

FRUIT-FEEDING BUTTERFLY ASSEMBLAGES IN A NEOTROPICAL SAVANNA: ASSESSING PHENOLOGICAL PATTERNS USING BAITED TRAPS

A. V. L. FREITAS^{1,2*}, D. G. MUNIZ^{1,3}, J. Y. O. CARREIRA¹, P. S. OLIVEIRA¹

¹ Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas

² Museu de Diversidade Biológica, Instituto de Biologia, Universidade Estadual de Campinas

³ Present address: LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo

*Corresponding Author Email: baku@unicamp.br

ABSTRACT. The cerrado savanna is currently one of the most endangered Neotropical biomes, yet while information for many butterfly groups are available from forested habitats, data from savannas and other non-forested habitats remain deficient. The present study assesses the species composition and phenology of fruit-feeding, nymphalid butterfly assemblages in a cerrado reserve at the southern limit of the Brazilian savanna distribution. Butterfly collections were carried out with 20 baited traps organized in four lines of five traps each, from November 2009 to October 2010. In total, 597 individuals from 39 species belonging to all fruit-feeding Nymphalidae clades were captured. Total butterfly abundance peaked at the middle of the wet season, and lowest abundances were recorded in mid dry season. Temperature and precipitation were good predictors of total community abundance and richness, but the most common species showed distinct relationship to these parameters. Species richness in the study site was equivalent or higher to those reported for other cerrado areas, and lower compared to forested habitats. Although interesting patterns emerged from comparative data of fruit-feeding butterfly assemblages, further investigation in diverse Neotropical habitats is needed to produce a more precise picture about the geographical ecology of this insect guild..

Additional key words: insect seasonality; Lepidoptera; Nymphalidae; temporal variation

Covering about 2 million km², the Neotropical cerrado savanna comprises a wide range of physiognomies, from grassy fields to tall forest vegetation, all interspersed by gallery forests and other moist vegetation following the watercourses (Oliveira-Filho & Ratter 2002). The climate in the region of the cerrado domain is highly seasonal, with a hot and rainy season alternating with a cold and dry period (Ratter et al. 1997, Oliveira-Filho & Ratter 2002). Accordingly, many cerrado plants usually shed their leaves during the dry season, and leaf production is concentrated in the late dry season and early rainy season (Morais et al. 1995, Batalha & Mantovani 2000).

The cerrado savannas are currently one of the most endangered Neotropical formations, and according to Strassburg et al. (2017) the cerrado biome has already lost 46% of its original area and only 19.8% remain as well-preserved areas. This rampant process of destruction was stressed by Cavalcanti & Joly (2002), who also called attention to the fact that conservation of the cerrados has been largely neglected. These authors provided a list of priority areas for conservation together with recommendations for conservation strategies, but very few have been adopted since then. Consequently, a large portion of cerrado species richness and endemism are threatened and can be lost in the near future, with high impacts to this unique biodiversity hotspot (Myers et al. 2000, Brown & Gifford 2002, Cavalcanti & Joly 2002, Klink & Machado 2005, Strassburg et al. 2017).

Facing the critical scenario of degradation of many tropical habitats, there is a need to understand the remaining biological communities and to maintain their viability (DeVries et al. 2012). Given the quick destruction of the cerrado savannas and the lack of detailed information about most animal communities within this vegetation, focus should be directed to biological indicator groups, which can be informative of the overall disturbance level of the environment (Pearce & Venier 2006). Ideally, a bioindicator group should be easily sampled in relatively high numbers, also have a stable taxonomy, and be easily identifiable (Pearce & Venier 2006). In most tropical and subtropical vegetation formations, the guild of fruit-feeding butterflies attends to all these criteria (Bonebrake et al. 2010, Freitas et al. 2014). In addition, fruit-feeding butterflies feed on rotting fruits and other decaying material, which make them easy to capture with baited traps (DeVries 1987, 1988, Freitas et al. 2014).

Information on fruit-feeding butterfly assemblages is available from numerous studies in tropical forests around the world, including Africa, Southeast Asia, India, and Central and South America (Freitas et al. 2014 and references therein). In contrast, data from non-forest habitats are lacking and only three studies have been carried out in the Brazilian cerrados so far (Pinheiro & Ortiz 1992, Silva et al. 2012, Freire Jr. 2015). The present study assesses the community of fruit-feeding butterflies in a cerrado reserve at the

southern limit of the savanna distribution (see Oliveira-Filho & Ratter 2002). Since the cerrado is characterized by strong seasonality, we also assess the temporal variation in species composition of fruit-feeding butterfly assemblages. Therefore, the objectives of the present study were: (1) to quantitatively describe the community of fruit-feeding butterflies in a cerrado area; (2) to describe the seasonality of the community, estimating when fruit-feeding butterflies should be more abundant; (3) to test if the observed seasonal patterns are associated with climate; and finally (4) to compare our results with those available from other cerrado areas and forested habitats as well, summarizing the available knowledge so far.

MATERIAL AND METHODS

Study site. Field work was carried out in a cerrado reserve near Itirapina, São Paulo State, Southeast Brazil (22.266111°S, 47.794167°W, 800 m altitude). The area is located near the southern limit of the cerrado biome, where a wide strip of cerrado runs through the middle of the state of São Paulo (IBGE, 2004). Nevertheless, the vegetation of the study area is very similar to northern areas at the core of the cerrado domain (Reys et al. 2013). The study area is a 51-ha fragment embedded in a heterogeneous matrix of agriculture, *Pinus* (Linnaeus) and sugar cane plantations, and cerrado fragments. The vegetation consists of a scrub of shrubs and trees (canopy about 3 to 5 m high), corresponding to the cerrado sensu stricto physiognomy (Oliveira-Filho & Ratter 2002). A hot and rainy season occurs from October to March (spring-summer, hereafter wet season), and a cool and dry season from May to September (fall-winter, hereafter dry season) (see Fig. 1). Local climatic data were obtained from the climatological station of Instituto Florestal (Fig. 1). Long term data confirmed that the climate during the study period is typical for the region (Instituto Nacional de Meteorologia 2018).

Sampling procedures. Fruit-feeding nymphalid butterflies are rarely seen visiting flowers, and the adults commonly feed on rotting fruits, plant sap, and decaying material such as mammal excrement and carrion (DeVries 1987, 1988). Due to their diet, these butterflies are easily captured with baited traps. Also, they have been subject of many studies in the last decades (see references in Freitas et al. 2014).

Butterfly collections were carried out with baited traps, following DeVries (1988) and Uehara-Prado et al. (2007). Butterflies were sampled from November 2009 to October 2010, using 20 portable butterfly traps organized in four lines of five traps. Traps were deployed in a grid formed by four linear transects 30 m apart from each other, and baited with a standard mixture of banana

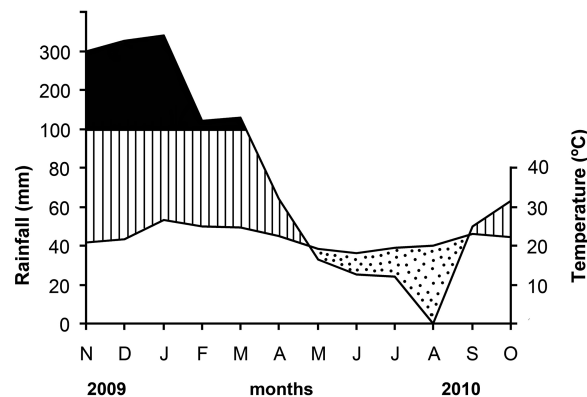


FIG. 1. Climatic diagram of the study site in Itirapina, São Paulo State, SE Brazil (see methods) during the study period (format following Walter 1985). Dotted = dry periods; hatched = humid periods; black = super-humid periods.

and sugarcane juice fermented for 48 h. Each trap was suspended from low branches such that the platform hung at 1–1.5 m above the ground, and at least 110 m from the cerrado edge. Collections were carried out weekly, and all traps were kept simultaneously open for 24 h each week each month (96 h per month). In November 2009 only three trapping sessions were performed. Overall, samplings comprised 940 trap-days (47 days in one year [12 months x 4 days – 1] x 20 traps). With the exception of three common, easily identifiable species, most trapped butterflies were collected and identified in the laboratory.

Fruit-feeding butterfly taxonomy follows Freitas & Brown (2004) modified after Wahlberg et al. (2009), including the subfamilies Biblidinae, Charaxinae, Satyrinae (tribes Morphini, Brassolini and Satyrini), and Nymphalinae (more details in Freitas et al. 2014).

Data analysis.

Species richness and diversity

Community species diversity was estimated using the Fisher Alpha, an index chosen for its robustness (Magurran 2004). Community species richness was estimated using the non-parametric Chao1 index, which does not assume species-abundance models, and has been considered more efficient than other indices (Colwell & Coddington 1994, Magurran 2004). A Whittaker plot was designed to compare relative species abundance and identify dominant species. Rarefaction curves were used to compare species richness. All these analyses were performed using the software PAST® version 3.16 (Hammer et al. 2001).

Seasonal patterns and climatic correlations

Circular statistics was used to describe the seasonal pattern of abundance. Specifically, the Rao test was used to estimate mean occurrence dates and to test the hypotheses that butterfly abundance was not evenly distributed along the year (Bergin 1991). The Rao test was performed for the whole community and for the five more common species using the software Oriana 4.02 (Kovach 2011).

In order to investigate the relationship between climatic data and butterfly richness and abundance, a model selection approach was adopted (Burnham & Anderson 2002). In this analysis, each field trip was used as a data point (field trips occurred approximately weekly during the sampling period) and the predictor variables were mean rainfall and mean temperature prior to each observation. To explore the time scale in which climate influences the butterfly community, mean rainfall and temperature were calculated in three different periods in relation to the date of each observation: (1) last 15 days, (2) last 30 days and (3) a 30-day period ending 30 days before the beginning of each observation. In the cerrado, the rainy season is also the hottest season, so that there is a high correlation between rainfall and temperature (Oliveira-Filho & Ratter 2002). To deal with this, a linear regression between mean temperature and rainfall for each time scale was performed, and the residuals were used as a measure of rainfall independent of temperature (following Graham 2003). This measure of residual rainfall is interpretable as how more (or less) rainy a period was than expected by its temperature.

Seven response variables were analysed separately: observed species richness, total butterfly abundance, and the abundances of each of the five most abundant species in the sample. The following models were built for each of these variables: 1) separate models for each time scale, 2) a saturated model containing rainfall, temperature, and their interaction for each time scale, and 3) competing models including all possible combinations of variables within the same time scale. In addition, in the case of the abundance of *Ypthimoides patricia* (Hayward), models containing a quadratic effect of temperature were added, because the data suggested a non-monotonic relationship between these variables. Competitor models were ranked according to the Akaike Information Criterion (AIC) and models with $\Delta AIC < 2$ were considered as equally plausible. In all models, a negative binomial distribution was assumed, which is an adequate distribution for count-data with high variance (White & Bennets 1996). All these analyses were performed in the software R 3.4.2 (R Development Core Team 2013) using the packages MASS (Venables & Ripley 2002) and MuMIn (Barton 2016).

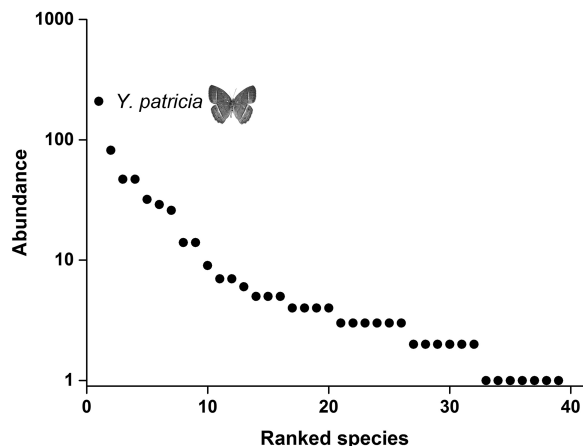


FIG. 2. Whittaker plot for total sample of fruit-feeding Nymphalidae captured in the study site in Itirapina, São Paulo State, SE Brazil.

Comparison with other cerrado sites

The data from the present study (hereafter SP) were compared with similar data from three other cerrado sites: (1) Silva et al. (2012) – a study in a cerrado area near Belo Horizonte, Minas Gerais State, southeastern Brazil (hereafter MG); (2) Pinheiro & Ortiz (1992) – a study in the cerrado reserve of the Brasília Botanical Garden, Brasília, Distrito Federal, Central Brazil (hereafter DF1); and (3) Freire (2015) – a study (partially published in Freire & Diniz 2015) in the “Fazenda Água Limpa” reserve, Brasília, Distrito Federal, Central Brazil (hereafter DF2) (see Appendix 1). The MG site and the present study are located in a transitional region where the cerrado and the Atlantic Forest are interspersed (the “blend zone” of Brown & Mielke (1968), a region combining faunal elements from the Atlantic Forest and from the cerrados). The two sites in Brasília are adjacent areas located in the “core region” of cerrado in the Central Brazil plateau (see Brown & Mielke 1967, 1968). These data were all gathered using the same standardized sampling methods for fruit-feeding butterflies. Data from other cerrado sites were not included in the analysis because complete datasets, with abundance data for each species, were not available. Species composition similarity among cerrado sites was calculated using the Morisita similarity index (using PAST®). Based on existing literature (Andrade et al. 2017) and field experience, all butterfly species from the four studies were categorized as one of the following: forest specialist, cerrado specialist, and generalist.

TABLE 1. Abundance of all 39 species of fruit-feeding butterflies captured between November 2009 and October 2010 in Itirapina, São Paulo State, SE Brazil.

	2009			2010										Total
	Nov	Dec		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	
Biblidinae														
<i>Callicore astarte</i>	1	2		7	14	5		1			1		1	32
<i>Callicore sorana</i>	1	3		3	5	4	2		2			2	4	26
<i>Catonephele acontius</i>					2		1							3
<i>Catonephele numilia</i>				2										2
<i>Eunica bechina</i>					3	2	1					2	1	9
<i>Eunica tatila</i>							1	1	1					3
<i>Myscelia orsis</i>							1							1
<i>Temenis laothoe</i>					1		1							2
<i>Hamadryas amphinome</i>		1				2		2	1					6
<i>Hamadryas arete</i>						1								1
<i>Hamadryas epinome</i>		1						1						2
<i>Hamadryas februa</i>	3	1			1	3	11	19	18	4	9	13		82
Charaxinae														
<i>Archaeoprepona demophon</i>				3		1							1	5
<i>Archaeoprepona demophoon</i>						1								1
<i>Fountainea ryphea</i>						2		1						3
<i>Hypna clymnestra</i>								1						1
<i>Memphis acidalia</i>						1		1						2
<i>Memphis appias</i>											1			1
<i>Memphis moruus</i>						1	1	2			2		1	7
<i>Siderone galanthis</i>				1										1
<i>Zaretis strigosus</i>					2	1								3
Nymphalinae														
<i>Historis odius</i>		2		1				1	1					5
<i>Smyrna blomfieldia</i>	1	1			1		1	1	1				1	7
Satyrinae: Brassolini														
<i>Caligo illioneus</i>	1	2		2	2	3	12	7						29
<i>Opsiphanes invirae</i>		1			1	1				1				4
Satyrinae: Morphini														
<i>Morpho helenor</i>	6	6				17	10	2					6	47
Satyrinae: Satyrini														
<i>Cissia phronius</i>		1		1							1			3
<i>Euptychoides castrensis</i>	1													1
<i>Herneuptychia sp.</i>		1			2			2						5
<i>Moneuptychia soter</i>				1									1	2
<i>Nhambikuara cerradensis</i>				1	1	1	2	1	1	3	3	1		14
<i>Paryphthimoides poltys</i>	3	6		3	13	3	5			2	4	6	2	47
<i>Pharneuptychia sp.</i>				1		1	1		1					4
<i>Taygetis laches</i>				1	4		3	3		1	1	1		14
<i>Yphthimoides affinis</i>	1							1			1		1	4
<i>Yphthimoides celmis</i>				1		1								2
<i>Yphthimoides patricia</i>	1	31		118	34					1	17	6	1	209
<i>Yphthimoides renata</i>					2							1	1	4
<i>Yphthimoides straminea</i>				1	1								1	3
Total abundance	19	59		147	89	51	53	47	26	12	40	32	22	597
Total species richness	10	14		16	17	19	15	17	8	6	10	8	13	39

RESULTS

Community description. A total of 597 individuals from 39 species, belonging to all fruit-feeding Nymphalidae clades, were captured in the studied cerrado site (Table 1). The most abundant group was Satyrinae (66% of the total), followed by Biblidinae (28%), Charaxinae (4%) and Nymphalinae (2%) (Table 1). The tribe Satyrini alone contributed to 52% of all sampled butterflies, with a single species, *Ypthimoides patricia*, representing about one third of all captured individuals (Table 1, Fig. 2). A third of the captured species were singletons or doubletons; only nine species were represented by 10 or more individuals (Table 1, Fig. 2). The five most common species were *Y. patricia* (Satyrini), *Hamadryas februa* (Hübner) (Biblidinae), *Morpho helenor* (Cramer) (Morphini), *Paryphthimoides poltys* (Prittwitz) (Satyrini), and *Callicore astarte* (Cramer) (Biblidinae) (Table 1). The species abundance curve did not reach an asymptote (Fig. 3a). The observed richness represents 92.9% of total species richness estimated by Chao 1 index (42 species, S.D. = 5.38) and the Fisher Alpha index was 9.35.

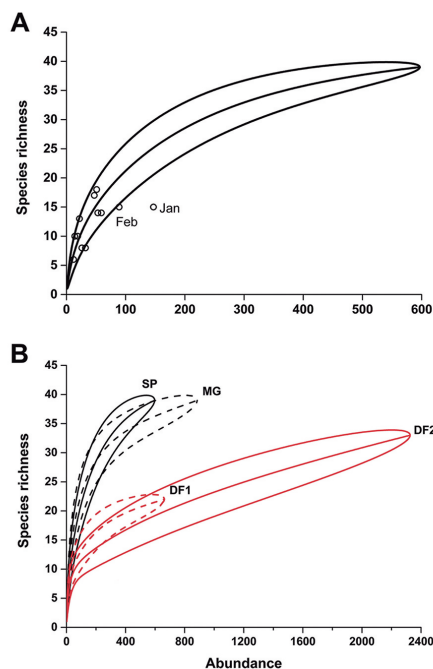


FIG. 3. Rarefaction analyses of the fruit-feeding butterfly assemblages in the present study. **A)** Actual monthly species richness plotted against an individual-based accumulation curve for the total assemblage; Jan = January; Feb = February. **B)** Rarefaction curves comparing species richness among four cerrado sites in Brazil. SP = Itirapina, São Paulo (present study); MG = Belo Horizonte, Minas Gerais; DF1 = Brasília Botanical Garden, Brasília, Distrito Federal; DF2 = "Fazenda Água Limpa", Brasília, Distrito Federal.

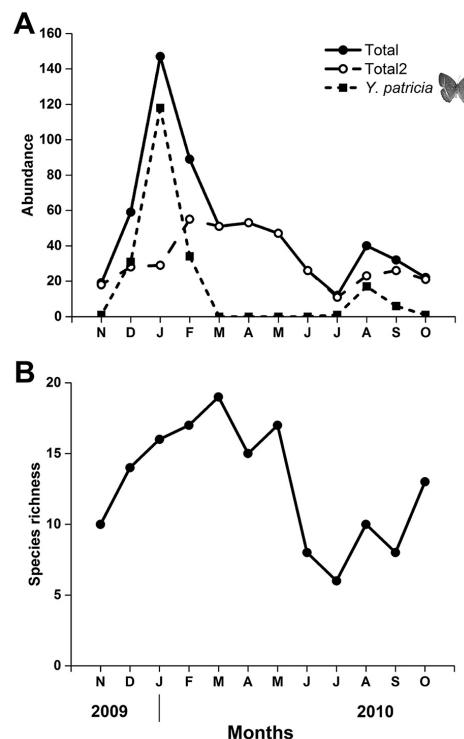


FIG. 4. Temporal variation in abundance (**A**) and richness (**B**) of fruit-feeding butterflies in Itirapina, São Paulo State, SE Brazil, along one sampling year. Solid circles = all species pooled; open circles = butterfly abundance by removing *Ypthimoides patricia* (showed separately); solid squares = *Y. patricia* abundance.

Seasonal patterns and climatic correlations.

Total butterfly abundance was not uniformly distributed along the year (Table 2), with a clear peak of abundance occurring in the middle of the wet season (January), and the lowest abundances recorded in the middle of the dry season (July) (Fig. 4a). By removing the most abundant species, *Y. patricia*, the temporal pattern of abundance distribution is much more stable, with higher abundances evenly distributed from February to May (see "Total 2" in Fig. 4a). Species richness showed a different pattern of distribution, with higher values through the wet season, and with the period from June to September presenting the lower number of species (Fig. 4b). Although monthly species richness varied from six to nineteen species, assemblages from most months were not different from the total community richness, except for January 2010, a month that presented a very high dominance of *Y. patricia* (Fig. 3a, 4b).

None of the five most abundant species occurred uniformly through the year (Table 2, Fig. 5), and three patterns emerged from them: (1) *Y. patricia*, *P. poltys*,

TABLE 2. Circular statistics and Rao s test results for the five most common species, and total abundance of fruit-feeding butterflies captured in the study site. S.D. = Standard Deviation. The mean date is based on the mean angle representing the peak for each species according to the circular analysis (see text).

	Mean date	S.D. (days)	Rao's <i>U</i>	<i>P</i>
<i>Callicore astarte</i>	04/02/2010	41.9	233.11	< 0.01
<i>Hamadryas februa</i>	16/06/2010	67.6	240.48	< 0.01
<i>Morpho helenor</i>	16/02/2010	71.0	252.37	< 0.01
<i>Yphthimoides patricia</i>	10/01/2010	41.9	322.11	< 0.01
<i>Paryphthimoides poltys</i>	05/01/2010	87.0	202.00	< 0.01
Total abundance	02/02/2010	79.9	327.44	< 0.01

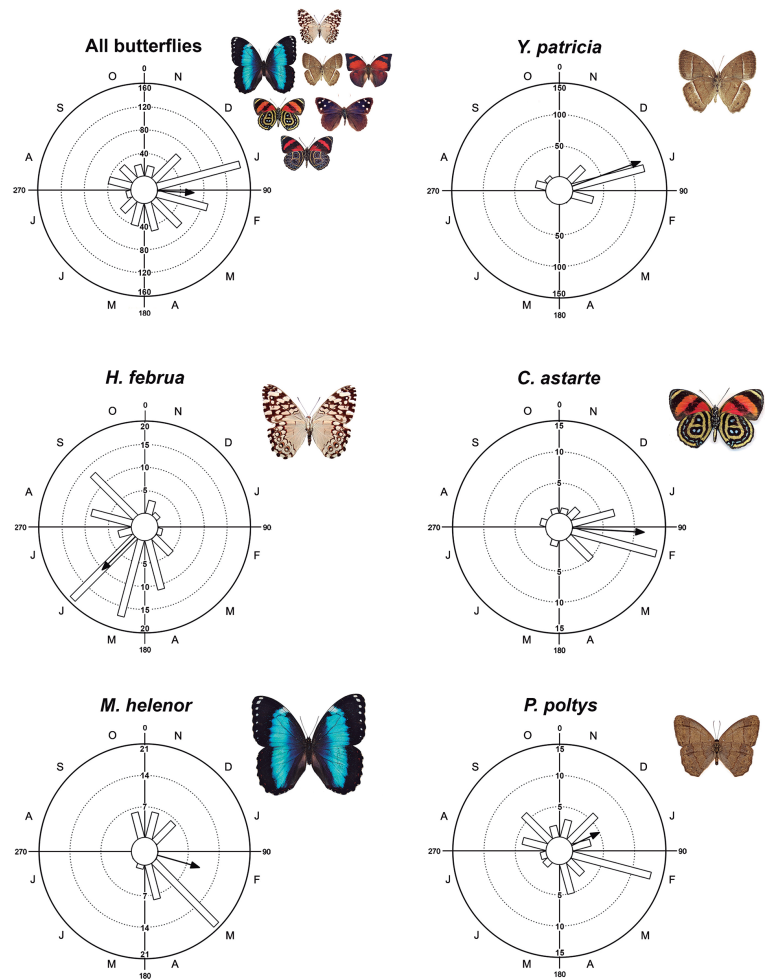


FIG. 5. Circular histogram of the number of individuals observed for the total fruit-feeding butterfly community and the five most abundant species, based on one year of samplings in Itrapina, São Paulo State, SE Brazil. The arrows represent the average vector length (*r*) of each taxon and indicate the average dates.

and *C. astarte* peaked in the middle of the wet season; (2) *M. helenor* presented a nearly bimodal distribution, with a large peak in March/April and a second lower peak from October to December (Fig. 5); and (3) *H. februa* was the commonest species in dry season, with higher numbers occurring from April to September (Fig. 5).

Relative contribution of the different clades to abundance and richness varied markedly along the year (Fig. 6). Satyrini was the most abundant group in most months, except from March to June and from September to November. Biblidinae were abundant from March to September, whereas Brassolini + Morphini presented a bimodal pattern of abundance (March-April and October-November), and Charaxinae + Nymphalinae presented low abundance all year round (Fig. 6a). The variation in species richness was much more stable, with an increase in Satyrini species in January and also from July to September (Fig. 6b).

The variables within the most plausible model for each predictor variable are listed in Table 3. Additionally, the complete model selection tables and values of model parameters are provided in the Online Resource 1. All the best ranked models had Akaike

weights above or equal to 0.3 and the null model was never considered as a plausible model. The AIC of the null model for the abundance of *P. poltys* was 4.56, and its Akaike weight was 0.03, but for all other response variables the AIC of the null model was above 10 and its Akaike weight was below 0.001. In the best model, species richness was showed a positive relationship with temperature in time scale 2 (previous 30 days) but no relationship with precipitation (Figs. 7a and 7b). Total abundance showed positive relationship with both precipitation and temperature in time scale 1 (previous 15 days) (Figs. 7c and 7d).

Among the five most abundant species, all showed relationship with some climatic variable, and those were usually positive. The abundance of *Y. patricia* showed a quadratic relationship with temperature and a positive relationship with precipitation in time scale 3 (Figs. 8a and 8b). The precipitation slope on the most plausible model for *Y. patricia* abundance is negative (Table S3), although the overall effect of precipitation is positive due to the interaction term with temperature, which explains the positive curve on Fig. 8b). *H. februa* was the only species to show negative relationships with precipitation and temperature (in time scale 2, Figs. 8c

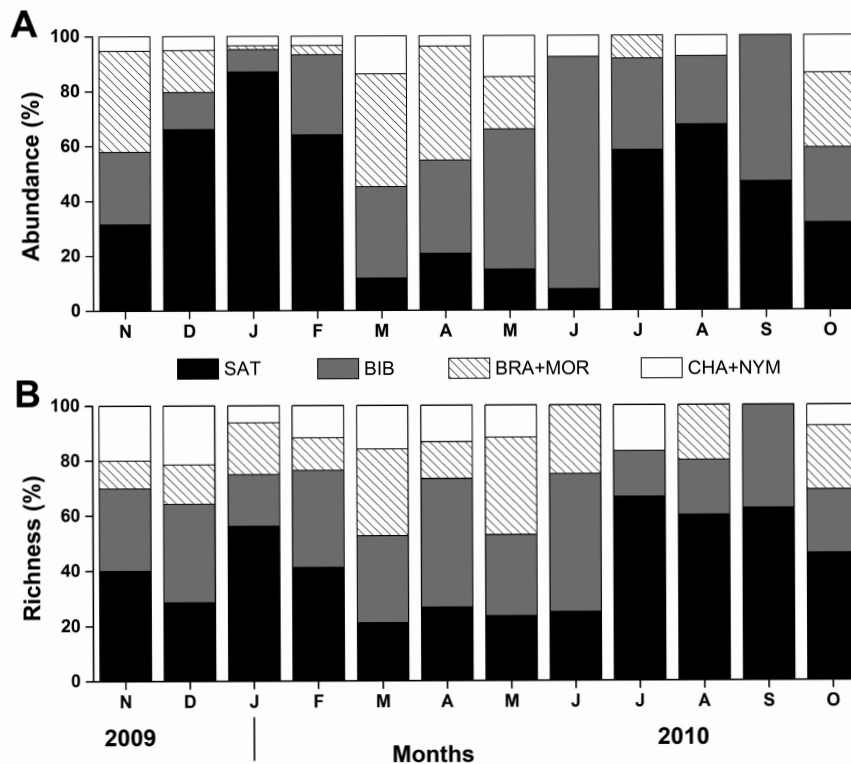


FIG. 6. Monthly variation in the relative contribution (as percentage of total) of each fruit-feeding butterfly group in the abundance (A) and richness (B) in Itirapina, São Paulo State, SE Brazil. SAT = Satyrini; BIB = Biblidinae; BRA + MOR = Brassolini + Morphini; CHA + NYM = Charaxinae + Nymphalinae.

TABLE 3. Summary of the models correlating fruit-feeding butterfly species richness, total abundance, and abundance of the five most abundant species with climatic variables. The table shows the variables present in the best model (ranked by AIC), the time scale in which the variables best explained the response variable, and the Akaike weight of the best ranked model. Plus signs (+) represent additive effects, and multiplication signs (×) represent an additive effect plus a statistical interaction. Time scale 1 refer to the 15 days immediately before each observation; time scale 2 refer to the 30 days immediately before each observation, and time scale 3 refers to a 30-day period ending 30 days before each observation.

Response variable	Predictor variables in the selected model	Time scale	Akaike weight
Species richness	temperature	2	0.34
Total abundance	precipitation × temperature	1	0.69
Species abundances			
<i>Ypthimoides patricia</i>	precipitation × (temperature + temperature ²)	3	0.72
<i>Hamadryas februa</i>	precipitation + temperature	2	0.70
<i>Morpho helenor</i>	precipitation × temperature	2	0.99
<i>Callicore astarte</i>	precipitation	3	0.30
<i>Paryphtimoides poltys</i>	precipitation + temperature	1	0.31

and 8d). The number of captures of *M. helenor* was influenced by temperature, precipitation and their interaction, showing a positive relationship with both temperature and precipitation on time scale 2 (Figs. 8e and 8f). Abundance of *C. astarte* was positively related to precipitation on time scale 3 and showed no relationship with temperature (Figs. 8g and 8h). Finally, the abundance of *P. poltys* was positively correlated with both temperature and rainfall (time scale 1, Figs. 8i and 8j).

Comparison with other cerrado sites. Comparing the available data for other cerrado areas, the reported species richness in the present study (39 species) is the same to that reported by Silva et al. (2012) (39 species) for MG. These numbers are higher than those reported in the Brasília region in DF1 (22 species, not considering the two species of non-fruit-feeding *Adelpha* Hübnér), and DF2 (33 species considering canopy and understory) (Fig. 3b). Based on the habitat categories, the present study and MG presented a

slightly larger proportion of generalists compared to DF1 and DF2, which, conversely, present a higher contribution of cerrado species (Fig. 9). The Morisita similarity index showed that sites in the same region (SP and MG versus DF1 and DF2) are more similar to one another than sites from different regions (Table 4). A summary of diversity parameters for each of the four sites (species richness, Chao-1 and Fisher) is presented in Table 5.

DISCUSSION

The species richness reported in the present study (S = 39) is equivalent to that reported for other cerrado areas in “blend zone” (Appendix 1). The higher species richness reported in the two transitional sites (SP and MG) compared to the two sites in the “core region” of the cerrados (DF1 and DF2) can be related to the infusion of species typical from the southeast coastal montane forests present near the cerrado of this region, a pattern already discussed by Brown and Mielke

TABLE 4. Morisita similarity indices among the four compared studies in cerrado vegetation. SP = present study; MG = Silva et al. (2012); DF1 = Pinheiro and Ortiz (1992); DF2 = Freire (2015).

	SP	MG	DF1
MG	0.79	---	---
DF1	0.47	0.30	---
DF2	0.30	0.28	0.82

TABLE 5. Summary of diversity parameters for the four studies on fruit-feeding butterflies in cerrado vegetation, showing number of sampled species, estimated richness based on Chao 1 and Fisher . SP = present study; MG = Silva et al. (2012); DF1 = Pinheiro and Ortiz (1992); DF2 = Freire (2015).

	SP	MG	DF1	DF2
Species	39	39	22	33
Chao-1	42	67	27	68
Fisher α	9.35	8.35	4.38	5.45

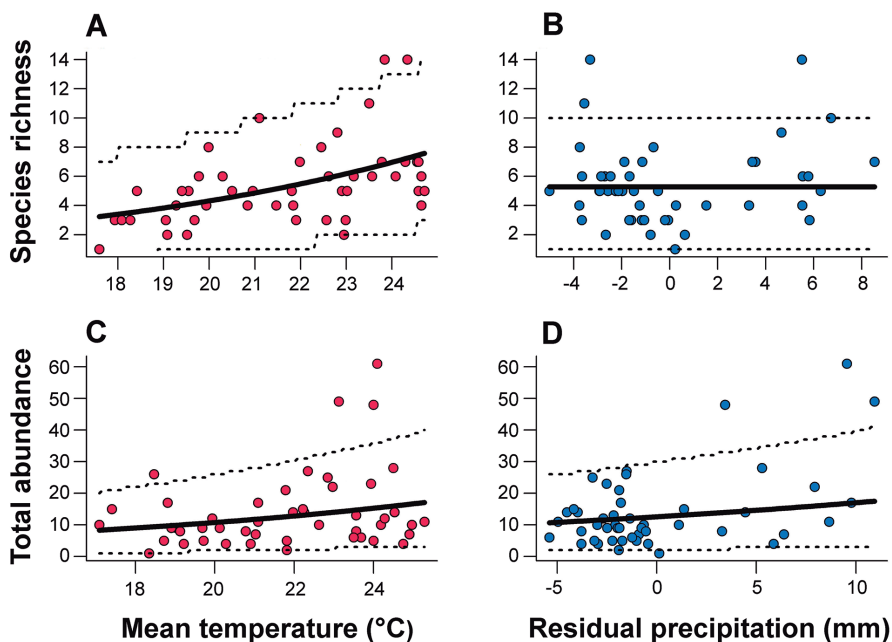


FIG. 7. Relationship between the weekly species richness, total abundance and climatic variables of fruit-feeding butterflies in Itirapina, São Paulo State, SE Brazil. Climatic variables were measured in different time scales, and only the data for the scale that best explained the data is presented. Solid lines represent the mean expectation according to the best model (ranked by AIC) and dashed lines represent the 95% interval predicted by the model. In **A** and **B**, climatic data refer to the 30 days immediately before each observation; in **C** and **D** climatic data refer to a 30-day period ending 30 days before each observation.

(1968). Conversely, although exhibiting lower species richness, the two sites in the cerrado “core region” present a higher number of cerrado specialists (Fig. 9). Accordingly, because of the different species composition, sites in the same region were shown to be more similar to one another than sites from different regions (Table 4). This pattern was previously reported by Brown and Gifford (2002), using qualitative data (presence-absence data) for three different butterfly groups (but the pattern was not supported for Saturniidae moths). This hypothesis can be further examined as more detailed quantitative data for other cerrado areas become available.

Nevertheless, even considering the estimated species number for the four cerrado areas compared here (Table 5), the values are much lower than those reported in forest areas, where fruit-feeding butterfly richness easily surpasses 80 species and can reach values up to 200–300 species, as reported for the upper Amazon (Brown & Freitas 2000, Brown 2005). However, cerrado assemblages are not a subsample of forest assemblages, but include several typical species that if are not exclusive, are clearly predominant in cerrado areas if compared to forest sites. Examples of

these species are *Godartiana armilla* (Butler), *Pharneptychia innocentia* (C. Felder & R. Felder), *Ypthimoides celmis* (Godart), *Y. patricia*, *Nhambikuara cerradensis* Freitas, Barbosa & Zacca (Satyrini), *Callicore sorana* (Godart), *Eunica bechina* (Hewitson), and *Eunica cuvierii* (Godart) (Biblidinae) (see also Appendix 1).

As evidenced in Figure 2, the fruit-feeding butterfly assemblage in SP showed a preponderance of less abundant species, a pattern reported for fruit-feeding butterflies in the three cerrado sites here compared (see Appendix 1), and for other Neotropical forests (e.g. DeVries et al. 1997, Barlow et al. 2007, Uehara-Prado et al. 2007, DeVries et al. 2012, Ribeiro & Freitas 2012). A similar pattern was also reported in tropical forests in Africa (Fermon et al. 2000, 2003, Molleman et al. 2006, Aduse-Poku et al. 2012) and Southeast Asia (Tangah et al. 2004, Dumbrell & Hill 2005, Fermon et al. 2005, Bobo et al. 2006). Therefore, this community structure in cerrado is similar to those found in forest areas elsewhere, reinforcing the typical species rareness in the Tropical region.

Considering the relative contribution of each taxon in the local assemblages, the pattern usually reported in

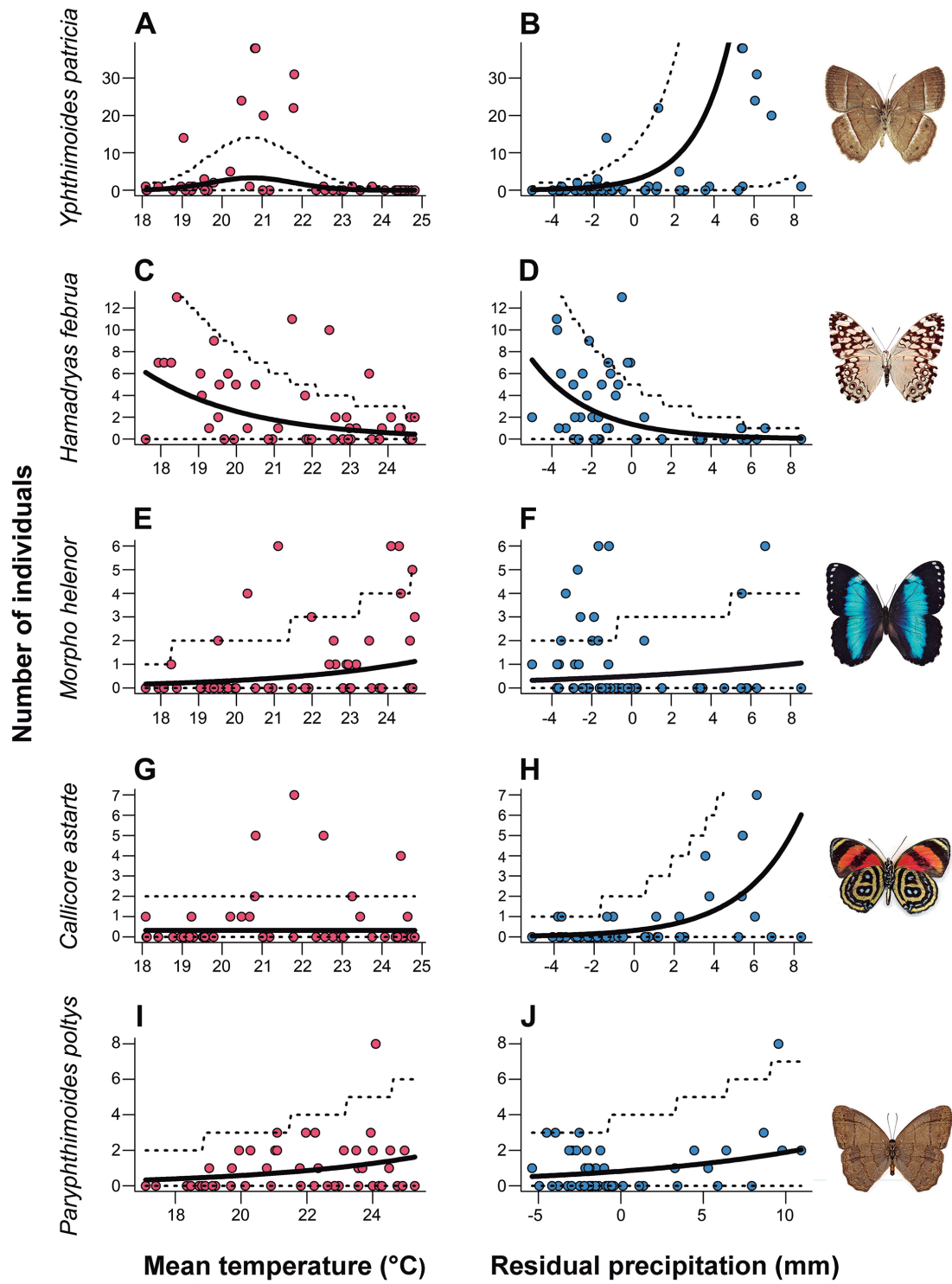


FIG. 8. Relationship between the number of weekly captures and climatic variables for the five most abundant species of fruit-feeding butterflies in Itirapina, São Paulo State, SE Brazil. Climatic variables were measured in different time scales, and only the data for the scale that best explained the occurrence of each species is presented. Solid lines represent the mean expectation according to the best model (ranked by AIC) and dashed lines represent 95% range predicted by the model. In **A**, **B**, **G** and **H**, climatic data refer to a 30-day period ending 30 days before each observation (time scale 3); in **C**, **D**, **E** and **F**, climatic data refer to the 30 days immediately before each observation; and in **I** and **J**, climatic data refer to the 15 days immediately before each observation.

Neotropical forests includes Biblidinae (DeVries 1988, DeVries & Walla 2001, Uehara-Prado et al. 2007, Ribeiro et al. 2010, Ribeiro & Freitas 2012), Charaxinae (Nobre et al. 2012) and Brassolini (Ribeiro & Freitas 2012) as the dominant butterfly groups. In the present study, however, the tribe Satyrini was the dominant group, representing about half of all sampled butterflies. The same pattern of Satyrini dominance was reported in other cerrado sites, such as the MG (Appendix 1), a cerrado area in central Minas Gerais (Beirão 2016), and in some disturbed sites in the Amazon (DeVries et al. 1997, Barlow et al. 2007). Ribeiro et al. (2012) showed that the high pasture cover in the surrounding 100 m radius was the best predictor of the variation in abundance of Satyrini in the Atlantic Forest. Accordingly, it is very likely that the high abundance of Satyrini in the above studies is related to the abundance of Poaceae in the sampled sites surroundings, as would be expected in forest edges, disturbed sites, and in the cerrados (whose understory is dominated by grasses). Despite the high abundance of Satyrini, the two cerrado areas in the “core region” contained Biblidinae as the most abundant taxon because the expressive abundance of two species of *Hamadryas* Hübner. Although not investigated in detail, this high prevalence of *Hamadryas* in both study areas above could be explained by the close proximity of large forest patches where its host plant vines in the genus *Dalechampia* L. (Euphorbiaceae) are abundant in the sunny edges (G. B. Freire Jr. pers. comm. and AVLFPers. obs. based on visits to both study areas). Additional quantitative studies with bait traps should improve our understanding on the key factors structuring fruit-feeding butterfly communities in the Neotropics.

Several factors are involved in the seasonal abundance patterns of arthropods in tropical areas, mainly photoperiod, temperature, and rainfall (Wolda 1988). Usually, for seasonal sites, the highest abundances of adults (and consequent high species richness) are usually reported during the wet season (Wolda 1988, Pinheiro et al. 2002, Ferreira et al. 2013). Indeed, rainfall was reported as an important factor influencing insect abundance even on non-seasonal tropical sites (Kishimoto-Yamada & Itioka 2015). In the present study, species richness showed a positive relationship with temperature during the previous 30 days, suggesting a possible influence on larval growth and survival during the period of high resource availability, and consequently the number of live adults from different species. Species abundance was best explained by precipitation and temperature in the shorter time scale, indicating an effect of recent climate not only on butterfly development, but also on

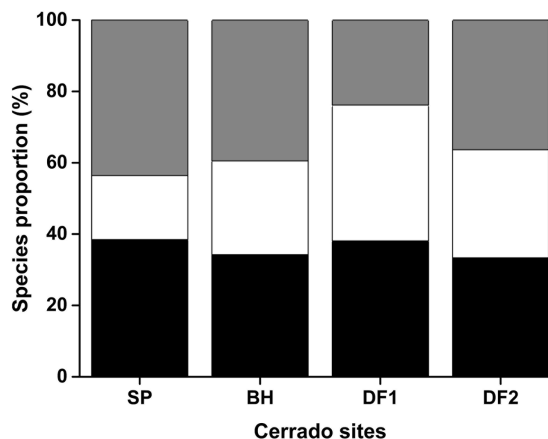


FIG. 9. Proportion of species classified in the three habitat categories in each cerrado site. Forest specialist = black; Cerrado specialist = white; Generalist = grey. SP = Itirapina, São Paulo (present study); MG = Belo Horizonte, Minas Gerais (Silva et al. 2012); DF1 = Brasília Botanical Garden, Distrito Federal (Pinheiro & Ortiz 1992; DF2 = "Fazenda Água Limpa", Brasília, Distrito Federal (Freire 2015).

individual activity, since butterflies are more active in warm periods (Kammer 1970, Douwes 1976).

Even though the pattern of high arthropod abundance during the warm/wet season was commonly reported in tropical areas (see above), this is not the broad pattern reported for fruit-feeding butterflies. From the available studies on temporal patterns of fruit-feeding butterflies, only a few (including the present study) reported a pattern of high abundance during the warm/wet season (e.g. DeVries & Walla 2001, Freire & Diniz 2015). Other studies showed that variations in abundance did not follow the seasonal patterns of rainfall (Willott et al. 2000, Molleman et al. 2006, Grøtan et al. 2012), or reported a bimodal pattern of abundance (Ribeiro et al. 2010, Valtonen et al. 2013, Carreira 2015, Santos et al. 2017).

This increase in insect abundance during the rainier periods is usually associated with plant leaf phenology. Leaf production is usually increased in the wet periods of the year in the tropics, and as the new leaves are usually softer and more nutritious, herbivorous insects often peak in this period (Janzen & Schoener 1968, Wolda 1988). In the cerrado, leaf production by woody plants anticipates the wet season and begins in the late cool dry season and continues through the early wet season, whereas grasses only produce new leaves after the first rains (Morais et al. 1995, Batalha & Mantovani 2000, Marquis et al. 2001, Florencio et al. 2009). In sum, it makes young leaf availability highest in the rainy season, probably favouring butterfly development (see also Muniz et al. 2012). The abundance peak observed

in the wet season was propelled principally by the satyrine *Y. patricia*. Larvae of most satyrines feed on grasses (e.g. Braby 1995, Beccaloni et al. 2008, AVLFPers. obs.), plants whose growth and nutritional content are highly associated with rain (Braby 1995, Florencio et al. 2009). Thus, grasses may become adequate resources for the larvae just after the first heavy rains start, resulting in the high satyrine adult abundance reported in the mid rainy season (see Figs. 4 and 6).

Janzen (1973) points out that many herbivorous tropical insects undergo periods of reproductive diapause during the dry season, resuming reproductive activity when conditions improve. In the same area of the present study, Silva & Oliveira (2010) observed the bug *Edessa rufomarginata* (De Geer) (Hemiptera: Pentatomidae) as reproducing adults and growing nymphs only during the wet season, and proposed the occurrence of a reproductive diapause during the dry season. This may be the case of *M. helenor* in the study area and could explain the bimodal pattern found. In this case, early wet season adults may correspond to the recently emerged imagoes coming from diapausing larvae or pupae, whereas the ones captured by the end of the wet season could be their offspring. Interestingly a similar nearly bimodal pattern in the abundance of Morphini has been reported for other three Neotropical sites (Ribeiro et al. 2010, Freire et al. 2014, Carreira 2015). However, this hypothesis awaits additional natural history data on immature stages of *M. helenor*.

Hamadryas februa was the only species to peak during the dry season. This can be explained by a combination of high longevity of individuals (up to three months) and continuous development of new individuals during the dry season. Larvae of *H. februa* feed on *Dalechampia* (Linnaeus) (Euphorbiaceae), which may be evergreen in the cerrados (Marquis et al. 2001). The abundance of *H. februa* was the only to show negative relationships with temperature and precipitation. Moraes et al. (1999) found a pattern of increased abundance of lepidopteran larvae in the cerrado during the dry season, hypothesizing it may be a mechanism to temporally escape from predators, and this could be the case of *H. februa*.

Although some interesting patterns emerge from this comparative study on butterfly assemblages, there is an overall lack of information for neotropical habitats in general, and for the cerrado in particular. For instance, while there are dozens of published papers on fruit-feeding butterflies in forested habitats (see references above), only four published studies are available for cerrado (including the present paper), and they cover only a very small area of this savanna in three distant regions. In recent years, data on community structure of

fruit-feeding butterflies have been used as important subsidies for several conservation programs, since they can help in habitat diagnostic and monitoring (e.g. Santos et al 2016). Accordingly, the present data add to this scenario by providing valuable data that can be used in future conservation programs focused on cerrado areas. We hope the present study will be an incentive for future studies in other cerrado areas through the Neotropics, allowing a better understanding of how butterfly assemblages are structured in diverse vegetation types.

ACKNOWLEDGMENTS

The authors thank Geraldo Freire Jr., Carlos E. G. Pinheiro, André R. M. Silva and Marina Beirão for sharing specimens and/or pictures of several species collected in previous studies, allowing the faunistic comparisons in the present paper. We are also thankful to Aline. P. Ataíde, Danilo Ribeiro, Daniela Rodrigues, Douglas Enrique, Hélio Soares Jr., Mariana Brito, Poliana Vasconcellos, and Ricardo Aguiar, for help during the fieldwork. Lee Dyer kindly revised a previous version of the manuscript. We also thanks Enrique A. S. Ortega and an anonymous referee for the valuable suggestions and corrections in the submitted version. JYOC thanks the “Coordenação de Aperfeiçoamento de Pessoal de Nível Superior” (CAPES) – Finance Code 001 and the CNPq for graduate fellowships. DGM was supported by FAPESP (no. 2009/02451-4). PSO was supported by research grants from the Brazilian Research Council – CNPq (no. 301853/2009-6, 306115/2013-1, 302219/2017-0) and FAPESP (no. 2008/54058-1, 2011/18580-8, Biota-Fapesp grant 2014/23141-1, 2017/16645-1). AVLFP was supported by research grants from FAPESP (Biota-Fapesp grants 2011/50225-3, 2012/50260-6, 2013/50297-0, 2014/50316-7), CNPq (no. 302585/2011-7 and 303834/2015-3), and from the National Science Foundation (DEB-1256742). This publication is part of the RedeLep ‘Rede Nacional de Pesquisa e Conservação de Lepidópteros’ SISBIOTA-Brasil/CNPq (563332/2010-7). Butterfly species are registered at the SISGEN A3E008C.

LITERATURE CITED

- ADUSE-POKU, K., O. WILLIAM, S. K. OPFONG, T. LARSEN, C. OFORI-BOATENG, & F. MOLLEMAN. 2012. Spatial and temporal variation in butterfly biodiversity in a West African forest: lessons for establishing efficient rapid monitoring programmes. *Afr. J. Ecol.* 50:326–334.
- ANDRADE, R. B., J. K. BALCH, J. Y. O. CARREIRA, P. M. BRANDO, & A. V. L. FREITAS. 2017. The impacts of recurrent fires on diversity of fruit-feeding butterflies in a south-eastern Amazon forest. *J. Trop. Ecol.* 33:22–32.
- BARLOW, J., W. L. OVERAL, I. S. ARAUJO, T. A. GARDNER, & C. A. PERES. 2007. The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *J. Appl. Ecol.* 44:1001–1012.
- BARTON, K. 2016. *MuM In: Multi-Model Inference*. R package version 1.15.6. Available from: <https://CRAN.R-project.org/package=MuMIn>.
- BATALHA, M. A., & W. MANTOVANI. 2000. Reproductive phenological patterns of cerrado plant species at the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and woody floras. *Rev. Bras. Biol.* 60:129–145.
- BECCALONI, G. W., A. L. VILORIA, S. K. HALL, & G. S. ROBINSON. 2008. Catalogue of the Hostplants of the Neotropical Butterflies/Catálogo de las Plantas Huésped de las Mariposas Neotropicales. Sociedad Entomológica Aragonesa, Zaragoza. 536 pp.
- BEIRÃO, M. V. 2016. Distribuição espaço-temporal de borboletas

- frugívoras em ambientes tropicais sazonais. Ph.D. Dissertation, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais.
- BERGIN, T. M. 1991. A comparison of goodness-of-fit tests for analysis of nest orientation in Western Kingbirds (*Tyrannus verticalis*). *Condor* 93:164–171.
- BOBO, K. S., M. WALTERT, H. FERMON, J. NJOKAGBOR, & M. MÜHLENBERG. 2006. From forest to farmland: butterfly diversity and habitat associations along a gradient of forest conversion in Southwestern Cameroon. *J. Insect Conserv.* 10:29–42.
- BONEBRAKE, T. C., L. C. PONISIO, C. L. BOGGS, & P. R. EHRLICH. 2010. More than just indicators: a review of tropical butterfly ecology and conservation. *Biol. Conserv.* 143:1831–1841.
- BRABY, M. F. 1995. Seasonal changes in relative abundance and spatial distribution of Australian lowland tropical Satyrine butterflies. *Aust. J. Zool.* 43:209–229.
- BROWN JR, K. S. 2005. Geologic, evolutionary, and ecological bases of the diversification of neotropical butterflies: implications for conservation. pp. 166–201. *In* Dick, C. W., & G. Moritz (eds.), *Tropical Rainforest: past, present, and future*. The University of Chicago Press, Chicago, Illinois.
- BROWN JR, K. S., & A. V. L. FREITAS. 2000. Atlantic forest butterflies: indicators for Landscape Conservation. *Biotropica* 32:934–956.
- BROWN JR, K. S., & D. R. GIFFORD. 2002. Lepidoptera in the Cerrado landscape and conservation of vegetation, soil and topographical mosaics. pp. 201–222. *In* Oliveira, P. S., & R. J. Marquis (eds.), *The Cerrados of Brazil: ecology and natural history of a Neotropical savanna*. Columbia University Press, New York, New York.
- BROWN JR, K. S., & O. H. H. MIELKE. 1967. Lepidoptera of the Central Brazil Plateau. I. Preliminary list of Rhopalocera: Introduction, Nymphalidae, Libytheidae. *J. Lepid. Soc.* 21:77–106.
- BROWN JR, K. S., & O. H. H. MIELKE. 1968. Lepidoptera of the Central Brazil plateau. III. Partial list for the Belo Horizonte area, showing the character of the southeastern "blend zone". *J. Lepid. Soc.* 22:147–157.
- BURNHAM, K. P., & D. R. ANDERSON. 2002. *Model Selection and Multimodel Inference: A practical information-theoretic approach*. Springer, New York, 488 pp.
- CARREIRA, J. Y. O. 2015. Dinâmica temporal e sazonalidade de borboletas frugívoras na Mata Atlântica. M.S. Thesis, University of Campinas, Campinas, São Paulo.
- CAVALCANTI, R. B., & C. A. JOLY. 2002. Biodiversity and conservation priorities in the Cerrado region, pp. 351–367. *In* Oliveira, P. S., & R. J. Marquis (eds.), *The Cerrados of Brazil: ecology and natural history of a Neotropical savanna*. Columbia University Press, New York, New York.
- COLVELL, R. K., & J. A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. T. R. Soc. B.* 345:101–118.
- DEVRIES, P. J. 1987. The butterflies of Costa Rica and their natural history: Papilionidae, Pieridae, and Nymphalidae. Princeton University Press, Princeton, 327 pp.
- DEVRIES, P. J. 1988. Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *J. Res. Lepid.* 26:98–108.
- DEVRIES, P. J., D. MURRAY, & R. LANDE. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding nymphalid butterfly community in an Ecuadorian rainforest. *Biol. J. Linn. Soc.* 62:342–364.
- DEVRIES, P. J., L. G. ALEXANDER, I. A. CHACON, & J. A. FORDYCE. 2012. Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. *J. Animal Ecol.* 81:472–482.
- DEVRIES, P. J., & T. R. WALLA. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. *Biol. J. Linn. Soc.* 74:1–15.
- DOUWES, P. 1976. Activity in *Heodes virgaureae* (Lep., Lycaenidae) in relation to air temperature, solar radiation, and time of day. *Oecologia* 22:287–298.
- DUMBRELL, A. J., & J. K. HILL. 2005. Impacts of selective logging on canopy and ground assemblages of tropical forest butterflies: implications for sampling. *Biol. Conserv.* 125: 123–131.
- FERMON, H., M. WALTERT, T. B. LARSEN, U. DALL'ASTA, & M. MÜHLENBERG. 2000. Effects of forest management on diversity and abundance of fruit-feeding nymphalid butterflies in south-eastern Côte d'Ivoire. *J. Insect Conserv.* 4:173–189.
- FERMON, H., M. WALTERT, & M. MÜHLENBERG. 2003. Movement and vertical stratification of fruit-feeding butterflies in a managed West African rainforest. *J. Insect Conserv.* 7:7–19.
- FERMON, H., M. WALTERT, R. I. VANE-WRIGHT, & M. MÜHLENBERG. 2005. Forest use and vertical stratification in fruit-feeding butterflies of Sulawesi, Indonesia: impacts for conservation. *Biodivers. Conserv.* 14:333–350.
- FERREIRA, A. S., B. C. BELLINI, & A. VASCONCELLOS. 2013. Temporal variations of Collembola (Arthropoda: Hexapoda) in the semiarid Caatinga in northeastern Brazil. *Zoologia* 30:639–644.
- FLORENCIO, C., R. ARRUDA, & R. A. FIGUEIREDO. 2009. Phenology of herbaceous species in cerrado comparisons between intact, burnt, and reforested areas. *Naturalia* 32:1–12.
- FREIRE, G. B. JR. 2015. Dinâmica temporal e espacial da comunidade de borboletas frugívoras (Nymphalidae) do Cerrado. Ph.D. Dissertation, Universidade Federal de Brasília, Brasília, Distrito Federal.
- FREIRE, G. B. JR., & I. R. DINIZ. 2015. Temporal dynamics of fruit-feeding butterflies (Lepidoptera: Nymphalidae) in two habitats in a seasonal Brazilian environment. *Fla. Entomol.* 98:1207–1216.
- FREIRE, G. B. JR., A. R. NASCIMENTO, I. K. MALINOV, & I. R. DINIZ. 2014. Temporal occurrence of two *Morpho* butterflies (Lepidoptera: Nymphalidae): influence of weather and food resources. *Environ. Entomol.* 43:274–282.
- FREITAS, A. V. L., & K. S. BROWN JR. 2004. Phylogeny of the Nymphalidae (Lepidoptera). *Syst. Biol.* 53:363–383.
- FREITAS, A. V. L., C. A. ISERHARD, J. P. SANTOS, J. Y. O. CARREIRA, D. B. RIBEIRO, D. H. A. MELO, A. H. B. ROSA, O. J. MARINI-FILHO, G. M. ACCACIO, & M. UEHARA-PRADO. 2014. Studies with butterfly bait traps: an overview. *Rev. Colomb. Entomol.* 40:203–212.
- GRAHAM, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815.
- GRÖTAN, V., R. LANDE, S. ENGÉN, B. E. SÆTHER, & P. J. DEVRIES. 2012. Seasonal cycles of species diversity and similarity in a tropical butterfly community. *J. Anim. Ecol.* 81:714–723.
- HAMMER, O., D. A. T. HARPER, & P. D. RYAN. 2001. *Past: paleontological statistics software package for education and data analysis*. *Palaeontol. Electron.* 4:1–9.
- IBGE, INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA. 2004. Mapa de Biomas e de Vegetação do Brasil. Available from <http://www.ibge.gov.br/> (September, 2020)
- INSTITUTO NACIONAL DE METEOROLOGIA. 2020. Dados meteorológicos. Available from: <https://portal.inmet.gov.br/> (September, 2020).
- JANZEN, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54:687–708.
- JANZEN, D. H., & T. W. SCHOENER. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49:96–110.
- KAMMER, A. E. 1970. Thoracic temperature, shivering, and flight in the monarch butterfly, *Danaus plexippus* (L.). *Z. Vgl. Physiol.* 68:334–344.
- KISHIMOTO-YAMADA, K., & T. ITIOKA. 2015. How much have we learned about seasonality in tropical insect abundance since Volda (1988)? *Entomol. Sci.* 18:407–419.
- KLINK, C. A., & R. B. MACHADO RB. 2005. Conservation of the Brazilian Cerrado. *Conserv. Biol.* 19:707–713.
- KOVACH, W. L. 2011. *Oriana – Circular Statistics for Windows*. Version 4. Pentraeth, Kovach Computing Services.
- MAGURRAN, A. E. 2004. *Measuring Biological Diversity*. Blackwell Science, Oxford, 256 pp.
- MARQUIS, R. J., I. R. DINIZ, & H. C. MORAIS. 2001. Patterns and correlates of interspecific variation in foliar insect herbivory and pathogen attack in Brazilian Cerrado. *J. Trop. Ecol.* 17:127–148.

- MOLLEMAN, F., A. KOP, P. M. BRAKEFIELD, P. J. DEVRIES, & B. J. SWAAN. 2006. Vertical and temporal patterns of biodiversity of fruit-feeding butterflies in a tropical forest in Uganda. *Biodivers. Conserv.* 15:107–121.
- MORAIS, H. C., I. R. DINIZ, & L. BAUMGARTEN. 1995. Padrões de produção de folhas e sua utilização por larvas de Lepidoptera em um Cerrado de Brasília. *Rev. Bras. Bot.* 18:163–170.
- MORAIS, H. C., I. R. DINIZ, & D. M. S. SILVA. 1999. Caterpillar seasonality in a central Brazilian Cerrado. *Rev. Biol. Trop.* 47:1025–1033.
- MUNIZ, D. M., A. V. L. FREITAS, & P. S. OLIVEIRA. 2012. Phenological relationships of *Eumica bechina* (Lepidoptera: Nymphalidae) and its host plant, *Caryocar brasiliense* (Caryocaraceae), in a Neotropical savanna. *Stud. Neotrop. Fauna Environ.* 47:111–118.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. FONSECA, & J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- NOBRE, C. E. B., L. IANNUZZI, & C. SCHLINDWEIN. 2012. Seasonality of fruit-feeding butterflies (Lepidoptera, Nymphalidae) in a Brazilian semiarid area. *Int. Sch. Res. Notices Zoo.* 2012:1–8.
- OLIVEIRA-FILHO, A. T., & J. A. RATTER. 2002. Vegetation physiognomies and the woody flora of the Cerrado biome, pp. 91–120. *In* Oliveira, P. S., & R. J. Marquis (eds.), *The Cerrados of Brazil: ecology and natural history of a Neotropical savanna*. Columbia University Press, New York, New York.
- PEARCE, J. L., & L. A. VENIER. 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. *Ecol. Indic.* 6:780–793.
- PINHEIRO, C. E. G., & J. V. C. ORTIZ. 1992. Communities of fruit-feeding butterflies along a vegetation gradient in central Brazil. *J. Biogeogr.* 19:505–511.
- PINHEIRO, F., I. R. DINIZ, D. COELHO, & M. P. S. BANDEIRA. 2002. Seasonal pattern of insect abundance in the Brazilian Cerrado. *Austral. Ecol.* 27:132–136.
- R DEVELOPMENT CORE TEAM. 2013. R: A language and environment for statistical computing.
- RATTER, J. A., J. F. RIBEIRO, & S. BRIDGEWATER. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. *Ann. Bot. - London.* 80: 223–230.
- REYS, P., M. G. G. DE CAMARGO, M. T. GROMBONE-GUARATINI, A. DE P. TEIXEIRA, M. A. ASSIS, & L. P. C. MORELLATO. 2013. Estrutura e composição florística de um Cerrado sensu stricto e sua importância para propostas de restauração ecológica. *Hoehnea* 40: 449–464.
- RIBEIRO, D. B., & A. V. L. FREITAS. 2012. The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. *J. Insect Conserv.* 16:733–744.
- RIBEIRO, D. B., P. I. PRADO, K. S. BROWN JR., & A. V. L. FREITAS. 2010. Temporal diversity patterns and phenology in fruit-feeding butterflies in the Atlantic Forest. *Biotropica* 42:710–716.
- RIBEIRO, D. B., R. BATISTA, P. I. PRADO, K. S. BROWN JR., & A. V. L. FREITAS. 2012. The importance of small scales to the fruit-feeding butterfly assemblages in a fragmented landscape. *Biodivers. Conserv.* 21:811–827.
- SANTOS, J. P., O. J. MARINI-FILHO, A. V. L. FREITAS & M. UEHARA-PRADO. 2016. Monitoramento de Borboletas: o Papel de um Indicador Biológico na Gestão de Unidades de Conservação. *BioBrasil* 6:87–99.
- SANTOS, J. P., C. A. ISEHARD, J. Y. O. CARREIRA, & A. V. L. FREITAS. 2017. Monitoring fruit-feeding butterfly assemblages in two vertical strata in seasonal Atlantic Forest: temporal species turnover is lower in the canopy. *J. Trop. Ecol.* 33:345–355.
- SILVA, A. R. M., C. O. CASTRO, P. O. MAFIA, M. O. C. MENDONÇA, T. C. C. ALVES, & M. V. BEIRÃO. 2012. Borboletas frugívoras (Lepidoptera: Nymphalidae) de uma área urbana (Área de Proteção Especial Manancial Cercadinho) em Belo Horizonte, Minas Gerais, Brasil. *Biota Neotrop.* 12:292–297.
- SILVA, D. P., & P. S. OLIVEIRA. 2010. Field Biology of *Edessa rufomarginata* (Hemiptera: Pentatomidae): phenology, behavior, and patterns of host plant use. *Environ. Entomol.* 39:1903–1910.
- STRASSBURG, B. B. N., T. BROOKS, R. FELTRAN-BARBIERI, A. IRIBARREM, R. CROUZEILLES, R. LOYOLA, A. E. LATAWIEC, F. J. B. OLIVEIRA-FILHO, C. A. M. SCARAMUZZA, F. R. SCARAN, B. SOARES-FILHO, & A. BALMFORD. 2017. Moment of truth for the Cerrado hotspot. *Nat. Ecol. Evol.* 1, 99.
- TANGAH, J., J. K. HILL, K. C. HAMER, & M. M. DAWOOD. 2004. Vertical distribution of fruit-feeding butterflies in Sabah, Borneo. *Sepilok Bull.* 1:17–27.
- UEHARA-PRADO, M., K. S. BROWN JR., & A. V. L. FREITAS. 2007. Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. *Global Ecol. Biogeogr.* 16:43–54.
- VALTONEN, A., F. MOLLEMAN, C. A. CHAPMAN, J. R. CAREY, M. P. AYRES, H. ROININEN. 2013. Tropical phenology: bi-annual rhythms and interannual variation in an Afrotropical butterfly assemblage. *Ecosphere* 4: 36.
- VENABLES, W. N., & B. D. RIPLEY. 2002. *Modern Applied Statistics with S*. Springer, New York, 510 pp.
- WAHLBERG, N., J. LENEVEU, U. KODANDARAMAIAH, C. PEÑA, S. NYLIN, A. V. L. FREITAS, & A. V. Z. BROWER. 2009. Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. *P. Roy. Soc. B - Biol. Sci.* 276:4295–4302.
- WALTER, H. 1985. *Vegetation of the earth and ecological systems of the geo-biosphere*. Springer-Verlag, Berlin, 300 pp.
- WHITE, G. C., & R. E. BENNETTS. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* 77:2549–2557.
- WILLOTT, S. J., D. C. LIM, S. G. COMPTON, S. L. SUTTON. 2000. Effects of selective logging on the butterflies of a Bornean Rainforest. *Conserv. Biol.* 14:1055–1065.
- WOLDA, H. 1988. Insect seasonality: why? *Annu. Rev. Ecol. Syst.* 19:1–18.

Submitted for publication 25 May 2020; revised and accepted 8 September 2020.

See APPENDIX on next two pages

Please see additional supplementary material online at
https://www.lepsoc.org/journal/Freitas_et_al_2021_Supplement.docx

APPENDIX 1. Butterfly species of the four compared studies in cerrado vegetation. SP = present study; MG = Silva et al. (2012); DF1 = Pinheiro and Ortiz (1992); DF2 = Freire (2015). All species of MG and DF2 studies have been revised for comparative purposes (except for some species of DF1 study, since part of the voucher material is no longer available). Habitat categories following Andrade et al. (2017) and AVLFE expertise. For additional details, see text.

	Habitat	SP	MG	DF1	DF2
Biblidinae		169	148	387	1160
<i>Biblis hyperia</i> (Cramer, 1779)	forest	0	39	0	0
<i>Callicore astarte</i> (Cramer, 1779)	generalist	32	0	0	0
<i>Callicore sorana</i> (Godart, [1824])	cerrado	26	69	36	155
<i>Catonephele acontius</i> (Linnaeus, 1771)	forest	3	0	0	1
<i>Catonephele numilia</i> (Cramer, 1775)	forest	2	0	0	0
<i>Diaethria candrena</i> (Godart, [1824])	forest	0	1	0	0
<i>Diaethria clymena</i> (Cramer, 1775)	forest	0	7	0	0
<i>Eunica bechina</i> (Hewitson, 1852)	cerrado	9	1	6	2
<i>Eunica cuvierii</i> (Godart, 1819)	cerrado	0	1	5	24
<i>Eunica tatila</i> (Herrich-Schäffer, [1855])	generalist	3	0	4	1
<i>Hamadryas amphinome</i> (Linnaeus, 1767)	forest	6	8	0	0
<i>Hamadryas arete</i> (E. Doubleday, 1847)	forest	1	0	0	0
<i>Hamadryas epinome</i> (C. Felder & R. Felder, 1867)	generalist	2	0	0	0
<i>Hamadryas februa</i> (Hübner, [1823])	generalist	82	10	157	122
<i>Hamadryas feronia</i> (Linnaeus, 1758)	forest	0	4	177	846
<i>Myscelia orsis</i> (Drury, 1782)	forest	1	0	0	0
<i>Paulogramma pygas</i> (Godart, [1824])	forest	0	3	0	1
<i>Temenis laothoe</i> (Cramer, 1777)	generalist	2	5	2	8
Charaxinae		24	43	46	122
<i>Archaeoprepona demophon</i> (Linnaeus, 1758)	generalist	5	4	0	0
<i>Archaeoprepona demophoon</i> (Hübner, [1814])	forest	1	0	1	0
<i>Prepona laertes</i> (Hübner, [1811])	forest	0	0	3	0
<i>Fountainea glycerium</i> (E. Doubleday, [1849])	cerrado	0	0	4	1
<i>Fountainea ryphea</i> (Cramer, 1775)	generalist	3	24	0	1
<i>Hypna clymnestra</i> (Cramer, 1777)	forest	1	0	0	1
<i>Memphis acidalia</i> (Hübner, [1819])	forest	2	0	0	0
<i>Memphis appias</i> (Hübner, [1825])	forest	1	0	0	0
<i>Memphis moruus</i> (Fabricius, 1775)	generalist	7	7	1	1
<i>Siderone galanthis</i> (Cramer, 1775)	generalist	1	3	37	118
<i>Zaretis strigosus</i> (Gmelin, 1790)	generalist	3	5	0	0
Nymphalinae		12	6	4	3
<i>Colobura dirce</i> (Linnaeus, 1758)	generalist	0	1	0	1
<i>Historis odius</i> (Fabricius, 1775)	generalist	5	4	3	0
<i>Smyrna blomfieldia</i> (Fabricius, 1781)	forest	7	1	1	2

Continued on next page

APPENDIX I. Continued

	Habitat	SP	MG	DF1	DF2
Satyrinae: Brassolini		33	25	1	69
<i>Blepolenis batea</i> (Hübner, [1821])	generalist	0	1	1	0
<i>Caligo illioneus</i> (Cramer, 1775)	forest	29	0	0	3
<i>Eryphanis reevesii</i> (E. Doubleday, [1849])	forest	0	3	0	0
<i>Opoptera syme</i> (Hübner, [1821])	forest	0	1	0	0
<i>Opsiphanes invirae</i> (Hübner, [1808])	generalist	4	20	0	66
Satyrinae: Morphini		47	9	0	3
<i>Morpho helenor</i> (Cramer, 1776)	generalist	47	9	0	3
Satyrinae: Satyrini		312	656	225	969
<i>Cissia phronius</i> (Godart, [1824])	forest	3	11	0	1
<i>Cissia terrestris</i> (A. Butler, 1867)	forest	0	0	0	1
<i>Euptychoides castrensis</i> (Schaus, 1902)	forest	1	1	0	0
<i>Forsterinaria quantius</i> (Godart, [1824])	forest	0	0	0	1
<i>Godartiana armilla</i> (Butler, 1867)	cerrado	0	0	37	0
<i>Godartiana muscosa</i> (A. Butler, 1870)	forest	0	14	0	0
<i>Hermeuptychia</i> sp.	generalist	5	0	64	512
<i>Moneuptychia itapeva</i> Freitas 2007	cerrado	0	19	0	0
<i>Moneuptychia soter</i> (A. Butler, 1877)	forest	2	0	0	0
<i>Nhambikuara cerradensis</i> Freitas, Barbosa & Zacca, 2018	cerrado	14	46	0	72
<i>Pareuptychia ocirrhoe</i> (Fabricius, 1776)	forest	0	0	1	5
<i>Paryphthimoides numeria</i> (C. Felder & R. Felder, 1867)	cerrado	0	0	7	1
<i>Paryphthimoides poltys</i> (Prittwitz, 1865)	cerrado	47	5	0	4
<i>Pharneuptychia innocentia</i> (C. Felder & R. Felder, 1867)	cerrado	0	12	0	0
<i>Pharneuptychia</i> sp. 1	cerrado	0	93	0	0
<i>Pharneuptychia</i> sp. 2	cerrado	0	52	0	0
<i>Pharneuptychia</i> sp. 3	cerrado	4	0	0	0
<i>Taygetis chiquitana</i> Forster, 1964	forest	0	0	0	1
<i>Taygetis laches</i> Fabricius, 1793	forest	14	24	0	0
<i>Taygetis rectifascia</i> Weymer, 1907	forest	0	12	0	0
<i>Yphthimoides affinis</i> (A. Butler, 1867)	forest	4	0	0	0
<i>Yphthimoides celmis</i> (Godart, [1824])	cerrado	2	31	0	0
<i>Yphthimoides mimula</i> (Hayward, 1954)	cerrado	0	0	0	1
<i>Yphthimoides ochracea</i> (A. Butler, 1867)	generalist	0	10	0	0
<i>Yphthimoides pacta</i> (Weymer, 1911)	cerrado	0	0	33	78
<i>Yphthimoides patricia</i> (Hayward, 1957)	cerrado	209	262	78	284
<i>Yphthimoides renata</i> (Stoll, 1780)	forest	4	62	0	7
<i>Yphthimoides straminea</i> (A. Butler, 1867)	generalist	3	0	0	1
Satyrinae sp.	----	0	0	5	0
Total abundance		597	885	663	2326
Total species richness		39	39	22	33

To make it possible some general comparisons, all species of *Hermeuptychia* have been combined under "*Hermeuptychia* sp." All "*Y. celmis*" from Pinheiro and Ortiz (1992) have been transferred to *Y. patricia*. Taxonomy follow Lamas (2004), and Neild (1996), modified after specific revisions of the genera.