

Temporal dynamics of the butterfly Heliconiinae assemblage in a typical ruderal environment in Southeastern Brazil

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ABSTRACT

This study aimed to verify the response of the Heliconiinae assemblage and of the flowering plants used as food resources for these butterflies to climate and weather conditions during 2019 along a dirt road in the Atlantic Forest. Many parts of the dirt roadside are occupied by anthropogenic ruderal vegetation. Climate conditions in that period were very different to climate normals mainly in respect to rainfall, spring 2019 being wetter and autumn drier. Flowers of at least 33 plant species were used by Heliconiinae butterflies during the study with six species being flowering in all seasons. In autumn (April to June) all 16 Heliconiinae species were on the fly. Flowering was affected by the accumulated rainfall and photoperiod availability of the previous three months. Acraeini species were less sensitive to bad weather conditions than Heliconiini. Heliconiinae species responded negatively to photoperiod.

KEY WORDS

Acraeini; diversity; flowering; photoperiod; seasonality.

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INTRODUCTION

In the Neotropical region, Heliconiinae (Papilionoidea: Nymphalidae) has more than 140 butterfly species distributed in three tribes: Acraeini, Argynnini and Heliconiini (Brower, 2000; Penz & Pegg, 2003; Wahlberg et al., 2003; Lamas, 2004). Although the species of these tribes are phylogenetically close since they diverged after the K-Pg event less than 55 million years ago (Wahlberg et al., 2009), their ecological characteristics are quite different. In the Neotropics, most Heliconiini species are K strategists (sensu MacArthur & Wilson, 1967; Pianka, 1970) linked to the interior of forest systems (Brown-Jr, 1981;

Gondeck et al., 2021) while Acraeini species are r strategists more linked to more open edges or ruderal systems (Francini, 1989; Silva-Brandão et al., 2008; Gondeck et al., 2021).

A total of 26 species are listed for these taxa in the Metropolitan Region of Santos (MRS) (Francini et al., 2011). Richness and diversity of Heliconiini and Acraeini are related to the richness and diversity of their larval food-plants (Gilbert & Singer, 1975), the first in the genus *Passiflora* (Passifloraceae) with more than 540 host plant species (Jiggins & Lamas, 2016) and the second in species of various genera of Asteraceae (Francini, 1989, 1992; Francini & Penz, 2006).

Adults of these butterflies in MRS use nectar or pollen of plants of different families, some common to both taxa (Francini, 2010). Adults of some Heliconiini species of the genus *Heliconius* have high longevity which can reach several months (Gilbert & Singer, 1975). This longevity, their chemical defense processes, and continuous capacity to produce eggs can be linked to the amino acids extracted from consumption of pollen grains (Gilbert, 1972; Dunlap-Pianka et al., 1977). On the other hand, other Heliconiini and all Acraeini adults of the genus *Actinote* live for a few days and consume only nectar (Francini, 1989; Francini et al., 2005).

The flowering patterns of trees and climbers in Neotropical forests are strongly correlated with climatic seasonality, however the proximate factors stimulating flowering are not yet well known but there is evidence that rainfall is a key factor in the release, timing and synchronization of anthesis by tropical trees and shrubs (Frankie and Baker, 1976; Morellato & Leitão-Filho, 1996). Photoperiodism in plants is known since 1852 (Henfrey, 1852) and today flowering of many angiosperms species responds to changes in day length synchronized to dry or rainy periods, even in tropical latitudes (Thomas & Vince-Prue, 1997). In animals, photoperiodism have also an important role regarding phenology together with other environmental conditions as temperature and rainfall (Bradshaw & Holzapfel, 2007).

Various models proposed by the Intergovernmental Panel on Climate Change predict increase in world temperature for the next 100 years (IPCC, 2021). However, nowadays, Climate Change has caused drastic changes on distributions and abundances of many species, which may be directly correlated with physiological tolerance in relation to increase in temperature, or in relation to expansion and retractions of their food supplies (Pateman et al., 2012). Butterflies are highly sensitive to climate change, consequently temperature variations can affect their phenological cycles, causing a damaging mismatch in relation to the phenology of their host plants or floral resources (Pateman et al., 2012; Caldas, 2014) or even changes on their resource use patterns (Ramos et al., 2021). The climate change and the anthropogenic processes of fragmentation and modification of natural habitats have changed the environmental conditions having a significant impact on butterfly populations (Kwon et al., 2010; Santos et al., 2020). These problems have alerted to the development of new

monitoring techniques using climate data or applying modern modeling techniques to predict and prioritize the conservation actions (Caldas, 2014, Sobral-Souza et al., 2015). Considering that insects are ectothermic organisms, changes in temperature affects their development (Gilbert & Rawort, 1996). Studies on forest fragmentation from anthropogenic origin show that variations on edge abiotic conditions, such as wind, humidity and solar irradiation can affect the structure and composition of trees, increasing their mortality rates, causing forest clearings, favoring non-forest species establishment and leading to microclimate changes (Li et al., 2018; Parra-Sanchez et al., 2020). Human actions can also alter the supply of food resources for larvae by planting passion fruit species that can be used by Heliconiini species (Gondeck, 2017; Gondeck et al., 2021).

The objective of this study was to verify the response of the Heliconiinae assemblage and of the flowering plants used as food resources for these butterflies to climate and weather conditions during 2019 along a dirt road in the Atlantic Forest.

MATERIAL AND METHODS

Study area

The study area covered the entire length of a dirt road that runs along the right bank of the Quilombo River, in the continental area of the municipality of Santos, São Paulo, Brazil (geographical coordinates: -23.858503° and -046.352081° to -23.817125° and -046.301656°; see Francini, 2010; and Gondeck et al., 2021).

Climate, weather, and vegetation of the study area

Photoperiod of study area was calculated based on sunrise/sunset tables (NOAA, 2020a) totaling monthly daylength in minutes. In the latitude of the study area, total monthly daylength has peak in summer (February; day length = 817 minutes), diminishing towards winter (July, day length = 640 minutes) (Fig. 1). The normal climate diagram followed the standards proposed by Walter (1984), being constructed with data from 30 years of observations, from 1970 to 2000, based on Worldclim data (Hijmans et al., 2005 Harris et al., 2014,

Worldclim, 2020). This data indicates that the study area has an Af type climate in the Köppen classification (Peel et al., 2007; Alvares et al., 2013) with average annual rainfall of 2550 mm and average annual temperature of 22.0 °C (Fig. 2).

The rainiest month was February (331 mm), in the summer and the driest July (100 mm), in the winter. Climate of the area during the study was based on the rainfall data for 2016–2019 period recorded by the Cemaden rain gauge 354850014A (CEMADEN, 2020) located at Neves Farm (Sítio das Neves, in Portuguese) (coordinates -23.88°, -046.31°). Hourly temperature and solar radiation data were obtained from the CETESB automatic station in Santos (coordinates -23.58°, -046.19°) (CETESB, 2020), the closest (7 to 15 km) to the study area. Daily conditions were classified to permit inferences between weather and probability of butterfly activity. Number of bad days in the study area for the butterfly flight during 2019 was estimated considering: total daily rainfall above 10 mm (RAIN); maximum mean solar radiation less than 500 J/m²/s during sampling period (RMAX); percentage of moisture during sampling period less than 40% (RHMI); daily dew point above 27 °C (DEWP); minimum temperature at shade during sampling period less than 18 °C (TMIN). These numbers permitted to calculate percentages of monthly bad days and percentage of samplings done during bad days.

The predominant vegetation in the studied area was originally composed by Submontane Ombrophilous Forest (Urrahy et al., 1987), but currently many parts of the dirt roadside are occupied by anthropogenic ruderal vegetation.

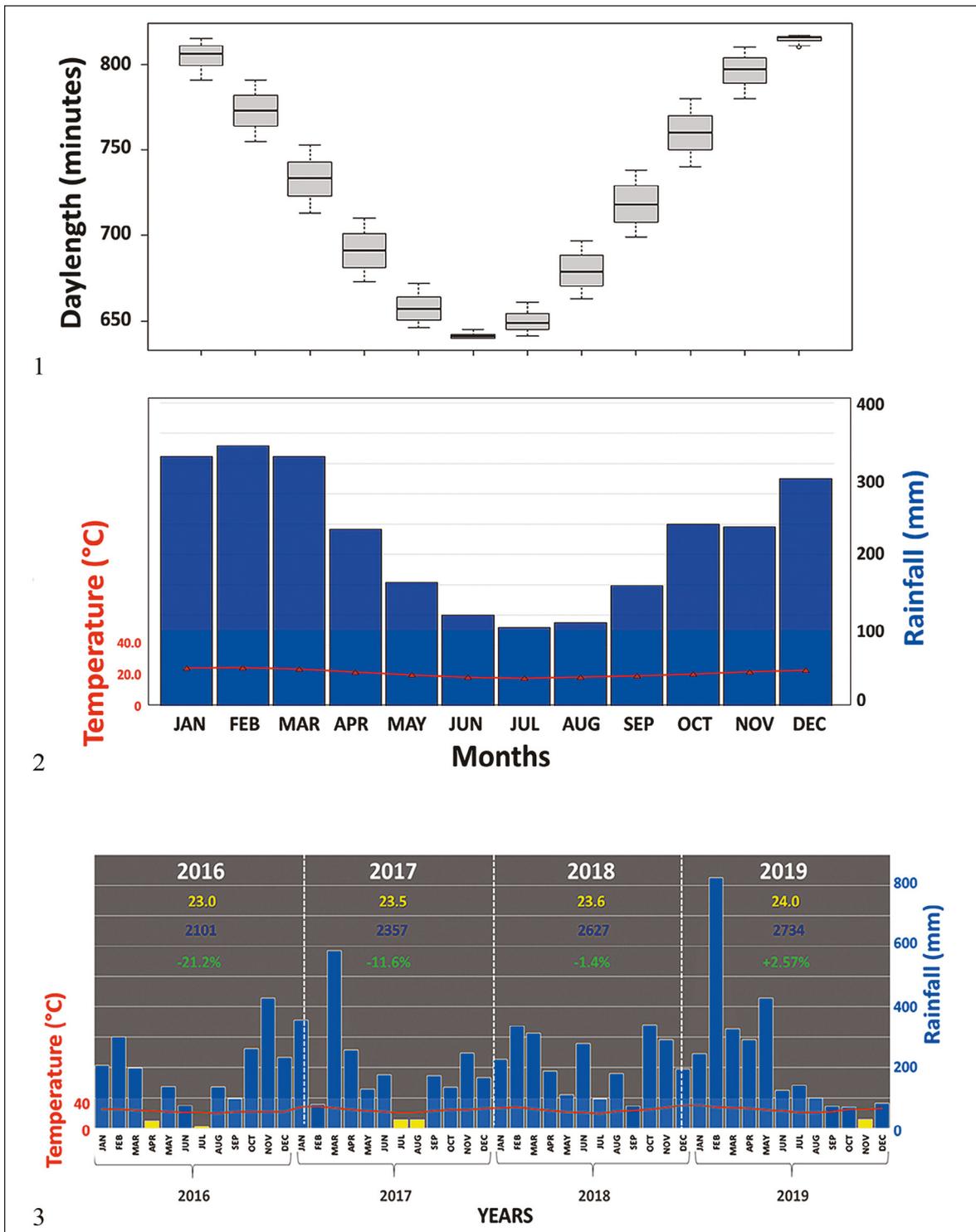
Samplings

Samplings encompassed all seasons totalizing 92 days (13,340 min), from January to December 2019. Accounting the presence of species at each 1000 m segment, accomplished using a motor vehicle traveling between 10 and 20 km/h which was stopped whenever a butterfly was spotted. Whenever a higher concentration of butterflies was observed due to the presence of resources, stops of several minutes were done until all the present species were identified or collected. Data was collected using digital photographic equipment with camera lenses up to 2000 mm focal length which allowed the identification of an individual of a species that was resting at up to 50m. Even though most days had good

weather and clear skies without clouds, cloudy or even rainy days were also sampled. Sampling effort usually covered the morning period (08:00h to 13:00h). The observations were made in both directions and edges of the road, that is, along the 8.6 km long transection. During this work all butterfly species, including non-nectarivores, were recorded in the study area, but here only the *Heliconiinae* assemblage was studied. Other taxa will be subject of other works. The number of researchers in each sample varied between one and four, but always together at the same point in the segment so that the observations were unique.

Data analysis

Final analysis considered only the presence or absence of species in each sampling. Data was analyzed using R software v. 3.6.3 (R Development Core Team, 2020) and RStudio interface v. 1.3.959 (RStudio.com, 2020) with packages *vegan* (Oksanen et al., 2017), *biodiversityR* (Kindt, 2019), *ggplot2* (Wickham, 2019), *FactoMineR*, v. 2.3 (Le et al., 2008; Husson et al., 2020), *factoextra*, v. 1.0.7 (Mundt, 2020), and *mgcv* (Wood, 2019). Data normality was tested by the Shapiro Wilk test. Relationships between variables were tested using Generalized additive (mixed) models (GAM) (Wood, 2017). The independent variables were tested in different combinations and the choice of the best model was made using the one with the lowest value of the Akaike Information Criterion (AIC). Principal component analysis (PCA) was used to show the strength of climate conditions during the study. After the exclusion of weak or too correlated environmental variables, nine were used in different analysis: monthly rainfall in mm (TRAIN), monthly number of rainy days (RAIND), total rainfall of previous season in mm (PREV), average temperature in °C (TMED), integrated temperature in °C (TINT), integrated daylength in hours (PHOTO), integrated solar radiation in J/m²/s (RINT), and average solar radiation in J/m²/s (RMED), daily minimum solar radiation in J/m²/s (RMIN). Dependent variables were richness of *Heliconiinae* assemblage (RICH) or frequency of each species. Flower richness (FLOWER) was also used as independent variable because it could affect the food availability for butterflies, but in one analysis, it was considered dependent of other abiotic conditions.



Figures 1–3. Climatic profile of study area. Fig. 1: total monthly daylength (minutes) based on sunrise/sunset tables (NOAA 2020a). In the latitude of the study area, total monthly daylength has peak in February (summer) diminishing towards July (winter). Fig. 2: climate diagrams of the study area based on Walter (1984). Climate normals from 1970-2000 (WORLDCLIM, 2020) showing that drier season began on the autumn end to the middle winter. Fig. 3: climate diagrams of the study area from 2016 to 2019 (data from CETESB 2020 and CEMADEN 2020), based on Walter (1984). Yellow numbers are mean annual temperature (°C), blue numbers are annual total rainfall (mm), and green numbers are percentage of differences between the total annual rainfall (mm) for each year from climate normals.

RESULTS

Analysis of the weather and climate of 2016–2019

Although this study covers only the period of 2019, data from temperature and rainfall from 2016 to 2019 were used here to give an idea of the variation of these parameters in the study area. The annual rainfall from 2016 to 2019 (Fig. 3) increased from 2101 mm to 2734 mm with 2016 to 2018 being drier than normal and 2019 wetter (Supplemental material 1A). July 2016 and July and August 2017 being extremely dry.

The separation of climate data by seasons permitted a most particular analysis. In this study we considered that summer encompasses January, February and March; autumn, April, May and June; winter, July–August and September, and spring, October, November and December.

In relation to the climate normals, for rainfall the percentage of difference ranged from spring 2019 being +76.80% more wet and autumn 2019 being 63.76% more dry. The comparison between seasons' rainfall showed significant differences and only autumn 2017–2018, and winter 2016–2017 were exceptions (2.94%). A clear pattern is shown in relation to the rainfall during autumn which increased from 2016 to 2019 (Supplemental material 1B). Temperature averages were different (Fig. 1C) except between winter 2017–2018, and spring 2017–2018. Mean annual temperatures were 1.5 °C to 1.9 °C higher than normal (Fig. 3).

Regarding the photoperiod (minutes) in the geographical coordinates of the study area, summer day length had the average of 770.0 minutes which drops to 663.2 minutes in autumn. The values drop and reaches 640 minutes in winter (June 20) then increase again to 817 minutes until the end of Spring (December 21; Fig. 1).

During 2019, the winter received low rainfall as expected but, from September to December (spring) there was a drought period characterized by hydric deficit mainly during November (Fig. 4). Despite lower rainfall, the integrated solar radiation which should increase after winter, maintained lower than expected due to the continuous cloudiness (Fig. 5).

In the Principal Component Analysis of monthly climate conditions (Fig. 6) for 2019 sam-

pling period the first two dimensions of analyses expressed 89.51% of the total dataset's inertia which is relatively high and both first planes well represent the data variability, being greater than the reference value and thus highly significant. The cluster 1 grouped spring months 10 (October), 11 (November) and December (12) and is characterized by high values for the variable PHOTO and low values for the variables RINT and TRAIN. The cluster 2 grouped one autumn months 6 (June), and two winter 7 (July) and 8 (August) and is characterized by low values for the variables TMED and PHOTO.

The cluster 3 grouped summer months 1 (January) and 2 (February) and is characterized by high values for the variables TRAIN and TMED. This scenario is an indication of the breaking of the expected seasonal pattern for autumn because June was attracted to cluster 2.

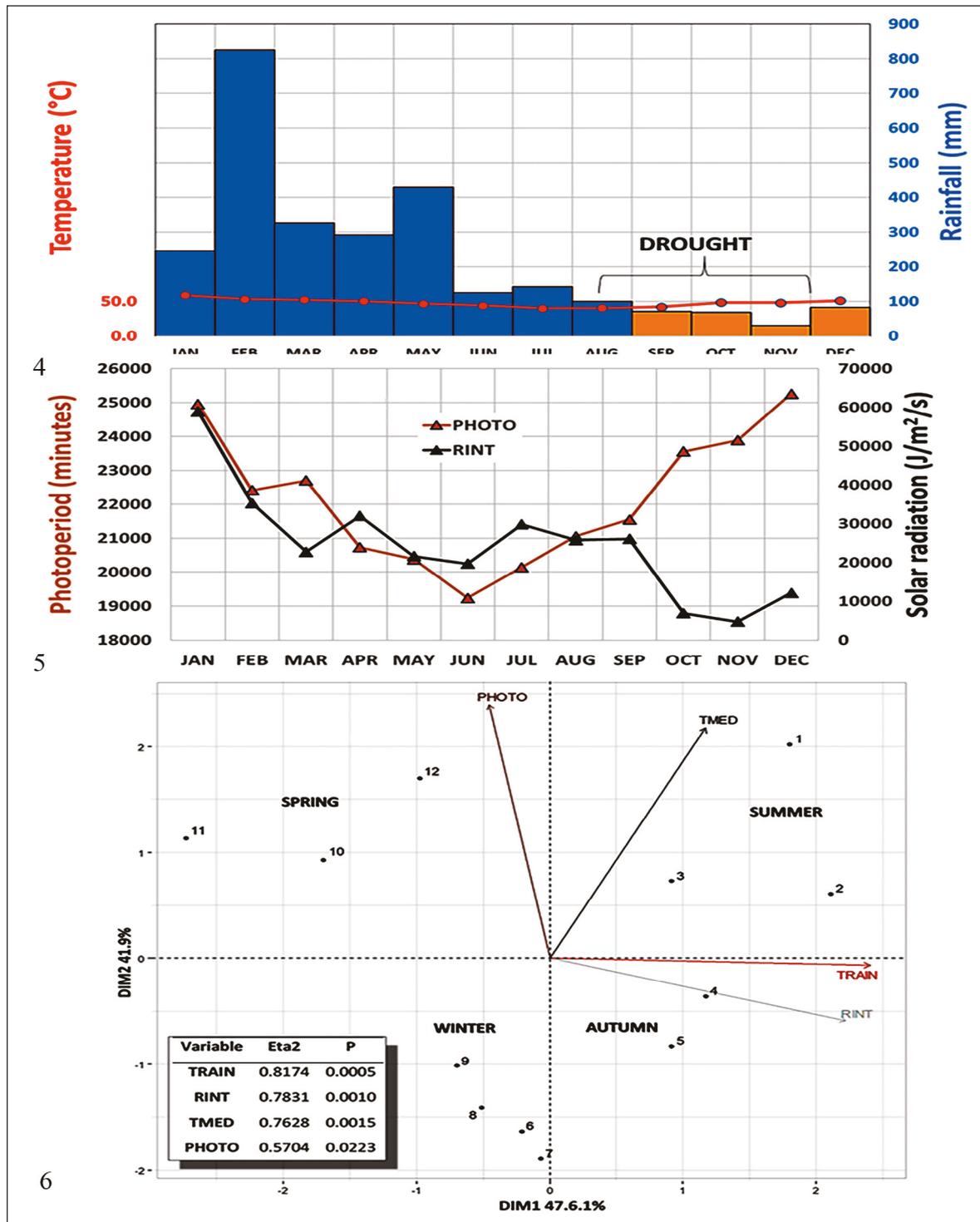
Samplings

A total of 42 samplings (45.7%) were done under bad days conditions, and in August 77.8% of samplings were done under these conditions (Fig. 7). Percentage of bad days in the study area for the butterfly flight during 2019 was 48.8%. Among seasons percentages were: 73.9% in winter, 48.4% in autumn, 41.1% in summer, and 31.5% in spring (Fig. 8). However, at sampling day level, there was no significant difference between the number of species recorded in bad and "normal" days (Wilcoxon rank sum test with continuity correction; $W = 710.5$; $p = \text{NS}$).

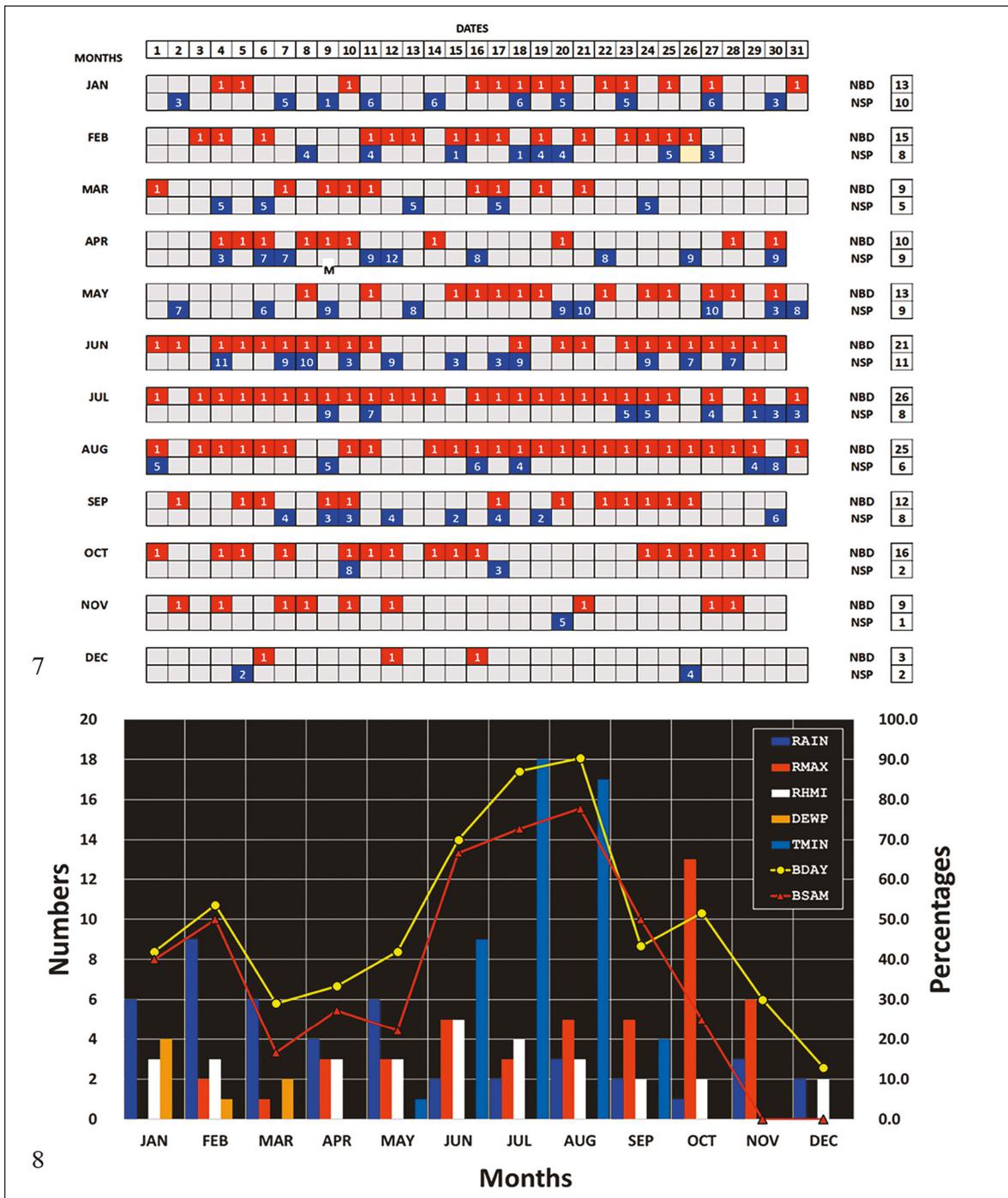
The regression between sampling effort in minutes (in each sampling) and recorded species number was marginally significant (adjusted $R = 0.17$; $t = 2.022$; $p = 0.046$) therefore was not considered.

Flowering plants

At least 33 plant species were used by adult butterflies in the area during the study concentrating in autumn (Table 1). Six species, *Bidens alba*, *Asclepias curassavica*, *Mikania lundiana*, *Impatiens walleriana*, *Sanchesia speciosa* and *Malvaviscus arboreus* presented flowers in all seasons. Autumn and winter concentrated 27 species of flowering plants; the highest number recorded. Asteraceae species ($S = 15$) concentrated 46.9% of all species.



Figures 4–6. Monthly description of abiotic environmental variables in the study area during 2019 showing (Fig. 4) the pronounced drought during spring due to ombrothermic relationships (Walter and Lieth, 1960) between mean temperature (TMED) and rainfall (TRAIN) and (Fig. 5) the low values of integrated solar radiation (RINT) in the same period with integrated photoperiod (PHOTO) showed only to permit comparison. (Fig. 6) Principal Component Analysis of monthly environmental variables in the study area during 2019. Numbers represent months. Variable codes: (RINT) integrated solar radiation; (PHOTO) integrated photoperiod; (TMED) mean monthly temperature; (TRAIN) monthly rainfall. Table at bottom left are correlations values.



Figures 7, 8. Response of butterflies to critical weather conditions. Fig. 7: Red cells indicate a bad day for the butterfly flight. Considering daily rainfall above 20 mm (RAIN); maximum mean solar radiation less than 500 J/m²/s during sampling period (RMAX); percentage of moisture during sampling period less than 40% (RHMI); daily dew point above 27°C (DEWP); and minimum temperature at shade during sampling period less than 18°C (TMIN). (NBD) number of monthly samplings. Decimals inside boxes indicate percentages of monthly bad days (BDAY). Deep blue cells indicate number of species in that sampling. Sequence of more than four bad days indicates a worst condition to butterflies appearing during May (1), June (2), July (2), August (2), September (1), and October (1). Fig. 8: Bars indicate the monthly number of bad days in the study area for the butterfly flight during 2019 considering daily rainfall above 20 mm (RAIN); maximum mean solar radiation less than 500 J/m²/s during sampling period (RMAX); percentage of moisture during sampling period less than 40% (RHMI); daily dew point above 27°C (DEWP); minimum temperature at shade during sampling period less than 18°C (TMIN). Line indicates percentages of monthly bad days (BDAY) and sampling done during bad days (BSAM).

PLANT SPECIES	FAMILY	SUM	AUT	WIN	SPR	TX	HABIT	STATUS
<i>Sanchesia speciosa</i> Leonard	Acanthaceae	1	3	2	2	H	SHR	AUTC
<i>Asclepias curassavica</i> L.	Apocynaceae	1	2	3	1	AH	HER	AUTC
<i>Cordyline terminalis</i> (L.) Kunth	Asparagaceae	0	1	0	0	H	SHR	EXOT
<i>Ageratina conyzoides</i> L.	Asteraceae	0	0	1	0	H	HER	AUTC
<i>Austro eupatorium inulaefolium</i> (Kunth) R.M.King & H.Rob.	Asteraceae	0	2	0	0	AH	SHR	AUTC
<i>Bidens alba</i> (L.) DC	Asteraceae	3	3	3	3	AH	HER	AUTC
<i>Bidens pilosa</i> L.	Asteraceae	0	2	0	0	AH	HER	AUTC
<i>Chromolaena laevigata</i> (Lam.) R. M. King & H. Rob.	Asteraceae	0	1	0	0	AH	SHR	AUTC
<i>Cyrtocymura scorpioides</i> (Lam.) Pers.	Asteraceae	0	0	1	1	AH	VIN	AUTC
<i>Elephantopus mollis</i> Kunt	Asteraceae	3	2	0	0	H	HER	AUTC
<i>Emilia forsbergi</i> Nicolson	Asteraceae	0	1	1	0	H	HER	AUTC
<i>Mikania cordifolia</i> (L.f.) Willd.	Asteraceae	1	1	0	0	AH	VIN	AUTC
<i>Mikania lundiana</i> DC	Asteraceae	1	3	1	2	H	VIN	AUTC
<i>Mikania micrantha</i> Kunth	Asteraceae	0	3	0	1	AH	VIN	AUTC
<i>Mikania pilosa</i> Baker	Asteraceae	0	0	1	0	AH	VIN	AUTC
<i>Tithonia diversifolia</i> (Hemsl.) A. Gray	Asteraceae	0	3	0	0	H	SHR	EXOT
<i>Vernonanthura beyrichii</i> (Less.) H.Rob.	Asteraceae	0	2	0	0	AH	SHR	AUTC
<i>Wedellia paludosa</i> DC	Asteraceae	0	1	1	0	AH	HER	AUTC
<i>Impatiens walleriana</i> Hook.f.	Balsaminaceae	3	3	3	3	AH	HER	AUTC
<i>Tilandsia</i> sp.	Bromeliaceae	0	2	0	0	H	EPI	AUTC
<i>Rhipsalis baccifera</i> (J. S. Muell.) Stearn	Cactaceae	0	0	1	0	AH	EPI	AUTC
<i>Costus speciosus</i> J. Koenig	Costaceae	3	3	0	0	AH	SHR	AUTC
<i>Helmontia</i> sp.	Curcubitaceae	0	0	2	0	AH	VIN	AUTC
<i>Malvaviscus arboreus</i> Cav.	Malvaceae	3	3	3	3	AH	SHR	EXOT
<i>Malvaviscus rosa-sinensis</i> L.	Malvaceae	0	2	0	0	H	SHR	EXOT
<i>Bougainvillea spectabilis</i> Willd.	Nyctaginaceae	0	1	0	0	H	SHR	AUTC
<i>Rubus rosaefolius</i> Sm. not Stokes	Rosaceae	0	1	3	0	H	HER	AUTC
<i>Psychotria nuda</i> (Cham. & Schldl.)	Rubiaceae	0	2	0	0	H	TRE	AUTC
<i>Citrus</i> sp.	Rutaceae	0	0	1	0	H	TRE	AUTC
<i>Cupania oblongifolia</i> Mart.	Sapindaceae	0	3	1	0	H	TRE	AUTC
<i>Acnistus arborescens</i> (L.) Schldl.	Solanaceae	0	1	0	0	AH	SHR	AUTC
<i>Lantana camara</i> L.	Verbenaceae	0	2	1	0	AH	SHR	AUTC
<i>Stachytarpheta cayennensis</i> (L.C. Rich.) Vahl	Verbenaceae	1	3	1	0	H	HER	AUTC
	TOTAL FREQUENCY	20	56	30	16			
	SPECIES NUMBER	10	27	18	8			

Table 1. Season flowering phenology of plants whose flowers were used by Heliconiinae butterflies in the study area during 2019 showing the frequency of each species by season. Codes: Summer (SUM); Autumn (AUT); Winter (WIN); Spring (SPR); Taxon which utilizes (TX); Used by Heliconiini (H); Used by Acraeini (A); Herbaceous (HER); Shrub (SHR); Vine (VIN); Tree (TRE). Autochthonous (AUTC); Exotic (EXOT).

Number of flowering plants with shrub habit was 12 (36.36%), followed by ten herbaceous (30.30%), six vines (18.18%), three trees (9.09%), and two epiphytes (6.06%). Four species (12.12%) were exotic.

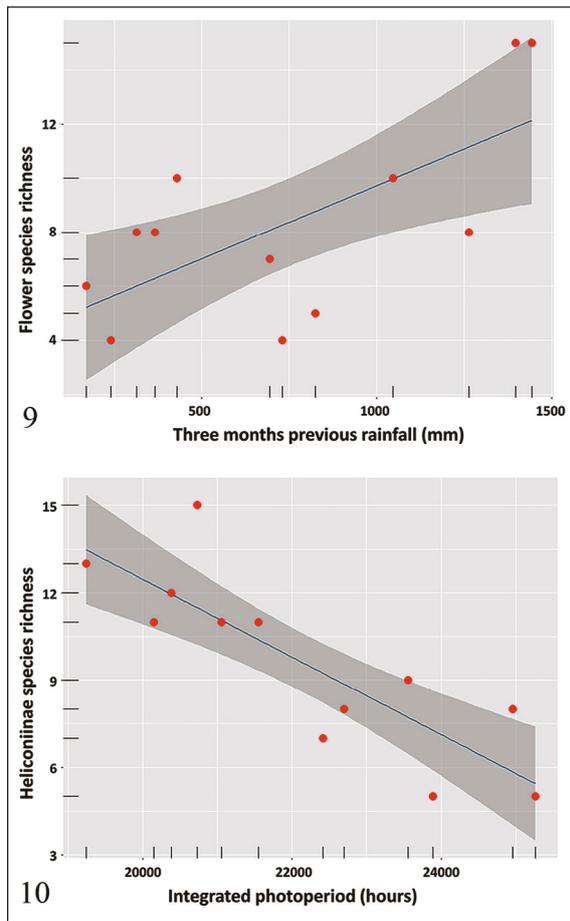
Also, *Vernonanthura beyrichii* is not affected because grows far from the edges as well as *Malvaviscus arboreus* and *Sanchesia speciosa* which are shrubby bushes that form large stands.

Flowering plants used by Heliconiinae assemblage was positively correlated with the accumulated rainfall of previous three months (PREV; $r^2 =$

0.56; $F = 8.53$; $p < 0.1$; $AIC = 60.03$) with the photoperiod appearing in the sequence (PHOTO; $r^2 = 0.4$; $F = 8.36$; $p < 0.1$; $AIC = 63.12$) (Supplemental material 2; Figs. 9, 10).

The Heliconiinae assemblage

During this study, 16 species of Heliconiinae were observed in the study area (Figs. 11–29): *Actinote pellenea pellenea* Hübner, [1821]; *A. brylla* Oberthür, 1917; *A. parapeles* Jordan, 1913; *A. discrepans* D'Almeida, 1958; *Agraulis vanillae macu-*



Figures 9, 10. Increase of the flower species richness in function of the integrated three months (Fig. 9) previous rainfall showing that high richness values are in the interval above 1200 mm of rainfall corresponding to autumn months (PREV; $r^2 = 0.56$; $F = 8.53$; $p < 0.1$; $AIC = 60.03$). Fig. 10: Decrease of the Heliconiinae species richness in function of the integrated photoperiod showing that high richness values are in the interval where less than 21000 hours corresponding to the autumn and winter months (PHOTO; $r^2 = 0.67$; $F = 23.5$; $p < 0.001$; $AIC = 51.79$).

losa (Stichel, [1908]); *Dione juno juno* (Cramer, 1779); *Dryas iulia alcionea* (Cramer, 1779); *Dryadula phaetusa* (Linnaeus, 1758); *Philaethria wernickei* (Röber, 1906); *Eueides aliphera aliphera* (Godart, 1819); *E. isabella dianasa* (Hübner, [1806]); *E. pavana* Ménétrés, 1857; *Heliconius erato phyllis* (Fabricius, 1775); *H. ethilla narcaea* Godart, 1819; *H. numata robigus* Weymer, 1875; *H. sara apseudes* (Hübner, [1813]).

Five species presented percentages (relative frequency) above 10%: *H. sara apseudes*, *H. erato phyllis*, *D. juno juno*, *H. ethilla narcaea* and *A. pel-lenea pellenea* (Fig. 30).

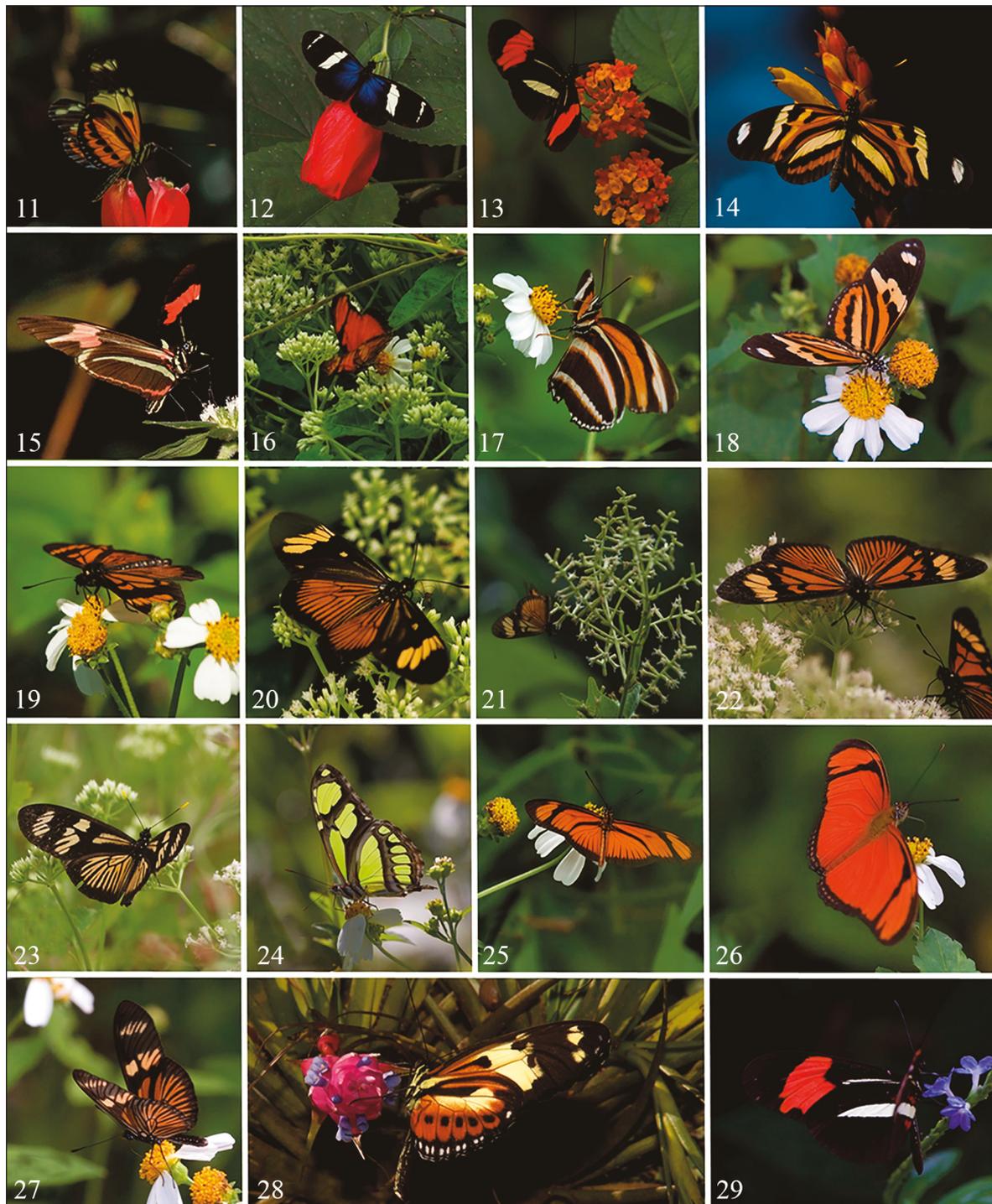
SPECIES	SUMMER	AUTUMN	WINTER	SPRING	
VAN	**	****	**	*	CODE 0.0 1-25% 26-59% > 59%
ALI	***	***	**	**	
ISA	*	****	**	**	
PAV	**	****	**	*	
DIO	**	****	**	**	
DRY	***	***	**	**	CODE *
PHA	**	****	*	*	
ERA	***	***	**	**	
ETI	**	****	**	**	
NUM	*	****	***	*	
SAR	***	***	**	**	***
PHI	***	***	*	*	****
PEL	***	***	**	**	
BRY	*	****	**	**	
PAR	*	****	*	*	
DIS	*	****	*	*	

Table 2. Season phenology of Heliconiinae butterflies in the study area during sampling periods of 2019.

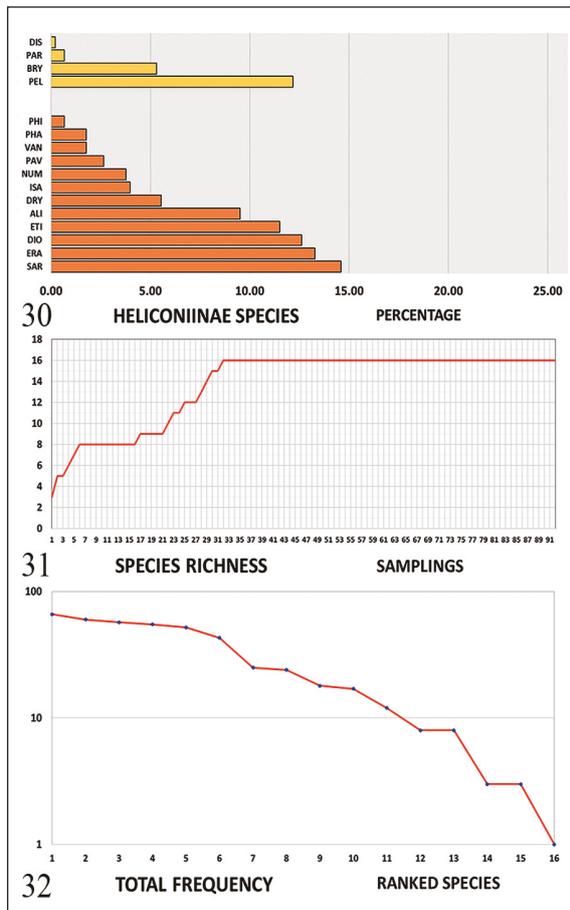
The collectors' curve for sampling period reached asymptote in sample 32 on April 14, 2019 (Fig. 31). The Whittaker plot showed a relatively smooth convex decline showing the relatively high diversity (0.98) estimated by Simpson index of this assemblage (Fig. 32).

The peak of Heliconiinae species richness was during autumn (April to June) reaching 16 species. Despite this, the species percentage (relative frequencies) along the seasons was extremely variable (Table 2).

The logistic regression analysis of the presence / absence data in each of the 92 samples from 2019 showed that the four *Heliconius* species had different patterns (Supplemental material 3). Both *H. ethilla narcaea* (FLOWER; $Z = 4.18$; $p < 0.0001$; $AIC = 96.11$; Fig. 33 ETI FLOWER; PHOTO; $Z = -4.39$; $p < 0.00001$; $AIC = 100.62$; Fig. 33 ETI PHOTO) and *H. numata robigus* (PHOTO; $Z = -3.46$; $p < 0.001$; Fig. 33 NUM PHOTO; $AIC = 79.73$; RMIN; $Z = -2.71$; $p < 0.01$; $AIC = 88.49$; Fig. 33 NUM RMIN) being more seasonal due to their strong responses to the daylength (photoperiod), but responding secondarily to flower richness or low values of solar radiation, respectively. Both *H. erato* ($Z = 1.98$; $p < 0.05$; $AIC = 111.07$; Fig. 33 ERA FLOWER), and *H. sara* ($Z = 2.06$; $p < 0.05$; $AIC = 100.41$; Fig. 33 SAR FLOWER) responded marginally only to FLOWER. *Actinote* and *Eueides* species



Figures 11–29. Heliconiinae species found in the study area during the study. (11) *Heliconius numata robigus* in *Costus speciosus*. (12) *Heliconius sara apseudes* in *Malvaviscus arboreus*. (13) *Heliconius erato phyllis* in *Lantana camara*. (14) *Heliconius ethilla narcaea* in *Sanchesia speciosa*. (15) *Heliconius besckey* was not present during the study but was found in previous years. (16) *Dione juno juno* in *Mikania cordifolia*. (17) *Dryadula phaetusa* in *Bidens alba*. (18) *Eueides isabella dianasa* in *Bidens alba*. (19) *Actinote pellenea pellenea* in *Bidens alba*. (20) *Actinote discrepans* in *Mikania micrantha*. (21) *Actinote brylla* *Mikania lundiana*. (22) *Actinote paraphelus* in *Mikania micrantha*. (23) *Eueides pavana* [female] in *Mikania micrantha*. (24) *Philaethria wenickey* in *Bidens alba*. (25) *Eueides aliphera aliphera* in *Bidens alba*. (26) *Dryas iulia alcyonea* in *Bidens alba*. (27) *Eueides pavana* [male] in *Bidens alba*. (28) *Heliconius numata robigus* in an unidentified Bromeliaceae. (S) *Heliconius erato phyllis* in *Stachytarpheta cayennensis*.



Figures 30–32. Percentage of Heliconiinae species in the study area in samplings during 2019. Species codes: (ERA) *Heliconius erato phyllis*. (ETI) *Heliconius ethilla narcaea*. (BES) *Heliconius besckeyi*. (NUM) *Heliconius numata robigus*. (SAR) *Heliconius sara apseudes*. (PHI) *Philaethria wernickei wernickei*. (DRY) *Dryas iulia alcyonea*. (AGR) *Agraulis vanillae maculosa*. (DIO) *Dione juno juno*. (PHA) *Dryadula phaetusa*. (ISA) *Eueides isabella dianasa*. (ALI) *Eueides aliphhera aliphhera*. (PAV) *Eueides pavana*. (PEL) *Actinote pellenae pellenae*. (BRY) *Actinote brylla*. (PAR) *Actinote parapheles*. (DIS) *Actinote discrepans*. Fig. 32: collector’s curve reached asymptote in sample 32 and (C) Whittaker plot of Heliconiinae assemblage which showed high diversity in the study area during 2019 (Simpson index = 0.98).

are more flowering-dependent than *Heliconius* species due to their capacity of pollen feeding which increases their longevity and survival.

Using the GAM, the model which better explained the correlation of Heliconiinae species’ richness with environmental conditions was the model which had a significant negative correlation with the photoperiod (PHOTO; $r^2 = 0.67$; $F = 23.5$; $p < 0.001$; AIC = 51.79; Supplemental material 4;

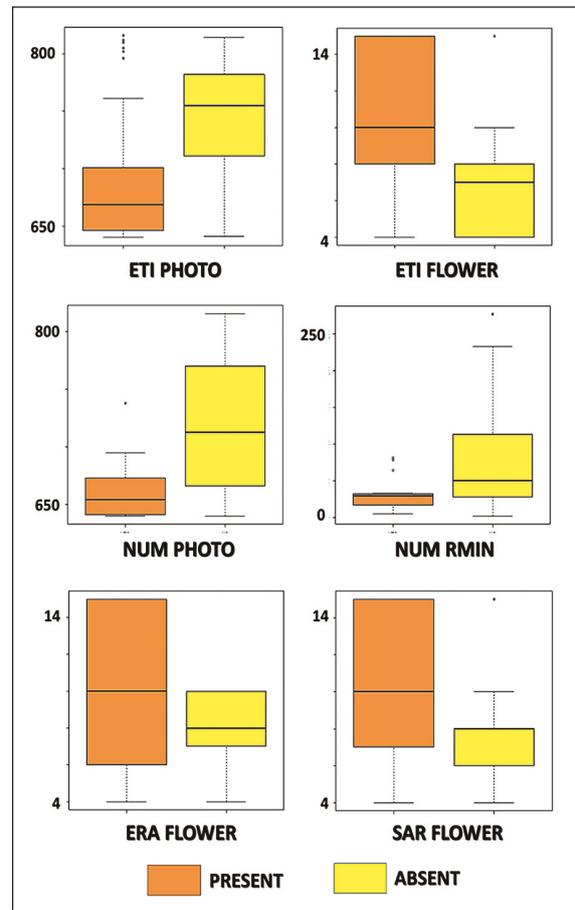


Figure 33. Boxplots of presence/absence of the four *Heliconius* species detected during 2019 in the study area. *H. ethilla narcaea* (ETI) presented significant response to photoperiod (PHOTO; Wilcoxon rank sum test with continuity correction; $W = 378.5$; $p = ***$) and flowering plant richness (FLOWER; $W = 15.975$; $p = ***$). *H. numata robigus* (NUM) high significant response to photoperiod (PHOTO; $W = 266$; $p = ***$) and to low solar radiation values (RMIN; $W = 370$; $p = ***$). Other two species, *H. erato phyllis* and *H. sara apseudes* responded only marginally to flowering plant richness (FLOWER) due to their continuous presence along the year.

Fig. 10) followed by a positive response to flowering (FLOWER, $r^2 = 0.67$; $F = 70.2\%$; AIC = 52.02).

The cluster analysis using the matrix of monthly species frequency showed that Heliconiinae species richness was concentrated in the autumn and early winter months (Fig. 34) and *E. aliphhera aliphhera*, *H. ethilla narcaea*, *H. sara apseudes*, *A. pellenae pellenae*, *D. juno juno* and *H. erato phyllis* in the cluster of higher frequency (Fig. 35).

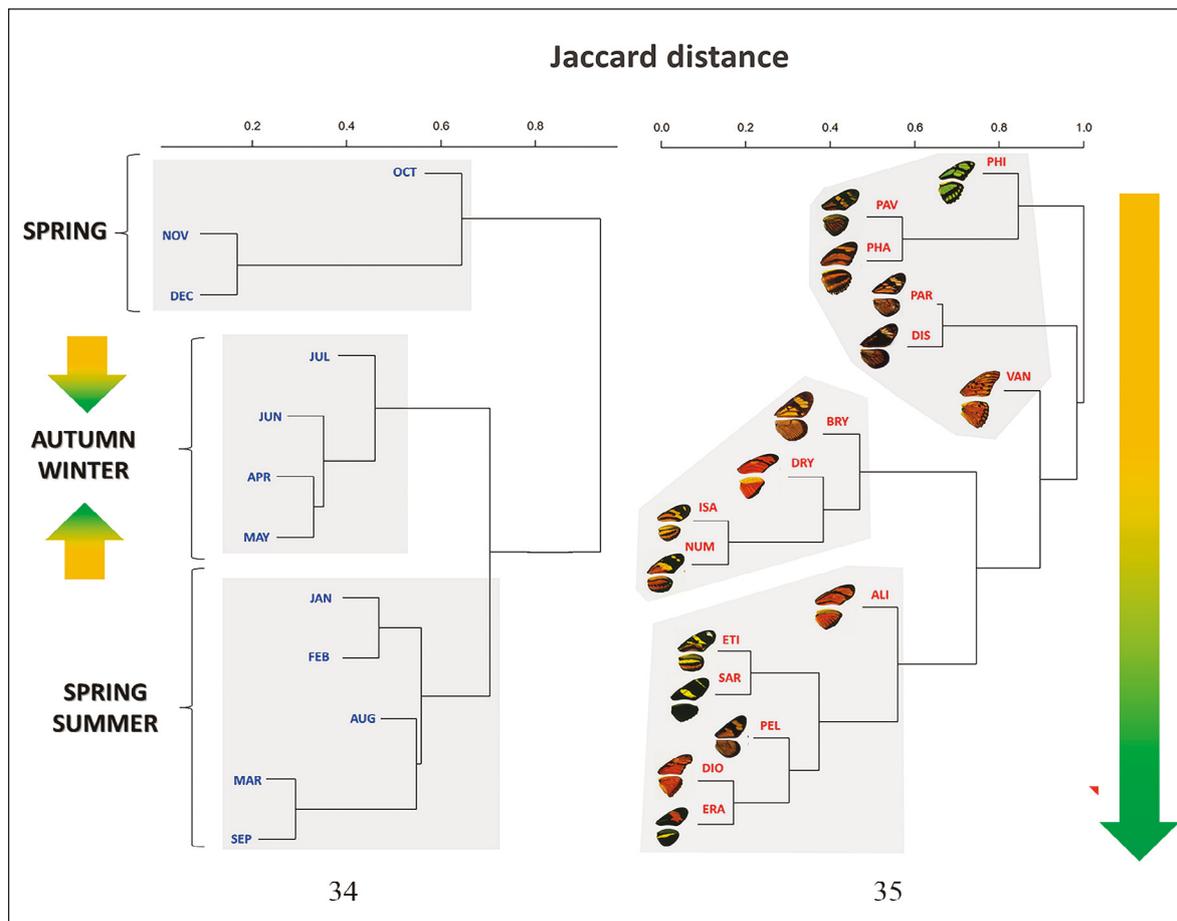


Figure 34. Cluster analysis using Jaccard distance and complete clustering. (A) Months' clustering showing that Autumn months (April, May, and June) and July were grouped because the richness is higher. Arrows indicate months richness. Figure 35. Species clustering showing the formation of three groups with increasing frequency indicated by the arrow.

DISCUSSION

Climate and weather 2016–2019

The climate of the study area is highly inconstant because of its geographical position at 45 km south of Tropic of Capricorn and the presence of Serra do Mar mountains as a barrier to cold fronts arriving from south pole.

Data on temperature anomalies (°C) from the National Climatic Data Center of the National Oceanic and Atmospheric Administration, from 1880 to 2018, in cell 23S - 46W show a clear positive increase of temperature from the 1970s (Menne et al., 2012ab). Also, recently, during two consecutive rainy summer seasons (2013–2014 and 2014–2015), periods without rain or dry spells played a central role in one of the most severe droughts in decades that struck South-eastern Brazil. During the first season, there was an interruption of rainfall for approximately 45 days,

from the beginning of January until mid-February (Cunningham, 2020). Finally, it is important to consider the effects of the El-Niño phenomenon that acted in an intermediate way during the first half of 2019 (NOAA, 2020b). At long term, the increase of temperature and rainfall should change phenological patterns of both plants and butterflies as well as affecting their local ranges (Gondeck et al., 2021). Although the behavior of passion vine butterflies can adjust itself according to resource availability, periods of severe drought can also impact the local populations through the reduction of alternative host plants, which are fundamental to maintain their larval populations according to the season (Ramos et al., 2021).

Samplings

Our study showed that almost half of the samples were taken on days considered initially to be

Supplemental material 1. Differences between the total rainfall (mm) of each season from normal (A) and between them (B) in the study area from 2016 to 2019.

A					B			
DIFFERENCE FROM NORMAL					DIFFERENCE BETWEEN SEASONS			
SEASON	YEAR	TOTAL	DIFF1	%	SEASON	YEARS	DIFF2	%
SUMMER	2016	707	-294	29.37	SUMMER	2016_2017	-312	30.62
SUMMER	2017	1019	18	-1.8	SUMMER	2016_2018	-168	19.2
SUMMER	2018	875	-126	12.59	SUMMER	2016_2019	-690	49.39
SUMMER	2019	1397	396	-39.56	SUMMER	2017_2018	144	-16.46
NORMAL	-----	1001	0	0	SUMMER	2017_2019	-378	27.06
AUTUMN	2016	235	-766	54.46	AUTUMN	2016_2017	-326	58.11
AUTUMN	2017	561	45	-8.72	AUTUMN	2016_2018	-343	59.34
AUTUMN	2018	578	62	-12.02	AUTUMN	2016_2019	-610	72.19
AUTUMN	2019	845	329	-63.76	AUTUMN	2017_2018	-17	2.94
NORMAL	-----	516	0	0	AUTUMN	2017_2019	-284	33.61
WINTER	2016	238	-278	36.02	WINTER	2016_2017	8	-3.48
WINTER	2017	230	-142	38.17	WINTER	2016_2018	-112	32
WINTER	2018	350	-22	5.91	WINTER	2016_2019	-75	23.96
WINTER	2019	313	-59	15.86	WINTER	2017_2018	-120	34.29
NORMAL	-----	372	0	0	WINTER	2017_2019	-83	26.52
SPRING	2016	922	550	-18.81	SPRING	2016_2017	374	-68.25
SPRING	2017	548	-228	29.38	SPRING	2016_2018	97	-11.76
SPRING	2018	825	49	-6.31	SPRING	2016_2019	742	-412.22
SPRING	2019	180	-596	76.8	SPRING	2017_2018	-277	33.58
NORMAL	-----	776	0	0	SPRING	2017_2019	368	-204.44

Supplemental material 2. Generalized additive model testing the effects of climate environmental variable and their associated interactions on the flowering of plant used by *Heliconiinae* in the study area during 2019.

MODEL	PARAMETER	F	p	deviance explained (%)	r ²	AIC
FLOWER~s(PREV)	PREV	8.53	*	63.1	0.56	60.03
RICH~s(PHOTO)	PHOTO	8.36	*	45.5	0.40	63.12
RICH~s(TRAIN)	TRAIN	3.25	NS	44.7	0.33	65.05
RICH~s(RMED)	RMED	4.08	NS	30.1	0.23	66.15
RICH~s(RINT)	RINT	2.36	NS	29.3	0.21	66.62
RICH~s(TMED)	TMED	0.95	NS	8.7	0.00	69.33
RICH~s(RAIND)	RAIND	0.31	NS	3.0	-0.07	70.05
Family: gaussian						
Link function: identity						
Formula: FLOWER ~ s(PREV)						
(intercept)	Estimate SE		t		p	
8.33	0.71		11.75		***	
Smooth term	edf	Ref. df	F		p	
PREV	1.79	1.96	8.53		*	
Adjusted r ²	Deviance explained	GCV	Scale est	n		
0.56	63.10%	7.86	6.03	12		

Supplemental material 3. Results of the logistic regression modeling of presence/absence of the four Heliconiinae species detected during 2019 in the study area showing the best models with lower AIC values.

MODEL glm(ETI~VAR) family = binomial (link = "logit")					MODEL glm(ERA~VAR) family = binomial (link = "logit")				
		Z	P	AIC		Z	P	AIC	
ETI	FLOWER	4.18	0.00003	96.11	ERA	FLOWER	1.98	0.04790	111.07
ETI	PHOTO	-4.39	0.00001	100.62	ERA	TRAIN	1.37	NS	112.79
ETI	LMIN	-3.28	0.00105	112.23	ERA	TMED	1.39	NS	113.38
ETI	TMED	-3.12	0.00183	113.68	ERA	LMAX	1.31	NS	113.60
ETI	RMIN	-3.04	0.00237	113.99	ERA	LMED	1.11	NS	114.10
ETI	LMED	-3.01	0.00264	114.57	ERA	PORVMAX	0.93	NS	114.50
ETI	PORVMAX	-2.17	0.03020	119.48	ERA	LMIN	0.71	NS	114.86
ETI	LMAX	-2.27	0.02320	119.57	ERA	RMIN	-0.44	NS	115.17
ETI	URDIF	1.80	NS	121.76	ERA	URDIF	-0.39	NS	115.21
ETI	TRAIN	-1.27	NS	123.52	ERA	PHOTO	-0.13	NS	115.35
ETI	URMIN	-0.10	NS	125.20	ERA	URMIN	-0.05	NS	115.36

MODEL glm(NUM~VAR) family = binomial (link = "logit")					MODEL glm(SAR~VAR) family = binomial (link = "logit")				
		Z	P	AIC		Z	P	AIC	
NUM	PHOTO	-3.46	0.00054	79.73	SAR	FLOWER	2.06	0.03950	100.41
NUM	RMIN	-2.71	0.00680	88.49	SAR	URDIF	1.99	0.04630	100.66
NUM	FLOWER	3.13	0.00174	91.98	SAR	PHOTO	-1.80	NS	101.92
NUM	TRAIN	-1.66	0.09785	93.58	SAR	URMIN	-1.50	NS	102.81
NUM	LMIN	-2.54	0.01110	95.77	SAR	TRAIN	-1.25	NS	103.69
NUM	URDIF	2.58	0.00996	95.82	SAR	LMIN	-1.12	NS	103.76
NUM	TMED	-2.11	0.03470	97.99	SAR	RMIN	-0.92	NS	104.40
NUM	LMED	-2.04	0.04140	98.40	SAR	LMAX	0.84	NS	104.50
NUM	LMAX	-1.23	NS	101.28	SAR	PORVMAX	0.32	NS	105.12
NUM	PORVMAX	-1.21	NS	101.38	SAR	LMED	-0.16	NS	105.19
NUM	URMIN	-1.12	NS	101.59	SAR	TMED	-0.03	NS	105.21

Supplemental material 4. Generalized additive model testing the effects of climate environmental variables interactions on the Heliconiinae species richness in the study area during 2019. Photoperiod was what better explained the richness.

MODEL	PARAMETER	F	p	deviance explained (%)	r ²	AIC
RICH~s(PHOTO)	PHOTO	23.50	***	70.2	0.67	51.79
RICH~s(FLOWER)	FLOWER	17.37	***	70.2	0.67	52.04
RICH~s(PREV)	PREV	2.23	NS	62.8	0.44	59.73
RICH~s(RINT)	RINT	3.06	NS	44.4	0.35	60.30
RICH~s(RMED)	RMED	3.582	NS	41.6	0.34	60.42
RICH~s(TMED)	TMED	2.33	NS	18.9	0.11	63.79
RICH~s(TRAIN)	TRAIN	0.78	NS	20.0	0.06	64.97
RICH~s(RAIND)	RAIND	1.14	NS	10.2	0.01	65.00

Family: gaussian Link function: identity Formula: RICH ~ s(PHOTO)						
(intercept)	Estimate	SE	t	p		
9.58		0.52	18.58	***		
Smooth term	edf	Ref. df	F	p		
PHOTO	1	1	23.5	***		
Adjusted r ²	Deviance explained	GCV	Scale est	n		
0.67	70.20%	3.83	3.19	12		

bad, which were mainly concentrated in winter but were above 30% in other seasons. However, the species of Acraeini can fly even in these conditions as shown by the results. Also, the day sampling effort in minutes do not appear as important to detect all flying species in that date.

Flowering plants

Due to its continuous availability, *B. alba* is a key species in the area because it is used by all species of the Heliconiinae assemblage. Its importance is complemented by *Asclepias curassavica*, *Sanchesia speciosa*, and the trees *Cupania oblongifolia*, and *Psychotria nuda*.

Other studies showed the positive correlation of nectarivorous butterflies with flower richness. The first, with populations of *Parnassius apollo* in Finland (Fred et al., 2006), another with an assemblage of 85 Nearctic species in the Muddy River drainage, in the US (Fleishman et al., 2005). The last, with two species, *Maniola jurtina* and *Lycaena virgaureae*, showed that was adult resource density, and not patch size or larval food plant abundance which influenced the numbers and the fractions of residents, emigrants, and immigrants (Schneider et al., 2003). They also suggest that relatively limited data sets may allow us to draw reliable inferences for adaptive management in the context of ecological restoration and rehabilitation. In two different works, Brown Jr. (Brown-Jr, 1992; Brown-Jr & Dias-Filho, 2009) emphasized the role of rainfall to Lepidoptera communities, certainly due to the growing of their larval and adult foodplants.

Heliconiinae assemblage

During this study, 61.54% of total Heliconiinae ($n = 26$) recorded for the “Baixada Santista” area (Francini et al., 2011) were observed. However, the absent species have never been observed in the study area since 1972 according to RBF personal observations. Autumn followed by winter were seasons which showed the greatest richness in Heliconiinae species in the study area and the environmental conditions in April are decisive in the structuring this community.

It has been previously shown that flowering of the plant species used by the Heliconiinae assemblage was correlated with the amount of rainfall in the three months preceding that considered. Also, the

past availability of larval food plants will probably affect the frequency of Heliconiinae species at present. Additionally, the seasons can change the quality of plants and therefore the interactions between females and their host plants (Ramos et al., 2021).

So, we can infer that the species richness of the Heliconiinae is not independent of historical biogeographic factors. This means, that the most common species will always be detected even with relatively small sampling effort. On the other hand, the frequency of the individuals of each species depends on how many floral resources are available in addition to adequate conditions (environmental temperature and solar radiation; see also Gondeck et al., 2021) that allow these butterflies to fly. Also, many species' flowering depends on the amount of rain from the previous season which allows the necessary energy accumulation for reproduction, in addition to the duration of the day (photoperiod) that serves as a trigger for this event. Indirectly, due to the dependency of plants to day length, the photoperiodism have an important role in butterfly phenology. Because they are ectothermic, both plants and butterflies depend on the amount of solar radiation for their development or other activities.

Finally, is not possible to study seasonality of butterflies and their foodplants without knowing the role of photoperiod. This is particularly important in regions where day length is more variable between seasons, as in subtropical areas.

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