




Article

Marked Differences in Butterfly Assemblage Composition between Forest Types in Central Amazonia, Brazil

Isabela Freitas Oliveira ^{1,2,*}, Fabricio Beggiato Baccaro ³ , Fernanda P. Werneck ⁴ , Thamara Zacca ⁵ and Torbjørn Haugaasen ² 

¹ Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia—INPA, Av. André Araújo, 2936, Manaus 69067-375, Brazil

² Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences—NMBU, P.O. Box 5003, 1432 Ås, Norway; torbjorn.haugaasen@nmbu.no

³ Departamento de Biologia, Universidade Federal do Amazonas—UFAM, Av. Gen. Rodrigo Octávio, 6200, Manaus 69080-900, Brazil; fabricera@gmail.com

⁴ Coordenação de Biodiversidade, Programa de Coleções Científicas Biológicas, Instituto Nacional de Pesquisas da Amazônia—INPA, Av. André Araújo, 2936, Manaus 69067-375, Brazil; fewerneck@gmail.com

⁵ Departamento de Entomologia, Museu Nacional—UFRJ, Rua Gen. Herculano Gomes, Rio de Janeiro 20941-360, Brazil; zacca.butterfly@gmail.com

* Correspondence: isabela.biologia@gmail.com

Abstract: Amazonia comprises a mosaic of contrasting habitats, with wide environmental heterogeneity at local and regional scales. In central Amazonia, upland forest (*terra firme*) is the predominant forest type and seasonally flooded forests inundated by white- and black-water rivers (*várzea* and *igapó*, respectively) represent around 20% of the forested areas. In this work, we took advantage of a natural spatial arrangement of the main vegetation types in central Amazonia to investigate butterfly assemblage structure in *terra firme*, *várzea* and *igapó* forests at the local scale. We sampled in the low- and high-water seasons, combining active and passive sampling with traps placed in both the understory and canopy. *Terra firme* supported the highest number of butterfly species, whereas *várzea* forest provided the highest number of butterfly captures. The high species richness in *terra firme* may reflect that this forest type is floristically richer than *várzea* and *igapó*. *Várzea* is a very productive environment and may thus support a higher number of butterfly individuals than *terra firme* and *igapó*. Most butterfly species (80.2%) were unique to a single forest type and 17 can be considered forest type indicator species in this landscape. Floodplain forest environments are therefore an important complement to *terra firme* in terms of butterfly species richness and conservation in Amazonia.

Keywords: butterflies; floodplain forest; indicator species; lepidoptera; species composition



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1. Introduction

Amazonia is widely recognized as the most biodiverse biome in the world [1–3]. This high diversity is associated with the massive size of the biome, but is also partly explained by its high habitat heterogeneity. Due to the differences in topography, soil and water properties, high forest heterogeneity may be observed at both the local and regional scales [4–6] with consequences for the associated fauna [7].

At the regional scale, the main macrohabitats are unflooded forests (hereafter, *terra firme*) and seasonally flooded forests inundated by white- and black-water rivers (hereafter, *várzea* and *igapó*, respectively). *Terra firme* forests lie above the maximum flood levels of lakes and rivers and account for more than 82% of Amazonia [8]. In contrast, flooded forests are situated on floodplains and cover approximately 17% of the basin [9]. The biota in these forests must endure floods for up to 6 months per year [10]. However, *várzea* and *igapó* forests differ significantly due to the type of water that inundate them [11,12]. White-water rivers flooding *várzea* forests carry large amounts of nutrient-rich sediments from the Andes and pre-Andean regions [13,14]. These floodplains are therefore exceptionally productive

due to the deposition of these sediments with the annual floods [14]. The black-water rivers inundating *igapó* forests are, on the other hand, relatively nutrient poor and more acidic [11,14].

These environmental differences lead to pronounced changes in forest structure and in floral and faunal composition between the different forest types. Previous studies have, for example, shown that assemblages of trees [11,12,15], ants [16], primates [17], bats [18,19], birds [20], and terrestrial vertebrates [21] differ significantly between these forest types. Typically, *terra firme* contains the highest number of species, followed by *várzea* and *igapó*. However, the Amazonian floodplain forests are probably some of the most species-rich flooded forests in the world [11,22].

At local scales, habitat heterogeneity may also be high. The topographic gradient of the floodplains influences the height and duration of the flood pulse [12,23], which has been shown to be an important predictor of tree alpha diversity and tree species distributions for both *várzea* [13,22,24,25] and *igapó* [26,27]. Many ecological processes, such as flowering and fruiting cycles, are similarly closely tied to the seasonal floods [28,29]. Small topographic differences may also induce habitat heterogeneity in *terra firme* forests that, in turn, may affect several terrestrial taxa [30–33].

Model organisms are good alternatives to standardize and/or delimit ecological patterns among heterogeneous environments and their associated biotas [34,35]. Butterflies are often recognized as good model organisms due to a relatively robust taxonomic resolution, their great abundance and diversity, and intimate host plant specificity in the larval stage [36,37]. This renders them a relevant indicator group of environmental change [38,39], such as changes in microclimate and host plant availability [35,40,41]. Most butterfly species therefore have a clear environmental preference. For example, some species are found largely in open areas, others in forest environments. In forests, some are more adapted to the forest understory, others to the canopy [42–44]. Although butterflies are charismatic animals and well-known animals [35,38], there is a conspicuous lack of inventories and ecological studies of these organisms in the Brazilian Amazon [45,46].

In this study, we present the first comparison of butterfly assemblage composition in adjacent *terra firme*, *várzea*, and *igapó* forests. More specifically, we investigated whether species richness and abundance differed, and how assemblage composition varied among the forest types. We expected to find that each forest type has a characteristic assemblage composition, reflecting their environmental uniqueness. Species richness was expected to be highest in *terra firme* due to the greater forest heterogeneity and lack of seasonal floods, whereas abundance was expected to be highest in *várzea* and lowest in *igapó* due to their contrasting productivity. Results are interpreted considering the differences experienced by seasonal flooding, soil fertility, and forest structure. Finally, we list potential indicator species of each forest type in this Amazonian landscape.

2. Materials and Methods

2.1. Study Area

This study was conducted at Uauaçu Lake (4°14' S, 62°17' W), located in the lower Purus region near the confluence between the Purus and Solimões Rivers, central Amazonia, Brazil (Figure 1). Most of the sampling area is part of the Piagaçu-Purus Sustainable Development Reserve and data collection was carried out from October to November 2018 (low-water season) and from May to June 2019 (high-water season). The forests in this area remain largely undisturbed and include a unique landscape mosaic containing *terra firme*, *várzea*, and *igapó*. Despite being located close to two major white-water rivers, Uauaçu Lake itself is a large crescent-shaped, black-water lake fed by water draining from the surrounding *terra firme* forest [15]. *Igapó* forests are located on the floodplains along the lake margins, whereas an extensive *várzea* forest occurs on the floodplain squeezed between the Purus and Solimões Rivers (Figure 1).

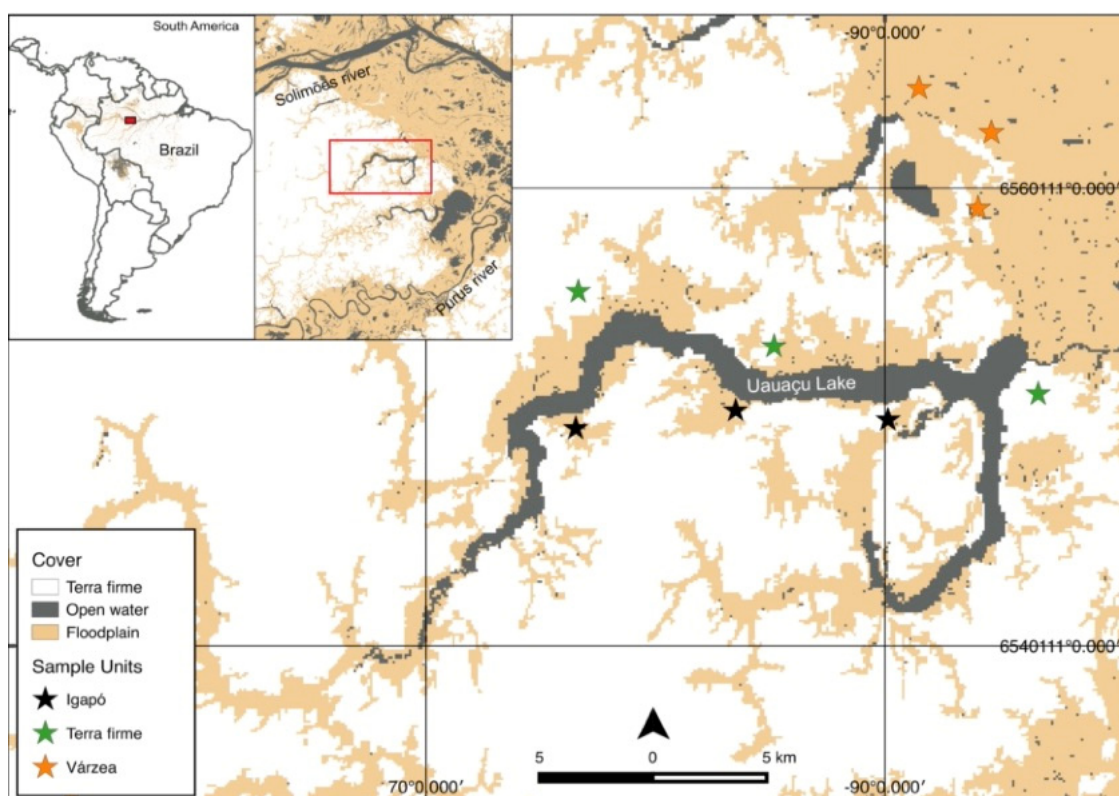


Figure 1. Location of the study and sampling points in the Uauaçu Lake region, state of Amazonas, Brazil. Black stars = *igapó*, green stars = *terra firme*, and orange stars = *várzea*.

2.2. Sampling Design

Butterfly sampling was performed along three 2 km transects in each forest type (Figure 1). We sampled the same transects in both the low-water and high-water season using cylindrical Van Someren-Rydon type traps [47] and an entomological net. Traps were installed and checked using a canoe in flooded forests during the high-water season. Twenty traps (ten in the canopy and ten in the understory) containing bait composed of fermenting bananas and brown sugar were placed 200 m apart along each transect. Canopy trap heights varied according to the local forest stature. Each trap was kept open for four days and checked every 48 h, totaling 1440 trap days. This sampling effort is sufficient to detect approximately 70% of the fruit-feeding butterfly species in the region [48]. In order to sample individuals from other families and feeding guilds, we also used standardized active searches with an entomological net. During active searches (performed simultaneously with checking traps), the collector covered the transects at 1 km/h and collected all butterflies sighted up to 2.5 m on each side of the transect [49,50]. In flooded forests during the high-water season, active searches were performed from a canoe. The active searches were performed at different times of the day (e.g., early morning, late morning, early afternoon, and late afternoon) to sample species with different activity patterns and were rotated among forest types.

Butterflies were identified to species and subspecies level using online guides (e.g., www.butterfliesofamerica.com, www.neotropicalbutterflies.com) and the taxonomic literature [51–55]. We used taxonomic references to confirm the current taxonomy of cryptic butterflies [56–63] and all butterfly identifications were verified by an expert taxonomist. All collected butterflies were deposited in the Entomological Collection of the National Institute of Amazonian Research (INPA) and some individuals of the most abundant species were also deposited in the Zoological Collection of the Federal University of Amazonas (UFAM) and at the National Museum (UFRJ).

2.3. Statistical Analysis

All butterflies sampled by active searches and in traps (both strata) were pooled by transect. The sample unit for all analyses is therefore transect in each season. We used rarefaction curves to compare and estimate species richness among forest types with different numbers of individuals collected [64]. The interpolated and extrapolated values are based on Hill numbers ($qD = 0$) generated in the iNEXT package [65].

To check whether butterfly species composition differed within and between forest types, we performed a permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarity measure. Forest type (*terra firme*, *várzea*, and *igapó*) was the dependent variable, and *p*-values were calculated based on 999 permutations. To visualize the assemblage composition in each forest type, we plotted a non-metric multidimensional scaling (NMDS) ordination using the Bray–Curtis dissimilarity index, using metaMDS function in the vegan package [66].

We performed an IndVal analysis [67] using the *multipatt* function in the *indicspecies* package to identify indicator species of each forest type. In this case, IndVal components “A” and “B” reflect how specific a species is to a particular forest type and how frequently it is found in sample units belonging to this forest type, respectively [68]. All analyses were performed using the R Studio program [69].

3. Results

3.1. The Uauaçu Lake Butterfly Community

We sampled a total of 726 individuals from 192 species representing six butterfly families: Nymphalidae (102 species, 526 individuals), Riodinidae (50 species, 141 individuals), Hesperidae (18 species, 26 individuals), Lycaenidae (12 species, 17 individuals), Pieridae (5 species, 10 individuals), and Papilionidae (5 species, 6 individuals, Table S1). The most abundant subfamily was Satyrinae (384 individuals, 51 species), followed by Riodininae (119 individuals, 42 species), and Biblidinae (60 individuals, 15 species). The most abundant subfamily in each forest type was Satyrinae with 154, 191, and 39 individuals in *terra firme*, *várzea*, and *igapó*, respectively. The most abundant species in each forest type was *Pierella lena brasiliensis* (C. Felder & R. Felder, 1862) (*terra firme*), *Taygetis mermeria* (Cramer, 1776) (*várzea*), and *Chloreuptychia chlorimene* (Hübner, 1819) (*igapó*).

3.2. Butterfly Richness and Abundance

Terra firme supported the highest number of species ($n = 101$), followed by *várzea* ($n = 74$) and *igapó* ($n = 65$). *Várzea* had the highest butterfly abundance ($n = 297$), followed by *terra firme* ($n = 287$) and *igapó* ($n = 142$). Rarefaction curves did not reach an asymptote for any of the forest types (Figure 2), suggesting that more species would likely be added to the species inventory with increased sampling effort. However, the interpolated and extrapolated curves show that *terra firme* has a steeper increase in expected number of species and *igapó* would have more species than *várzea* if the sampling effort was increased (Figure 2).

Few species were found in more than one environment (Figure 3). *Várzea* and *terra firme* shared the same number of species ($n = 12$) with *igapó*. Species exclusive to *terra firme* comprised 39.1% ($n = 75$) of the sampled species richness, whereas 25% ($n = 48$) and 16.1% ($n = 31$) of species were exclusive to *várzea* and *igapó*, respectively (Figure 3). In addition, most species were rare. Overall, 124 species were singletons ($n = 95$) or doubletons ($n = 29$) accounting for 64.6% of the total species richness, but only 21% of the sampled individuals ($n = 153$). The five most abundant species in *terra firme*, *várzea*, and *igapó* accounted for 31% ($n = 88$), 41% ($n = 123$), and 30% ($n = 43$) of all individuals captured in each forest type, respectively.

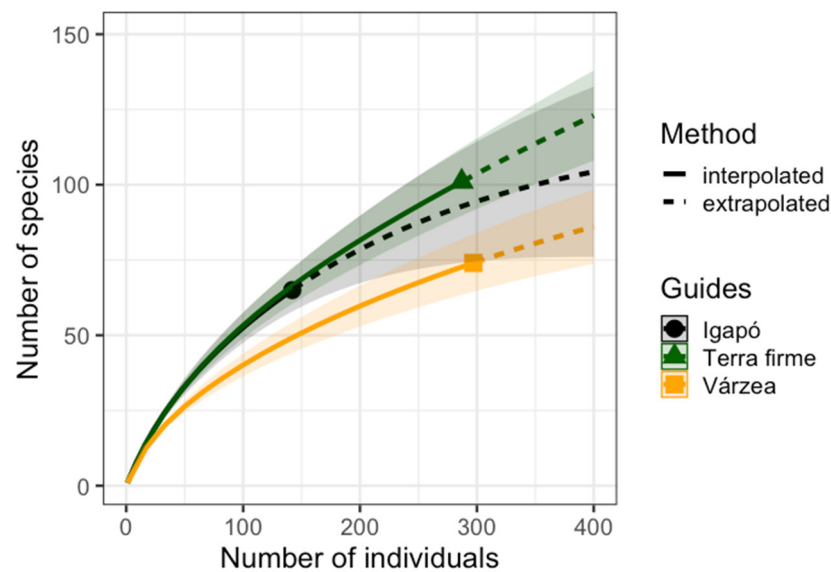


Figure 2. Species accumulation curves (interpolated and extrapolated) for the butterfly assemblages in three forest types in the lower Purus region, central Amazonia, Brazil. The solid lines show the cumulative number of species as a function of the number of individuals sampled in *terra firme* (green triangle and lines), *várzea* (yellow square and lines), and *igapó* (black circle and lines). Dashed lines indicate the extrapolated species number with a standardized number of individuals ($n = 400$) in each forest type and the shaded areas represent 95% confidence intervals.

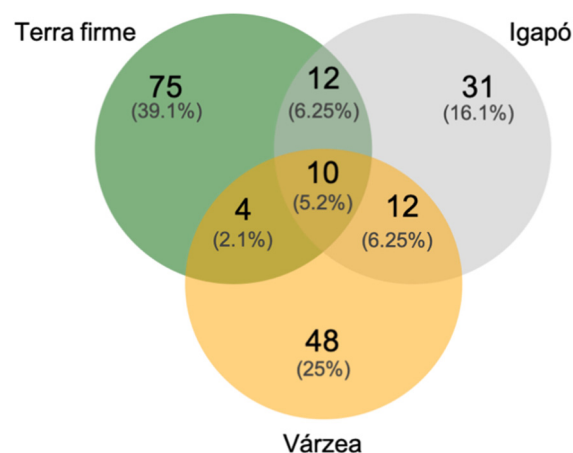


Figure 3. Venn diagram of the number and percentage of species exclusive to or shared between each forest type at Uauaçú Lake, central Amazonia, Brazil.

3.3. Butterfly Assemblage Composition

Butterfly assemblage composition differed between *terra firme*, *várzea*, and *igapó* (PERMANOVA, $F_{2,17} = 4.47$, $p = 0.001$). This can be clearly observed in the NMDS diagram, which shows that samples distinctly cluster by forest type (Figure 4).

The indicator species analysis identified 17 species that can be considered forest type indicators (Table 1). *Terra firme* had nine indicator species, *várzea* had five, and *igapó* had three.

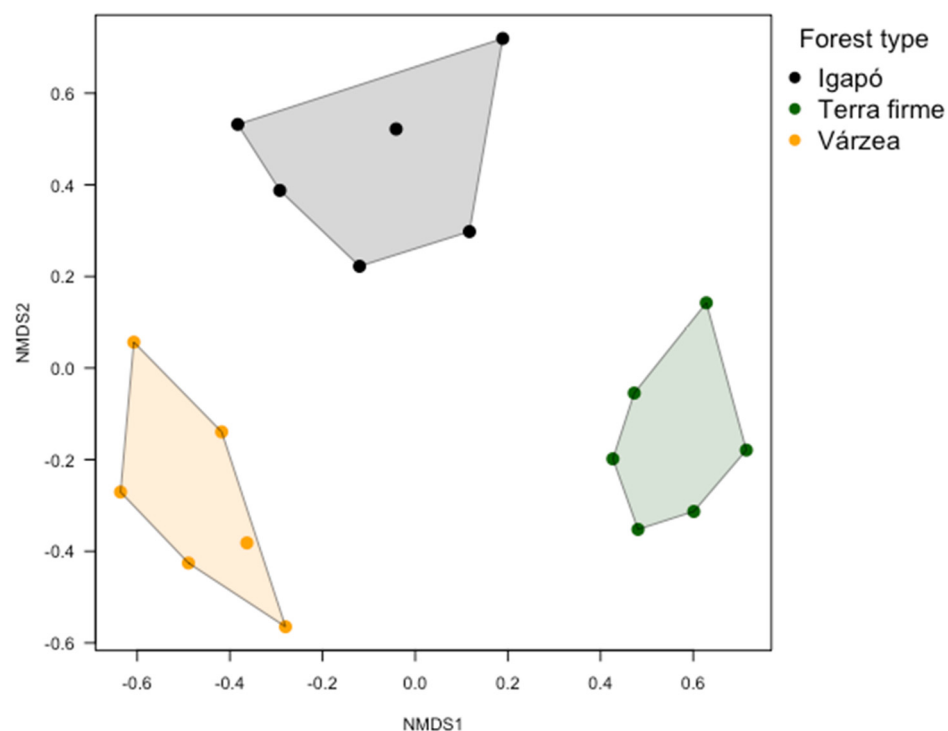


Figure 4. NMDS ordination of the butterfly assemblages in *terra firme*, *várzea*, and *igapó* at Uauaçu Lake, central Amazonia, Brazil. Green circles are *terra firme*, orange circles are *várzea*, and grey circles are *igapó* sample units.

Table 1. Butterfly indicator species for the three forest types at Uauaçu Lake, central Amazonia, Brazil. Records = species abundance and number of sample units in which the species was sampled (in parenthesis). Stat = the percentage of the IndVal combination of “A” (specificity) and “B” (fidelity). p = probability of the indicator value.

Indicator Species	Forest Type	Records	Stat	p
<i>Nubila nortia</i> (Hewitson, 1862)	<i>Terra firme</i>	20 (6)	100%	0.001
<i>Bia actorion</i> (Linnaeus, 1763)	<i>Terra firme</i>	19 (5)	91.3%	0.004
<i>Pierella lena brasiliensis</i> (C. Felder & R. Felder, 1862)	<i>Terra firme</i>	21 (5)	91.3%	0.005
<i>Cithaeris aurora</i> (C. Felder & R. Felder, 1862)	<i>Terra firme</i>	9 (4)	81.6%	0.009
<i>Nymphidium baeotia</i> (Hewitson, 1853)	<i>Terra firme</i>	7 (7)	83.3%	0.010
<i>Haetera piera</i> (Linnaeus, 1758)	<i>Terra firme</i>	5 (4)	81.6%	0.014
<i>Pierella chalybaea</i> (Godman, 1905)	<i>Terra firme</i>	18 (4)	81.6%	0.018
<i>Scriptor sphenophorus</i> (Lamas & Nakahara, 2020)	<i>Terra firme</i>	6 (4)	81.6%	0.018
<i>Taygetis laches</i> (Fabricius, 1793)	<i>Terra firme</i>	4 (4)	81.6%	0.019
<i>Pseudodebis marpessa</i> (Hewitson, 1862)	<i>Várzea</i>	22 (6)	100%	0.001
<i>Taygetis mermeria</i> (Cramer, 1776)	<i>Várzea</i>	42 (5)	91.3%	0.004
<i>Magneuptychia ocnus</i> (A. Butler, 1867)	<i>Várzea</i>	15 (4)	81.6%	0.018
<i>Taygetis rufomarginata</i> (Staudinger, 1888)	<i>Várzea</i>	9 (4)	81.6%	0.016
<i>Pseudodebis valentina</i> (Cramer, 1779)	<i>Várzea</i>	22 (7)	80.2%	0.020
<i>Archaeoprepona demophon demophon</i> (Linnaeus, 1758)	<i>Igapó</i>	6 (5)	91.3%	0.002
<i>Heliconius antiochus</i> (Linnaeus, 1767)	<i>Igapó</i>	12 (6)	83.3%	0.014
<i>Hermeuptychia undulata</i> ¹ (A. Butler, 1867)	<i>Igapó</i>	6 (4)	81.6%	0.014

¹ Recently removed from *Paryphthimoides* [61] and placed in *Hermeuptychia* (Zacca et al., unpubl. data).

4. Discussion

This is the first study to investigate how the butterfly community is structured in adjacent, yet very distinct, *terra firme*, *várzea*, and *igapó* forests in central Amazonia, highlighting the relevance of environmental heterogeneity even at the local scale. As hypothesized, our results revealed a marked difference in butterfly assemblages between forest types,

underlining a high association between butterfly species and a specific forest type present in the region.

4.1. Species Richness and Abundance

Terra firme supported the highest number of butterfly species, whereas *várzea* forest provided the highest number of butterfly captures. This is a common pattern seen for several different faunal taxa in the region, such as primates, birds, bats, and ants [16–18,70]. The slightly higher number of species sampled in *terra firme* may reflect that this forest type is floristically richer than *várzea* and *igapó* [11,13]. Previous studies showed that herbivore species richness is tightly linked to floristic diversity [71].

Due to the seasonal inundation, *várzea* and *igapó* contain fewer tree species [11,13] and may thus contain fewer potential food and larval host plants. In addition, the seasonal inundation effectively limits the use of understory habitats for up to 6 months annually, potentially leading to an impoverished understory butterfly fauna in seasonally flooded forests. Yet, the species accumulation curves did not reach an asymptote and it is likely that further butterfly species will be detected with increased sampling. Although the total number of species registered was the lowest in *igapó*, the species accumulation curves suggest that *igapó* may contain more species than *várzea*. A potential explanation for this finding is that *igapó* forests in the region are small in extent and located along the Uauaçu Lake margin and large streams entering the lake, and therefore intersect *terra firme* forest. In contrast, the large tract of *várzea* forest extends for many kilometers and most areas are thus far from *terra firme*. Species largely residing in *terra firme* forest may therefore opportunistically use *igapó* for resources or for simply traversing the area. A similar pattern has been observed in primates in the same study area [17,72].

Várzea forest provided the highest number of butterfly captures, despite supporting fewer species than *terra firme*. This high abundance is a common phenomenon found in several other taxa [17,19] and is largely linked to the annual deposition of nutrient-rich silt in *várzea* forest that make these systems exceptionally productive [10]. As the floodwaters recede, large amounts of decomposing fruits are deposited on the forest floor [72,73], potentially providing plentiful resources for adult butterflies.

4.2. Butterfly Assemblage Composition

Butterfly assemblages in each forest type were markedly different. This result is consistent with previous work on other taxa in the region, such as birds [74], bats [19], and large mammals [17]. The difference between *terra firme* and the two floodplain forests was largely driven by the higher number of understory species, which prefer to fly close to the ground, occurring in this forest type. This is reflected by the indicator species analysis where understory species, such as low-flying Haeterini, were important indicators of *terra firme*. *Terra firme* also had more species from other butterfly tribes, such as Nymphidiini, Satyrini, Epicaliini, and Brassolini, possibly due to the higher floristic diversity in this forest type.

Várzea also supported unique assemblage but had more species in common with *igapó* than with *terra firme*, perhaps reflecting the higher floristic similarity between these two forest types compared to *terra firme* [15]. Interestingly, all indicator species captured in *várzea* belong to the Satyrini tribe. These are understory butterflies readily collected via baited traps and sweep-nets, and their host plants are mainly from the Poaceae family that are abundant in flooded environments after the water recedes [75,76].

In *igapó*, the most representative butterfly tribe was Preponini, and *Archaeoprepona demophon demophon* (Linnaeus, 1758) was an important indicator species. Despite being host-plant generalists, some of its host plants are representatives of the Fabaceae and Leguminosae families (for *Prepona* spp.), common in *igapó* [15,77], and the immature *Archaeoprepona* spp. are polyphagous and feed on more than one plant family [41,78]. Preponini have agile flight, and individuals usually stay above the canopy and visit the ground only to feed on fermented fruits and/or animal feces [79]. *Igapó*, which has a more open canopy and understory compared to other environments [15], seems to be an ideal

environment for this group, providing more light to acquire energy and fewer obstacles in the forest for flight [18,80,81]. Other important species that were considered an indicator of *igapó* were *Heliconius antiochus* (Linnaeus, 1767) and *Hermeuptychia undulata* (A. Butler, 1867). The former lives in riparian forests in Amazonia and roosts over water [82]. The latter feeds *Panicum* sp. (Poaceae) and *Schlera* sp. (Cyperaceae) species, frequently found in *igapó* during the low-water season [12,78].

The most abundant species of each forest type and the indicator species in our study are commonly found in other regions of Amazonia. However, in this landscape context, they clearly show high forest type specificity. Despite the butterfly fauna in the Brazilian Amazonia having been studied for almost two centuries [83–85], there is a relatively small number of community ecology studies in central Amazonia that use butterflies as model organisms [44,80,86–89]. Most of these studies only sampled fruit-feeding butterflies with baited traps, which favors some Nymphalidae species. The similarity of Nymphalidae species between our study and other studies in Amazonia [87,88,90–93] is only 35%–60%. This is likely due to our rapid inventories in each season and limited sample sizes, as most other studies were long-term inventories [80,94] that allow a more complete sample of the butterfly fauna. However, few other studies encompassed other butterfly families [47] and our study therefore fills an important gap, presenting an updated list of all butterfly families (except Hedyliidae) for this Amazonian region.

5. Conclusions

Our results show that each forest type contains unique species assemblages, underlining a high level of habitat specificity among butterfly species present in the region. These findings have contributed to a better understanding regarding the Amazonian butterfly fauna, its ecological specificities, and assemblage structure across different forest types in central Amazonia. Our study therefore highlights the importance of floodplain forests to the regional species pool and the importance of protecting these forests to conserve Amazonian biodiversity.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f12070942/s1>, Table S1: Butterfly species abundance in each forest type.

Author Contributions: Conceptualization and methodology, I.F.O., F.B.B. and T.H.; investigation, data curation and formal analysis, I.F.O.; writing—original draft preparation, I.F.O., F.B.B., F.P.W. and T.H.; writing—review and editing, I.F.O., F.B.B., T.Z., F.P.W. and T.H. All authors have read and agreed to the published version of the manuscript.

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