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Article

Butterfly Assemblages Differ among Vegetation Types in Southern Amazonia

Luísa L. Mota ^{1,*} , Jessie P. Santos ¹ , Keith R. Willmott ² and André V. L. Freitas ¹ 

¹ Departamento de Biologia Animal, Universidade Estadual de Campinas—UNICAMP, Campinas 13083-862, SP, Brazil; jessiepereira@gmail.com (J.P.S.); baku@unicamp.br (A.V.L.F.)

² McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA; kwillmott@flmnh.ufl.edu

* Correspondence: lulismota@yahoo.com.br

Abstract: Environmental heterogeneity is considered an important factor supporting the evolution and maintenance of biodiversity. At small scales, such heterogeneity is thought to promote species co-existence through an increase in niche opportunities. Amazonia, the largest and most biodiverse rainforest in the world, presents a large number of vegetation types within its territory. Here, we tested the hypothesis that butterfly assemblages differ among five vegetation types at a small scale (less than 1 km²) in a region of Southern Amazonia. The vegetation types studied were forest gap, terra firme, igapó, semi-deciduous forest, and bamboo forest. The richest and most abundant community was in forest gap; igapó was the least rich, but held the second most abundant community and the only one with nine indicator species instead of two or three. Assemblage composition differed among all vegetation types, with the exception of forest gap and bamboo forest. Different light levels, temperatures, humidity, and host plant availability among vegetation types are likely relevant factors influencing these butterfly assemblages. The results suggest that the presence of various vegetation types in the region promotes the coexistence of butterfly species, and that specific threats to each vegetation type should be addressed to conserve the region's biodiversity.

Keywords: Amazon forest; environmental heterogeneity; habitat diversity; tropical



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1. Introduction

Understanding the origins and maintenance of biological diversity is an essential objective of ecology, and environmental heterogeneity is regarded as an important factor related to both, depending on the scale considered [1,2]. At large spatial and temporal scales, heterogeneity is thought to promote speciation, while at smaller, within-community scales, it is believed to enhance species co-existence through an increase in available niche space. Accordingly, positive correlations between diversity and environmental heterogeneity have been found for a variety of taxa and regions [2–4], although negative relationships also occur in some contexts [3,5]. Environmental heterogeneity is, in fact, a complex term itself, encompassing many aspects of physical and biological variation in space, such as topography, climate, and human use of the land, but one of its best studied facets is habitat diversity, which refers to the presence of different forms of land cover, such as vegetation types, in a given area [6]. Vegetation type is especially relevant for many groups of animals, since the vegetation defines the physical structure of the environment and the availability of food for herbivores and, potentially, their predators and parasites [7–9]. Within forested habitats, for instance, the vegetation type includes the presence of natural gaps that are formed by, among other causes, the falling of canopy trees, which allows for greater light entrance in the understory and initiates a succession process [10–13]. Moreover, a single phytogeographic domain may have several characteristic vegetation physiognomies that can occur in close proximity to each other and are often associated with abiotic conditions such as soil composition, water retention, and fire frequency e.g., [14].

Amazonia is the most diverse rainforest in the world [15,16] and is an example of a biome that contains multiple vegetation physiognomies [17–19]. The best-known vegetation types are evergreen, non-flooded forests known as “terra firme”, which account for most of the Amazonian territory, and the floodplain forests that are seasonally inundated by the rise of river or lake levels [20–22]. However, with more than 4,000,000 km² within Brazil alone [23], Amazonia also contains several lesser-known vegetation types, such as fields, savannic formations, white-sand habitats [19,24,25] and forests heavily dominated by woody bamboo species of the genus *Guadua* Kunth [26,27]. In Southern Amazonia, where the dry season is more severe and lasts longer than in Central Amazonia, areas of deciduous and semi-deciduous forests are also present [28–30].

The existence of this variety of vegetation types is one of the reasons behind Amazonia’s great diversity, and this vegetation diversity has been shown to affect the assemblages of several animal taxa, including anurans [31], bats [32], primates [33], and birds [34,35]. Recent studies regarding butterflies have found different assemblages between terra firme and floodplain forests in Central Amazonia [36–38], and taxonomic and functional responses to an environmental gradient between terra firme and white-sand habitats in Northern Amazonia [39]. Butterflies are considered an especially good model to test assemblage associations to environmental characteristics, since they are a relatively well-known group of invertebrates, easy to collect, and many are largely dependent on specific host plants and habitats [40–43]. However, the effects of the great environmental heterogeneity of Southern Amazonia on its particularly rich butterfly community remain unexplored.

In the present study, we tested the hypothesis that butterfly assemblages differ in diversity measures and composition among five types of vegetation (*terra firme*, *igapó*, *semi-deciduous forest*, *bamboo forest*, and *forest gap*), all of which are found as a mosaic within less than 1 km² in the region of the river Cristalino, in Southern Amazonia. We also tested for the presence of species associated with particular vegetation types, and discuss these results in relation to the characteristics of each kind of vegetation, butterfly natural history, and conservation.

2. Materials and Methods

2.1. Study Area

Cristalino Lodge (9°35′51″ S, 55°55′52″ W) is located in the Brazilian Southern Amazonia in the municipality of Alta Floresta, Mato Grosso State. While the Amazonia in this state has suffered great deforestation rates in recent decades [23], Cristalino Lodge is situated in the midst of a continuous area of forest delimited by its associated private reserves (72 km²) and other larger conservation areas located to the North.

The region is warm and humid, but with a dry season that lasts between 3 and 5 months. The average annual temperature is between 26 °C and 27 °C, and the annual rainfall is over 2300 mm [44,45]. The altitude varies between 100 m and 400 m (on the tops of hills locally called “serras”) [46,47].

The vegetation is characterized by the presence of many different physiognomies [30]. Most of the area is covered by evergreen, terra firme forests, which have a high floristic diversity, a canopy height of 25–35 m, and a moderate number of lianas. However, there are also enclaves of deciduous forests (Figure 1A) that occur on rocky outcrops and on the tops of the “serras”. Between these areas, there are semi-deciduous, transitional forests that have a combination of perennial and deciduous species and a higher prevalence of lianas in the understory. Floodplain forests are found at low elevations near the rivers and are periodically flooded, presenting a relatively open understory [30]. Patches of vegetation heavily dominated by bamboos, called bamboo forests or “tabocais”, are found within the terra firme forest (Figure 1D).

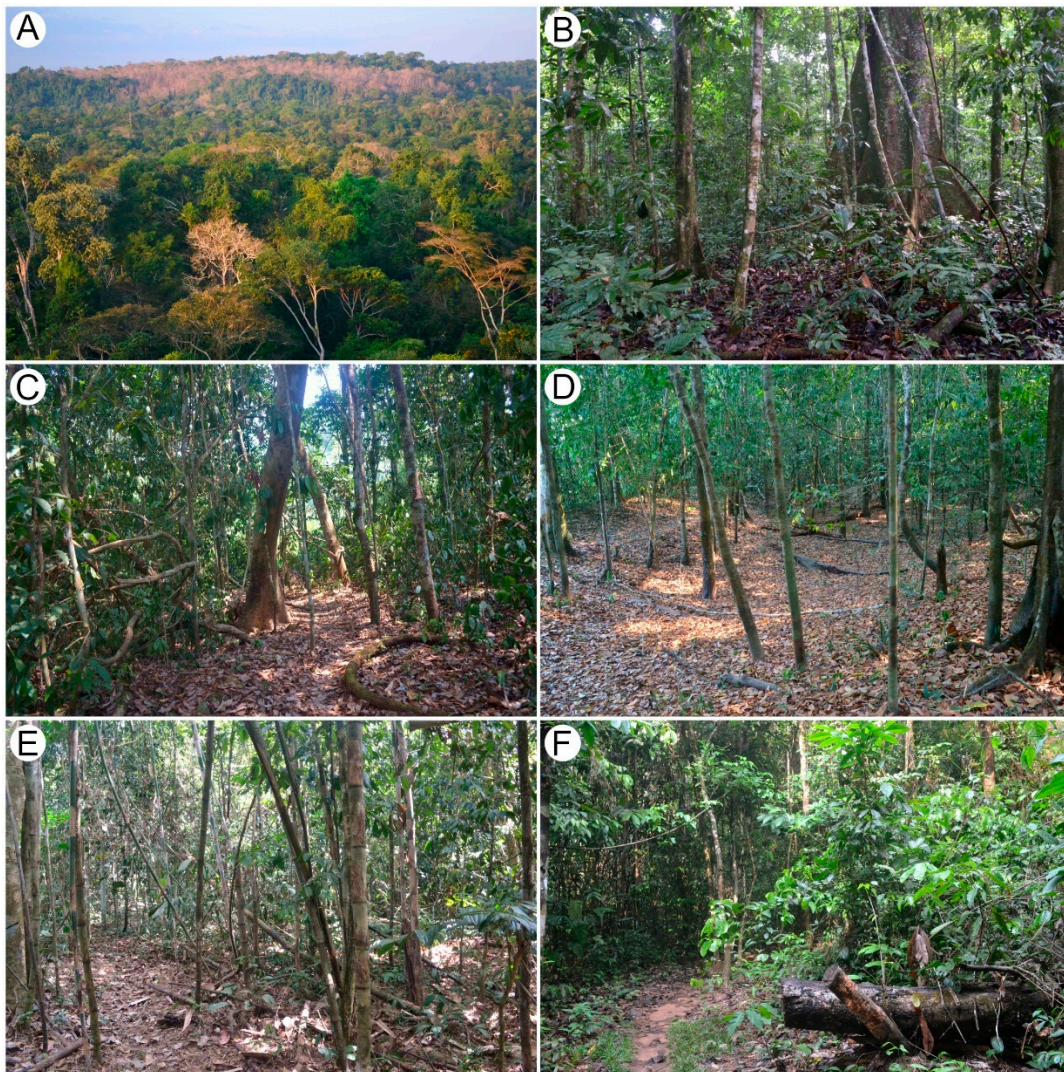


Figure 1. Vegetation types that occur at Cristalino Lodge (Alta Floresta, Mato Grosso, Brazil), in Southern Amazonia. (A) View of *terra firme* and deciduous forest (dry vegetation in the background) from a 50 m observation tower; (B) *terra firme*; (C) *semi-deciduous forest*; (D) *igapó* (floodplain forest) during the dry season; (E) *bamboo forest*; (F) *forest gap*.

The butterfly fauna of the region is relatively well known, with more than 1000 species (Table S1) recorded by butterfly watchers, ecotourists, and researchers since the opening of the lodge in 1991. The most taxonomically diverse families are Hesperidae and Nymphalidae, followed by Riodinidae [48].

2.2. Butterfly Sampling and Identification

The main trails that are accessible from the Lodge were walked several times by LLM between September and November 2015 for better familiarity with the local vegetation and butterfly fauna. We focused the study on five vegetation types, although there are others present in the region [30,46,47]. Fifty plots of 10×5 m were delimited along the trails, 10 plots for each of the five vegetation types studied: (1) *terra firme* (evergreen, non-flooded forest) (Figure 1A,B), (2) *semi-deciduous forest* (Figure 1C), (3) *igapó* (floodplain forest periodically inundated by the black-water river Cristalino) (Figure 1D), (4) *bamboo forest* (Figure 1E), and (5) *forest gap* (natural treefall gaps within *terra firme*; considered as a distinct “vegetation type” for the purposes of this work because of the distinct plant structure and composition) (Figure 1F). The size of the plots was measured with a retractable tape measure, and yellow tape was glued around tree trunks at the edges of the plots to provide

spatial reference. Because some vegetation types occurred only as limited patches along the trails, some of the plots were contiguous; however, the plots never intersected. The polygon delineated by the plots is less than 1 km² and the maximum distance between plots is less than 1.5 km. From April 2016 onwards, two plots of *semi-deciduous forest* had to be substituted due to drastic habitat changes. Each trail was walked multiple times between November 2015 and September 2016, and plots located on the same trails were observed on the same days between 8 am and 5 pm.

Observations of the same plot were made after a period of at least 48 h, but usually after five or more days. The minimum number of observations from each plot was 24; plots that had more observations than this had data from randomly selected observations excluded, so that all plots had a total of 24 observations, and all vegetation types had a total of 240 observations. Each observation consisted of 10 min of slowly walking back and forth along the plot, paying attention to the presence of butterflies, and all fieldwork was conducted by LLM to avoid differences in collecting and identification ability among observers.

Temperature and humidity were measured using an Instrutherm© digital thermo-hygro-anemometer in the center of the plot immediately after the end of each 10 min observation. Individuals found inside the plot or that flew through it were collected using an entomological net with handles plus rim diameter of 2.5 m or, if collection was not possible, had the lowest taxonomic group of certainty recorded in a notebook. Butterflies were only recorded if within the height reach of the collector with the net, so the data for all vegetation types were restricted to the understory. However, we believe that most butterfly specimens present at each observation, under the height considered in this study, could be successfully detected. Species that could be easily identified in the field and that were already represented by collected specimens were not always captured, or were frequently released after capture. Collected specimens were deposited in the zoological collection of the Museu de Diversidade Biológica, Universidade Estadual de Campinas (Unicamp), Campinas, São Paulo, Brazil. These specimens were used, with other data, for a recently published inventory of the butterflies of Cristalino Lodge (Mota et al., 2022) [48].

Identifications were made by specialists and the authors of this study, and details on identification and taxonomy are provided in [48]. Taxonomy of the nymphalid subtribe Eupychiina was updated after [49]. Due to difficulty in the capture, identification, or taxonomic uncertainty of some taxa, some species were merged and treated as a single entity for the purposes of this study, and some others could only be identified as “morphospecies” (Table S2). For simplicity, each of the entities considered in the present study will be denoted as a “species” hereafter, except where appropriate in the Discussion section.

2.3. Data Analyses

We used abundance, species richness, and species composition as diversity parameters to compare the butterfly assemblages among the five vegetation types. For this purpose, all sampled butterflies were pooled by plot. In the case of the two *semi-deciduous forest* plots that had to be substituted because of habitat changes, the butterflies sampled in the original plots were pooled with the ones sampled subsequently in the substitute plots (which belonged to the same vegetation type).

To test whether species richness differed among vegetation types, we used rarefaction curves based on sampled coverage and the interpolation and extrapolation method of Jost [50]. The diversity among vegetation types was calculated through Renyi’s Entropy, which gives different diversity measures based on species richness ($q = 0$), equability ($q = 1$), and dominance ($q = 2$).

We used a permutational multivariate analysis of variance (PERMANOVA) based on the Morisita dissimilarity measure to compare the species composition among vegetation types. A non-metric multidimensional scaling (NMDS) based on the Morisita dissimilarity index was used for visualization. A canonical ordination was made to visualize the association of plots and vegetation types to a gradient of humidity and temperature.

To identify species associated with specific vegetation types, we used an IndVal (“indicator species”) analysis. To avoid occasional and weak associations, we only considered species with at least five records and probability values of $p \leq 0.01$.

Analyses were made in the software PAST [51] or using the R Studio program [52].

3. Results

A total of 1571 individuals belonging to 322 species and all 7 butterfly families (including moth-like butterflies, Hedyliidae) were recorded (Table S1). The richest and most abundant family was Nymphalidae, with 112 species and 972 records. The second richest family was Hesperidae, with 90 species and 181 records, but the second most abundant family was Riodinidae, with 84 species and 337 records. These families were followed by Lycaenidae (23 species, $n = 46$), Pieridae (7 species, $n = 17$), Papilionidae (5 species, $n = 16$), and Hedyliidae (1 species, $n = 2$ records) (Table 1). The most abundant subfamily was Satyrinae, and the tribe Satyrini had the two most abundant species, *Hermeuptychia* sp. ($n = 109$) and *Euptychia westwoodi* Butler, 1867 ($n = 104$).

Table 1. Richness and abundance (between parentheses) of each butterfly family for five vegetation types at Cristalino Lodge (Alta Floresta, Mato Grosso, Brazil), in Southern Amazonia.

	<i>Terra Firme</i>	<i>Semi-Deciduous Forest</i>	<i>Igapó</i>	<i>Bamboo Forest</i>	<i>Forest Gap</i>	Total
Nymphalidae	46 (173)	49 (203)	36 (204)	60 (197)	57 (195)	112 (972)
Hesperidae	23 (30)	29 (36)	23 (30)	22 (23)	41 (62)	90 (181)
Riodinidae	28 (72)	38 (60)	26 (81)	22 (43)	36 (81)	84 (337)
Lycaenidae	6 (6)	5 (9)	2 (11)	0	16 (20)	23 (46)
Pieridae	1 (4)	2 (2)	5 (6)	2 (4)	1 (1)	7 (17)
Papilionidae	0	2 (4)	4 (9)	2 (2)	1 (1)	5 (16)
Hedyliidae	1 (1)	0	0	1 (1)	0	1 (2)
All butterflies	105 (286)	125 (314)	96 (341)	109 (270)	152 (360)	322 (1571)

Most of the species were sampled only once or a few times: 132 species were singletons and 65 were doubletons, representing 41% and 20.2% of all species, respectively. Singletons and doubletons, together, accounted for 61.2% of the species, but only 16.7% of the total records ($n = 262$). In total, 68 (21.2%) species were recorded at least 5 times, and 35 (10.9%), at least 10 times. All the vegetation types had at least 50% of singletons (species recorded only once in that vegetation type, but that might also be represented in other vegetation types), with more than 60% in the *forest gap*, the *bamboo forest*, and *terra firme* (which had the highest percentage, of 62.2%). Of the 190 species with at least two records, 41 (21.6%) were found in a single vegetation type, and of the 68 species with five records or more, only 7 (10.3%) were exclusive to one vegetation.

The most abundant vegetation type was the *forest gap*, with 360 records, followed by *igapó* ($n = 341$), *semi-deciduous forest* ($n = 314$), *terra firme* ($n = 286$), and *bamboo forest* ($n = 270$) forests (Table 1). All vegetation types showed the same pattern regarding the most abundant families, with Nymphalidae being the most abundant, followed by Riodinidae and then Hesperidae. The most abundant species in both *terra firme* and the *semi-deciduous forest* was *Euptychia westwoodi*, while *Hermeuptychia* sp. was the most abundant in *igapó*, *Morpho* sp. in *forest gap*, and *Eunica pusilla* H. Bates, 1864 in *bamboo forest*.

In terms of species richness, the richest vegetation type was also *forest gap*, with 152 species, followed by *semi-deciduous forest* (125 species), *bamboo forest* (109 species), *terra firme* (105 species), and *igapó* (96 species) (Table 1). Rarefaction curves (Figure 2) suggest that more species would be added to all vegetation types if the sampling effort was increased. Interpolated and extrapolated curves confirm *forest gap* as the richest vegetation type and the *igapó* as the least rich, while the richness of the other three vegetation types is not significantly different. *Forest gap* and *bamboo forest* were the most diverse vegetation types (Figure 3). Despite some intersection between plot clusters of different vegetation types in the NMDS diagrams (Figure 4), butterfly composition differed among all vegetation types,

except between *forest gap* and *bamboo forest*. In the canonical ordination, *terra firme* was generally associated with higher humidity and lower temperatures, while the other types were more variable and, overall, less humid and with higher temperatures (Figure S1).

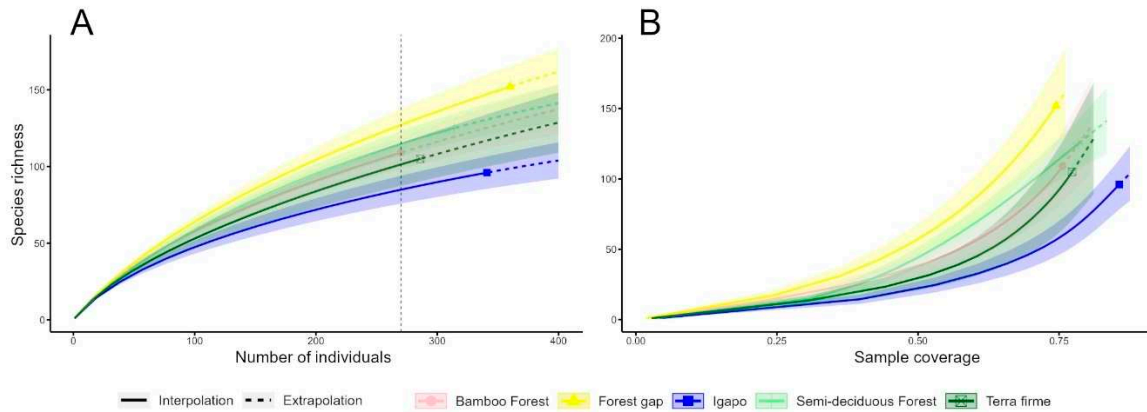


Figure 2. Species accumulation curves (interpolated in solid lines and extrapolated in dashed lines) comparing butterfly assemblage richness among five vegetation types at Cristalino Lodge (Alta Floresta, Mato Grosso, Brazil), in Southern Amazonia, based on the number of individuals (A) or sample coverage (B). Shaded areas represent confidence intervals ($\pm 95\%$). Pink: *bamboo forest*; yellow: *forest gap*; dark green: *terra firme*; blue: *igapó*; light green: *semi-deciduous forest*.

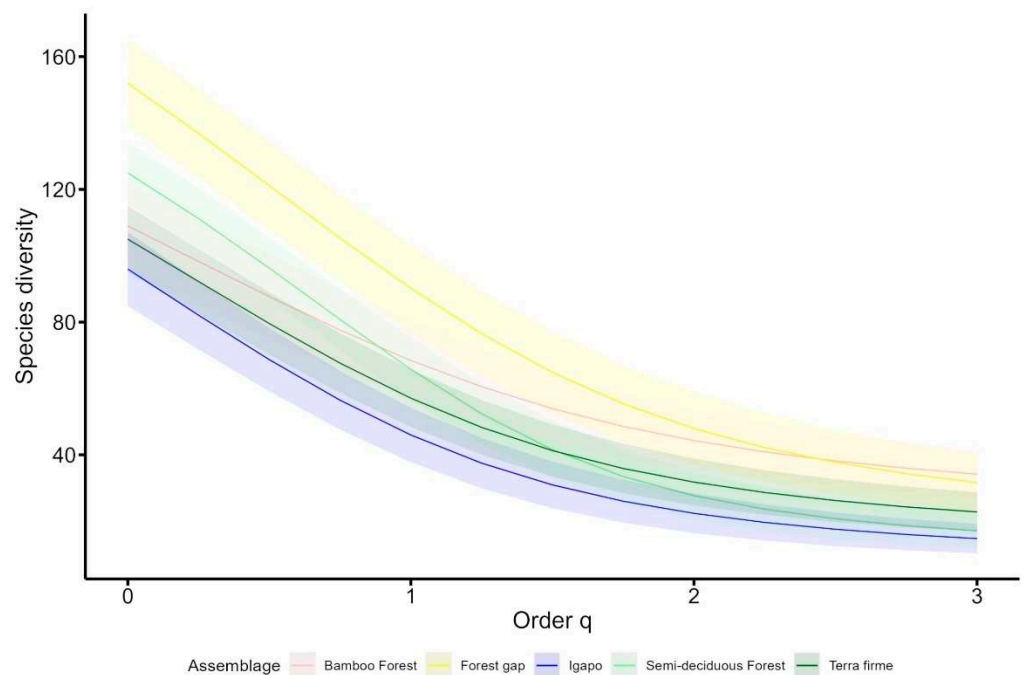


Figure 3. Entropy of Renyi calculated from the richness and abundance data of the butterfly assemblage of five vegetation types at Cristalino Lodge (Alta Floresta, Mato Grosso, Brazil), in Southern Amazonia. Pink: *bamboo forest*; yellow: *forest gap*; dark green: *terra firme*; blue: *igapó*; light green: *semi-deciduous forest*.

The IndVal analysis recovered 18 species as indicators of vegetation types, 9 of which were indicators of *igapó*, 3 of *terra firme*, and 2 of each of the other vegetation types (Table 2). Although the associations of these species with a vegetation type were significant ($p < 0.01$), the IndVal values were generally low, usually below 50%; a single species, *Nymphidium caricae* (Linnaeus, 1758), indicator of *igapó*, had an IndVal value greater than 70%. Most of

the indicator species belonged to the Nymphalidae ($s = 12$), in addition to four Riodinidae and two Lycaenidae. The other butterfly families had no species recovered as indicators.

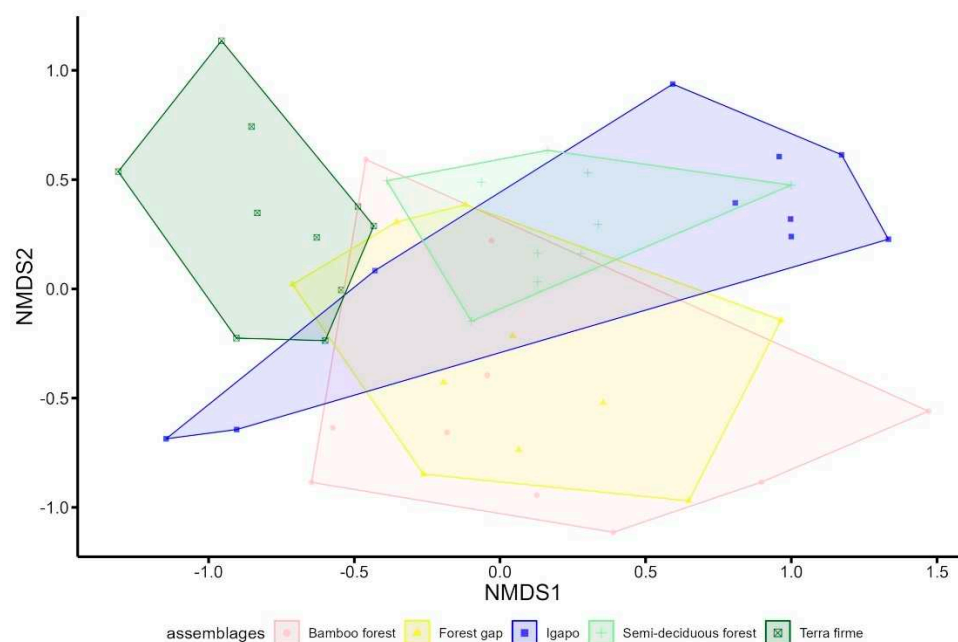


Figure 4. Non-metric multidimensional scaling ordination (NMDS) of butterfly assemblages among five vegetation types at Cristalino Lodge (Alta Floresta, Mato Grosso, Brazil), in Southern Amazonia. Pink: *bamboo forest*; yellow: *forest gap*; dark green: *terra firme*; blue: *igapó*; light green: *semi-deciduous forest*.

Table 2. Butterfly indicator species for five vegetation types at Cristalino Lodge (Alta Floresta, Mato Grosso, Brazil), in Southern Amazonia. N: species abundance (number of sampling plots where it was recorded in parenthesis). IndVal (%): indicator value. p (raw) probability of the indicator value.

Family	Indicator Species	Vegetation Type	N	IndVal (%)	p (Raw)
Nymphalidae	<i>Amphidecta calliomma</i> (C. Felder & R. Felder, 1862)	Bamboo forest	12 (4)	55	0.0001
Nymphalidae	<i>Splendeuptychia</i> sp.	Bamboo forest	10 (4)	40	0.0014
Nymphalidae	<i>Morpho</i> sp.*	Forest gap	56 (23)	40	0.0021
Riodinidae	<i>Mesosemia lacernata</i> Stichel, 1909	Forest gap	5 (4)	40	0.001
Lycaenidae	<i>Calycopis</i> msp.1 *	Igapó	6 (5)	50	0.0002
Lycaenidae	<i>Calycopis</i> msp.2 *	Igapó	9 (8)	27.78	0.0043
Nymphalidae	<i>Pseudeuptychia herseis</i> (Godart, 1824) *	Igapó	32 (21)	35	0.0031
Nymphalidae	<i>Heliconius erato</i> (Linnaeus, 1758)	Igapó	18 (9)	46.67	0.0002
Nymphalidae	<i>Hermeuptychia</i> sp.	Igapó	109 (25)	33.39	0.0077
Nymphalidae	<i>Deltaya ocypete</i> (Fabricius, 1776)	Igapó	5 (4)	40	0.0007
Nymphalidae	<i>Pierella hyalinus</i> (Gmelin, 1790)	Igapó	11 (7)	29.09	0.0063
Nymphalidae	<i>Vila emilia</i> (Cramer, 1779)	Igapó	15 (6)	60	0.0001
Riodinidae	<i>Nymphidium caricae</i> (Linnaeus, 1758)	Igapó	32 (11)	72.5	0.0001
Nymphalidae	<i>Euptychia westwoodi</i> A. Butler, 1867	Semi-deciduous forest	104 (35)	38.46	0.0008
Nymphalidae	<i>Heliconius aoede</i> (Hübner, 1813)	Semi-deciduous forest	5 (5)	32	0.004
Nymphalidae	<i>Pierella astyoche</i> (Erichson, 1849)	Terra firme	19 (12)	34.74	0.0025
Riodinidae	<i>Mesosemia marisa</i> (Hewitson, 1858)	Terra firme	26 (5)	38.46	0.0015
Riodinidae	<i>Stalactis calliope</i> (Linnaeus, 1758)	Terra firme	24 (15)	33.33	0.0053

* Lumped species or morphospecies; see more details in Table S2.

4. Discussion

In total, close to one-third of the butterfly community known from Cristalino Lodge was recorded in the present study. This is a reasonable representation of the total fauna, considering that this community has been explored for more than two decades, in an area much larger than the combination of our 50 plots (which is less than 1% of the

Cristalino private reserves), and includes many species that are rare and have only been recorded once [48]. In our study, most species were also recorded a single or a few times, with only a few species being abundant and accounting for a great number of records. This pattern was the same for all vegetation types, and is consistent with the known rarity of many butterfly species in diverse tropical forests, such as Amazonia [40]. The richest family was Nymphalidae, even though, in the whole Cristalino community, the number of known Hesperidae species slightly surpasses that of Nymphalidae. This is also expected in Neotropical forests, where the Hesperidae are usually the richest family, but only when there is sufficient sampling effort to register the rarer species or the use of specific methods [53–55]. Indeed, the Hesperidae were less abundant than the third-richest family, Riodinidae, which is typically an important component of the Amazonian butterfly fauna [56–58]. With the exception of two Lycaenidae morphospecies, all of the species recovered as indicators were nymphalids and riodinids, probably, in part, because these two families had more species in sufficient numbers to reveal an observable pattern.

Our results show that butterfly assemblages differ among vegetation types distributed within less than 1 km² in Southern Amazonia. These differences relate to richness and abundance, species composition, and particular species that are more associated with some vegetation types than others (indicator species). They are not, in general, as marked as what has been found for butterflies between three vegetation types in Central Amazonia, where few species were recorded in more than one vegetation type [36]. This result was expected because of the small scale of the present work, meaning that vegetation types were all in close proximity to one another and that some were found as small, limited patches contained within others. In this regard, it is reasonable to think that butterflies which use preferentially one or some vegetation types could be found in others, in part, due to dispersal movements, to having overall life areas larger than the patches of the vegetation types in question, or to the opportunistic use of resources and intermittent environmental conditions (such as flowers, fallen fruits, and sunlight spots). Indeed, we believe that butterflies could potentially move between any vegetation type in the study area. This, combined with the fact that no baits were used, and records were therefore of specimens that were spontaneously utilizing a particular vegetation type at a particular moment, make our results a strong indication that butterflies in Southern Amazonia are sensitive to this aspect of the environmental heterogeneity. Although we did not test whether a greater number of vegetation types correlated with greater species richness and diversity in this region, these results are consistent with the hypothesis that environmental heterogeneity creates more niche opportunities and therefore aids in species coexistence.

Many abiotic and biotic factors could explain the differences found between vegetation types, such as temperature, humidity, availability of host plants, and the community of predators. Luminosity is probably of particular relevance since tropical butterflies can be broadly divided according to the light levels at which they typically fly, with light-loving species being found in environments such as forest canopies, edges, and gaps, while shade-loving species are usually found in forest understories [40,59–61]. Indeed, tropical, closed-canopy forests are widely known to have a strong gradient of abiotic conditions between the canopy and the understory [62,63], which relates to the vertical stratification found in tropical butterfly communities around the world e.g., [64–73]. Even though we only considered the lower *stratum* of all the vegetation types studied, these abiotic conditions also varied between them, with *terra firme* being the only one consistently associated with relatively low temperatures and high humidity, probably as a consequence of its canopy allowing for less light penetration than the other vegetation types. It is noteworthy that some light-loving groups of butterflies that were present in other vegetation types, even if in low numbers, were absent in *terra firme*. This was the case of the fruit-feeding nymphalids of the tribe *Anaeni*, which are usually associated with forest canopies and edges [59], and of the *Coliadinae* (*Pieridae*), a group that is typically found in open habitats or canopies [74]. Notably, this was the only vegetation type with no records of *Morpho* sp., which is an amalgamation of three closely related species, the common *Morpho helenor*

(Cramer, 1776) and the less abundant *Morpho achilles* (Linnaeus, 1758) and *Morpho deidamia* (Hübner, 1819) (Table S2). In the present study, *Morpho* sp. was common in the *bamboo forest* and the *semi-deciduous forest*, but especially in the *forest gap*, to the point that it was recovered as an indicator species of this vegetation type, in accordance with what was found for *M. helenor* in Peru [75]. Another interesting case is that of the *terra firme* indicator riordinid, *Mesosemia marisa* (Hewitson, 1858). The males of this species are easily confused in the field with the co-occurring *Mesosemia croesus* (Fabricius, 1776), but are consistently found in leks in shaded *terra firme* understory, while *M. croesus*, which was not associated with any particular vegetation type, is usually seen in lighter and hotter areas instead (pers. obs.). The fact that species and entire groups of butterflies associated with lighter habitats were found in several vegetation types, but absent or particularly rare in *terra firme*, is evidence of the importance of the low light levels, low temperatures, and high humidity of this vegetation type in structuring its butterfly fauna. In this regard, *terra firme* is unique among the five vegetation types studied here. This uniqueness may result from the temporal stability observed in *terra firme*'s understory, since this vegetation type does not experience seasonal flooding in the rainy season or significant leaf loss during the dry months, maintaining approximately the same environmental conditions throughout the year. The *semi-deciduous forest*, for instance, has a rather similar vegetation structure, with a high canopy and dense understory, but differs in that the canopy loses a greater part of its leaves during the dry season [30], leading to higher light entrance and explaining why it was not associated with similar humid and cool conditions. In the region, this vegetation type is considered to be a transitional forest between *terra firme* and the dry forests on rocky outcrops. Despite this intermediate characteristic, it showed a butterfly assemblage composition distinct in comparison with the other vegetation types considered in the study, which could result, in part, from the great influence that seasonality is expected to have in the luminosity conditions of *semi-deciduous forest*.

In contrast to both forest types, *forest gap* lacks a closed canopy and therefore is associated with high luminosity during the entire year. In the present study, this was the richest and most abundant vegetation type; additionally, it was one of the most diverse. Indeed, previous studies from different parts of the world suggest that tropical forest gaps have rich and diverse butterfly communities, which differ in composition to the forest understory and comprised mostly of light-loving groups [40,75–80]. For instance, a richer community of butterflies in natural gaps compared to the understory has been found previously in Costa Rica [76] and Peru [75]; a study in Borneo found no difference in richness, but a more diverse gap community in terms of evenness [78]; and more species associated with gaps than with the forest understory were recorded in some cases [75,80]. The high abundance and richness found in the *forest gap* in this study is in accordance with the intermediate disturbance hypothesis [10,81], and is probably due to a combination of causes. For instance, the entrance of light in areas previously beneath closed canopy increases the quantity of flowers and vegetative growth, providing resources for nectar-feeding butterflies and abundant host plants for some species [40]. It has also been observed that butterflies overall stay longer in gap than in understory patches [80], which could make them easier to observe in the present study if this phenomenon is also true for this region. In addition, environmental heterogeneity between gaps might result from differences such as size, succession stage, and plant composition, leading to different community compositions among them [75,80]. Such turnover could contribute to a high total richness in this vegetation type. Finally, butterflies could use forest gaps for different reasons, resulting in a concentration of species and individuals in these limited spaces. It is known that canopy species are frequently observed closer to the ground in forest edges and gaps, which they treat as “extensions” of the canopy [59,73,76,82,83]. This seems to be the case, here, in the genera *Memphis* and *Zaretis* (Nymphalidae: Anaeni), and the heliconiine *Dryas alcionea* (Cramer, 1779), which belongs to a mimicry ring that flies above the trees [64]. However, the composition of gap butterfly communities has also been found to be different from that of the nearby forest canopy, meaning that such communities are

not composed exclusively of canopy species [75,78]. The aforementioned *Morpho* sp., for example, belongs to a group of species within the genus that typically does not fly in the canopy [84], as confirmed in many studies of vertical stratification e.g., [42,82,85]. A study in Borneo showed that gaps are used by different butterflies to perform an array of distinct behaviors, such as patrolling, resting, basking, and courting, and that, even though gaps and closed-canopy understories have different butterfly communities, many species need both environments to exhibit their full range of behaviors [80]. This could explain why some species widely regarded as forest understory inhabitants were occasionally found in the *forest gap* in the present study, such as transparent and translucent-yellow ithomiines [64,86]. The riodinid *Mesosemia lacernata* Stichel, 1909, on the other hand, was recorded as gap indicator and seems to be more dependent on this vegetation type, using it for territories or lekking areas (pers. obs.). These examples illustrate the complex interaction between open and closed-canopy areas, and the importance of the natural gap dynamics for the maintenance of a rich and diverse butterfly fauna in tropical forests [40].

Another aspect of each vegetation type that is likely to influence its butterfly community is the presence and abundance of host plants e.g., [87]. In our study area, this factor is expected to be especially important in the *bamboo forest*, since, as the name suggests, they are highly dominated by a single plant species, a woody bamboo in the genus *Guadua*. The abundance of this bamboo species may favor butterflies that are capable of utilizing this resource as a host plant for their immature stages, which is known to be the case for many Satyrini [88]. Accordingly, both species associated with bamboo forests in the indicator species test are satyrs: an undescribed *Splendeuptychia*, and *Amphidecta calliomma* (C. Felder & R. Felder, 1862). Two other species in the latter genus, *Amphidecta pignerator* A. Butler, 1867 and *Amphidecta reynoldsi* Sharpe, 1890 were also observed during this study only in this vegetation type, although not in sufficient numbers for any association to be found. The same is true of *Cristalinaia vitoria* Mota, Zacca & Freitas, 2019, a species whose first discovered individual was a *Guadua*-feeding caterpillar, and that has only been recorded so far in the *bamboo forest* [89]. It is not known, however, if all the species mentioned do feed on the dominant *Guadua* species or are using other common Poaceae found in this vegetation type. Even the species that do use *Guadua* as host plants are not necessarily specific to *bamboo forest*, since many euptychiines have been recorded feeding on more than one species of Poaceae or even plant families, which could be found in other vegetation types as well. Therefore, it is possible that some species are highly associated with bamboo forests due to the abundance of a suitable plant resource, but not exclusive, while other species could be indeed specialized and dependent on this vegetation type. In fact, the community composition of *bamboo forest* did not differ from that of *forest gap*, this vegetation pair being the only one for which this was true. This could be a result of *bamboo forest* having a very low and patchy canopy, with many areas where light reaches the understory, creating somewhat similar abiotic conditions to the *forest gap*; nevertheless, it is probably influenced by plant composition as well, since bamboos and grasses are also abundant in gaps and butterfly groups that feed on Poaceae as larvae could find host plants in both vegetation types. In terms of richness and abundance, however, the butterfly community differed between these two vegetation types, because *bamboo forest* was less rich and had a particularly low abundance, possibly a consequence of a less diverse plant composition and of fewer flowers and less abundant vegetative growth. It is interesting to note that a study in Vietnam also found bamboo forest butterfly communities to be species-poor and to have lower abundance than other nearby vegetation types [90], and to comprise mainly satyr species. Bamboo forests, dominated by different bamboo species, are found throughout the tropical world but support as yet little-studied butterfly communities [90]; future studies might clarify whether low richness, low abundance, and prevalence of Satyrini represent a common syndrome of these forests, and to what extent there are butterfly species that are dependent on them. It would be particularly interesting to study the butterfly community in the bamboo-dominated forests of Southwestern Amazonia, where this vegetation type is most prevalent and occupies more than 160,000 km² [27].

Butterfly assemblages have been shown to differ between floodplain and terra firme forests in Amazonia, with the flooding acting as an environmental filter [36–38]. Contrary to várzea forests, which receive nutrient input from the inundation by muddy water and therefore are highly productive, igapó forests are flooded by poor, acidic black-waters, and are comparatively species-poor and unproductive [91–93]. The igapó area studied in the present work is not as large or flooded by as high-water levels as in other regions of Amazonia (the sampling plots were barely underwater in the rainy season when the collection took place), but it presents the typical open understory and low plant richness [30]. Therefore, instead of the direct presence of water covering the ground during part of the year, the small availability of plant resources, such as flowers or host plant species and biomass, is a possible reason why igapó presented the lowest butterfly richness among the five vegetation types. The structural simplicity of the open understory may also offer few places for some butterfly species to perch, rest, court or exhibit other behaviors in accordance with their specific requirements. On the other hand, this vegetation type is the one that showed the highest dominance, and, while all the other vegetation types had two or three indicator species, it was the only one with nine. This result suggests that this vegetation type has a very distinctive butterfly assemblage, with relatively few species in total, but including some that are highly associated with this particular vegetation type. These are probably species that can feed on host plants tolerant of this vegetation type's nutrient-poor soils and can either survive flooding periods, or rapidly colonize areas after flooding. For instance, the biblidine *Vila emilia* (Cramer, 1779) has been recorded feeding on *Dalechampia* sp. (Euphorbiaceae) in a floodplain forest at the Teles Pires river, not far from the Cristalino Lodge [94]. Both this and previous studies have found satyr species to be indicators of or particularly common in floodplain forests, probably because these butterflies feed on fast-growing grasses that occur in such forests during the dry season [36–38]. Finally, it is interesting to note that the genus *Calycopis* belongs to a group of detritivorous Lycaenidae, whose larvae are capable of feeding on dead leaves on the ground [95–97]. These butterflies are possibly favored by the slow leaf decomposition and consequent thick litter of igapó forests [22], exemplifying how the characteristics of each vegetation type might benefit different butterfly groups.

Conservation Remarks

The presence of different vegetation types is an important feature of Amazonia, and the maintenance of this vegetation heterogeneity is expected to be crucial for the conservation of Amazonia's unmatched biodiversity. In this sense, it is important to address both the threats that are common to all vegetation types and the ones that are specific. For instance, floodplain forests may be disproportionately impacted by the construction of hydroelectric dams, which alter the flood pulse downstream and can lead to tree mortality, change in composition, and loss of habitats [98,99], being also shown to affect butterfly communities [100]. This is relevant considering the large number of hydroelectric dams planned to be constructed in the Amazon region [101]. Regarding Southern and Southeastern Amazonia, there is also evidence that the dry seasons are lasting longer than previously, and it is predicted that a savannization process of forest areas may take place if some deforestation, temperature, and other "tipping-points" are transgressed [102–107]. In the case of butterflies, this could be especially threatening to the species associated with the humid and cool temperatures of terra firme forests, and even more so if the natural gap dynamics of this vegetation type are also affected, considering that it has been shown that butterfly communities are sensitive to changes in forest dynamics due to selective logging, for instance [72,79]. Butterflies therefore represent an ideal group of organisms for long-term studies on the environmental modifications happening in Southern Amazonia due to climate change and deforestation.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15050624/s1>, Figure S1: Canonical ordination of sampling plots of five vegetation types at Cristalino Lodge (Alta Floresta, Mato Grosso, Brazil), Southern Amazonia, in a gradient of humidity and temperature; Table S1: List and abundance of butterfly species recorded in five vegetation types at Cristalino Lodge (Alta Floresta, Mato Grosso, Brazil), in Southern Amazonia; Table S2: List of butterfly morphospecies and species that were lumped under single species names.

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