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Temporal dynamics of fruit-feeding butterflies (Lepidoptera: Nymphalidae) in two habitats in a seasonal Brazilian environment

Geraldo de B. Freire Júnior^{1,*} and Ivone Rezende Diniz²

Abstract

The Cerrado Biome comprises many habitats, the most common being the savanna type. This biome presents an intense dry season that imposes difficulties on organism survival. The Cerrado's wet season is the period of greatest abundance and richness of species, including the Lepidoptera. In Brazil, most studies on Nymphalidae seasonality have been conducted in biomes other than the Cerrado. Thus, the pattern of the Nymphalidae seasonality in the Cerrado is unknown. The aim of this study was to describe the temporal dynamics of these butterflies in both savanna and gallery forest habitats in the Cerrado, comparing our findings to those previously reported from other Brazilian biomes, and to discuss the effects of weather and habitat structure on temporal dynamics. Thirty bait-traps were distributed in 2 vertical strata (understory and canopy) in each habitat type (savanna and gallery forest; thus, 60 bait-traps were distributed during 6 d each month from Jul 2012 to Jun 2013). In total, 3,459 individuals of 62 species were captured. The transition between the wet and dry season presented the greatest abundance and species richness and was the period of lowest evenness in the Nymphalidae community. Two distinct assemblages were found in the savanna and gallery forest. Moreover, greater butterfly species turnover was found over time in the gallery forest than in the savanna habitat. These results highlight the importance of climatic seasons, plant phenology, and habitat structure as important predictors of the temporal dynamics of these butterflies in the Cerrado Biome. Furthermore, the floristic and structural distinctiveness of the savanna and gallery forest, and the biological requirements of the butterfly species, could explain a large portion of the species turnover observed in the gallery forest.

Key Words: assemblage; Cerrado; gallery forest; savanna; seasonality

Resumo

O Cerrado é formado por várias fitofisionomias e a mais comum é o habitat do tipo savana. Apresenta um período seco intenso e prolongado, o que impõe dificuldades à sobrevivência de organismos. No cerrado, a maior abundância e riqueza de insetos, incluindo os lepidópteros ocorrem no período chuvoso. No Brasil, a maioria dos estudos sobre sazonalidade dos Nymphalidae foi desenvolvido em outros biomas, portanto, o presente estudo visa preencher essa lacuna no Cerrado. Os objetivos foram: 1) descrever a dinâmica temporal dessas borboletas em dois habitat do Cerrado, cerrado *sensu stricto* (vegetação tipo savana) e mata de galeria e 2), comparar a dinâmica temporal dos Nymphalidae do Cerrado com o encontrado em outros biomas. Sessenta armadilhas foram distribuídas nos dois habitats, em duas alturas (sub-bosque e dossel) e acompanhadas por seis dias a cada mês, em um ano. Foram capturadas 3.459 borboletas de 62 espécies. A maior abundância e riqueza de espécies, e a menor equitabilidade na distribuição das abundâncias dos Nymphalidae foram encontradas na transição entre a estação seca e a chuvosa. Entretanto, não houve variação significativa na diversidade ao longo do tempo. A composição de espécies de borboletas foi distinta entre os dois habitats, com maior substituição temporal na mata de galeria. A composição estrutural e florística, as características fenológicas das plantas da mata de galeria, e o requerimento biológico desses ninfalídeos são fatores que explicaram as variações nas comunidades presentes na mata e no cerrado *sensu stricto*.

Palavras Chave: assembléia; cerrado; comunidade; mata de galeria; sazonalidade

The Cerrado Biome once occupied about 22% of Brazilian national territory. It is composed of a mosaic of different habitat types, ranging from open grassland and savanna-like vegetation (this is known as Cerrado *sensu stricto*, or Cerrado ss.) to woodland (gallery forest) (Oliveira-Filho & Ratter 2002). Climate, soil fertility, and the frequency of wildfires are the determinant factors that define and shape the Cerrado. Moreover, this biome has an intense dry season that imposes difficulties on the animal communities present (Marquis et al. 2002). Water availability is one of the most important factors affecting plant development and flower/fruit phenology patterns, both of which, in turn, influence the temporal dynamics of associated animal commu-

nities, especially insect communities (Pinheiro et al. 2002; Silva et al. 2011b).

In Central Brazil, the transition period between the dry and wet seasons (Sep–Nov) corresponds with a peak in insect abundance (Silva et al. 2011b). However, this pattern may change depending on the insect order (Pinheiro et al. 2002; Silva et al. 2011b) or the stage of insect development. For example, Coleoptera and Lepidoptera are abundant in the wet season and generally respond positively to an increase in air temperature and precipitation (Silva et al. 2011b), Hymenoptera peak in the late dry season (Pinheiro et al. 2002; Silva et al. 2011b), and Lepidoptera larvae are abundant in the first half of the dry season (Morais

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et al. 1999). Other orders like Orthoptera, Hemiptera, and Diptera occur homogeneously through the year (Pinheiro et al. 2002).

The fruit-feeding butterfly guild is often used in ecological studies in the Neotropics (DeVries & Walla 2001), including Brazil (Brown & Freitas 2000; Uehara-Prado et al. 2007; Ribeiro & Freitas 2011). As a consequence, the temporal dynamics of this guild are well known, especially in the Atlantic and Equatorial Amazon Forest (DeVries et al. 1997, 2011; DeVries & Walla 2001). In general, the Nymphalidae are evenly distributed all the year round, but show 2 peaks in their abundance, the 1st between Sep and Oct and the 2nd in Feb and Mar (Ribeiro et al. 2010). However, some variations can be observed among Nymphalidae subfamilies, with differences in average body size delineating differences in the temporal dynamics of these subfamilies (Ribeiro & Freitas 2011).

Although the temporal dynamics of the Nymphalidae are well known in the Neotropical forests, their seasonal distribution in the Cerrado Biome remains to be investigated. Thus, the present study aimed to describe the temporal pattern of the Nymphalidae in 2 habitats of the Cerrado, with specific attention given to the role of habitat structure on temporal dynamics in both habitat types. Additionally, the difference in temporal dynamics between subfamilies, tribes, and species are discussed.

Based on previous studies, we hypothesized that the abundance of Nymphalidae in the Cerrado would have 2 peaks through the year, associated with the hot and wet periods (as in other Brazilian biomes). If this was not the case, we expected that the climatic characteristics of the Cerrado could explain any potential differences between Nymphalidae distribution patterns found in the Cerrado and patterns found in other biomes. Additionally, we examined how habitat structure impacts the temporal dynamics of butterflies in the Cerrado. We predicted less temporal variation in butterfly communities in the forest (gallery forest) compared with those in a savanna habitat, because the dense canopy that covers the gallery forest promotes high shade levels (Kanegae et al. 2000) and greater microclimate stability, reinforcing earlier findings of less temporal variation of insects in this habitat compared with their savanna relatives (Diniz & Kitayama 1998; Tidon 2006; Scherrer et al. 2013).

Materials and Methods

STUDY SITE

This study was performed from Jul 2012 to Jun 2013 on 2 contiguous ecological reserves, Fazenda Água Limpa (4,500 ha; 15°56'23"S, 47°56'17"W) and Reserva Ecológica do Roncador (1,350 ha; 15°56'64"S, 47°52'94"W). The study site is inside a 10,000 ha protected area composed of 3 ecological reserves: Fazenda Água Limpa, Reserva Ecológica do Roncador, and Jardim Botânico de Brasília (Fonseca & Silva-Júnior 2004). The annual precipitation ranges from 1,400 to 1,500 mm, with the highest rain volume occurring between Oct and Mar (Castro et al. 1994; Silva et al. 2008).

NYMPHALIDAE CAPTURE

In order to encompass a large portion of the floristic and structural variation present in each habitat, 15 plots distributed in 5 linear transects (200 m) were installed in each habitat (savanna: C1–C5; gallery forest: F1–F5). In each of these 30 plots, bait-traps were installed at 2 heights (canopy: ~8 m; understorey: ~1.5 m); thus, 60 bait-traps were spread across the study area. Transects were located at least 1 km apart (Suppl. Fig. 1, available online at <http://purl.fcla.edu/fcla/ento>

mologist/browse). The largest known dispersion distance of butterflies present within the study area is 870 m (Marini-Filho & Martins 2010); hence, transects may be regarded as independent sampling units.

A mixture of bananas and sugarcane (~50 mL) was fermented for 48 h and included in each bait-trap. This followed the longstanding collecting protocol for these Nymphalidae (see DeVries et al. 1999). The Nymphalidae were collected during 6 d of the 1st week each month, with the first 2 d spent installing bait-traps. The traps in both the savanna and the gallery forest were visited and the bait changed every 48 h. Trapped butterflies were identified to the species level by comparison with specimens at the local entomological collection, by review of pertinent literature, and by species confirmation by a taxonomist (André Lucci Freitas, University of Campinas, Campinas, São Paulo, Brazil). The non-confirmed specimens were classified as morphospecies. All captured butterflies were deposited at the Entomological Collection of the Zoology Department of the Universidade de Brasília (UnB), Brasília, Brazil.

SEASONS AND COMMUNITY PARAMETERS

The transitional periods between the dry–wet season (T.dw.: Sep–Nov) and between the wet–dry season (T.wd.: Mar–May) were determined based on 8 yr of climatic profiling. Thus, the temporal dynamics of the Nymphalidae were examined over these 4 seasons: wet (Dec–Feb), T.wd, dry (Jun–Aug), and T.dw.

Rarefaction curves, constructed with MaoTau and Jackknife 1 with 1,000 randomizations without replacement, were used to verify and compare the species richness between the 4 seasons. The Jackknife 1 estimator was used because of its efficiency and reduced dependence on sample size (Colwell 2005). Temporal dynamics of Nymphalidae were tested using 5 community parameters: relative abundance (number of individuals), species richness (number of species—MaoTau and Jackknife 1), evenness (Pielou's—J), diversity (Shannon index), and species composition.

In Pielou's index, evenness values range from 0 to 1, representing the level of homogeneity of the relative abundance of each butterfly species. Values closer to 1 represent periods when the relative abundance is more homogeneously distributed across a given species (Magurran 2004). In this study, Pielou's index was calculated using the “vegan” packages of the R statistical software (R Development Core Team 2015).

STATISTICAL ANALYSES

Linear mixed-effect models (lme) were used to test the impact of seasons (wet, T.wd, dry, T.dw), habitats (savanna and gallery forest), and the interaction of habitat with season on the temporal variation of relative abundance, species richness, evenness, and diversity of fruit-feeding butterflies. The sample units and linear transects (C1–C5 and F1–F5) were used as random factors; the habitat (spatial) and season (temporal) were used as fixed factors.

The PERMANOVA analysis (1,000 randomizations) was used to test the possible dissimilarities in Nymphalidae species composition over the seasons and habitats. Non-metric dimensional scaling analysis was used to visualize those potential differences (Logan 2010). Additionally, we used the “INDVAL” approach of Dufrêne & Legendre (1997) to identify those species that best characterize each climatic season. The indicator value for each species provides a measure of its importance in a given temporal partition. The probability of obtaining a given indicator value (*P*-value) was determined using 1,000 randomizations followed by Holm correction for multiple comparisons. This analysis was conducted using the “labdsv” packages in the R statistical software (R

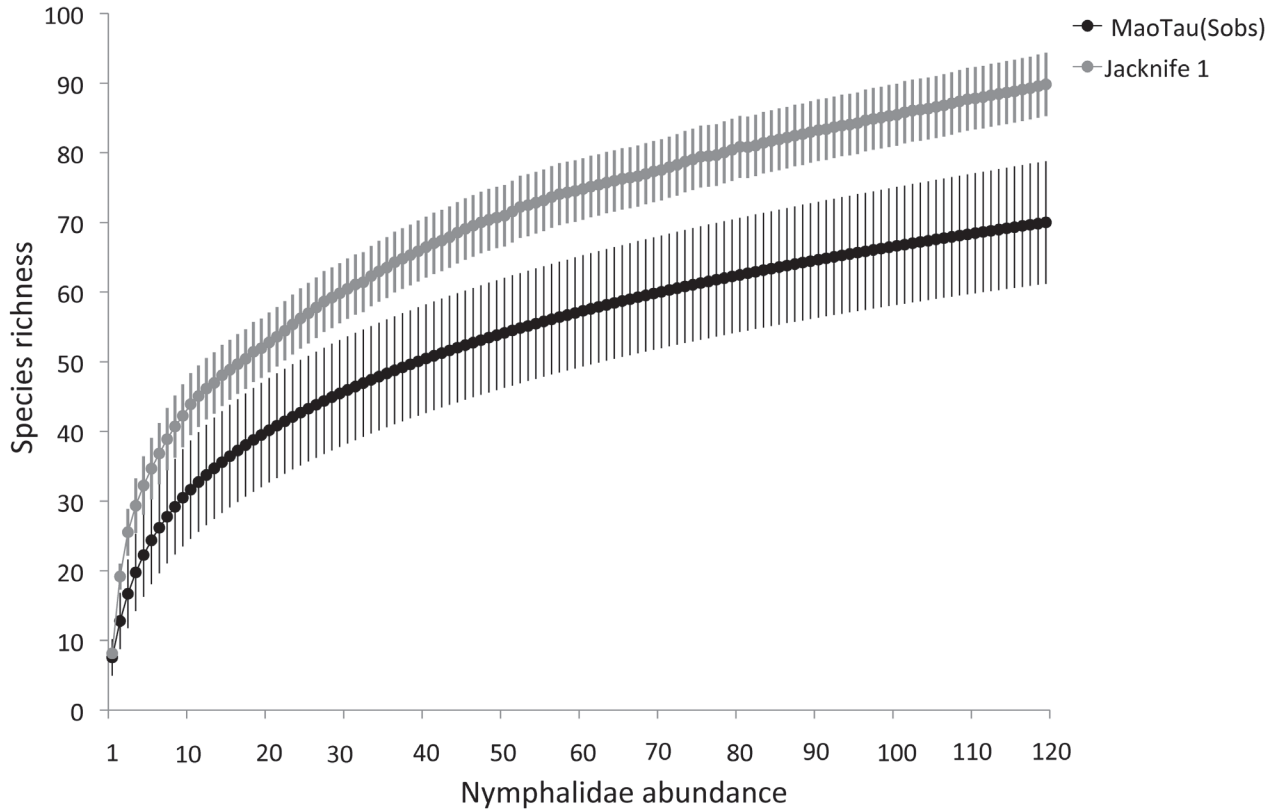


Fig. 1. Rarefaction curves, generated with 1,000 randomizations without replacement, based on the MauTau (Sobs, black circles) and “total” estimated (Jackknife 1, gray circles) values. The data of Nymphalidae species richness was acquired from Jul 2012 to Jun 2013 in the Fazenda Água Limpa and the Reserva Ecológica do Roncador, Brasília, DF.

Development Core Team 2015), and a significance level of $P \leq 0.05$ was used to refute the null hypothesis.

Results

In total, 3,459 individuals of 62 species (30 genera) were captured; the Satyrinae (1,795 individuals; 52%) was the most abundant subfamily, followed by Biblidinae (1,411; 41%), Charaxinae (204; 6%), and Nymphalinae (49; 1%). The sample effort applied in this study was sufficient to capture 80% of the total species richness as estimated by Jackknife 1 values (Fig. 1).

Nine Nymphalidae species showed a relative abundance greater than 100 individuals (Suppl. Table 1, available online at <http://purl.fcla.edu/fcla/entomologist/browse>). The 5 most abundant species were *Hamadryas feronia* L. (Biblidinae) (906 individuals), *Hermeuptychia hermes* F. (Satyrinae) (414 individuals), *Ypthimoides* sp.1 (Satyrinae) (302 individuals), *Pareuptychia ocirrhoe* F. (Satyrinae) (247 individuals), and *Callicore sorana* (Godart) (Biblidinae) (184 individuals). These 5 species accounted for 60% of all individuals captured. Fifteen species were moderately represented (24–85 individuals), and the other 38 species (61%) had a lower relative abundance (<14 individuals) (Suppl. Table 1, available online at <http://purl.fcla.edu/fcla/entomologist/browse>).

The temporal dynamics of Nymphalidae showed a non-homogeneous pattern (Rayleigh-Z: 268.6; $P < 0.0001$), with abundance peaks in the T.wd and the wet seasons (Fig. 2). Similar results were observed regarding the different subfamilies and tribes (Fig. 3). In general, around 20.3% of Satyrinae abundance occurred in Mar (T.wd), with some differences observed between the Satyrinae tribes: Brassolini were most

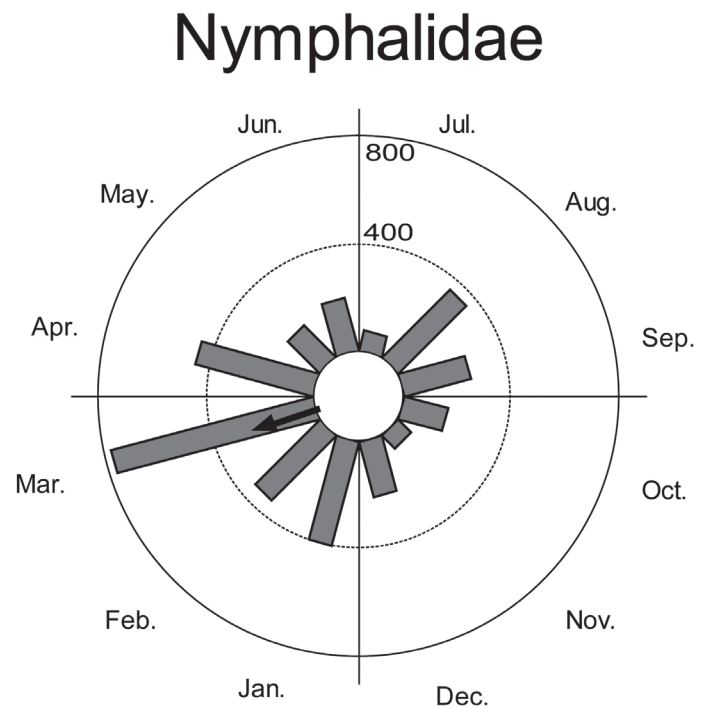


Fig. 2. Circular analysis of the number of individuals reflecting the abundance of Nymphalidae captured from Jul 2012 to Jun 2013 in the Fazenda Água Limpa and Reserva Ecológica do Roncador. In this analysis, each column’s length represents the observed abundance and the arrow the tendency of the highest abundance.

abundant in Aug (dry season: 20.5% of Brassolini abundance), and Morphini were most abundant in Nov (T.dw: 38% of Morphini abundance). Biblidinae (26.7%) and Nymphalinae (20.4%) were most abundant in Mar and Apr, respectively, whereas the Charaxinae (26.6%) peaked in Jul (dry season) (Fig. 3).

In general, the greatest relative abundance occurred in the transition between wet and dry seasons (T.dw: 1.389 individuals; 46 ± 40 individuals), followed by the wet season (943 individuals; 31 ± 22 individuals), the dry season (637 individuals; 21 ± 18 individuals), and the transition from dry to wet season (T.dw: 489 individuals; 16 ± 11 individuals) ($F_{1,26}: 26.87; P < 0.0001$). In relation to temporal variation in butterfly abundance, the savanna and gallery forest habitats showed a similar pattern (Fig. 4A), with greatest abundance in Mar (T.dw; Fig. 4B). However, the interaction between the temporal and spatial factors (Table 1) indicated that in the gallery forest (Fig. 4C), the variation in the relative abundance over the seasons was less than that found in the savanna areas (Fig. 4D).

The highest level of butterfly species richness was observed in the transition from the wet to the dry season, especially in Mar, when 55% of total species richness was captured (Fig. 5A). Also, the temporal variation in species richness was less in the gallery forest (Fig. 5B) than in the savanna areas (Fig. 5C).

The habitat, the season, and interaction between habitat and season affected the evenness of butterfly distribution (Table 1). In the

savanna, Nymphalidae species abundance was more homogeneously distributed in the dry season and in the transition period from dry to wet (T.dw) than in other seasons. On the other hand, no significant change was observed in evenness between seasons in the gallery forest (Fig. 6). Likewise, no effect of season on species diversity values was observed for this habitat (Table 1).

Season and the interaction between season and habitat explained 61% and 5% of the variation in butterfly species composition, respectively (Table 2). Each of the 2 habitats studied has distinctly seasonal butterfly species, but in the gallery forest a greater temporal turnover was observed compared with the savanna habitat (Fig. 7). Two temporally distinct species groups occurred in the gallery forest. The 1st group included *Archaeoprepona demophon* (Hübner), *Morpho helenor* (C. Felder & R. Felder), and *Paryphthimoides poltys* (Prittwitz), which all occurred in a greater proportion in the T.dw than in the other seasons. The 2nd species group was composed of *Catonephele acontius* (Prittwitz), *Cissia terrestris* (A. Butler), *Colobura dirce* (L.), *Diathria clymena janeira* (C. Felder), *Memphis moruus* (F.), *Pareuphytychia ocirrhoe* (F.), and *Temenis laothoe* (Cramer), and occurred mainly in the T.dw (Fig. 7; Suppl. Table 1, available online at <http://purl.fcla.edu/fcla/entomologist/browse>).

Considering the species with more than 10 individuals captured, the abundance of *Siderone marthesia* (Illiger) peaked in the dry season, *Hamadryas februa* (Hübner) and *M. helenor* in the T.dw, *Yphthimoides*

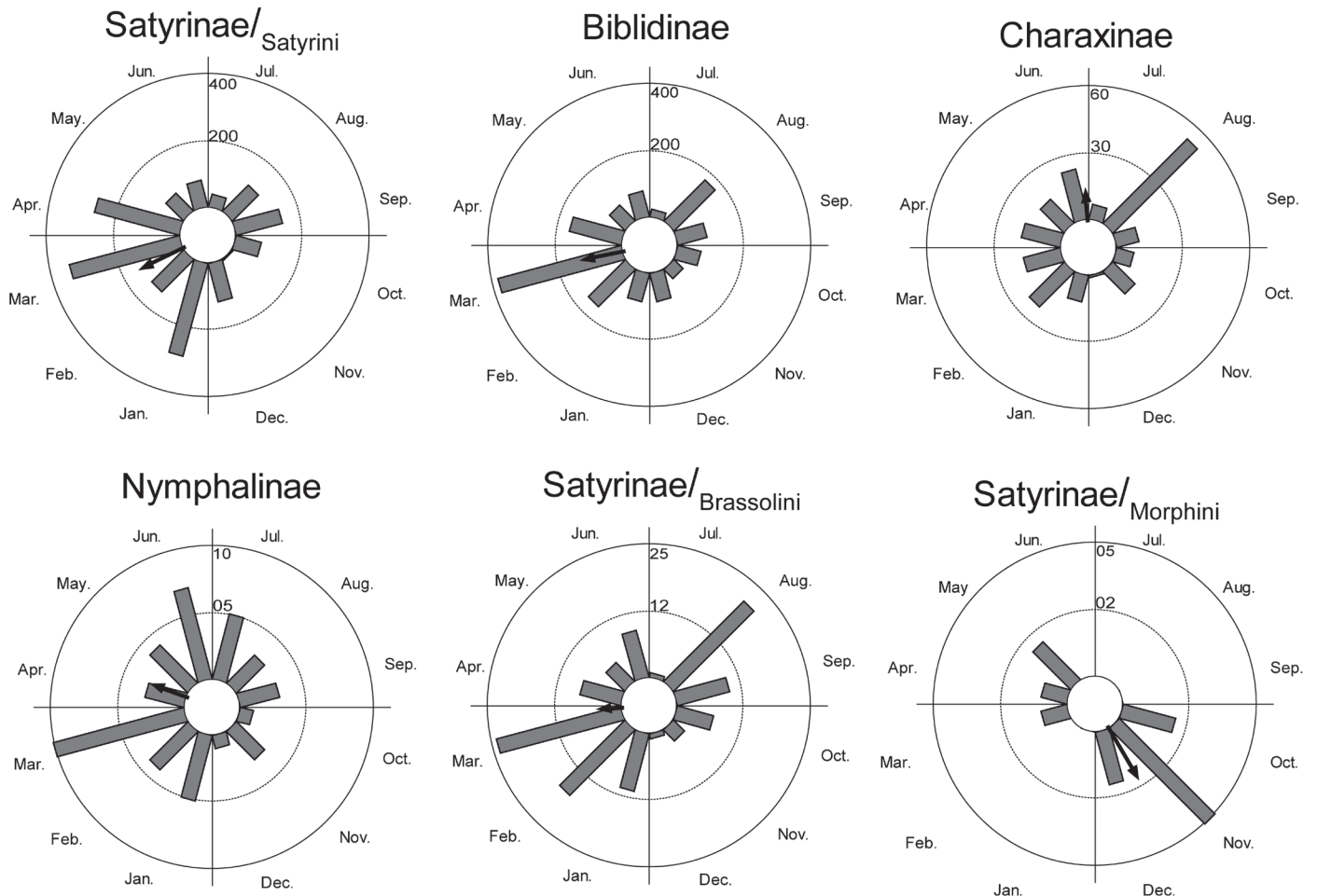


Fig. 3. Circular analysis of the number of individuals reflecting the abundance of the different Nymphalidae subfamilies and tribes captured from Jul 2012 to Jun 2013 in the Fazenda Água Limpa and Reserva Ecológica do Roncador. In this analysis, each column's length represents the observed abundance and the arrow the tendency of the highest abundance.

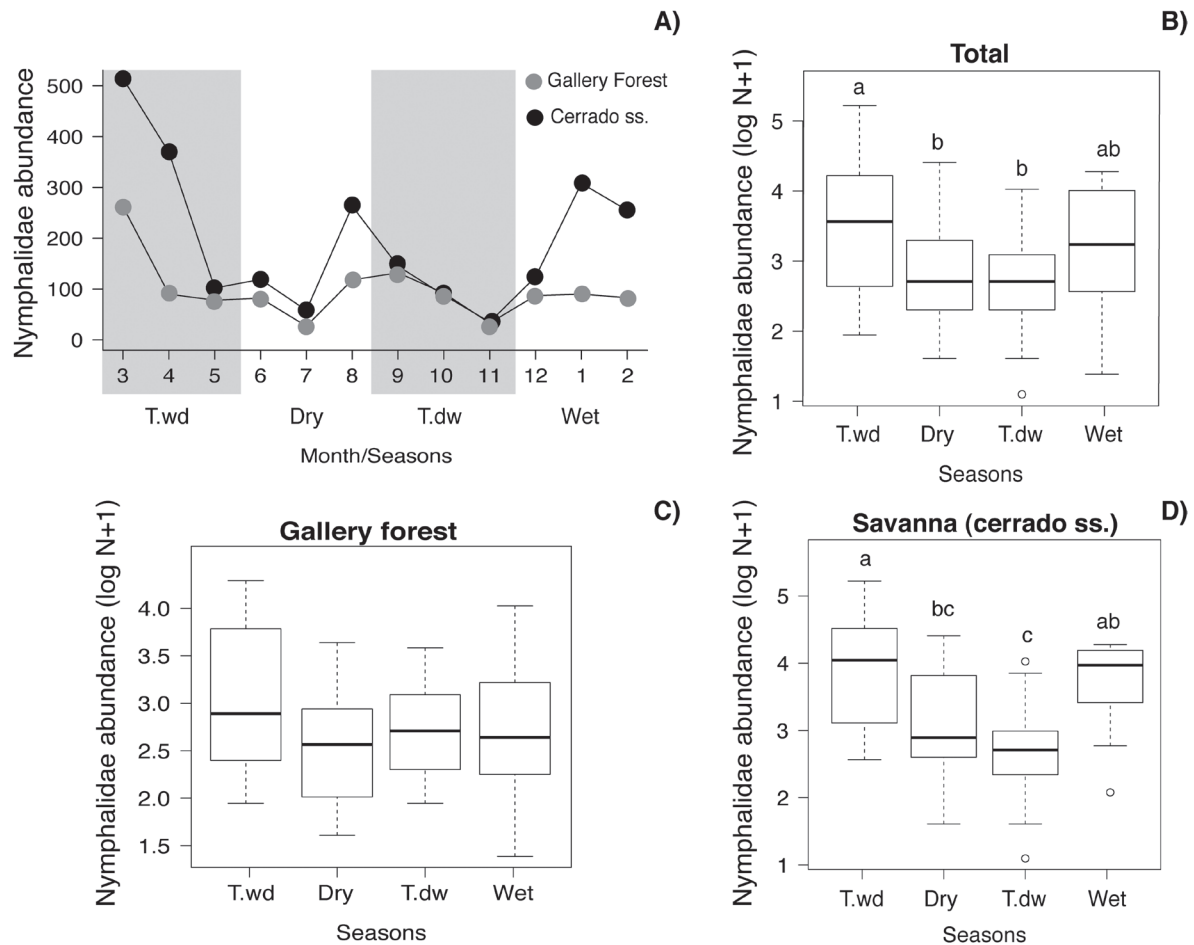


Fig. 4. A) Temporal variation in Nymphalidae abundance captured in the dry and wet seasons and in the 2 transitional periods between those seasons, from wet to dry (T.wd) and from dry to wet (T.dw), in savanna (Cerrado sensu stricto, ss) and forest (gallery forest) habitats of the Fazenda Água Limpa and the Reserva Ecológica do Roncador, Brasília, DF. The box plots show the differences between the 4 climatic periods, considering B) the total butterfly abundance (gallery forest + savanna), and that C) in the gallery forest and D) in the savanna separately. Different lowercase letters represent significant differences ($P < 0.05$).

sp.1 and *Ypthimoides pacta* (Weymer) in the wet season, and *Hama-dryas feronia* (L.) and *H. hermes* in the T.wd (Table 3).

Discussion

The number of traps installed (60 units), the size of the study area, the vertical strata (canopy and understory), and the 2 different habitats sampled (savanna and gallery forest) were all important factors in explaining the greater number of individuals and butterfly species found in this study than in a previous study in the same region (Pinheiro & Ortiz 1992). In the previous study, 1,034 individuals of 46 species were captured in 14 bait-traps installed in 1 linear transect of 700 m (Pinheiro & Ortiz 1992).

Satyrinae and Biblidinae were the most abundant subfamilies, accounting for 90% of all individuals captured in this study. This pattern is different from that of the Caatinga Biome (Nobre et al. 2012), in which these subfamilies accounted for 41% of all butterfly individuals captured, and Charaxinae as the most abundant subfamily accounted for 57% of all captures. Dissimilarities regarding the climate and the habitat structure of both biomes can help explain the differences. Habitats with forest structure are found more often in the Cerrado compared with the Caatinga, which could cause a greater abundance of Satyrinae, which are preferentially found in forest sites (Young 1973; DeVries 1987). Thus, the proportion of the

Table 1. Linear mixed-effect model (lme) parameters considering the effects of habitat, season, and the interactions between habitat and season on abundance, Pielou's evenness, and species diversity of Nymphalidae captured from Jul 2012 to Jun 2013 in the Fazenda Água Limpa and the Reserva Ecológica do Roncador, Brasília, DF.

Variables/factors	AIC	df _{numerator}	df _{denominator}	F	P
Abundance					
Intercept	255.2	1	84	384.14	<0.001 ***
Habitat		1	8	3.39	0.0461 *
Season		3	84	13.02	<0.001 ***
Habitat*season		3	84	4.89	0.0030 **
Pielou's evenness (J)					
Intercept	166.1	1	84	2228.70	<0.001 ***
Habitat		1	8	5.30	0.0400 *
Season		3	84	10.10	<0.001 ***
Habitat*season		3	84	5.60	0.0400 *
Diversity (Shannon)					
Intercept	128.1	1	84	913.25	<0.001 ***
Habitat		1	8	13.23	0.0060 **
Season		3	84	0.83	0.4797 NS
Habitat*season		3	84	1.38	0.2551 NS

AIC, Akaike information criterion; NS, non-significant; significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

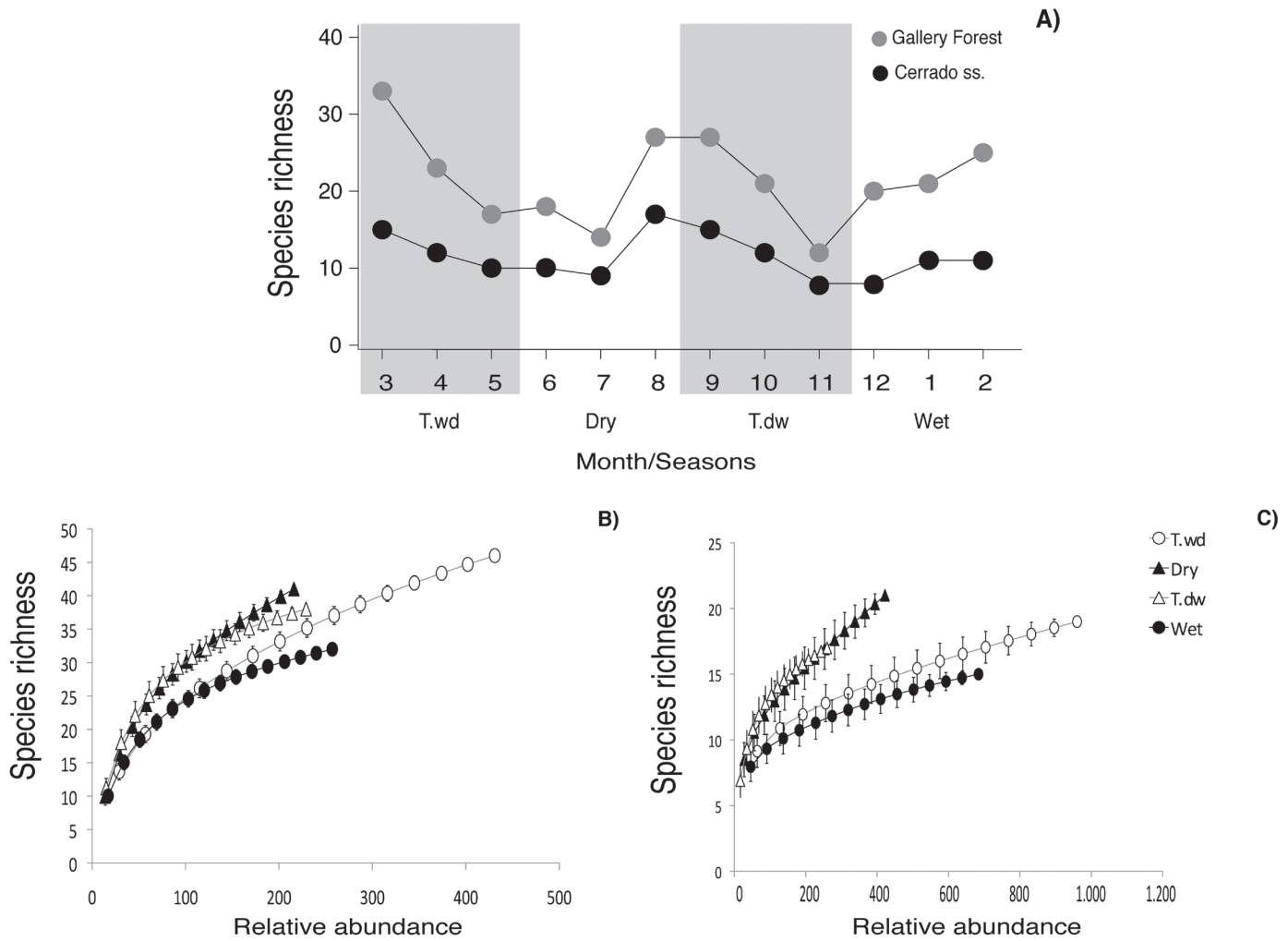


Fig. 5. A) Temporal variation in Nymphalidae species richness captured in the dry and wet seasons and in the 2 transitional periods between those seasons, wet to dry (T.wd) and dry to wet (T.dw), in savanna (Cerrado sensu stricto, ss) and gallery forest habitats in the Fazenda Água Limpa and the Reserva Ecológica do Roncador, Brasília, DF. The rarefaction curves compare the 4 climatic periods—dry (black triangles) and wet (black circles) seasons, and the transitional periods from wet to dry (T.wd, white circles) and from dry to wet (T.dw, white triangles)—in B) gallery forest and C) savanna separately.

butterfly subfamilies found in the present study is similar to the proportions previously reported in the Cerrado Biome (Pinheiro & Ortiz 1992; Marini-Filho & Martins 2010), Atlantic Forest (Ribeiro

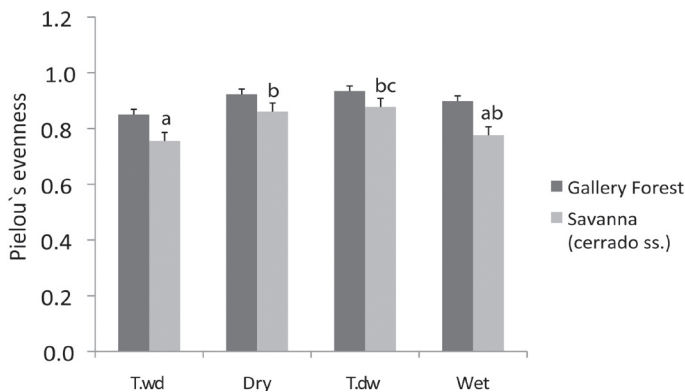


Fig. 6. Pielou's evenness values of the Nymphalidae species in the dry and wet seasons and in the transitional periods between these 2 seasons, from wet to dry (T.wd) and from dry to wet (T.dw), in savanna (Cerrado sensu stricto, ss) and forest (gallery forest) habitats in the Fazenda Água Limpa and the Reserva Ecológica do Roncador, Brasília, DF. Different lowercase letters represent significant differences ($P < 0.05$).

et al. 2012), and Equatorial Amazonia (DeVries et al. 1997, 2011; Barlow et al. 2008; Ribeiro & Freitas 2011) and could be explained by the important contributions of forest structure on the butterfly species richness of the Cerrado.

The temporal dynamics reported in this study (butterfly peaks in the wet season and in the T.wd) coincide with the abundance peaks of tropical insects (Brown 1991; Wolda 1992; DeVries et al. 1997, 2011) and with the Lepidoptera abundance peaks previously reported in the Cerrado Biome (Pinheiro et al. 2002; Silva et al. 2011b). The effect of weather conditions (air temperature and relative air humidity), natural enemies, and food resource availability are several factors that potentially explain the temporal dynamics observed (Morais et al. 1999; Silva et al. 2011b; Freire et al. 2014).

The Cerrado is characterized by a well defined and intense dry season that imposes difficulties on the animal communities present (Marquis et al. 2002), which is different from the wet weather in Amazonia and the Atlantic Forest (Ribeiro et al. 2010). Changes in weather potentially predict the temporal dynamics of butterflies within these habitats. For example, we showed that Satyrinae occurred at least 6 mo later in the Cerrado than in forest biomes (Atlantic Forest and Amazonia). Moreover, body size and high sensibility to periods of low air relative humidity, as is characteristic of the

Table 2. PERMANOVA results, obtained by 1,000 randomizations based on the Bray–Curtis dissimilarity matrix, showing the relative explanatory power of habitat, season, and the interaction between habitat and season for predicting composition of Nymphalidae captured from Jul 2012 to Jun 2013 in the Fazenda Água Limpa and the Reserva Ecológica do Roncador, Brasília, DF.

Factors	df	SS	MS	F (model)	Explanatory variable (%)	P
Habitat	1	536.09	536.09	1338.91	33	<0.001***
Season	3	971.84	323.95	809.07	61	0.002**
Habitat*season	3	70.20	23.40	58.44	5	0.05*
Residuals	32	12.81	0.40	0.01		
Total	39	1590.94	1			

MS, mean square; SS, sums of squares (in PERMANOVA analysis); significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Cerrado, could explain a large portion of the temporal variation in Satyrinae abundance (Braby 1995; Hill et al. 2003; Ribeiro & Freitas 2011).

The greater abundance during the dry season in the Cerrado may be a strategy by which larvae can avoid natural enemies (i.e., Hymenoptera) (Morais et al. 1999), which occur in greatest abun-

dance in the early wet season of the Cerrado (Pinheiro et al 2002; Silva et al. 2011b). As a consequence of greatest abundance of larvae in the dry season, adult emergence will occur most often in the beginning of wet season, a period in which the weather conditions favor flight and oviposition (Torres-Villa & Rodríguez-Molina 2002) and in which the leaves are younger than those in the dry season.

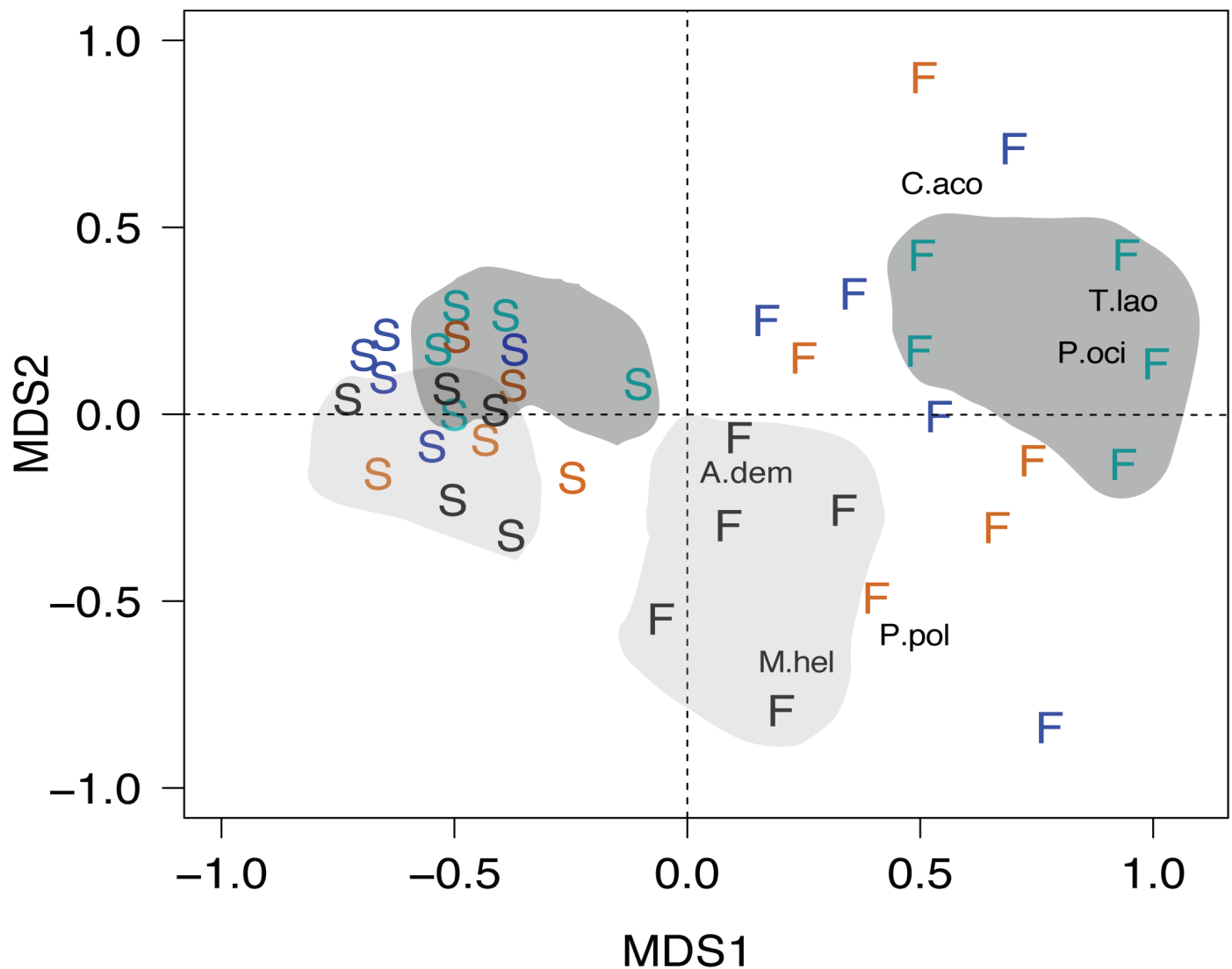


Fig. 7. Non-metric multidimensional scaling based on the Nymphalidae species composition captured in 4 climatic periods—wet (dark blue), dry (red), transition from wet to dry (T.wd, light blue), and transition from dry to wet (T.dw, black)—in 2 habitats, savanna (S) and gallery forest (F) in the Fazenda Água Limpa and the Reserva Ecológica do Roncador, Brasília, DF. A.dem, *Archeoprepona demophon*; M.hel, *Morpho helenor*; and P.pol, *Paripthimoides poltys* best characterize the T.dw, whereas C.aco, *Catonephele acontius*; P.oci, *Pareupthichia ocirrhoe*; and T.lao, *Temenis laothoe* best characterize the T.wd. Stress: 0.15.

Table 3. Temporal distribution of the 28 most abundant butterfly species ($n \geq 10$ individuals) in the Fazenda Água Limpa and the Reserva Ecológica do Roncador (Brasília, DF) in 4 climatic periods: wet, dry, transition from dry to wet (T.dw), and transition from wet to dry (T.wd). Also shown are values generated from INDVAL analysis and their significance (P).

Species	SF	T.wd	Dry	T.dw	Wet	Total	Season	INDVAL	P
<i>Archaeoprepona demophon</i>	C	2	1	8	3	14	T.dw	0.095	0.117 NS
<i>Caligo illioneus</i>	Sb	1	10	11	2	24	T.dw	0.097	0.207 NS
<i>Callicore pygas</i>	C	12	3	6	7	28	T.wd	0.100	0.297 NS
<i>Callicore sorana</i>	B	52	63	38	31	184	Dry	0.194	0.483 NS
<i>Catonephele acontius</i>	C	37	11	3	8	59	T.wd	0.251	0.006 **
<i>Cissia terrestris</i>	S	34	7	7	12	60	T.wd	0.076	0.625 NS
<i>Colobura dirce</i>	N	14	15	4	8	41	Dry	0.098	0.435 NS
<i>Diaethria clymena</i>	B	10	0	0	4	14	T.wd	0.095	0.064 NS
<i>Eunica curvierii</i>	B	2	7	12	3	24	T.dw	0.100	0.173 NS
<i>Hamadryas februa</i>	B	30	23	58	24	135	T.dw	0.158	0.450 NS
<i>Hamadryas feronia</i>	B	429	153	80	244	906	T.wd	0.331	0.049 *
<i>Hermeuptychia hermes</i>	S	268	5	8	133	414	T.wd	0.345	0.001 ***
<i>Memphis moruus</i>	C	15	8	8	6	37	T.wd	0.122	0.253 NS
<i>Morpho helenor</i>	Sm	1	0	7	2	10	T.dw	0.117	0.042 *
<i>Opsiphanes invirae</i>	C	31	20	9	25	85	T.wd	0.146	0.511 NS
<i>Pareuptychia ocirrhoe</i>	S	131	47	7	62	247	T.wd	0.248	0.025 *
<i>Paryphthimoides poltys</i>	S	15	9	21	0	45	T.wd	0.140	0.100 NS
<i>Satyrinae sp.1</i>	S	42	32	23	7	104	T.wd	0.144	0.381 NS
<i>Satyrinae sp.2</i>	S	117	51	8	0	176	T.wd	0.355	0.001 ***
<i>Siderone marthesia</i>	C	29	68	11	25	133	Dry	0.290	0.009 **
<i>Taygetis laches</i>	S	1	3	7	12	23	Wet	0.087	0.260 NS
<i>Temenis laothoe</i>	B	26	10	1	4	41	T.wd	0.338	0.001 ***
<i>Thaygetis sp.4</i>	S	0	4	3	3	10	Dry	0.040	0.766 NS
<i>Yphthimoides sp.1</i>	S	11	33	83	175	302	Wet	0.367	0.001 ***
<i>Yphthimoides mimula</i>	S	1	5	15	6	27	T.dw	0.093	0.198 NS
<i>Yphthimoides pacta</i>	S	0	0	0	78	78	Wet	0.267	0.001 ***
<i>Yphthimoides renata</i>	S	14	7	7	22	50	Wet	0.117	0.260 NS
<i>Yphthimoides straminea</i>	S	28	13	21	23	85	T.wd	0.110	0.709 NS
Total		1,353	608	466	929	3,356	—	—	—

Subfamilies (SF): Biblidinae (B); Charaxinae (C); Nymphalinae (N); S (Satyrinae); Sb (Satyrinae, tribe: Brassolini), and Sm (Satyrinae, tribe: Morphini). Significance level: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; NS, non-significant or $P > 0.05$.

In the gallery forest, the competition for light is important, thus plant species with more investment in biomass and leaf area are selected in this environment (i.e., *Alibertia macrophylla* K. Schum. [Gentianales: Rubiaceae]; *Ouratea castaneifolia* [DC.] Engl. [Malpighiales: Ochnaceae]; *Salacia elliptica* [Mart. ex Roem. & Schult.] G. Don [Celastrales: Celastraceae]) compared with the savanna habitat (Hoffmann & Franco 2003; Hoffmann et al. 2005). This selection results in different shade levels and supports the idea of more stable microclimate conditions in the forest than in the savanna (Diniz & Kitayama 1998; Tidon 2006). This may explain, in part, the lesser temporal variation in the Nymphalinae community parameters in the forest habitat, compared with their savanna relatives.

The first rains could act as a trigger inducing high insect activity (Wolda 1988), which may explain the higher species richness captured in the early wet season and in the T.wd. Additionally, the dry season and T.dw were the periods in which the relative abundances were distributed more homogeneously between butterfly species. More abundant species benefit from the wet season and grow in number until the T.wd. In this way, the response of the most abundant species could be associated with improved weather conditions caused by the first rains (Torres-Vila & Rodríguez-Molina 2002). The beginning of the wet season may indirectly impact the most abundant species due to the plant phenological response associated with the weather, because the wet season is the period when most zoochorical (animal-dispersed) plants present mature fruits (Batalha et al. 1997; Batalha & Mantovani 2000; Batalha & Martins 2004; Silva et al. 2011a).

Previous studies have reported that forested habitat has great temporal species turnover, suggesting that habitat structure is an important factor in the temporal dynamics of butterflies (Shahabuddin & Terborgh 1999; Hamer et al. 2005; Barlow et al. 2008; DeVries et al. 2011; Nobre et al. 2012). The results of the present study agree with this hypothesis and indicate that the open habitat surveyed (i.e., savanna), in contrast to the forested habitat surveyed, is spatially less diverse and, as a consequence, has a butterfly assemblage that is more homogeneously distributed over the seasons (Hamer & Hill 2000; Hamer et al. 2003).

Differences in the floristic and structural composition between the 2 habitats studied illustrate different eco-physiological responses of the plant community between the 2 habitats (Mesquita 2000; Hoffmann et al. 2005). For example, plants in the gallery forest present a greater leaf area (Hoffmann et al. 2005) and greater phenological synchrony (Goulart et al. 2005) compared with their savanna relatives. These factors could explain the greater species turnover of Nymphalinae found in the gallery forest compared with the savanna.

The savanna habitat is characterized by an open environment, making it more exposed to variation in weather compared with the gallery forest (Meyer & Sisk 2001; Hoffmann et al. 2005). Plant species found in climatically variable environments may have poor anti-herbivore defenses (Salmore & Hunter 2001; Zehnder et al. 2009), and consequently, wide diet breadth could be a common strategy among the herbivore community present in these environments (Coley & Aide 1991;

Pellissier et al. 2012). In accordance with ecological theory, communities composed primarily of species with narrow diet breadth are, in general, richer than those in which most species are generalists (Coley & Aide 1991; Dyer et al. 2007; Pellissier et al. 2012). Diet specialization and seasonality are positively related in a variety of arthropods; thus, species with narrow diet breadth may be more temporally restricted compared with polyphagous species (Novotny & Basset 1998; Forkner et al. 2008; Wardhaugh 2014).

The relative stability of climate (Oliveira-Filho & Ratter 2002), the greater species richness (Diniz & Kitayama 1998; Meyer & Sisk 2001; Hoffmann et al. 2005; Tidon 2006), and the marked temporal turnover in the butterfly community within the gallery forest are factors that reinforce diet specialization as a widespread strategy for forest butterflies. Although a long-term study (~20 yr) has been conducted examining the interactions between herbivores and host plants within the Cerrado (I. R. Diniz & H. C. Morais, unpublished) the study did not include gallery forest. Therefore, we recommend that studies of host-herbivore interactions include other habitats aside from the savanna in order to confirm or refute hypotheses presented here regarding relative host breadth between habitat types. The findings presented here confirm the role of the habitat heterogeneity found in the Cerrado Biome in maintaining the lepidopteran biodiversity (Brown & Gifford 2002) and reinforce the habitat heterogeneity as an important component in determining the Nymphalidae species richness and composition as found in moths (Braga & Diniz 2015). Thus, the integrity of Cerrado as a mosaic of different habitat types should be prioritized because each habitat plays a crucial role in maintaining the moth and butterfly biodiversity at the local and regional scale.

In conclusion, the greater temporal variation of examined butterflies was found in the savanna habitat than in the gallery forest. However, the gallery forest habitat, where the weather conditions were more stable (Oliveira-Filho & Ratter 2002; Tidon 2006; Scherrer et al. 2013), showed greater butterfly species turnover over the seasons. The present study is among the first to describe the temporal dynamics of Nymphalidae in the Cerrado Biome and indicates that the gallery forest is an important component of Nymphalidae diversity. Moreover, this study highlights the complex interaction between seasons, habitat structure, feeding behavior, and diet breadth on the temporal dynamics of these butterflies. Thus, based on our findings, we suggest that future studies regarding the fruit-feeding butterfly guild in the Cerrado should consider temporal and spatial factors in order to make more accurate predictions.

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