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Assemblage structure of fruit-feeding nymphalids (Lepidoptera, Nymphalidae) in floodplain and upland forest at Cocha Cashu, Peru

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Acknowledgements

So - this is it. This is the end (, beautiful friend). I have thoroughly enjoyed the last year. Even though wandering through one of the most pristine and biodiverse places on earth all day long quite clearly ranks as number one, the writing process comes surprisingly close.

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Abstract

The Amazon is widely recognised as the most biodiverse area in the world. Within the Amazon, large tracts of forest are flooded each year, resulting in two dominant forest types – *terra firme*, unflooded forest and *várzea*, flooded forest. Because of the inundation, *terra firme* and *várzea* differ in species composition, and *várzea* has a more open understorey and canopy. In this study, I compared fruit-feeding nymphalid species assemblages in *terra firme* and *várzea* forest in the Peruvian Amazon using fruit-baited traps placed in the understorey, midstorey and canopy. Total species richness was similar in both forest types, but more species were caught per trapping location in *terra firme*. There was a high species turnover between the two forest types; only 48 % of the species were shared between *várzea* and *terra firme* and an ANOSIM confirmed that species assemblages were significantly different. The butterfly community in *terra firme* contained more species adapted to the understorey than *várzea* and the understorey species assemblage was significantly different from both the midstorey and canopy assemblages in *terra firme*. All strata contained different species assemblages in *várzea*. This study is the first to examine differences in butterfly assemblage structure between these two dominant Amazonian forest types, and underlines that *várzea* forests plays a crucial role in maintaining biodiversity in the Amazon.

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Introduction

The Amazon is widely recognized as one of the most biodiverse areas in the world. The Amazon basin covers about 7 million km², and is the largest remaining tropical forest. However, the Amazon forest is comprised of several different forest types – with the two main forest types being flooded and unflooded forests. The unflooded forests (hereafter, terra firme) lies above the maximum flood levels of lakes and rivers. Terra firme is the dominant forest type in the Amazon, and account for more than 82 % of the Amazon forests (Melack & Hess 2010). In contrast, flooded forests are situated below the maximum flood level of lakes and rivers, and may thus experience seasonal inundation. The total floodable forest area in the Amazon is around 800.000 km² (Melack & Hess 2010). The forests that are flooded by nutrient rich white-waters are called várzea forests, and account for about 50 % of the flooded forests across the basin (Melack & Hess 2010).

A vast number of floral and faunal inventories are available for the Amazon, but surprisingly few of these have focused on differences in species composition between terra firme and várzea. In terms of the flora, the seasonal inundation in várzea forests has been shown to affect the forest in various ways, both in terms of floristic composition and forest structure. For example, várzea forests contain fewer plant species than terra firme, and the community composition differs between terra firme and várzea (Haugaasen & Peres 2006; Myster 2007). The flooding in várzea forests also affects the forest structure, for example by increasing the canopy and understorey openness (Haugaasen & Peres 2006; Bobrowiec et al. 2014), and reducing number of saplings in the understorey (Haugaasen & Peres 2006). In addition, várzea contains fewer, but larger trees (Balslev et al. 1987). In terms of the fauna, previous studies have shown that volant taxa, such as birds (Haugaasen and Peres 2008, Beja et al., 2010) and bats (Bobrowiec et al. 2014) have significantly different species assemblages in terra firme and várzea, but little or no difference in species richness. Haugaasen and Peres (2005a, b) found that terra firme harbours significantly more non-volant mammal species than várzea, but that várzea supported a much higher biomass. Gascon (1996) found no differences in species richness and abundance of leaf litter frogs, whereas várzea has been shown to harbour less species of spiders (Höfer 1997), termites (Martius 1997) and beetles (Gauer 1997; Adis et al. 2010).

More studies are therefore clearly needed in order to further assess differences between terra firme and várzea, and to my knowledge, no study to date has investigated butterfly assemblage structure and composition between these forest types.

Of all insects, butterflies (Lepidoptera) are probably the insect group best known taxonomically and ecologically (Thomas 2005). In the Neotropics alone, there are an estimated 7784 butterfly species, making it the richest butterfly fauna in the world (Lamas 2004). Of all butterflies in the Neotropics, fruit-feeding nymphalids are probably those that are best understood in terms of community composition and vertical stratification (DeVries et al. 2012). Due to differences in microclimatic conditions from the understorey up to the canopy, the butterfly fauna is divided between these two strata (Elton 1973; Parker 1995; DeVries et al. 1997). For butterflies, this translates into light-loving species in the canopy, and species restricted to shade in the understorey. It is therefore necessary to sample in both strata in order to obtain a precise estimation of species richness (e.g. DeVries & Walla, 2001).

As different butterfly species often have specific habitat requirements, such as larval host plant availability and light intensity (DeVries 1987), the butterfly species assemblage in a given habitat is a good indicator of the habitat condition. Butterflies have therefore readily been used as indicator species in relation to habitat degradation (Brown Jr & Hutchings 1997; Bonebrake et al. 2010). For example, fruit-feeding nymphalid community composition has previously been shown to differ between natural and disturbed forest (DeVries et al. 1997; Hamer et al. 1997; DeVries et al. 1999; Hill 1999; Willott et al. 2000; Lewis 2001; Fermon et al. 2003; Hamer et al. 2003; Dumbrell & Hill 2005; Fermon et al. 2005; Barlow et al. 2007; Cleary et al. 2009), contiguous and fragmented forests (Benedick et al. 2006; Uehara-Prado et al. 2007), and closed-canopy forests and treefall gaps (Hill et al. 2001; Pardonnet et al. 2013). Changes in forest structure, such as a decrease in canopy cover, disrupts the stratification of fruit-feeding nymphalids, resulting in species typically found in the canopy occurring at ground level as well (e.g. Fermon et al. 2005).

This study aims to identify the main differences and similarities between the fruit-feeding nymphalid species assemblages in terra firme and várzea forest. The main predictions of this study were:

- 1) TERRA FIRME WILL HARBOUR MORE FRUIT-FEEDING NYMPHALID SPECIES THAN VÁRZEA. An increase in larval host plant diversity has been linked with increased species richness of butterflies (Koh & Sodhi 2004). The floristic diversity in várzea is lower than in terra firme and this should result in terra firme being more species rich than várzea.

- 2) TERRA FIRME WILL HARBOUR MORE SPECIES THAT ARE ADAPTED TO A DENSE AND SHADED UNDERSTOREY. The seasonal inundation in várzea leads to a more open understorey. As many of nymphalid species are adapted and restricted to a dense and shaded understorey, this should in turn reduce the abundance of these species in várzea forests.

- 3) STRATIFICATION WILL BE MORE PRONOUNCED IN TERRA FIRME. Forest structure differs between terra firme and várzea (such as canopy and understorey openness) and this should be reflected in the stratification pattern of the fruit-feeding nymphalids.

2. Methods

2.1 Study area

The current study was carried out at the Cocha Cashu Biological Station (EBCC). Cocha Cashu is an oxbow lake, located in the two million hectare Manu National Park (11 ° 51'23''S 71 ° 43'17''W), in the south-eastern part of the Peruvian Amazon. The field station is located on the bank of the oxbow lake along the Manu river, a large white-water river connected with the huge Amazon River system. The average annual rainfall is about 2300 mm and the average temperature is 24 °C (Pardonnet et al. 2013). The study area covers over 16 km², which is served by around 60 km of trails. The várzea forest around EBCC is a 'mature floodplain', and only experience occasional flood pulses (Haugaasen & Peres 2005a).

2.2 Study taxon

Butterflies in the Neotropics can be divided into two feeding guilds - flower feeders and fruit-feeding nymphalids (DeVries 1987). Species belonging to the fruit-feeding guild gain more or less all of their nutrition by feeding on juices from rotting fruit or plant sap (DeVries et al. 1997). Although the division is uncertain, the fruit-feeding nymphalid guild is generally understood to consist of species in the subfamilies Biblidinae, Charaxinae, Nymphalinae and Satyrinae. Together they comprise 40-55 % of the nymphalid species in the Neotropics (DeVries 1987). It has been argued that the subfamily Limenitidinae should not be included in analysis of fruit-feeding nymphalid communities (Lucci Freitas et al. 2014), but at least 23 species have been reported feeding on fruits (Willmott 2003). Further, the amount captured in this study argues that this subfamily cannot be ignored (Table 3.2, Appendix 1). In other fruit-baiting studies in the Neotropics, a small number of species in the subfamily Ithomiinae has been observed in traps (DeVries et al. 1997), as was the case in this study. However, Ithomiines mainly feed on flower nectar and are thus not a part of the fruit-feeding guild (DeVries et al. 1999). All Ithomiines trapped in this study were excluded from the analyses.

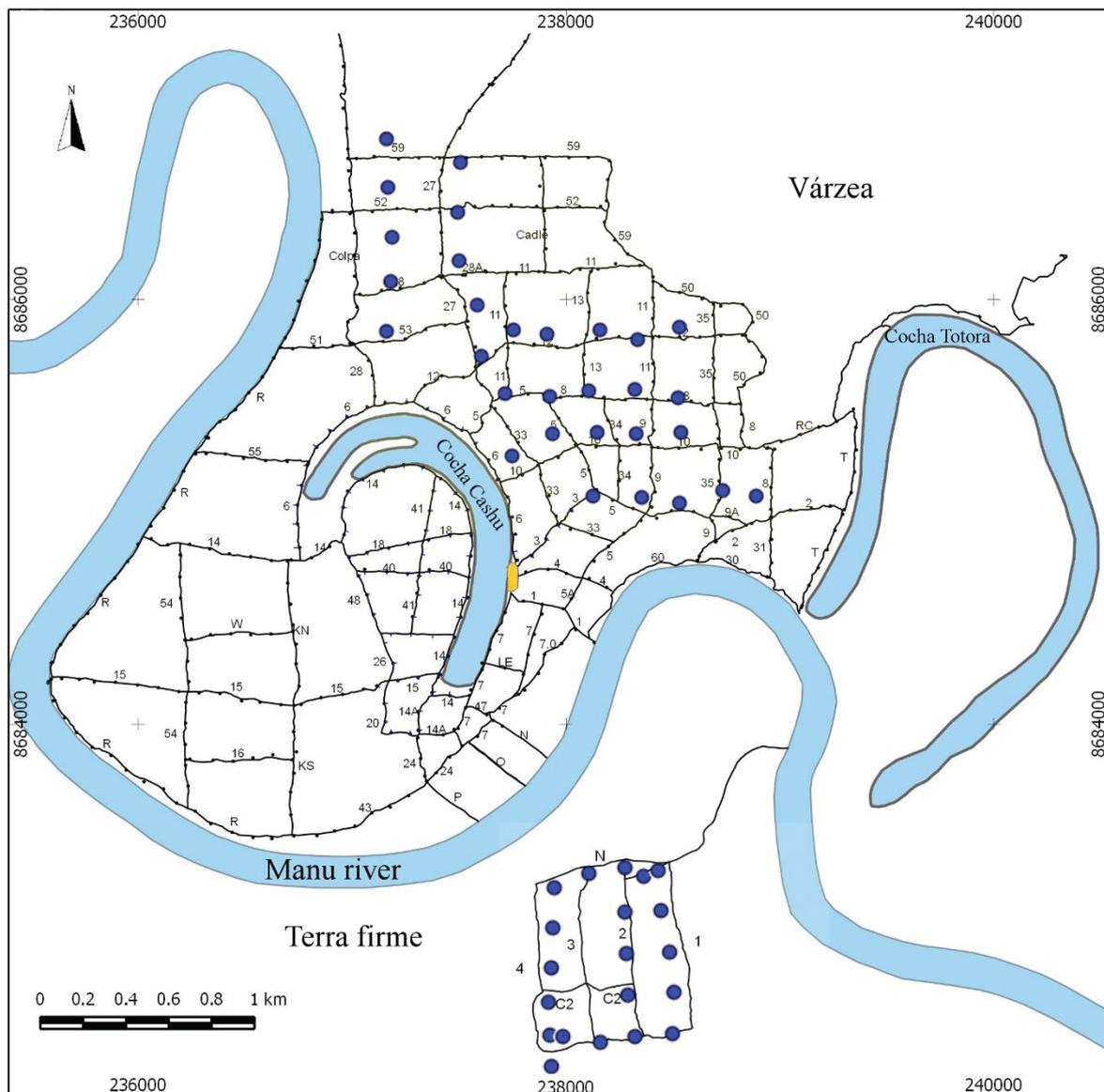


Figure 2.1: The Cocha Cashu Biological Station (yellow area) with lines indicating the existing trail grid and blue circles indicating the location of the butterfly trapping sites ($n = 30$ in várzea, $n = 20$ in terra firme). The area north of the Manu river is várzea forest and the area with a trail grid south of the river is terra firme forest. Map modified from C. E. Timothy Paine.

2.3 Study design

Within the Cocha Cashu trail system, I established 10 transect. Six of these were in várzea and four in terra firme. This was due to a much smaller trail system in terra firme (Fig. 2.1). Each transect consisted of five trap points, placed 250 meters apart in várzea and 200 meters apart in terra firme. Each trap point was fitted with three traps, one in the understorey (1 meter above ground), one in the midstorey and one in the canopy. This resulted in 60 traps in terra firme and 90 in várzea. The understorey traps were placed approx. 10 meters off the trail in order to reduce

the potential effect a trail would have on the sampling. Bow and arrow were used to attach a line above a branch in the canopy, and thus enabling me to lower and raise the midstorey and canopy traps. The traps were made following the design by DeVries (1987), had a height of ~60 cm, diameter of 30 cm, and were made of black nylon mesh net. A plastic plate was placed 3 cm below the net. The bait was made the day prior to its use and consisted of ripe or rotten plantains (as regular bananas were unavailable) and a dash of vanilla extract, mashed and mixed thoroughly. The traps were baited prior to the first day of sampling, and bait was added to the remaining bait in the trap each day of the sampling. Each sampling round consisted of two transects (n = 30 traps) if sampling in várzea and four transects (n = 60 traps) if sampling in terra firme. During one sampling round, traps were sampled for five consecutive days. All traps were sampled for 15 days each, and the sampling period lasted from the middle of July to the end of September 2015.

All butterflies were photographed dorsally and ventrally, before being individually marked with a felt-tipped pen following the 1-2-4-7 system (Ehrlich & Davidson 1960) and released. This was done in order to avoid specimen collection and to recognise re-captures. Photographs were used for subsequent identification of butterflies. All pictures were sent to various expert lepidopterists in order to ensure correct identification, as well as to identify unidentified individuals.

All species follow the classification and nomenclature of (Lamas 2004), except for *Taygetis oyapock* (Satyrinae) which first was described in 2007 (Brévignon 2007). Some difficulties occurred in identification of the genus *Taygetis* (Satyrinae). *Taygetis thamyra* and *T. laches* are more or less impossible to distinguish from one another with the use of photos only. These were therefore pooled together as *T. thamyra/laches*. Further, 9 individuals of *Taygetis* were pooled together as *T. spp.* as identification to species level was impossible.

2.4 Statistical analyses

Following DeVries & Walla (2001), rare species were defined as those with 4 or fewer observations.

I used rank abundance plots to describe species abundance distributions in the two forests. In order to evaluate sampling efficiency, I created sample-based species accumulation curves using EstimateS statistical software v9.10 (Colwell 2006). This was done for each forest type, and for each stratum within each forest type. As the sample effort was different in the two

forests ($n = 20$ for each stratum in terra firme, $n = 30$ for each stratum in várzea), I extrapolated the sample size in terra firme using the rarefaction function in EstimateS.

EstimateS was also used to estimate the total species richness for all strata in both forests types using Chao2. The Chao2 estimation is a conservative measure, and it is also thought to be among the least biased methods for estimating total species richness (Walther & Moore 2005). As the sample effort was different for the two forests ($n = 60$ in terra firme, $n = 90$ in várzea), Shannon H' was used as a diversity measure, as this method is independent of sample size (Jost 2006).

Non-metric multidimensional scaling (NMDS) with Bray-Curtis similarity measure was used to visually investigate within and between habitat differences in the assemblage structure at trap level. All species were entered as single entities. However, all abundance data were square-root transformed in order to reduce the impact of species with high abundance. An analysis of similarity (ANOSIM) with Bray-Curtis similarity measure was used to assess the level of difference between two forest types. To identify species that contributed the most to this difference I used a similarity percentage analysis (SIMPER), also using the Bray-Curtis measure. These analyses was done using PRIMER v.5 (Clarke 1993). A non-parametric Mann-Whitney U-test was used to compare abundances of species between the forest using Minitab v. 16 (Minitab-Inc. 2010).

3. Results

3.1 The Cocha Cashu fruit-feeding nymphalid community

In total, 1705 individuals and a minimum of 99 species in the subfamilies Satyrinae (41), Biblidinae (20), Charaxinae (19), Limenitidinae (12), Nymphalinae (6) and Apaturinae (1) were trapped during this study. Of these, 896 (52.5 %) were caught in várzea forest and 809 (47.5 %) in terra firme (Table 1). In várzea, six subfamilies were registered, while five were registered in terra firme. The most abundant sub-family in várzea and terra firme was Limenitidinae (396 individuals) and Biblidinae (538 individuals), respectively.

3.2 Species richness and abundance

The five most abundant species accounted for 73.25 % of all individuals (n = 1249). *Panacea prola* was the most abundant, and accounted for 40 % of all captures (n = 682), followed by *Adelpha jordani*, (21.93 % of all captures, n = 374), *Nessaia obrinus* (5.04 % of all captures, n = 86), *Pseudodebis valentina* (3.34 % of all captures, n = 57) and *Catoblepia berecynthia* (2.93 % of all captures, n = 50). The most abundant species in the várzea forest was *A. jordani* (366 individuals, 40.84 % of várzea captures) and *P. prola* (466 individuals, 57.6 % of terra firme captures) was most abundant in terra firme.

The rank abundance distribution for the two forests showed that most species caught were rare (fig. 3.1). Species with 4 or fewer captures accounted for 63 % of the species (n = 62), but only 6.9 % of the captured individuals (n = 117). In terra firme, rare species accounted for 69.33 % of the total species count and 11.61 % of the individuals (n = 94). In várzea this was even more pronounced, with rare species accounting for 76.38 % of the species caught and 10.15 % of the individuals (n = 91) (fig. 3.1).

There was a high species turnover between the two habitats: 24 species were only found in várzea, while 27 species were only found in terra firme (Table 3.1). Within each habitat, várzea had a higher level of turnover between strata than terra firme, with more species being restricted to one stratum (Table 3.1).

Each trapping point (understorey, midstorey and canopy combined) in terra firme captured significantly more species than in várzea (Mann-Whitney U test, $p < 0.0001$). Terra firme accumulated species faster than várzea and had a higher species richness in each stratum as well as for all strata combined (Fig. 3.2, Table 3.1). Further, the Shannon H' and Chao2

estimations indicates a higher level of diversity and a higher expected total species richness, in terra firme for all stratum and all strata combined (Table 3.1).

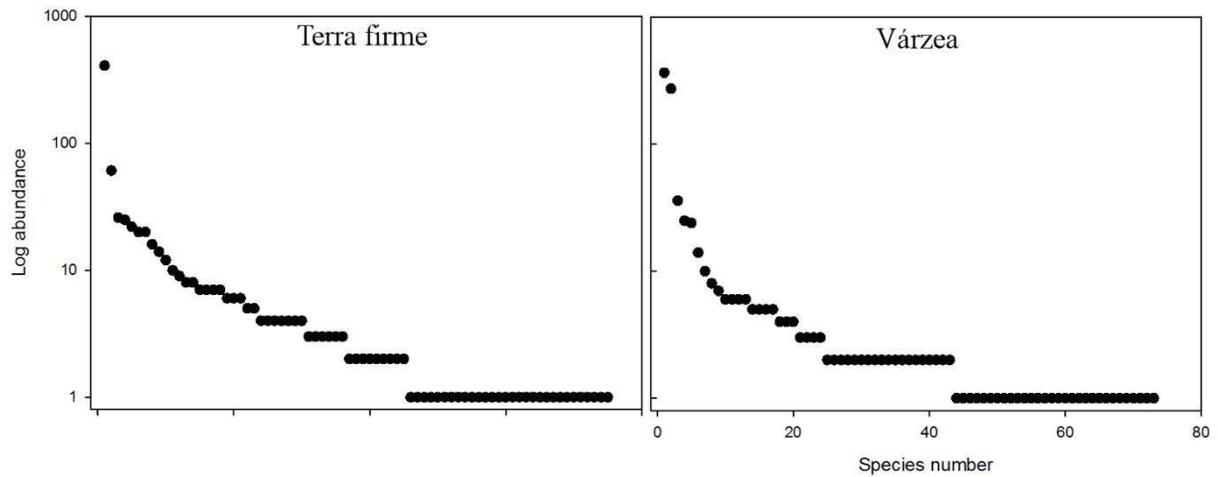


Figure 3.1: Rank abundance distribution for the total sample in terra firme (left panel) and várzea (right panel).

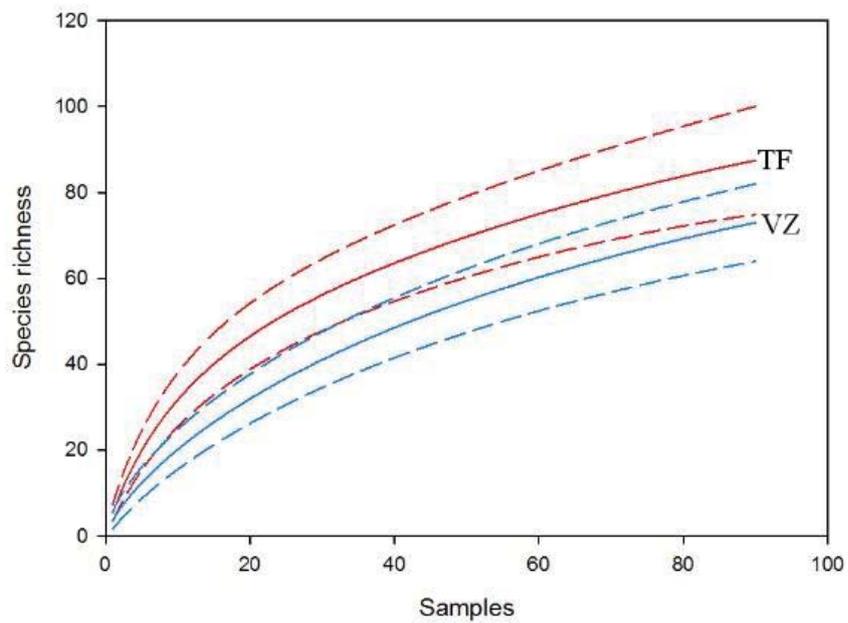


Figure 3.2: Sample-based species accumulation curves for terra firme (red line) várzea (blue line). Stippled lines indicate 95 % CI.

Table 3.1: Species richness, diversity and abundance in várzea and terra firme at Cocha Cashu, Peru. U = understorey, M = midstorey, C = canopy, Total = all strata within the forest type combined. Unique species are those present only in one stratum in a particular habitat ('U', 'M', 'C') or unique to a particular habitat ('total'). Rare species are those represented by ≤ 4 individuals, and common species are those represented by ≥ 5 individuals.

	Várzea				Terra firme			
	U	M	C	Total	U	M	C	Total
No. of species	53	30	13	72	57	36	18	75
No. of unique species	37	14	5	24	33	10	6	27
Rare species	43	27	11	55	39	34	17	52
Common species	10	4	2	17	18	2	1	23
Individuals	547	291	58	896	657	119	33	809
Shannon H'	2.17	1.48	1.67	2.12	2.24	2.59	2.36	2.47
Chao2	66.96	48.78	36.75	102.78	82.12	60.94	39.61	115.23

3.3 Butterfly assemblages and composition

Terra firme and várzea forest samples formed distinct clusters in the NMDS ordination (fig. 3.3). The ANOSIM confirmed that differences in the butterfly assemblages between terra firme and várzea were significant (Global R = 0.459, P = 0.001). The ten most important species contributing to the difference between terra firme and várzea explained 58.9 % of the difference between the forests. The difference was mainly due to a higher abundance of *A. jordani* in várzea and *P. prola* in terra firme (Fig. 3.4), together explaining 35.2 % of the difference.

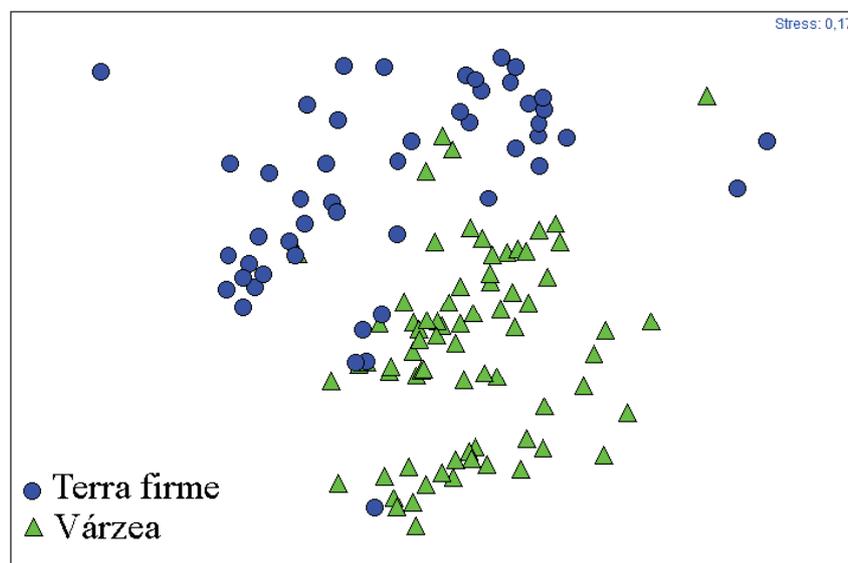


Figure 3.3: NMDS ordination of the fruit-feeding nymphalid community in terra firme (blue circles) and várzea (green triangles) forest at Cocha Cashu, Peru.

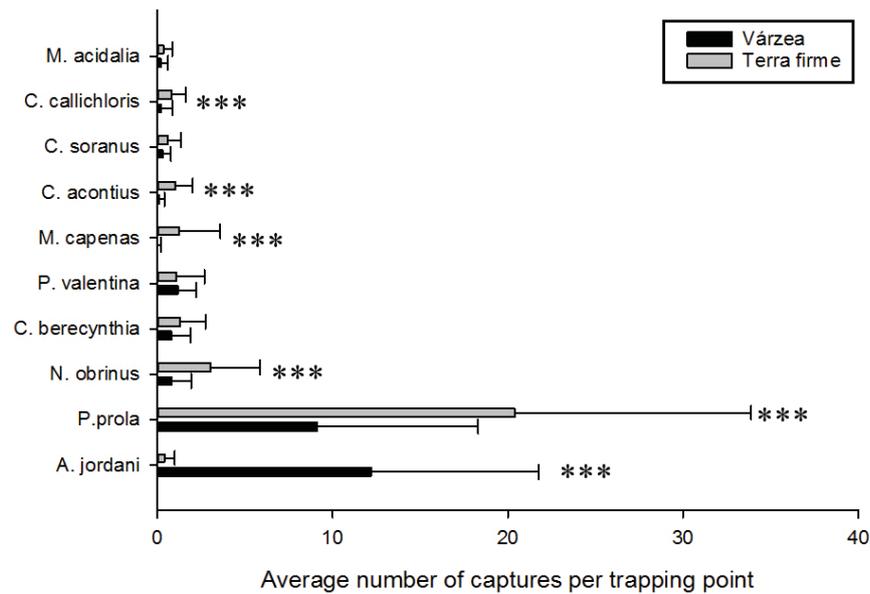


Figure 3.4: Average number of captures (\pm SE) per trapping point in várzea (black bars) and terra firme (grey bars) forest. Asterisks indicate significant differences: * $P < 0.05$, ** $P < 0.01$. *** $P < 0.001$.

3.3.1 Stratification

Most individuals were captured in the understorey, followed by the midstorey and the canopy (Table 3.1). The butterfly assemblages in terra firme and várzea combined were clearly stratified (Figure 3.5). The ANOSIM shows that the difference in assemblage structure between strata overall is significant (Global $R = 0.313$; $P = 0.001$). The understorey formed a distinct cluster, and was significantly different from both the midstorey and the canopy (ANOSIM pairwise tests – understorey vs midstorey: $R = 0.347$, $P = 0.001$ – understorey vs canopy: $R = 0.557$, $P = 0.001$). However, no significant difference was found between the midstorey and the canopy (ANOSIM pairwise tests – midstorey vs canopy: $R = 0.052$, $P = 0.059$).

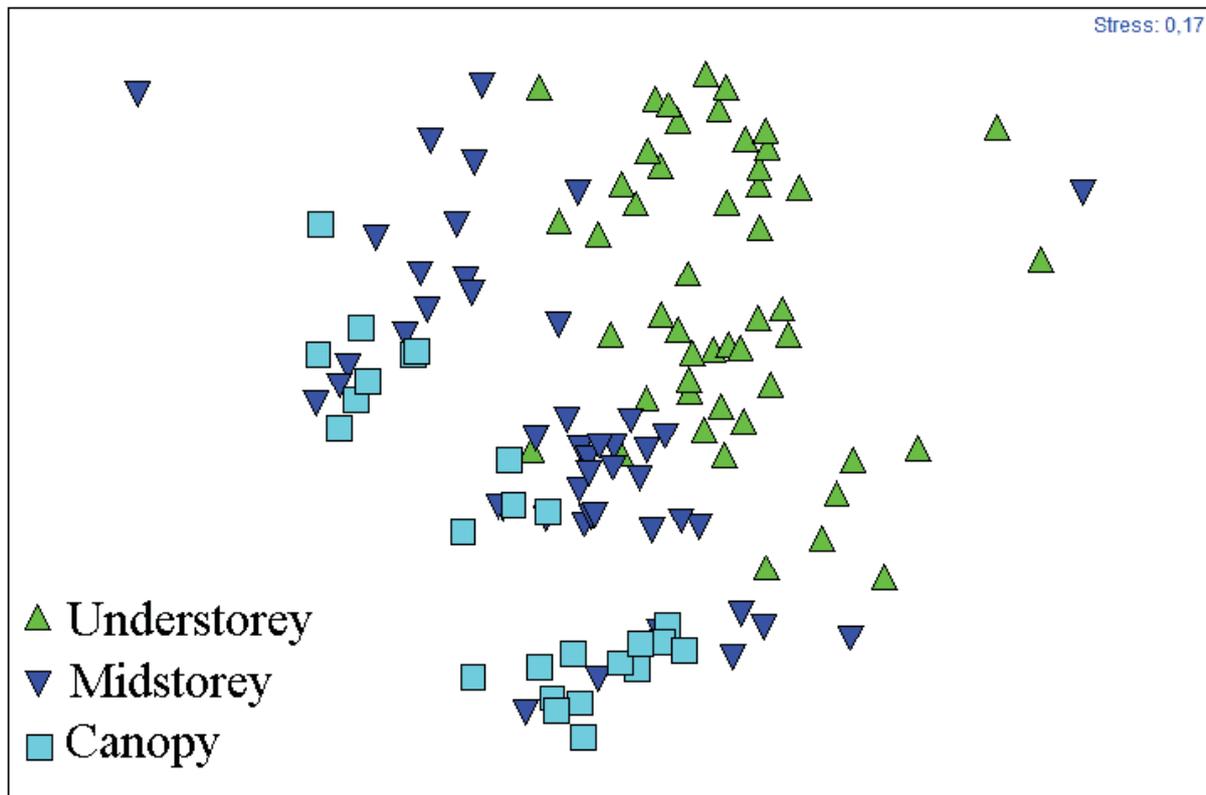


Figure 3.5: NMDS ordination of the understorey (green triangles), midstorey (blue triangles) and canopy (blue squares) fruit-feeding nymphalid community at Cocha Cashu, Peru.

Both terra firme and várzea showed a significant decrease in butterfly abundance (Spearman's rank correlation – terra firme (n = 60): $r_s = -0.878$, $p < 0.0001$; várzea (n = 90): $r_s = -0.788$, $P < 0.0001$) and number of species (terra firme: $r_s = -0.859$, $p < 0.0001$; várzea $r_s = -0.823$, $P < 0.0001$) with increasing trap height.

Results at the subfamily level show that there was a significant decrease in abundance and number of species with increasing trap height for all subfamilies in várzea. In terra firme, three subfamilies (Biblidinae, Charaxinae and Satyrinae) showed a significant decrease in both abundance and species richness with an increase in trap height, while Limenitidinae and Nymphalinae did not show any significant pattern (Table 3.2).

The species accumulation curves showed that understorey traps accumulated species faster than midstorey traps, and midstorey traps accumulated species faster than canopy traps (Figure 3.6). In addition, terra firme had a higher (estimated) species richness for all strata compared to várzea (Figure 3.6).

Table 3.2: Number of captures (number of species in parentheses) of each subfamily, including three tribes of Satyrinae, in terra firme and várzea forest at Cocha Cashu, Peru. U = understorey, M = midstorey, C = canopy, Total = all strata within the habitat combined. r_{sA} : Spearman rank correlation between abundance and trap height. r_{sB} : Spearman rank correlation between number of species and trap height. In terra firme, N = 60, in várzea, N = 90. N.S: not significant, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

	Várzea										Terra firme									
	U	M	C	Total	r_{sA}	Sig.	r_{sB}	Sig.	Total	C	M	U	Total	r_{sA}	Sig.	r_{sB}	Sig.			
Apaturinae	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-			
		(1)		(1)																
Biblidinae	258	66	7	331	-0.697	***	-0.638	***	538	15	72	451	538	-0.793	***	-0.666	***			
	(11)	(8)	(2)	(16)					(14)	(3)	(7)	(12)	(14)							
Charaxinae	23	11	7	41	-0.285	**	-0.255	**	53	8	13	32	53	-0.309	**	-0.313	*			
	(10)	(6)	(4)	(14)					(16)	(8)	(8)	(12)	(16)							
Limenitidinae	155	201	40	396	-0.406	***	-0.261	*	21	5	11	5	21	0.029	N.S.	0.030	N.S.			
	(8)	(6)	(3)	(10)					(9)	(3)	(6)	(4)	(9)							
Nymphalinae	9	3	1	13	-0.282	**	-0.28	**	14	2	5	7	14	-0.213	N.S.	-0.207	N.S.			
	(3)	(2)	(1)	(5)					(4)	(2)	(2)	(2)	(4)							
Satyrinae	102	9	3	114	-0.774	***	-0.77	***	183	3	18	162	183	-0.831	***	-0.827	***			
	(21)	(7)	(3)	(26)					(32)	(2)	(13)	(27)	(32)							
<i>Brassolini</i>	40	2	-	42	-	-	-	-	48	-	6	42	48	-	-	-	-			
	(6)	(2)		(6)					(8)		(3)	(8)	(8)							
<i>Morphini</i>	3	-	-	3	-	-	-	-	20	-	-	20	20	-	-	-	-			
	(2)			(2)					(1)		(1)	(1)	(1)							
<i>Satyriini</i>	59	7	3	69	-	-	-	-	11	3	12	100	11	-	-	-	-			
	(13)	(5)	(3)	(18)					(25)	(2)	(10)	(18)	(25)							

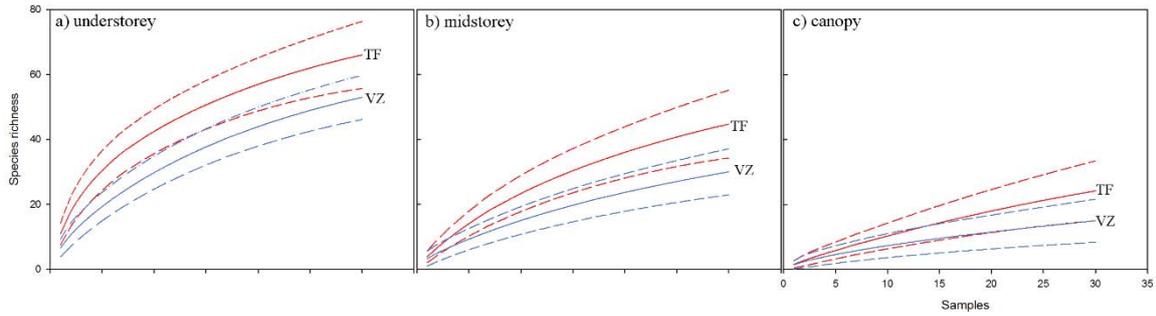


Figure 3.6: Species accumulation curves based on sample sites for each stratum in terra firme (red lines) and várzea (blue lines). Stippled lines indicate 95 % CI.

3.3.2 Differences between habitats

The vertical stratification seen in terra firme and várzea butterfly assemblages combined (Fig. 3.5), is upheld also within each forest type (Fig. 3.7). The terra firme understorey assemblage appears to be more homogenous than in várzea, since várzea understorey samples are more scattered in ordination space (Fig. 3.7). However, for midstorey and canopy samples this pattern appears to be reversed, with terra firme samples being highly variable in species composition and abundance. Interestingly, várzea samples appear to be divided into two separate clusters, each containing samples from all strata (Fig. 3.7).

Each individual stratum was significantly different between habitats (ANOSIM understorey: $R = 0.44$, $P = 0.001$; midstorey: $R = 0.575$, $P = 0.001$; canopy: $R = 0.48$, $P = 0.001$). The difference between understorey, midstorey and canopy samples across habitats was mainly due to a significantly higher number of captures of *A. jordani* in várzea and *P. prola* in terra firme (Fig. 3.8 a, b, c).

The ten species contributing most to differences between the terra firme and várzea understorey explained 56.9 % of the difference. In addition to *P. prola* (which explained 13.5 % of the difference) and *A. jordani* (10.2 %), the species largely consisted of species mainly found in terra firme (*N. obrinus*, 6.5 %; *M. helenor*, 3.8 %; *C. acontius*, 3.7 %; *C. callichloris*, 3.6 % and *T. thamyra/laches* 3.5 %) (Fig. 3.8 c).

In the midstorey and canopy, the ten species contributing most to the difference explained 62.4 % and 83.9 % of the difference, respectively. Apart from *A. jordani* (explaining 28.5 % of the difference in the midstorey and 34.8 % in the canopy) and *P. prola* (explaining 14.0 % of the difference in the midstorey and 22.5 % in the canopy), the difference was also in these strata largely caused by species being more abundant in terra firme (e.g. *B. aelius*, *M. capenas*, *C. acontius* and *M. antonoe*) (fig. 3.8 a, b).

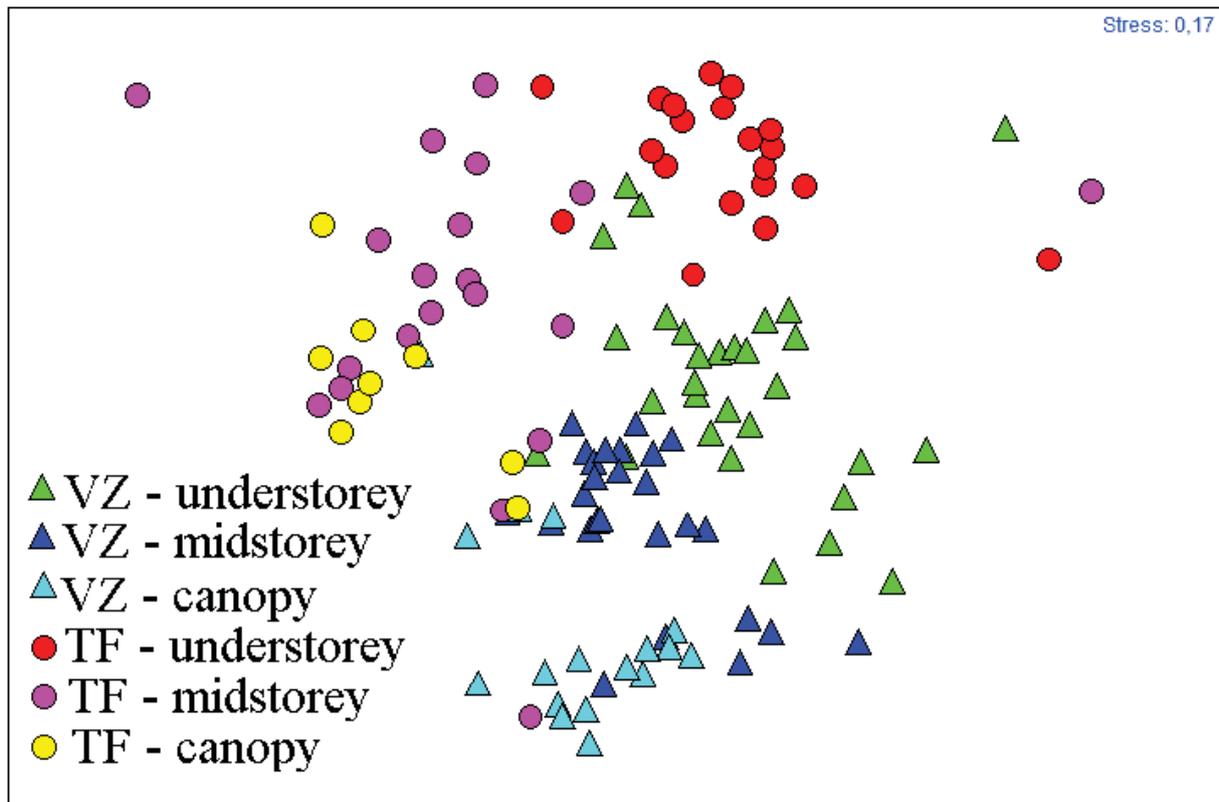


Figure 3.7: NMDS ordination of the Cocha Cashu butterfly assemblages in terra firme (TF - circles) and varzea (VZ - triangles), split into understorey (red circles, green triangles), midstorey (purple circles, dark blue triangles) and canopy (yellow circles, light blue triangles).

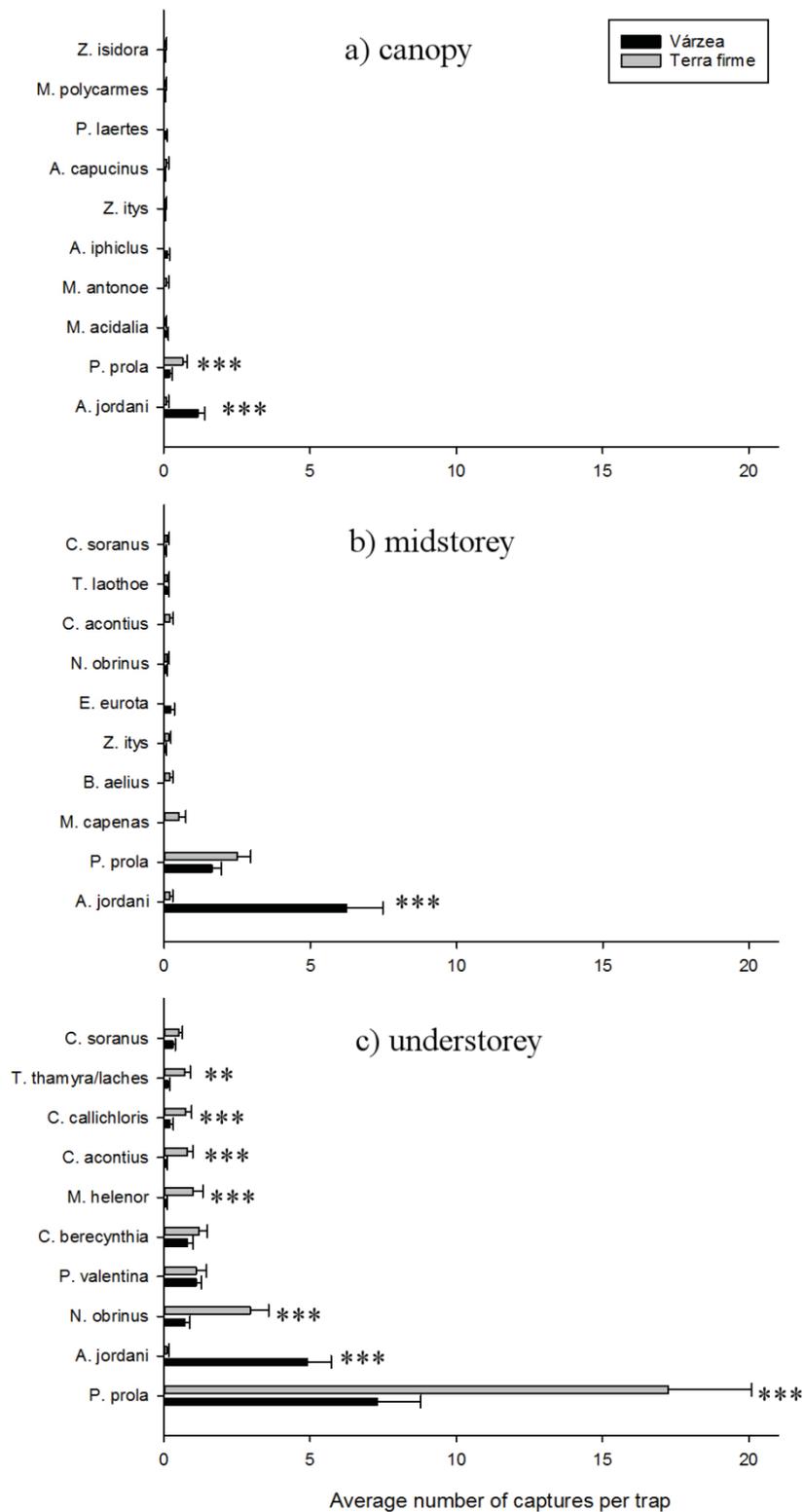


Figure 3.8: Average number of captures (\pm SE) per trap in the a) canopy, b) midstorey and c) understory of várzea (black bars) and terra firme (grey bars) forest. Asterisks indicate significant differences: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

3.3.3 Differences within habitats

In terra firme, the understorey samples formed a distinct cluster in the NMDS, while the midstorey and canopy varied a lot more in their species composition (Fig. 3.7). The within-habitat ANOSIM pairwise comparison test resulted in the understorey being significantly different from both the midstorey and the canopy, while no difference was found between the midstorey and canopy (Table 3.3). The ten most important species contributing to differences between the understorey and the midstorey and canopy explained 56.3 % and 60.4 % of the difference, respectively. The differences between the understorey and the other two strata was largely due to a very high number of *P. prola* captures in the understorey samples compared to the midstorey and canopy samples (Fig. 3.9 c, e). *Panacea prola* alone explained 15.9 % of the difference between understorey and midstorey and 18.4 % of the difference between understorey and canopy. In addition, several of the 10 most important species were restricted to the understorey samples. In fact, eight out of the 10 species contributing most to the difference between understorey and canopy only occurred in the understorey. Comparing the midstorey and canopy, the ten most important species accounted for 59.6 % of the difference (Fig. 3.9a). For nine of the 10 species, the difference was caused by a higher abundance in the midstorey (except *M. antonoe*). Here, *P. prola* again was the species explaining most of the difference (17.3 %).

All three strata in várzea were significantly different from each other (Table 3.3). The ten most important species contributing to differences between the understorey and midstorey and canopy explained 63.55 % and 68.21 %, respectively. The differences between strata was mainly due to very high abundances of *A. jordani* and *P. prola* in the understorey and *A. jordani* in the midstorey (Fig. 3.9 b, d, f). Most of the other species contributing to the differences between the understorey and the other two strata were species with a higher abundance in the understorey samples, and if present, occurring in very low numbers in the midstorey and canopy (Fig. 3.9 d, f). The ten species contributing most to the difference between the midstorey and canopy explained 75 % of the difference. This difference was largely due to *A. jordani* and *P. prola* being more abundant in the midstorey samples, together explaining 49.1 % of the difference.

Table 3.3: ANOSIM pairwise comparison between strata within terra firme and várzea forest showing R-values and P-values in parentheses. U: understory, M: midstorey, C: canopy.

Groups	Terra firme	Várzea
U, M	0.560 (0.001)	0.364 (0.001)
U, C	0.795 (0.001)	0.598 (0.001)
M, C	0.004 (0.390)	0.239 (0.001)

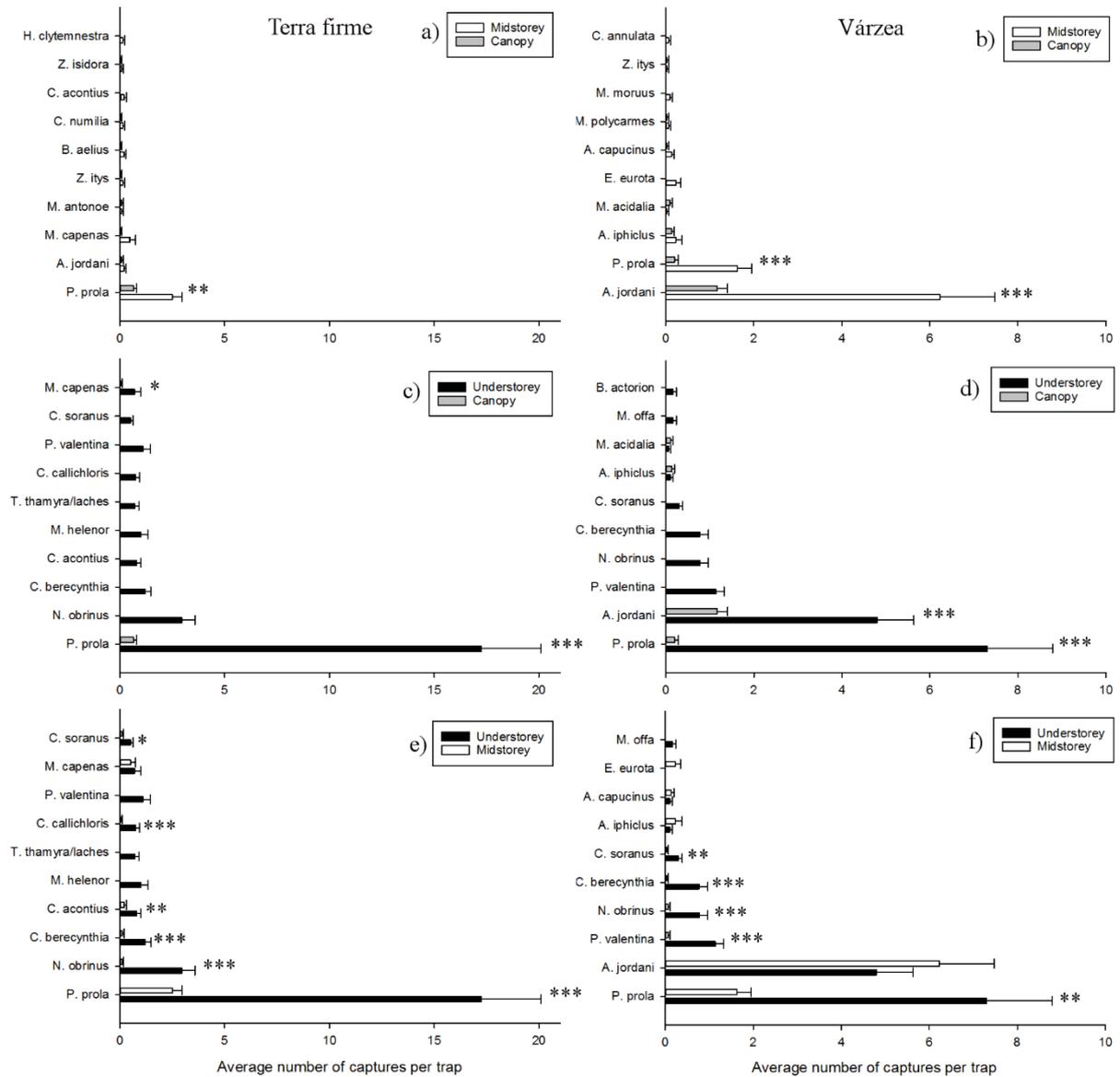


Figure 3.9: Differences in average number of captures (\pm SE) per trap between midstorey and canopy (a, b), understory and canopy (c, d) and understory and midstorey (e, f) of terra firme (left column) and várzea (right column) forest. Asterisks indicate significant differences: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

4. Discussion

4.1 Species richness and abundance

The butterfly species composition registered at Cocha Cashu in this study are similar to a previous study in the region (Pardonnet et al. 2013), as well as with other studies done at other locations in western Amazonia (DeVries et al. 1997; DeVries & Walla 2001). It has previously been registered 369 nymphalid species at a nearby field station (Robbins et al. 1996). 40 – 55 % of nymphalid species are thought to be fruit-feeding (DeVries 1987), suggesting that there should be about between 147-202 fruit-feeding nymphalid species in the area. This indicates that this study sampled approximately half of the possible species. However, butterfly communities vary both within and between years (Checa et al. 2009; DeVries et al. 2012; Grøtan et al. 2012), and thus a longer sampling period than what was possible in this study is necessary to achieve a more precise estimation of the total species richness. Further, the species accumulation curves for the total sample in both forest types did not reach an asymptote, although they appear to approach one (Fig. 3.2). This indicates that the sampling does not represent the full inventory of fruit-feeding nymphalids.

Total species richness was similar between the two forests, but on average more species were caught per trapping point in terra firme than in várzea. Only 48 % of species sampled in this study were shared between the two forest types. The species exclusive to each forest type (24 in várzea and 27 in terra firme) mainly consisted of species with fewer than five individuals (all but three species), indicating that rare species contributed significantly to the dissimilarity in assemblage. Indeed, rare species generally make up a large number of the sample in most studies (e.g. DeVries et al., 1997). In addition, the two forests were separated by the Manu river. Although the Manu river is a meandering river, and thus may transport species from one side to the other over time via meander cut-offs, the high turnover between the two forests may be due to the river acting as a dispersal barrier. Many butterfly species are restricted to the shaded understorey in closed canopy forest (DeVries 1987) and thus will not cross an area of approximately 200 meters of beach and river (Groenendijk et al. 2014).

Of the six subfamilies registered, Biblidinae was the most abundant ($n = 869$), largely due to *P. prola* ($n = 682$). This was expected, as *P. prola* has been registered in high numbers in other studies across western Amazonia (Devries & Walla 2001; Pardonnet et al. 2013). The abundance of Limenitidinae (*A. jordani* in particular) was surprising, as this subfamily is assumed to not be a part of the fruit-feeding guild. However, in this study 95 % of the

individuals in Limenitidinae and 98 % of *A. jordani* occurred in várzea forest (Appendix 1). In a study done in Yasuni National park in Ecuador, Checa (2006) found a similar distribution pattern (*A. jordani*: flooded forest n = 520, forest edge n = 3). While the reason for the affinity for flooded forests is unknown, it is possible that the larval host plant(s), which are currently unknown, are more abundant in flooded forests (Willmott 2003).

4.2 Butterfly assemblage structure and composition

I found that terra firme and várzea butterfly assemblages were significantly different, with a clear species turnover between forest types. These results are similar to those found for other taxa, such as birds (Haugaasen & Peres 2008; Beja et al. 2010), bats (Bobrowiec et al. 2014) and mammals (Haugaasen & Peres 2005a).

The overall difference in species composition between terra firme and várzea was mainly due to higher abundances of species belonging to Biblidinae and Satyrinae in terra firme, and Limenitidinae in várzea (Fig. 3.4, Appendix 1). *Myscelia capenas* is an uncommon species restricted to the upper Amazon basin (Jenkins 1984). In this study, *M. capenas* was significantly more abundant in terra firme than in várzea (Fig 3.4). Little information exist on the biology of this species (Jenkins 1984), and no records of the larval host plant are available (Robinson et al. 2010). However, *M. capenas* is known to show local restrictions on a small geographical scale. For example, DeVries & Walla (2001) found 75 % of this species in one of five closed placed sampling sites.

Moreover, assemblage differences between terra firme and várzea were largely driven by understorey species (Appendix 1), and consequently they were important for the observed difference in species assemblages in this stratum too (Fig. 3.8). In this study, *N. Obrinus* and *Catonephele acontius* were both more abundant in terra firme understorey than in várzea understorey (Fig. 3.8c). *Nessaea obrinus* and *C. acontius* are known to prefer undisturbed understorey (Ramos 2000) and to prefer forest over cerrado landscape (Pinheiro & Ortiz 1992). The higher abundances of these species in terra firme understorey thus suggest a more suitable habitat, but whether this is due to a more suitable microclimate or a better availability of larval host plants is uncertain.

In addition to *P. prola*, *N. obrinus* and *C. acontius*, the difference between terra firme and várzea in the understorey stratum was due to the higher abundance of individuals of the subfamily Satyrinae in terra firme (table 3.2, Figure 3.8 c). Satyrinae is generally restricted to understorey habitat (DeVries 1987; DeVries 1988; DeVries & Walla 2001), utilizing only

monocotyledonous plants as larval hostplants (Ackery 1988; Fiedler 1998). They are particularly sensitive to changes in humidity and moisture (Hill 1999). Many Satyrinae butterflies also have broad wings, which favour slow, agile flight (Betts & Wootton 1988), which Hill et al. (2001) suggested may aid manoeuvrability in dense understorey. As the seasonal flooding in várzea leaves the understorey entirely submerged, terra firme should host better overall conditions for Satyrinae species, for example boasting a higher abundance and diversity of larval host plants, and a denser understorey and canopy (Haugaasen & Peres 2006; Bobrowiec et al. 2014). For example, the genus *Taygetis* (Satyrinae, Satyrini), which consists of medium to large sized butterflies that are restricted to deeply shaded understorey (DeVries 1987), showed a clear preference for terra firme understorey compared to várzea understorey (Appendix 1).

The butterfly assemblages in terra firme and várzea were clearly stratified (Fig 3.7). The overall stratification patterns were similar in both forests, with an overall decrease in abundance and species richness from the understorey to the canopy (Table 3.2). This is partly consistent with other Neotropical studies investigating vertical stratification of fruit-feeding nymphalids. The abundance tends to be higher in understorey traps compared to canopy traps across studies, while the number of species varies between studies (DeVries et al. 1997; DeVries et al. 1999; DeVries & Walla 2001; DeVries et al. 2012). For example, DeVries et al. (2012) compared vertical stratification of fruit-feeding nymphalids between Costa Rica and Ecuador and found that Ecuador had significantly more species in the understorey, while Costa Rica had significantly more species in the canopy. Indeed, it appears that studies from the Amazon (DeVries et al. 1997; DeVries et al. 1999; DeVries & Walla 2001) tend to have higher species richness in the understorey than in the canopy, while the opposite appears to be true for Central America (DeVries 1988; DeVries et al. 2012).

One can expect that most rotting, fallen fruit should end up on the forest floor, and this may thus explain the higher abundance of butterflies captured in the understorey. Nevertheless, there are still fruit-feeding nymphalids that are upper strata specialists (e.g. *B. aelius*, Appendix 1), suggesting that there is a source of rotten fruits above understorey level. Schulze et al. (2001) suggested that epiphytes could act as traps for falling fruit, and in this way provide a more predictable source of fallen fruit above understorey level. Leimbeck and Balslev (2001) found significantly more epiphytes in várzea compared to terra firme. This might explain the higher abundance of captured individuals in midstorey and canopy in várzea compared to terra firme.

A few subfamilies portrayed differences in vertical stratification across forest types. While all subfamilies had a significant decrease in both abundance and species number in várzea with increasing trap height, Limenitidinae and Nymphalinae did not decrease in number of individuals or species with increasing trap height in terra firme (Table 3.2). In most other Neotropical studies, Nymphalinae and Charaxinae (and often Biblidinae) has been most abundant in the canopy, while Satyrinae has been most abundant in the understorey (DeVries et al. 1997; DeVries & Walla 2001). No data on stratification from fruit-trapping studies exist for Limenitidinae in the Neotropics, as this subfamily is generally not included in the fruit-feeding guild. However, Willmott (2003) states that most *Adelpha* (Limenitidinae) species prefer areas with high levels of sunlight, such as the canopy, as they use the sun as a source of heat in order to warm up their thoraxes. The absence of a significant stratification pattern in these subfamilies in terra firme can therefore be explained by a more closed canopy, resulting in sun loving species having to use the upper strata. In addition, it has been hypothesized that the availability of larval host plants has led to a specialisation to specific strata (Schulze et al. 2001). For example, the distribution of adult Ithomiinae butterflies in the Neotropics are known to be influenced by the vertical stratification of their host plants (Beccaloni 1997). While no floristic analyses were done in this study, the difference in stratification may, in addition to different light levels beneath the canopy, be due to a different stratification of the larval host plants between the two forests. However, both Limenitidinae and Nymphalinae have a wide range of larval host plants (Ackery 1988; Willmott 2003), and thus it is unlikely that the difference in stratification is caused by this alone. The sampling of fruit feeding nymphalids mainly captures individuals when they are feeding, and can thus not provide information on their behaviour when not feeding, e.g. during courtship. For example, DeVries (1988) observed that males of *Morpho cypris*, a species only trapped in the understorey, spent much of the time patrolling in the canopy, presumably looking for females.

In this study, the midstorey and canopy strata had lower species richness compared to the understorey. Apart from *A. jordani* and *P. prola*, the main drivers of difference between terra firme and várzea, the difference was made up by species very low in numbers (Fig 3.6). While some of these species were exclusive to either forest (e.g. *E. eurota* in várzea midstorey), most species occurred in both forests, but in very low numbers in these strata (Appendix 1). This reflects the ecology of these ‘upper strata’ species. Species found in canopies typically have a wide thorax and small wings (Schulze et al. 2001), which make them fast flyers (Chai & Srygley 1990; Srygley & Chai 1990). This is especially important in the canopy, where increased predation pressure from e.g. insectivorous aerial-hawking birds (Schulze et al. 2001)

and higher wind speed (Parker 1995) should favour species capable of fast flight. Furthermore, Schulze et al. (2001) found a higher variability in the species assemblage of fruit-feeders in the canopy compared to the understorey. They suggested this was due to a more varied availability of rotting fruits in the canopy, which caused the canopy feeders to have wider niches and thus occurring in lower abundances and a more varied species composition. This is in accordance with results found for terra firme in this study, which showed a relatively high variability in assemblage composition within the midstorey and canopy samples. In várzea, midstorey and canopy samples were much more clustered – probably an artefact of *A. jordani* being highly abundant in these strata, and thus causing the samples to cluster in ordination space.

In terra firme, the understorey species assemblage was significantly different from both the midstorey and canopy assemblages, while the midstorey and canopy did not differ from each other (Table 3.3). This is in line with previous studies showing a high species turnover rate between the understorey and the two upper strata (Fermon et al. 2003, 2005). In addition, the understorey samples in terra firme in this study formed a very compact cluster, indicating a very homogenous species assemblage across sampling sites. This is confirmed by the high number of common species as well as the high Shannon diversity value (Table 3.1). In contrast, the midstorey and canopy had few common species, but still attained a high Shannon diversity value, indicating that also the assemblages in these strata were diverse and that the common species did not dominate the assemblage to a very large degree.

Midstorey and canopy samples in terra firme were very similar. Indeed, there was a higher assemblage variation within each stratum than between strata (Fig. 3.7). The similarity of midstorey and canopy samples, in addition to the significantly different understorey samples suggests that there are two fruit-feeding nymphalid communities in terra firme – understorey and ‘upper strata’.

In várzea, butterfly assemblages differed significantly between all three strata (Table 3.3). This was unexpected, as the more open canopy in várzea compared to terra firme (Bobrowiec et al. 2014) should cause a disruption of the vertical stratification due to increased light levels beneath the canopy (Fermon et al. 2005). In South East Asia, studies comparing vertical stratification of fruit-feeding nymphalids in undisturbed and selectively logged forests have found mixed communities along the vertical gradient in the selectively logged forests (Fermon et al. 2005; Luk et al. 2011). As selective logging reduces canopy cover (Hill 1999), it was expected that the same pattern would occur in várzea in this study. However, differences in the general forest

structure between Neotropical and South East Asian rainforests, as well as potential differences in how selective logging and flooding of the understorey affect the forest structure, may explain the lack of similarity.

While the reason for the apparent distinct midstorey community is unknown, it is likely to result from vegetation characteristics not recorded in this study. However, within the scope of this study, there are two possible explanations for why a distinct midstorey community only occurred in várzea:

- 1) The higher number of epiphytes in várzea (Leimbeck & Balslev 2001) that potentially can act as traps for fallen rotting fruit (Schulze et al. 2001), might support a higher number of midstorey specialists in várzea, resulting in a distinct midstorey community. Indeed, there were more species restricted to the midstorey stratum in várzea than in terra firme.
- 2) Schulze et al. (2001) found the midstorey stratum to be the most species rich, and stated that this was due to the understorey and canopy assemblages overlapping. While this overlap may partially explain the intermediate position of the midstorey samples in the NMDS ordination (Fig. 3.7), a high number of midstorey restricted species, as well as a low species richness, indicate that this is not the reason for the distinct midstorey community in várzea in this study.

Nevertheless, this hypothesis remains untested in this study, but is a promising topic for future studies, and indicates that vertical stratification studies in the Neotropics benefit from including the midstorey stratum as a sampling height.

The Cocha Cashu várzea forest is not a ‘true várzea’ but a ‘mature floodplain’, only experiencing occasional flood pulses (Haugaasen & Peres 2005a). This results in a mosaic of different habitats, where some forest areas resemble terra firme with a denser understorey, and other areas are more similar to true várzea (*pers. obs.*). This was reflected in the NMDS, where the várzea samples formed two distinct clusters (fig. 3.7). A subsequent SIMPER analysis (data not shown) revealed *A. jordani* and *P. prola* to be the most important species in determining the difference between these two clusters. While *A. jordani* was more abundant in the outermost cluster, *P. prola* was far more abundant in the more central cluster. These two species together explained 59.2 % of the difference. Apart from these two dominant species, the rest of the difference was made up by species associated with terra firme being more abundant in the central cluster (e.g. *N. obrinus* and *C. berecynthia*), and species associated with várzea (e.g. *A. iphichlus* and *A. capucinus*) being more abundant in the outermost cluster. The outermost cluster consisted mainly of traps located along transects located closest to the meandering Manu river

(Fig 2.1). It is possible that the apparent division between the várzea samples has arisen as a result of edge effects caused by the river, such as changes in microclimatic conditions (Laurance et al. 1998), or due to increased flooding levels in the rainy season.

4.3 Conclusion

Although terra firme trapping locations on average caught more species than in várzea, the total species richness was similar, and thus my first prediction was not confirmed. My second prediction was confirmed, as terra firme hosted more understorey adapted species. The third prediction was not confirmed, as the species communities in all strata were different from each other in várzea, whereas the midstorey and canopy communities were similar in terra firme.

Terra firme and várzea species assemblages were significantly different in this study – only 48 % of the species captured were shared between the forest types. In terra firme, the understorey assemblage was significantly different from both the midstorey and canopy assemblages, while all strata were different in várzea, indicating a midstorey community seldom sampled in the Neotropics. These results further underline the value of várzea forests in maintaining biodiversity in the Amazon, due to their distinct species communities, which also has been found for plants (Balslev et al. 1987; Haugaasen & Peres 2006; Myster 2007), birds (Haugaasen & Peres 2008; Beja et al. 2010) and mammals (Haugaasen & Peres 2005a; Haugaasen & Peres 2005b). Várzea forests are one of the most threatened ecosystems in the Amazon due to timber extraction and conversion to agriculture (Schöngart & de Queiroz 2010), but the accumulating evidence for várzea forests as an important part of Amazonian biodiversity suggests a better protection of these forests are long overdue.

5. References

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6. Appendix 1

Table A1: Captures of all species caught at Cocha Cashu, Peru, 14.7-28-9 2015.

	Várzea			Terra firme			Total
	U	M	C	U	M	C	
Apaturinae							
<i>Doxocopa agathina</i>	0	1	0	0	0	0	1
Biblidinae							
<i>Catonephele acontius</i>	2	0	1	16	4	0	23
<i>Catonephele numilia</i>	1	0	0	0	3	1	5
<i>Epiphile lampethusa</i>	0	1	0	0	0	0	1
<i>Dynamine chryseis</i>	0	0	0	1	0	0	1
<i>Eunica eurota</i>	0	7	0	0	0	0	7
<i>Eunica marsolia</i>	0	1	0	2	0	0	3
<i>Eunica orphise</i>	0	0	0	1	0	0	1
<i>Eunica sydonia</i>	0	0	0	0	1	0	1
<i>Hamadryas arinome</i>	0	2	0	0	0	0	2
<i>Hamadryas chloe</i>	0	0	0	4	0	0	4
<i>Myscelia capenas</i>	1	0	0	14	10	1	26
<i>Nessaea hewitsonii</i>	2	0	0	6	0	0	8
<i>Nessaea obrinus</i>	23	2	0	59	2	0	86
<i>Panacea prola</i>	219	49	6	345	50	13	682
<i>Panacea regina</i>	1	0	0	1	0	0	2
<i>Pyrrhogyra crameri</i>	2	0	0	0	0	0	2
<i>Pyrrhogyra edocla</i>	1	0	0	1	0	0	2
<i>Pyrrhogyra otolais</i>	4	0	0	0	0	0	4
<i>Temenis laothoe</i>	2	3	0	1	2	0	8
<i>Temenis pulchra</i>	0	1	0	0	0	0	1
Charaxinae							
<i>Archaeoprepona demophoon</i>	2	0	0	4	0	0	6
<i>Archaeoprepona demophon</i>	2	0	0	3	0	0	5
<i>Archaeoprepona licomedes</i>	1	0	0	0	0	0	1
<i>Coenophlebia archidona</i>	0	0	0	0	1	0	1
<i>Consul fabius</i>	4	0	0	2	0	0	6
<i>Fountainea ryphea ryphea</i>	0	0	0	0	1	1	2
<i>Hypna clytemnestra</i>	0	0	0	0	3	0	3
<i>Memphis acidalia</i>	2	1	3	5	1	1	13
<i>Memphis cathinka</i>	0	0	0	3	0	1	4
<i>Memphis glauce</i>	1	0	0	2	0	1	4
<i>Memphis moruus</i>	2	3	0	1	0	1	7
<i>Memphis offa</i>	5	0	0	0	1	0	6
<i>Memphis phantes vicinia</i>	1	0	0	1	0	0	2
<i>Memphis polycarmes</i>	0	2	0	3	1	1	7
<i>Memphis praxias</i>	0	0	0	1	0	0	1
<i>Memphis xenocles</i>	0	2	0	0	0	0	2
<i>Prepona laertes</i>	0	0	2	0	0	0	2

Table A1 cont.

Zaretis isidora	3	2	1	3	2	1	12
Zaretis itys	0	1	1	4	3	1	10
Limentidinae							
Adelpha capucinus	3	4	1	0	0	2	10
Adelpha cocala	0	0	0	1	0	0	1
Adelpha cytherea	0	0	0	1	0	0	1
Adelpha erotia	0	1	0	0	1	0	2
Adelpha heraclea	1	0	0	0	0	0	1
Adelpha iphicus	3	7	4	0	0	0	14
Adelpha jordani	144	187	35	2	4	2	374
Adelpha malea	1	0	0	0	1	0	2
Adelpha mesentina	0	1	0	0	1	0	2
Adelpha naxia	1	0	0	0	0	0	1
Adelpha pleasure	1	0	0	1	3	0	5
Adelpha thesprotia	1	1	0	0	1	1	4
Nymphalinae							
Baeotus aelius	0	0	1	0	4	1	6
Baeotus deucalion	0	0	0	0	0	1	1
Colobura annulata	1	2	0	0	0	0	3
Colobura dirce	2	0	0	1	0	0	3
Smyrna blomfieldia	0	1	0	0	0	0	1
Tigrida aesta	6	0	0	6	1	0	13
Satyrinae							
<i>Brassolini</i>							
Bia actorion	5	0	0	1	0	0	6
Caligo eurilochus	2	0	0	0	0	0	2
Caligo idomenides	0	0	0	1	0	0	1
Catoblepia berecynthia	23	1	0	24	2	0	50
Catoblepia soranus	8	1	0	10	2	0	21
Catoblepia xanthicles	1	0	0	0	0	0	1
Eryphanis automedon	0	0	0	2	0	0	2
Opoptera aorsa	0	0	0	1	0	0	1
Opsiphanes invirae	0	0	0	2	2	0	4
Opsiphanes quiteria	1	0	0	1	0	0	2
<i>Morphini</i>							
Morpho achilles	1	0	0	0	0	0	1
Morpho helenor	2	0	0	20	0	0	22
<i>Satyrini</i>							
Amphidecta pignerator	0	0	0	1	0	0	1
Caeruleptychia scopulata	1	0	1	0	0	0	2
Chloreuptychia arnaca	0	0	0	1	0	0	1
Chloreuptychia callichloris	6	0	0	15	1	0	22
Chloreuptychia herseis	2	0	0	3	0	0	5
Chloreuptychia marica	0	0	0	6	1	0	7
Cissia myneca	0	1	0	0	1	0	2
Cissia terrestris	0	1	1	0	0	0	2

Table A1 cont.

Erichthodes antonina	0	0	0	0	1	0	1
Harjesia n. sp.	1	0	0	0	0	0	1
Magneuptychia fugitiva	0	2	0	1	0	0	3
Magneuptychia sp.	0	0	0	0	1	0	1
Manataria hercyna	1	0	0	0	0	0	1
Megeuptychia antonoe	1	0	0	0	2	2	5
Pareuptychia spp.	0	1	0	1	1	0	3
Posttaygetis penelea	0	0	0	2	0	0	2
Pseudodebis celia	0	0	0	1	0	0	1
Pseudodebis valentina	33	2	0	22	0	0	57
Splendeuptychia n. sp.	0	0	1	0	0	0	1
Taygetis angulosa	0	0	0	0	0	1	1
Taygetis echo	0	0	0	3	0	0	3
Taygetis elegia	2	0	0	1	0	0	3
Taygetis n. spp.	2	0	0	1	0	0	3
Taygetis oyapock	1	0	0	5	2	0	8
Taygetis sosis/cleopatra	0	0	0	9	1	0	10
Taygetis spp.	0	0	0	8	1	0	9
Taygetis sylvia	2	0	0	0	0	0	2
Taygetis thamyra/laches	4	0	0	14	0	0	18
Taygetis virgilia	3	0	0	6	0	0	9



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