species where the adult butterflies obligately feed on pollen (Fig. 5) were more important in primary forest, rare in cultivated land, and intermediate in secondary forest.

Discussion

Species diversity of La Gamba and the Esquinas Rainforest – rapid assessment of a local fauna drawn from a regional species pool with high diversity

A total of 118 butterfly species were recorded during the brief standardised surveys, while the estimated total (ICE & Chao2) is about 180; this suggests that within the short assessment periods about 66% of the Papilionoidea species were observed. Table 2 shows however that completeness varies greatly between butterfly families. The coverage for the family Pieridae is nearly complete. In Costa Rica, few Pieridae species occur in lowland rainforest; most pierids are either confined to higher altitudes (genera *Archonias*, *Leodonta*, *Pereute* and *Catasticta*) or are found in open habitats where they can easily be recorded. Slightly more than half of the recorded species belong to the large family Nymphalidae which was covered reasonably well ($S_{obs} / ICE = 75\%$). Most members of this family are large and conspicuous and thus easily recorded. The large subfamily Satyrinae is less conspicuous but most of its members are weak fliers, often resting on the ground and therefore easy to catch. Much less complete is the coverage for the remaining families. Members of the small family Papilion-

Table 7: Species contributions to similarity percentages for riverine forests (cut-off for low contributions: 90%)

Species	Average abundance	Average similarity	Similarity /SD	Contribution [%]	Cumulative contribution [%]
<i>Heliconius sapho</i>	1.67	4.08	1.54	15.34	15.34
<i>Archonias brassolis</i>	1.67	4.08	1.54	15.34	30.67
<i>Philaethria dido</i>	1.00	2.89	4.93	10.87	41.54
<i>Morpho menelaus</i>	1.00	2.89	4.93	10.87	52.40
<i>Eueides lybia</i>	1.00	2.89	4.93	10.87	63.27
<i>Eueides lineata</i>	1.33	2.38	0.58	8.94	72.21
<i>Hyposcada virginiana</i>	0.91	1.47	0.58	5.54	77.75
<i>Arawacus togarna</i>	1.24	1.47	0.58	5.54	83.29
<i>Laparus doris</i>	1.47	1.20	0.58	4.52	87.81
<i>Hermeuptychia hermes</i>	1.14	1.20	0.58	4.52	92.33
Average similarity: 26.63					

Table 8: Results of univariate ANOVAs for relative contributions of butterflies with various larval host plant traits across the three land use types (cultivated land, secondary forest, and primary forest), based on species and individuals. F and p values are shown, and significant results ($\alpha < 5\%$) are printed in bold.

Larval food	Species			Individuals		
	F	df	P	F	df	P
woody	1.42	2;10	0.287	0.51	2;10	0.613
vine/liana	4.85	2;10	0.034	9.58	2;10	0.005
herb monocot	1.50	2;10	0.270	4.13	2;10	0.049
herb dicot	12.84	2;10	0.002	14.98	2;10	0.001
grass	0.59	2;10	0.575	2.26	2;10	0.154
others	3.42	2;10	0.074	6.01	2;10	0.019

Table 9: Results of univariate ANOVA for relative contributions of butterflies with various adult resource traits across the three land use types (see Table 8 for further explanation)

Adult food	Species			Individuals		
	F	df	P	F	df	P
pollen+flowers	4.73	2;10	0.036	6.66	2;10	0.015
fruit/carrion	1.60	2;10	0.249	0.83	2;10	0.464
flowers	2.86	2;10	0.104	2.50	2;10	0.132

idae are strong fliers which mostly live in the forest canopy and therefore are difficult to record. Lycaenidae and Riodinidae, on the other hand, are mostly inconspicuous small butterflies which are easily overlooked. Unlike most other butterflies, many Riodinidae have a crepuscular behaviour and hide under leaves during the daytime. The estimated figures for these two families thus appear to be unreliable, and further specific recording efforts will be needed to provide more realistic insight into the representation of these butterfly families around La Gamba.

These two families were also excluded from the species inventory of the Corcovado National Park by DEVRIES (1978), the only intensive study of butterflies in a Pacific evergreen rainforest in Costa Rica, with a recorded total of 123 species during six months observations (including fruit baiting) in the dry season. This figure compares surprisingly well with 79 recorded (and an esti-

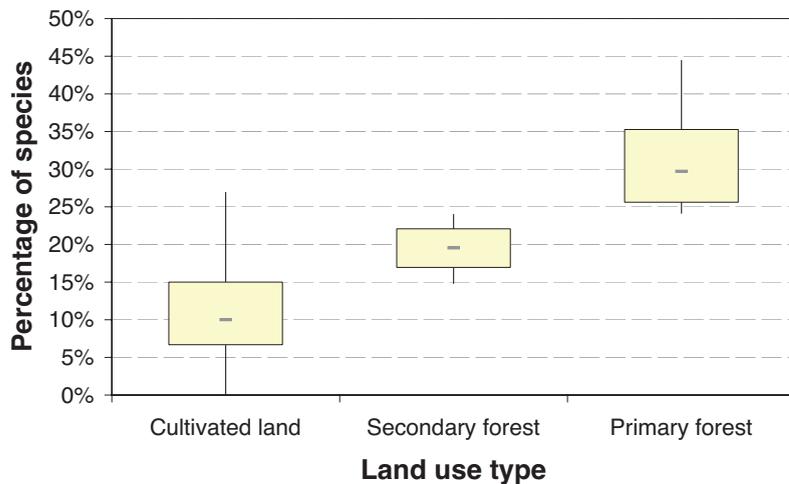


Fig. 3: Relative contribution of species whose larvae feed on "herb dicots" to the butterfly communities in the three land use types. Medians, interquartile ranges (box) and minima/maxima (whiskers) are given.

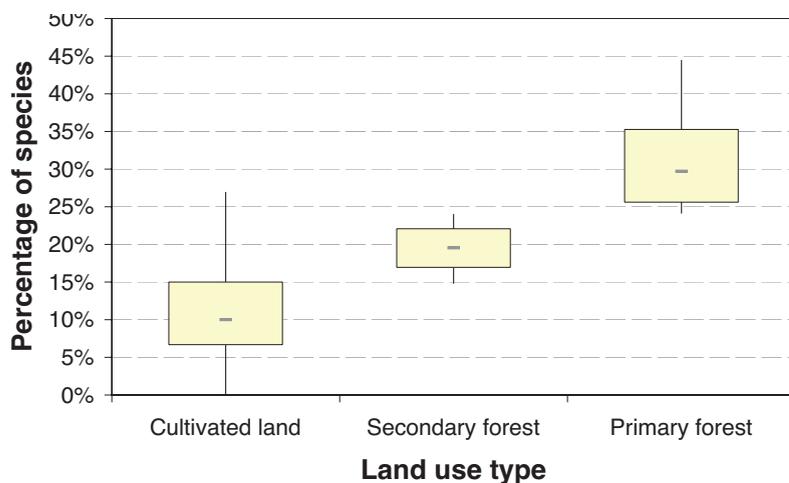


Fig. 4: Relative contribution of species whose larvae feed on "lianas/vines" to the butterfly communities in the three land use types. See Fig. 3 for further explanation.

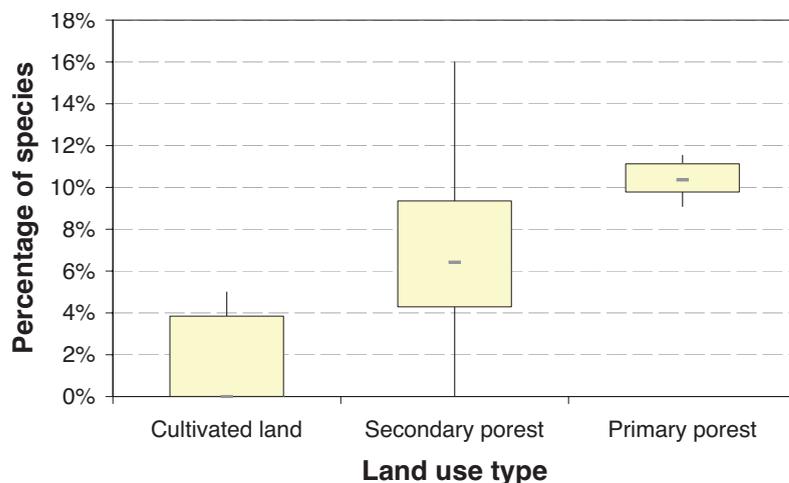


Fig. 5: Relative contribution of species whose adults obligately feed on pollen (besides floral nectar) to the butterfly communities in the three land use types. See Fig. 3 for further explanation.

mated ~100) species of the same families for La Gamba and the Esquinas rainforest. Clearly, the current estimates for the Esquinas rainforest (and surroundings) based on very brief biodiversity inventories are underestimates, and we expect species totals to approach those from the Corcovado National Park with further sampling. This can be deduced from the fact that the cumulative ICE estimate for both years is 25-45% higher than the estimate for a single year. Moreover, most estimator curves (Fig. 1) have not reached an asymptote. The upper bound 95% confidence curve for Chao2, however, seems to have reached an asymptote and the average value of the last six samples (246.6) appears to be a reasonable absolute upper limit for the number of butterfly species to be expected around La Gamba. Thus, this rather small area may be home to about one quarter of the entire butterfly fauna of Costa Rica. Our results also indicate that even short-term surveys may yield data that are amenable to analysis, in the framework of 'rapid biodiversity assessments' (e.g. KERR et al. 2000 for a case study from temperate zone butterflies), at least as long as emphasis is placed on the more conspicuous fraction of butterflies.

Species richness in different land use systems (alpha diversity)

Habitats that have been strongly altered by humans (i.e. pastures, oil palm plantations, roadside verges, and gardens) are relatively poor in butterfly species. This was expected, since many biodiversity studies in tropical landscapes indicate species losses in anthropogenically altered habitats (for a prominent example for Neotropical butterflies see DEVRIES et al. 1999) Even though most sample sites were in close proximity to primary forests, and records might thus include some vagrants from there, observed (47) as well as estimated (69-74) species numbers are much lower than for primary forest (70 observed, 121-130 estimated). These estimates appear to be quite reliable (low Chao2 standard deviations). Secondary forests appear to have an intermediate position, if species numbers are compared. The estimated species totals in secondary forest approach or even exceed those for the primary forest, but they appear to be less reliable with high standard deviations reaching a third of the estimated value.

Interestingly, however, the local diversity of nocturnal moths is sometimes even higher, or at least not significantly lower, at the margin of tropical rainforests than in adjacent forest habitats (e.g. BECK et al. 2002, FIEDLER et al 2007, HILT & FIEDLER 2008). This might indicate that diurnal butterflies are generally more sensitive to clearing or modification of forest than their nocturnal relatives (KOH 2007). The observed changes in butterfly species composition around La Gamba are in line with this suggestion (see below).

Comparison of species diversity between land use systems (beta diversity)

While a significant difference in the species composition of butterfly communities has been demonstrated between natural forest and disturbed habitats, species diversity is unexpectedly uniform between various types of anthropogenically disturbed habitats. This means that butterfly ensembles observed in secondary or gallery forests around La Gamba were largely the same as in the more strongly impacted habitats, and were quite dissimilar to the fauna of pristine forest. This is mainly due to a few dominant species which are common in open areas and mostly have a large distribution throughout the Neotropical and even southern parts of the Nearctic region. As a corollary, this means that the patches or strips of impacted forest around La Gamba are likely of lower conservation value for butterflies than one might hope for (see below).

One outlier with a quite divergent butterfly sample (regeneration forest 1) is explained by the fact that sampling was here only conducted in the interior of this very dense and secondary forest dominated by a single tree species (*Vochysia ferruginea*). The butterfly fauna of that site was impoverished and consisted of only 8 species, almost all of which were only found as single individuals. In contrast to 2006, the secondary forest sampled in 2007 was much more diverse in tree species and also situated in close proximity to primary forest. Butterfly species composition at this forest site was intermediate between the other disturbed habitats and riverine primary forests. Natural forests, on the other hand, are much less uniform than are disturbed habitats. Even sites in close proximity (like ridge forest 1 & 2) appear much less similar than structurally different disturbed habitats located at much higher distances from another. These observations all conform to the concept of biotic homogenisation, i.e. the loss of specialist species in human-impacted landscapes where only a few dominant and widespread species flourish (LOCKWOOD & MCKINNEY 2001). Such dominant species may reduce species diversity in disturbed habitats through direct competition for resources as demonstrated by KUNTE (2008) in an experimental approach carried out in a secondary coastal forest in Corcovado National Park. The removal of two dominant *Anartia* species lead to an increased species diversity due to an increase in nectar availability, a resource which was previously depleted by these two extremely abundant species, *Anartia fatima* and *A. jatrophae*.

The five butterfly species which make up more than half of the similarity between natural forests are all restricted to tropical rainforest of Central and northern South America, and two of them are endemic to Costa

Rica and Panama. Interestingly, these two *Heliconius* species are co-mimics (DEVRIES 1987) and, although they often fly together, seem to have different habitat preferences: While *H. cydno* dominates in the ridge forest, *H. sapho* is more common in riverine forest. The majority of species recorded from primary forest (41, 54.7%) have thus far not been found in disturbed habitats at all. Elsewhere studies have shown that populations of endemic tropical rainforest species are more strongly affected by severe disturbances to their habitat than widely distributed species (CLEARY & MOOERS 2006).

How indicative are surveys of tropical adult butterflies to infer their breeding habitats?

Adult butterflies and their larvae occupy different ecological niches. While larvae depend on their (usually specific) food plants, adults need to take up energy from flowers (nectar, pollen), fruit or carrion, which might not always be found in close proximity to the larval host plants. In contrast to their sedentary caterpillars, most adult butterflies are found in sunny spots, either because their flight activity requires solar energy, or because solar light is important in courtship behaviour. For these reasons, most butterfly species in rainforests are rarely encountered inside the dense forest, but are seen in forest gaps, along riversides, or in the canopy. The question thus arises whether butterflies found in disturbed habitats actually breed in these habitats, or are just visitors from the rainforest in search for important resources. If the latter behaviour dominates, the microdistribution of butterflies should be more strongly correlated with adult than with larval resources. Our analyses for various larval and adult life history traits reveals, however, that most of the significant differences are related to larval host plants. Specifically, there are more butterflies with herb dicot feeding larvae in cultivated habitats, whereas species with caterpillars on climbing or woody plants are more prevalent in the natural forest. These observations correlate well with the high prevalence of herb dicots in disturbed habitats which are nearly absent from primary forests.

The only significant deviation among the adult resource groups was for pollen feeders, all of which belong to the two closely related genera *Heliconius* and *Laparus* which feed on vines in the larval stage (DEVRIES 1987). These vines belong to the genus *Passiflora* which is mainly found in forests and at forest edges, and thus the larval resource use probably better explains the higher percentage of pollen-feeding butterflies in forests. While dispersal abilities in most tropical butterfly species are poorly investigated, butterflies of the genus *Heliconius* are known for their rather low rates of dispersal which is due to home range behaviour. MALLET

(1986), for example, estimated the dispersal parameter σ for *Heliconius erato* to be 296 ± 30 m – a surprisingly low value for a large butterfly that is apparently a strong flier.

Overall, our observations and analyses indicate that larval resources have a stronger influence on the microdistribution of butterflies around La Gamba than requirements of the adult butterflies. This means that forest species in particular show high habitat fidelity, which stands in stark contrast to the high mobility that one might expect for insects with such good flight ability as most butterflies. Moreover, this observation may be critical for the dispersal of butterflies out of persisting forest reserves.

Conclusions

The area of La Gamba with the Esquinas Rainforest harbours an estimated total of 180 (± 24) butterfly species, of which 129 species have been recorded so far. This figure appears to be a low estimate and might still rise with further sampling. The species richness appears to be similar to that in Corcovado National Park which is also situated in the Pacific evergreen forest region of Costa Rica. The area of La Gamba is thus home to about the same number of butterfly species as is the country of Austria, which is one of the most species-rich countries in Europe.

Butterfly diversity is reduced in disturbed habitats compared to primary forests. Secondary forests are more species rich than open pastures or oil palm plantations, but their species composition is much more similar to the surrounding open landscape matrix than to primary forests. Only species-rich secondary forests in direct neighbourhood to primary forests appear to have an intermediate butterfly diversity and species set. Butterfly diversity thus appears to show a similar gross pattern as tree diversity (WEISSENHOFER et al. 2001), which is probably caused by the resource requirements of the herbivorous larval stage. Although the adult stage is more mobile and able to colonise habitats in a distance of several kilometres, many of the true forest species do not regularly leave the closed forest. Most of them did not even show up in secondary forest patches or gallery forest strips in the vicinity to near-pristine closed forest. For forest corridors to be successful in connecting butterfly populations between fragments of remaining primary forest, these corridors should therefore be broad enough and include a high diversity of tree and climber species. Otherwise, it seems unlikely that individuals of these sensitive forest species will enter such corridors in sufficient numbers, e.g. as to stabilise metapopulation dynamics.

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Appendix

Preliminary checklist of the Butterflies of the Golfo Dulce Region (Papilionoidea & Hesperioidea). The table includes our own data (La Gamba) as well as published data from Corcovado National Park (Corcova-

do). Figures for La Gamba are minimum total numbers of specimens recorded in each land use system (including those recorded outside the survey periods). The checklist from DEVRIES (1978) excludes six species which appear to represent misidentifications because they are not listed in DEVRIES (1987).

Species (LAMAS 2004)	Differing taxon names according to DEVRIES (1987 & 1997), D'ABRERA (1995) or WARREN (in litt.)	La Gamba			TOTAL	Corcovado	
		Intensive land use	Secondary forest	Natural forest		DEVRIES (1978)	KUNTE (2008)
Hesperiidae:							
<i>Achlyodes mithridates</i> (FABRICIUS, 1793)							1
<i>Antigonus nearchus</i> (LATREILLE, 1817)							2
<i>Autochton bipunctatus</i> (GMELIN, 1790)							10
<i>Autochton neis</i> (GEYER, 1832)				1	1		
<i>Celaenorrhinus monartus</i> (PLÖTZ, 1884)		1			1		
<i>Celaenorrhinus stallingsi</i> FREEMAN, 1946					1		
<i>Cogia calchas</i> (HERRICH-SCHÄFFER, 1869)							119
<i>Helias cama</i> EVANS, 1953							3
<i>Heliopetes arsalte</i> (LINNAEUS, 1758)					1		47
<i>Hylephila phyleus</i> (DRURY, 1773)							10
<i>Mnasilus allubita</i> (BUTLER, 1877)				1	1		
<i>Molo mango</i> (GUENÉE, 1865)					1		
<i>Nisoniades rubescens</i> (MÖSCHLER, 1877)							1
<i>Nyctelius nyctelius</i> (LATREILLE, 1824)							4
<i>Ouleus fridericus</i> (GEYER, 1832)	<i>Ouleus panna</i>		1		1		
<i>Panoquina ocola</i> (EDWARDS, 1863)			1		1		
<i>Pompeius pompeius</i> (LATREILLE, 1824)		1			1		102
<i>Pyrgus oileus</i> (LINNAEUS, 1767)							286
<i>Pyrgus orcus</i> (STOLL, 1780)					1		
<i>Pyrrhopyge thericles</i> (MABILLE, 1891)	<i>Pyrrhopyge pseudophidias</i>	1			1		
<i>Pythonides jovianus</i> (STOLL, 1782)					1		
<i>Remella vopiscus</i> (HERRICH-SCHÄFFER, 1869)							4
<i>Timocharis trifasciata</i> (HEWITSON, 1868)							1
<i>Urbanus dorantes</i> (STOLL, 1790)							12
<i>Urbanus procne</i> (PLÖTZ, 1880)					1		
<i>Urbanus proteus</i> (LINNAEUS, 1758)							1
<i>Urbanus simplicius</i> (STOLL, 1790)							182
<i>Urbanus teleus</i> (HÜBNER, 1821)							1
<i>Xenophanes tryxus</i> (STOLL, 1780)					1		11
Lycaenidae:							
<i>Arawacus togarna</i> (HEWITSON, 1867)		3	7	5	15		
<i>Arumecla galliena</i> (HEWITSON, 1877)	<i>Thecla galliena</i>		1	11	12		
<i>Brangas caranus</i> (STOLL, 1780)			1		1		
<i>Calycopis demonassa</i> (HEWITSON, 1868)	<i>Thecla demonassa</i>		1		1		
<i>Calycopis isobea</i> (BUTLER & DRUCE, 1872)	<i>Thecla beon</i>		1		1		
<i>Calycopis trebula</i> (HEWITSON, 1868)	<i>Thecla trebula</i>			3	3		
<i>Cupido comyntas</i> (GODART, 1824)	<i>Everes comyntas</i>	6	3		9		
<i>Hemiargus hanno</i> (STOLL, 1790)	<i>Hemiargus ceraunus</i>	7	3		10		
<i>Ocaria thales</i> (FABRICIUS, 1793)	<i>Thecla thales</i>			1	1		
<i>Panthiades bathildis</i> (FELDER & FELDER, 1865)							8
<i>Panthiades phaleros</i> (LINNAEUS, 1767)	<i>Cydno phaleros</i>				1		
<i>Pseudolycaena damo</i> (DRUCE, 1875)							2
<i>Pseudolycaena marsyas</i> (LINNAEUS, 1758)		1			1		
<i>Siderus leucophaeus</i> (HÜBNER, 1813)	<i>Thecla leucophaeus</i>			2	2		

Species (LAMAS 2004)	Differing taxon names according to DeVRIES (1987 & 1997), D'ABRERA (1995) or WARREN (in litt.)	La Gamba			TOTAL	Corcovado	
		Intensive land use	Secondary forest	Natural forest		DEVRIES (1978)	KUNTE (2008)
<i>Theorema eumenia</i> HEWITSON, 1865				1	1		
<i>Theritas hemon</i> (CRAMER, 1775)				1	1		
<i>Theritas lissus</i> (STOLL, 1790)	<i>Thecla hisbon</i>		1		1		
<i>Theritas mavors</i> HÜBNER, 1818					1		
<i>Ziegleria syllis</i> (GODMAN & SALVIN, 1887)	<i>Strymon syllis</i>		1		1		
Nymphalidae:							
<i>Actinote lapitha</i> (STAUDINGER, 1885)						x	
<i>Adelpha basiloides</i> (BATES, 1865)							1
<i>Adelpha boeotia</i> (FELDER & FELDER, 1867)			1		1		
<i>Adelpha cocala</i> (CRAMER, 1779)				2	2	x	
<i>Adelpha cytherea</i> (LINNAEUS, 1758)		21	22	1	44	x	2
<i>Adelpha justina</i> (FELDER & FELDER, 1861)				2	2		
<i>Adelpha salmoneus</i> (BUTLER, 1866)				1	1		
<i>Adelpha serpa</i> (BOISDUVAL, 1836)							1
<i>Aeria eurimedia</i> (CRAMER, 1777)				2	2	x	
<i>Agraulis vanillae</i> (LINNAEUS, 1758)		1			1	x	
<i>Anartia fatima</i> (FABRICIUS, 1793)		41	38	1	80	x	1134
<i>Anartia jatrophae</i> (LINNAEUS, 1763)		58	31		89	x	471
<i>Anthanassa frisia</i> (POEY, 1832)	<i>Anthanassa tulcis</i>	18	7		25	x	53
<i>Antirrhoea philoctetes</i> (LINNAEUS, 1758)	<i>Antirrhoea tomasia</i>				1	x	
<i>Archaeoprepona demophon</i> (LINNAEUS, 1758)						x	
<i>Archaeoprepona demophoon</i> (HÜBNER, 1814)						x	
<i>Caligo atreus</i> (KOLLAR, 1850)						x	
<i>Caligo eurilochus</i> (CRAMER, 1775)						x	
<i>Caligo telamonius</i> (FELDER & FELDER, 1862)	<i>Caligo memnon</i>		1	2	3	x	
<i>Callicore texa</i> (HEWITSON, 1855)							1
<i>Callicore tolima</i> (HEWITSON, 1852)	<i>Callicore pacifica</i>					x	
<i>Callithomia hezia</i> (HEWITSON, 1854)						x	
<i>Castilia eranites</i> (HEWITSON, 1857)				1	1	x	
<i>Catoblepia orgetorix</i> (HEWITSON, 1870)				1	1		
<i>Catonephele numilia</i> (CRAMER, 1775)						x	
<i>Catonephele nyctimus</i> (WESTWOOD, 1850)	<i>Catonephele mexicana</i>					x	
<i>Ceratinia tutia</i> (HEWITSON, 1852)			1		1	x	
<i>Chloreuptychia arnaca</i> (FABRICIUS, 1776)	<i>Chloreuptychia arnaea</i>		10	9	19	x	
<i>Chlosyne hippodrome</i> (GEYER, 1837)							2
<i>Chlosyne janais</i> (DRURY, 1782)						x	
<i>Chlosyne lacinia</i> (GEYER, 1837)						x	8
<i>Chlosyne theona</i> (MÉNÉTRIÉS, 1855)	<i>Thessalia ezra</i>	1	1		2	x	8
<i>Cissia confusa</i> (STAUDINGER, 1887)				2	2	x	
<i>Cissia pompilia</i> (FELDER & FELDER, 1867)	<i>Cissia usitata</i>		2		2		
<i>Cissia pseudoconfusa</i> SINGER, DEVRIES & EHRLICH, 1983					1		
<i>Cithaeris pireta</i> (STOLL, 1780)	<i>Cithaeris menander</i>			1	1	x	
<i>Colobura dirce</i> (LINNAEUS, 1758)	*	2			2	x	
<i>Consul fabius</i> (CRAMER, 1776)		2			2	x	
<i>Danaus gilippus</i> (CRAMER, 1775)						x	7
<i>Danaus plexippus</i> (LINNAEUS, 1758)		1			1	x	
<i>Diaethria astala</i> (GUÉRIN-MÉNEVILLE, 1844)						x	
<i>Diaethria clymena</i> (CRAMER, 1775)	<i>Diaethria marchalli</i>					x	
<i>Dione juno</i> (CRAMER, 1779)		3		1	4		62
<i>Dircenna dero</i> (HÜBNER, 1823)						x	
<i>Dryadula phaetusa</i> (LINNAEUS, 1758)		1			1	x	1

Species (LAMAS 2004)	Differing taxon names according to DeVRIES (1987 & 1997), D'ABRERA (1995) or WARREN (in litt.)	La Gamba			TOTAL	Corcovado	
		Intensive land use	Secondary forest	Natural forest		DeVRIES (1978)	KUNTE (2008)
<i>Dryas iulia</i> (FABRICIUS, 1775)		4	4	2	10	x	13
<i>Dynamine agacles</i> (DALMAN, 1823)		1	2		3		
<i>Dynamine tithia</i> (HÜBNER, 1823)	<i>Dynamine salpensa</i>				1	x	
<i>Eresia eunice</i> (HÜBNER, 1807)	<i>Eresia mechanitis</i>					x	
<i>Eresia ithomioides</i> HEWITSON, 1864	<i>Eresia eutropia</i> & <i>Eresia melaina</i>		1	2	3		
<i>Eryphanis automedon</i> (CRAMER, 1775)	<i>Eryphanis polyxena</i>					x	
<i>Eueides aliphera</i> (GODART, 1819)						x	4
<i>Eueides isabella</i> (STOLL, 1781)		1			1		
<i>Eueides lineata</i> SALVIN & GODMAN, 1868				4	4		
<i>Eueides lybia</i> (FABRICIUS, 1775)			1	6	7	x	
<i>Eunica alpais</i> (GODART, 1824)	<i>Eunica excelsa</i>	1	1		2	x	
<i>Eunica chlororhoa</i> SALVIN, 1869	<i>Eunica mira</i>			1	1		
<i>Eunica sydonia</i> (GODART, 1824)	<i>Eunica caresa</i>		1		1		
<i>Eunica volumna</i> (GODART, 1824)	<i>Eunica venusia</i>					x	
<i>Euptoieta hegesia</i> (CRAMER, 1779)		1			1	x	51
<i>Euptychia insolata</i> BUTLER & DRUCE, 1872			1	4	5	x	
<i>Euptychia jesia</i> BUTLER, 1869		3	6	9	18		
<i>Euptychia westwoodi</i> BUTLER, 1867						x	
<i>Fountainea euryppyle</i> (FELDER & FELDER, 1862)	<i>Memphis euryppyle</i>	1			1		
<i>Godyris zavaleta</i> (HEWITSON, 1855)	<i>Godyris zygia</i>					x	
<i>Hamadryas amphinome</i> (LINNAEUS, 1767)						x	
<i>Hamadryas feronia</i> (LINNAEUS, 1758)		5		1	6		
<i>Hamadryas guatemalena</i> (BATES, 1864)						x	
<i>Heliconius charithonia</i> (LINNAEUS, 1767)	<i>Heliconius charitonius</i>					x	
<i>Heliconius cydno</i> (DOUBLEDAY, 1847)	<i>Heliconius pachinus</i>		2	11	13	x	
<i>Heliconius erato</i> (LINNAEUS, 1758)						x	16
<i>Heliconius hecale</i> (FABRICIUS, 1776)						x	20
<i>Heliconius ismenius</i> LATREILLE, 1817			1		1	x	
<i>Heliconius melpomene</i> (LINNAEUS, 1758)		1	4	1	6	x	
<i>Heliconius sapho</i> (DRURY, 1782)	<i>Heliconius hewitsoni</i>	1	4	10	15	x	
<i>Heliconius sara</i> (FABRICIUS, 1793)			1	1	2	x	29
<i>Hermeuptychia hermes</i> (FABRICIUS, 1775)	<i>Cissia hermes</i>	62	55	6	123	x	
<i>Historis acheronta</i> (FABRICIUS, 1775)						x	
<i>Historis odius</i> (FABRICIUS, 1775)		1			1	x	
<i>Hyposcada virginiana</i> (HEWITSON, 1855)			1	5	6	x	
<i>Ithomia patilla</i> HEWITSON, 1852						x	
<i>Janatella leucodesma</i> (FELDER & FELDER, 1861)						x	
<i>Junonia evarete</i> (CRAMER, 1779)		4			4		158
<i>Laparus doris</i> (LINNAEUS, 1771)	<i>Heliconius doris</i>			12	12	x	
<i>Lycorea halia</i> (HÜBNER, 1816)	<i>Lycorea cleobaea</i>		2	1	3		
<i>Magneuptychia gomezi</i> (SINGER, DeVRIES & EHRlich, 1983)	<i>Cissia gomezi</i>		1	1	2		
<i>Magneuptychia libye</i> (LINNAEUS, 1767)	<i>Cissia libye</i>	2	10		12	x	
<i>Marpesia berania</i> (HEWITSON, 1852)		1			1	x	
<i>Marpesia chiron</i> (FABRICIUS, 1775)		1			1	x	
<i>Marpesia furcula</i> (FABRICIUS, 1793)	<i>Marpesia iole</i>				1	x	
<i>Marpesia merops</i> (DOYÈRE, 1840)		4	2	3	9	x	
<i>Marpesia petreus</i> (CRAMER, 1776)						x	
<i>Mechanitis lysimnia</i> (FABRICIUS, 1793)							1
<i>Mechanitis polymnia</i> (LINNAEUS, 1758)		5	22	5	32	x	
<i>Megeuptychia antonoe</i> (CRAMER, 1775)				1	1	x	
<i>Melinaea lilis</i> (DOUBLEDAY, 1847)	<i>Melinaea scylax</i>			1	1	x	

Species (LAMAS 2004)	Differing taxon names according to DeVRIES (1987 & 1997), D'ABRERA (1995) or WARREN (in litt.)	La Gamba			TOTAL	Corcovado	
		Intensive land use	Secondary forest	Natural forest		DEVRIES (1978)	KUNTE (2008)
<i>Memphis forreri</i> (GODMAN & SALVIN, 1884)						x	
<i>Memphis oenomais</i> (BOISDUVAL, 1870)						x	
<i>Memphis xenocles</i> (WESTWOOD, 1850)		2			2		
<i>Morpho cypris</i> WESTWOOD, 1851						x	
<i>Morpho helenor</i> (CRAMER, 1776)	<i>Morpho peleides</i>			1	1	x	
<i>Morpho menelaus</i> (LINNAEUS, 1758)	<i>Morpho amathonte</i>			4	4	x	
<i>Morpho theseus</i> DEYROLLE, 1860						x	
<i>Nessaea aglaura</i> (DOUBLEDAY, 1848)				2	2	x	
<i>Nica flavilla</i> (GODART, 1824)						x	1
<i>Oleria rubescens</i> (BUTLER & DRUCE, 1872)						x	
<i>Opsiophanes tamarindi</i> FELDER & FELDER, 1861						x	
<i>Pareuptychia metaleuca</i> (BOISDUVAL, 1870)						x	
<i>Pareuptychia ocirrhoe</i> (FABRICIUS, 1776)	<i>Cissia hesione</i>	23	28		51		
<i>Perophtalma lasus</i> WESTWOOD, 1851				1	1		
<i>Philaethria dido</i> (LINNAEUS, 1763)		1		8	9	x	
<i>Pierella helvina</i> (HEWITSON, 1859)	<i>Pierella helvetia</i>			4	4	x	
<i>Pierella luna</i> (FABRICIUS, 1793)			1	5	6	x	
<i>Pteronymia alcmena</i> (GODMAN & SALVIN, 1877)	<i>Eunica alcmena</i>					x	
<i>Pteronymia aletta</i> (HEWITSON, 1855)	<i>Pteronymia agalla</i>					x	
<i>Pyrrhogyra crameri</i> AURIVILLIUS, 1882	<i>Pyrrhogyra crameri</i>			1	1	x	
<i>Pyrrhogyra otolais</i> BATES, 1864						x	
<i>Siproeta stelenes</i> (LINNAEUS, 1758)		3	2		5	x	
<i>Taygetis laches</i> FABRICIUS, 1793	<i>Taygetis andromeda</i>					x	
<i>Temenis laothoe</i> (CRAMER, 1777)						x	
<i>Thyridia psidii</i> (LINNAEUS, 1758)						x	
<i>Tithorea tarricina</i> HEWITSON, 1858			5	1	6	x	
<i>Ypthimoides renata</i> (STOLL, 1780)	<i>Cissia renata</i>					x	
Papilionidae:							
<i>Battus lycidas</i> (CRAMER, 1777)				1	1		
<i>Battus polydamas</i> (LINNAEUS, 1758)						x	
<i>Eurytides orabilis</i> (BUTLER, 1872)						x	
<i>Heraclides androgeus</i> (CRAMER, 1775)	<i>Papilio androgeus</i>						1
<i>Heraclides crespontes</i> (CRAMER, 1777)	<i>Papilio crespontes</i>					x	
<i>Heraclides thoas</i> (LINNAEUS, 1771)	<i>Papilio thoas</i>	1			1		18
<i>Mimoides ilus</i> (FABRICIUS, 1793)	<i>Eurytides ilus</i>			1	1		
<i>Parides childrenae</i> (GRAY, 1832)				5	5	x	1
<i>Parides eurimedes</i> (STOLL, 1782)	<i>Parides arcas</i>					x	
<i>Parides iphidamas</i> (FABRICIUS, 1793)						x	
<i>Parides panares</i> (GRAY, 1853)	<i>Parides lycimenes</i>			1	1		
<i>Protesilaus protesilaus</i> (LINNAEUS, 1758)	<i>Eurytides protesilaus</i>					x	
<i>Protographium calliste</i> (BATES, 1864)	<i>Eurytides calliste</i>					x	
<i>Protographium thyastes</i> (DRURY, 1782)	<i>Eurytides marchandi</i>					x	
<i>Pterourus menatius</i> (HÜBNER, 1819)	<i>Papilio cleotas</i> & <i>Papilio victorinus</i>						2
Pieridae:							
<i>Anteos clorinde</i> (GODART, 1824)						x	
<i>Aphrissa boisduvalii</i> (FELDER & FELDER, 1861)						x	
<i>Aphrissa statira</i> (CRAMER, 1777)		1		1	2	x	1
<i>Archonias brassolis</i> (FABRICIUS, 1776)	<i>Archonias tereas</i>			5	5		
<i>Ascia monuste</i> (LINNAEUS, 1764)						x	51
<i>Dismorphia theucharila</i> (DOUBLEDAY, 1848)			1	1	2		
<i>Enantia melite</i> (LINNAEUS, 1763)	<i>Enantia licinia</i>		1		1		

Species (LAMAS 2004)	Differing taxon names according to DeVRIES (1987 & 1997), D'ABRERA (1995) or WARREN (in litt.)	La Gamba			TOTAL	Corcovado	
		Intensive land use	Secondary forest	Natural forest		DeVRIES (1978)	KUNTE (2008)
<i>Eurema albula</i> (CRAMER, 1775)		6	2		8		20
<i>Eurema daira</i> (GODART, 1819)		34	20		54	x	
<i>Glutophrissa drusilla</i> (CRAMER, 1777)	<i>Appias drusilla</i>	3	1		4		
<i>Perrhybris pamela</i> (STOLL, 1780)	<i>Perrhybris pyrrrha</i>					x	
<i>Phoebis argante</i> (FABRICIUS, 1775)						x	
<i>Phoebis neocypris</i> (HÜBNER, 1823)	<i>Phoebis rurina</i>					x	
<i>Phoebis philea</i> (LINNAEUS, 1763)		3			3	x	
<i>Phoebis sennae</i> (LINNAEUS, 1758)		16		1	17		11
<i>Pyrisitia lisa</i> (BOISDUVAL & LE CONTE, 1830)	<i>Eurema lisa</i>						8
<i>Pyrisitia nise</i> (CRAMER, 1775)	<i>Eurema nise</i>	46	17		63		
<i>Pyrisitia proterpia</i> (FABRICIUS, 1775)	<i>Eurema proterpia</i>					x	
Riodinidae:							
<i>Calephelis browni</i> McALPINE, 1971		2			2		
<i>Calephelis laverna</i> (GODMAN & SALVIN, 1886)		1	4		5		
<i>Charis anius</i> (CRAMER, 1776)	<i>Charis auius</i>		4	2	6		
<i>Chimastrum argentea</i> (BATES, 1866)	<i>Chimastrum argenteum</i>				1		
<i>Detritivora gynaea</i> (GODART, 1824)	<i>Charis gynaea</i>			1	1		
<i>Eurybia elvina</i> STICHEL, 1910			1	1	2		
<i>Eurybia lycisca</i> WESTWOOD, 1851		2	7	3	12		
<i>Eurybia unxia</i> GODMAN & SALVIN, 1885		1			1		
<i>Euselasia aurantia</i> (BUTLER & DRUCE, 1872)			1		1		
<i>Juditha molpe</i> (HÜBNER, 1808)			4	1	5		
<i>Leucochimona lepida</i> (GODMAN & SALVIN, 1885)				1	1		
<i>Menander pretus</i> (CRAMER, 1777)				2	2		
<i>Mesene phareus</i> (CRAMER, 1777)			1		1		
<i>Mesene viz.phareus</i> (CRAMER, 1777)				1	1		
<i>Mesenopsis melanochlora</i> (GODMAN & SALVIN, 1878)				1	1		
<i>Mesosemia asa</i> HEWITSON, 1869				5	5		
<i>Mesosemia telegone</i> (BOISDUVAL, 1836)				1	1		
<i>Mesosemia zonalis</i> GODMAN & SALVIN, 1885				1	1		
<i>Napaea eucharila</i> (BATES, 1867)			1		1		
<i>Nymphidium ascolia</i> HEWITSON, 1853			5	1	6		
<i>Perophtalma lasus</i> WESTWOOD, 1851				5	5		
<i>Pirascca arbuscula</i> (MÖSCHLER, 1883)	<i>Stichelia arbuscula</i>		2		2		
<i>Sarota chrysus</i> (STOLL, 1781)	<i>Sarota dematira</i>			1	1		
<i>Sarota gyas</i> (CRAMER, 1775)		1			1		
<i>Thisbe lycorias</i> (HEWITSON, 1853)			3		3		
Total number of species		53	62	75	144	111	51

* Since DeVRIES (1987) *Colobura annulata* was discovered as a new species (WILLMOTT et al. 2001) which also occurs in Costa Rica and was previously confused with *Colobura dirce*.



Figs 6-14: Butterflies of the Piedras Blancas National Park and its vicinity. **(6)** *Heraclides thoas* is a widespread Neotropical swallowtail (family Papilionidae), whose larvae feed on pepper trees (*Piper*); almost indistinguishable is *Heraclides crespontes*, but its larvae feed on Rutaceae (e.g. lemon trees). **(7)** *Dismorphia theucharila* is an unusual Central American representative of the family Pieridae (the “whites & sulphurs”); it has transparent wings mimicking ithomiines of the family Nymphalidae. **(8)** *Arawacus togarna*, a hairstreak of the family Lycaenidae,

with a striped pattern similar to some satyrines of the family Nymphalidae (e.g. the following species). **(9)** *Pareuptychia ocirrhoe* is a Central American representative of the subfamily Satyrinae (family Nymphalidae) which is frequently found in forest habitats. **(10)** *Pierella helvina* is another Central American satyrine species (family Nymphalidae) which is well camouflaged when sitting on the forest floor; its upperside, however, contains a bright red patch which is displayed only during flight or when the butterfly is disturbed, probably startling attackers; this patch is visible in the photographed specimen due to wing damage. **(11)** *Hamadryas feronia* (Nymphalidae) and its very similar congeners are usually seen feeding on rotten fruit or sitting on tree bark where they are well camouflaged; most famous is the crackling noise produced by interacting individuals. **(12)** *Cithaerias pireta* is an almost transparent Central American member of the subfamily Satyrinae (family Nymphalidae) which is found in wet forests flying close to the ground. **(13)** *Charis anius* is an inconspicuous member of the Riodinidae, a family which is almost completely confined to the Neotropical region; its larvae feed on dead leaves. **(14)** *Urbanus teleus* represents the family Hesperidae whose members usually have a dull coloration; this (and some related) species bear tails like many swallowtails of the family Papilionidae.



Figs 15-25: Butterflies of the Piedras Blancas National Park and its vicinity. **(15)** *Anartia jatrophae* (Nymphalidae) is an indicator species of open disturbed habitats throughout the Neotropics and southern parts of the Nearctic region. **(16)** *Chloreuptychia arnaca* (Nymphalidae) is a Central American satyrine species indicative of natural rainforest habitats. **(17)** *Arumecla galliena* (Lycaenidae) is a hairstreak which flies around trees in primary rainforests and appears to prefer ridge forests over riverine forests. **(18)** *Laparus doris* (Nymphalidae) uses pollen as a nectar source like the members of the closely related genus *Heliconius*. **(19)** *Colobura dirce* (Nymphalidae) is a widespread Neotropical species which likes to feed on rotten fruits; a similar species (*C. dirce*) was only recently separated from *C. dirce* due to minor differences in wing pattern; these two mostly sympatric species are well differentiated in larval biology and behaviour. **(20)** *Historis odius* (Nymphalidae) is a strong flyer which only feeds on rotten fruits and dung; the specimen on the photo is attracted to a rotten banana at the field station. **(21)** *Dryas iulia* (Nymphalidae) larvae are feeding on leaves of passionfruit (*Passiflora*), a genus of vines which also comprises food plants for the closely related genus *Heliconius*. **(22)** *Cissia pseudoconfusa* (Nymphalidae) is a member of the subfamily Satyrinae, most of which feed on grasses. **(23)** *Morpho helenor* (Nymphalidae) is a forest species whose larvae feed on trees of the family Fabaceae. **(24)** *Anthanassa frisia* (Nymphalidae) is indicative of disturbed habitats and its larvae feed on herbs of the plant family Acanthaceae. **(25)** *Caligo memnon* (Nymphalidae) belongs to the Brassoliniinae ("owl butterflies"), a subfamily whose members are unusual among butterflies because of their crepuscular behaviour; *C. memnon* is often seen in banana plantations because its larvae feed on plants of the genera *Musa* and *Heliconia*, both of which are monocots.

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