

# Seasonal and diel variations in the activity of canopy insect herbivores differ between deciduous and evergreen plant species in a tropical dry forest

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**Abstract** This study evaluated whether herbivorous insects can be expected to have particular adaptations to withstand the harsh dry season in tropical dry forests (TDFs). We specifically investigated a possible escape in space, with herbivorous insects moving to the few evergreen trees that occur in this ecosystem; and escape in time, with herbivores presenting an increased nocturnal rather than diurnal activity during the dry season. We determined the variation in the free-feeding herbivorous insects (sap-sucking and leaf chewing) between seasons (beginning and middle of both rainy and dry seasons), plant phenological groups (deciduous and evergreen trees) and diel period (diurnal and nocturnal) in a Brazilian TDF. We sampled a total of 5827 insect herbivores in 72 flight-interception traps. Contrary to our expectations, we found a greater herbivore diversity during the dry season, with low species overlap among seasons. In the dry season, evergreen trees supported greater richness and abundance of herbivores as

compared to deciduous trees. Insects were also more active at night during the dry season, but no diel differences in insect abundance were detected during the rainy season. These results indicate that the strategies used by insect herbivores to withstand the severe climatic conditions of TDFs during the dry season include both small-scale escape in space and time, with evergreen trees playing a key role in maintaining resident insect herbivore populations in TDFs. Relatively more nocturnal activity during the dry season may be related to the avoidance of harsh climatic conditions during the day. We suggest that the few evergreen tree species occurring in the TDF landscape should be especially targeted for protection in this threatened ecosystem, given their importance for insect conservation.

**Keywords** Diel activity · Leaf-chewing insects · Sap-sucking insects · Temporal abundance · Plant functional groups

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## Introduction

Insects represent the most diverse and well-distributed group of organisms, comprising different trophic guilds, such as herbivores, detritivores, and predators. In tropical forests, the insects achieve their highest diversity (Basset et al. 2012), being an important part of living biomass from the soil to the emerging canopy trees (Basset et al. 2003, 2012). Due to their complex life forms, diverse feeding habits, dispersal capacity, and high diversity and biomass, insects participate in several processes (e.g. soil fertilization and aeration, seed dispersal, pollination and biological control) that are key for the functioning and maintenance of ecosystems (Losey and Vaughan 2006; Nichols et al. 2008). Specifically, herbivorous insects compose the most diverse

group of insects in tropical forests (Price 2002; Basset et al. 2012), with a wide array of feeding guilds that respond differently to seasonal changes (Didham and Springate 2003; Novotny et al. 2003; Leal et al. 2015). However, few studies have investigated particular adaptations about how insect herbivores cope with the harsh dry periods in seasonal ecosystems.

Tropical dry forests (TDFs) are characterized by a marked dry season (i.e. at least 3 months with less than 100 mm/month of rainfall) when deciduous plants drop more than 50% of their leaves (Murphy and Lugo 1986; Sánchez-Azofeifa et al. 2005). During this period, environmental conditions become harsh, with increasing insolation and wind intensity and decreasing humidity (Murphy and Lugo 1986; Lebrija-Trejos et al. 2011). In the case of free-feeding leaf insects (e.g. chewers and suckers), resource availability sharply decreases because deciduous plants dominate the landscape (Villalobos et al. 2013; Pezzini et al. 2014). These organisms exhibit two strategies to survive the prolonged dry season: (1) temporal adjustment via diapause or synchronization of their life cycle with the rainy season; or (2) spatial adjustment, moving to habitats with non-deciduous trees (Janzen 1973; Dirzo and Domínguez 1995; Silva and Neves 2014).

In spite of such strategies, there is a general reduction in insect herbivore diversity and activity during the dry season (Janzen 1973), suggesting that the temporal adjustment may prevail. In fact, finding leaves in TDFs during the dry season is not trivial. It involves long-distance migration to other vegetation types, such as semi-deciduous riparian forests, savannahs (the Cerrado in Brazil) or altitudinal fields (Leal et al. 2015); or searching for isolated evergreen or brevi-deciduous plants that compose a small proportion of TDF species (Silva and Neves 2014). In this way, these plant phenological groups may play a key role in the maintenance of at least some insect guilds during the dry season (Janzen 1973; Silva and Neves 2014). According to Villalobos et al. (2013), only a small fraction of the TDFs flora is evergreen, ranging between 1.1 and 9.7%. Despite the few species, this phenological group could contribute to diversity and ecosystem process maintenance in TDFs, and areas with a high abundance of these species could be prioritized for conservation. Changes in plant diversity and abundance in these threatened forests could underlie changes in herbivore abundance (Leal et al. 2016; Silva et al. 2016). Nevertheless, information on life history or movement patterns for insect species in the tropics are scant, and the relevance of non-deciduous plants to insect population dynamics in TDFs is still unclear. To our knowledge no detailed study has investigated the role of evergreen trees within TDFs in maintaining insect diversity during the severe dry season.

In addition to seasonal variations, insect activity shows small-scale temporal patterns (i.e. diel cycles) that are

frequently overlooked (Janzen 1973; Springate and Basset 1996; Basset et al. 2001). Several studies performed in tropical forests have revealed higher diel activity of arboreal insects, mostly herbivores, during the night (Basset and Springate 1992; Novotny et al. 1999; Wardhaugh 2014). Janzen (1983) proposed two non-exclusive hypotheses for a greater nocturnal activity of herbivores: (1) the existence of a “temporal window” of enemy-free space; and (2) the availability of higher leaf concentration of photoassimilates which have not yet been translocated or used in respiration. Moreover, specifically for TDFs, the intensity of diel variation in abiotic conditions, such as temperature and humidity, shows strong seasonal variations (Lebrija-Trejos et al. 2011). Hence, due to more adverse hygrothermal conditions (i.e. high temperatures and low relative humidity) and wider climatic diel range in the dry season, we expect that insect nocturnal activity would be more intense compared to the diurnal activity during this season.

This study evaluated temporal variations in the abundance and richness of herbivorous insects in the TDF canopy across different seasons (beginning and middle of rainy and dry seasons), plant phenological groups (deciduous and evergreen) and diel periods (day- and night-time). We addressed the following hypotheses: (1) there are changes in herbivorous species composition between seasons, with reduced abundance and richness of insects during the dry season; (2) the richness and abundance of herbivorous insects are greater on evergreen compared to deciduous tree species in the dry season; and (3) herbivorous insects have greater nocturnal activity compared to the diurnal activity in the dry season, whereas the inverse pattern is expected during the rainy season.

## Methods

### Study area and system

This study was conducted at the Mata Seca State Park (MSSP), created in 2000, and managed by the Instituto Estadual de Florestas (IEF—Forestry State Institute). The MSSP has an area of 15,466.44 ha and is located in the valley of the São Francisco River, Minas Gerais state, Brazil, between 14°48′36″–14°56′59″S and 43°55′12″–44°04′12″W, at an altitude between 400 and 500 m above sea level. The climate of the region is considered as tropical semi-arid (Aw in Köppen’s classification), with an average temperature of 24 °C, and average annual precipitation of 871 mm (Antunes 1994). The dry season extends from May to October, and rains are unevenly distributed along the rainy season from November to April (Antunes 1994). The precipitation in the rainy season is 744 mm in average, with only 60 mm during the

marked dry season (data available from 1936 to 2012 at the Mocambinho Station, situated at 15 km from the MSSP).

The MSSP is covered with a mosaic of TDFs in different successional stages, and this study was conducted in an old-growth forest. According to the former farm manager, forest structure has been the same since the beginning of the 1970s, although occasional selective logging and sparse free-ranging cattle occurred in the area until the park creation. This forest is characterized by two vertical strata: the first is composed of deciduous trees that reach more than 16 m in height and form a closed canopy. The second stratum is composed of a dense understory, with lianas, shade-tolerant adult trees, and juvenile canopy trees. The average basal area is  $22.0 \pm 2.3$  m<sup>2</sup>/ha and tree density is  $98.8 \pm 6.1$  individuals/0.1 ha (Madeira et al. 2009). The level and duration of deciduousness vary among tree species, but evergreen trees can hold their green leaves during the dry season (Pezzini et al. 2014). Previous floristic and phenological studies conducted at the MSSP registered the presence of four leaf-exchanger evergreen species (see Pezzini 2008): *Aspidosperma polyneuron* Müll. Arg. (Apocynaceae), *Goniorrhachis marginata* Taub. (Fabaceae-Ceasalpinioideae), *Machaerium scleroxylon* Tul. (Fabaceae-Faboideae) and *Ziziphus joazeiro* Mart. (Rhamnaceae). Individuals of these species retain their leaves for approximately 11.5 months of the year, and replace them within a few days at the end of the dry season (September) (Pezzini et al. 2014).

The beginning of the rainy season is characterized by rapid leaf production, with canopy formation ( $22.32 \pm 1.41\%$  of canopy openness) within 2 weeks after the occurrence of the first rains in October/November (Fig S1). In this period, there is a high abundance of leaf buds and expanding leaves with high nutritional quality for herbivores (Silva et al. 2012). In the peak of the rainy season (January) there is high foliage availability ( $16.47 \pm 1.68\%$  of canopy openness) with fully expanded green leaves. The onset of the dry season (May) is marked by rapid leaf senescence ( $40.54 \pm 3.18\%$  of canopy openness), with leaf nutrients being translocated to other plant organs (Silva et al. 2012). In the peak of the dry season (August), there is no precipitation and plants drop up to 95–100% of their leaves ( $70.18 \pm 1.80\%$  of canopy openness) (see Fig. S1).

### Sampling design

Samples were taken between 2011 and 2012 in the following periods: (a) middle of the dry season (August-2011), (b) beginning of the rainy season (October-2011); (c) middle of the rainy season (January-2012) and (d) beginning of the dry season (May-2012). We determined the month corresponding to each season through a cluster analysis (using complete linkage method for

amalgamation and Euclidean distance as the coefficient of association; see Madeira and Fernandes 1999), using the monthly rainfall recorded between 1976 and 2012 from Mocambinho Station (see Fig. S2).

Insects were collected with flight-interception traps, modified from Malaise and Window traps, set up in tree crowns (see Springate and Basset 1996; Novais et al. 2016; Fig S3). The main body of the trap consisted of a rectangular cross-panel of black netting (mesh width of 0.5 mm, collecting surface of 4.5 m<sup>2</sup>). A funnel was attached at both ends of the main body of the trap (upper and lower diameter of funnel of 90 and 75 cm, respectively) and connected to a collecting recipient (4 cm in diameter). The length of the trap, from the top of the upper collector to the base of the lower recipient, was 2.65 m. Collecting recipients were filled with ethanol 70% and glycerin 5%. This trap is very effective in capturing winged insects, but it is not appropriate to collect wingless adult insects or crawling larvae (see Grimbacher and Stork 2009).

We sampled three individuals of each one of the following evergreen tree species: *A. polyneuron*, *G. marginata* and *M. scleroxylon*. *Ziziphus joazeiro* was not sampled in this study due to its low abundance and absence among emerging and canopy trees (see Pezzini 2008; Madeira et al. 2009). Sampled individuals were at least 30 m apart from any other evergreen tree. We also sampled nine deciduous trees (regardless of species identity and paired to evergreen trees) at least 15 m distance from each trapped evergreen tree. We sampled 18 trees in each period (18 traps  $\times$  4 periods = 72 total traps), with one trap winched into the centre of the crown (see Fig. S3). Traps were raised and lowered using ropes passed over supporting branches. All trees were between 15 and 18 m tall and were trapped during five consecutive days. During each period, the traps were surveyed twice a day in the same sequence, with the surveys commencing at 6.00 a.m. and at 6.00 p.m. Thus, samples were separated into diurnal (from 6 a.m. to 6 p.m) and nocturnal (from 6 p.m. to 6 a.m.) catches. During this study, daily mean sunrise and sunset were respectively at 06.11 a.m. and at 6.25 p.m. (i.e. considering the coordinated universal time—in summer:  $-2.00$  and winter:  $-3.00$ ). On average, the inspection of the 18 traps in each daily survey was completed in 55 min.

All samples were taken to the laboratory and free-feeding herbivorous insects (chewing and sap-sucking) were identified to the family level and sorted into morphospecies (Rafael et al. 2012). We consider as herbivores all the insects from families in which the herbivorous habit predominates (see Moran and Southwood 1982; Neves et al. 2014).

## Statistical analyses

The family composition of free-feeding herbivorous insects (chewing and sap-sucking) was determined per trap and compared among different periods using nonmetric multidimensional scaling (NMDS). Since we used abundance data of different taxa simultaneously, the NMDS is indicated to calculate a matrix of dissimilarity for community composition data (Clarke 1993). This analysis to determine data dispersion is based on changes in the mean–variance relationship (Warton et al. 2012). A few morphospecies were captured per trap regardless of the season period, thus most morphospecies was scored as “zero” in the matrix. This could cause only small changes in the mean–variance between groups and generate misleading results when comparing seasonal groups. To solve this problem, traps from different seasons were ordered using the density of families of herbivorous insects calculated through the Bray–Curtis index. To test whether the community structure of different herbivore guilds differed among periods, we performed an analysis of similarity (ANOSIM; Clarke 1993). In this analysis, a nonparametric permutation procedure was applied to rank similarity matrices underlying sample ordinations (Clarke 1993). The calculated R-value (Clarke 1993) was obtained and used to determine similarity patterns between the insect communities sampled at each period. These analyses were conducted using the PAST software (Hammer et al. 2001).

The effects of seasonality (beginning and middle of both rainy and dry seasons) and phenological group (deciduous vs. evergreen trees) on the abundance and richness of free-feeding herbivores (chewing and sap-sucking) were evaluated using generalized linear models (GLMs). In these models, the abundance and richness of the insects were used as response variables, whereas the period, phenological group and their interaction were used as explanatory variables. Initially, all models were adjusted for Poisson error distribution (link-log function), followed by an adjustment when the data were overdispersed. Afterward, the junction of non-significant categorical treatments (amalgamation) was performed using a post hoc contrast analyses (Crawley 2007).

To verify the diel activity (diurnal vs. nocturnal) of the insect fauna, we constructed generalized linear mixed models (GLMMs). We used GLMMs due to the existence of a nested structure (diel shift/host plant) that was included in the model as the random effect (Crawley 2007). In these models, the abundance and richness of free-feeding herbivores (chewing and sap-sucking) were used as response variables and the error distribution was adjusted for the negative binomial family (count data), since our data showed overdispersion (GLMMADMB package). The diel period in each season was used as an explanatory variable.

All models were developed in R software (R Development Core Team 2014), followed by residual analyses and evaluation of error distribution adequacy (Crawley 2007).

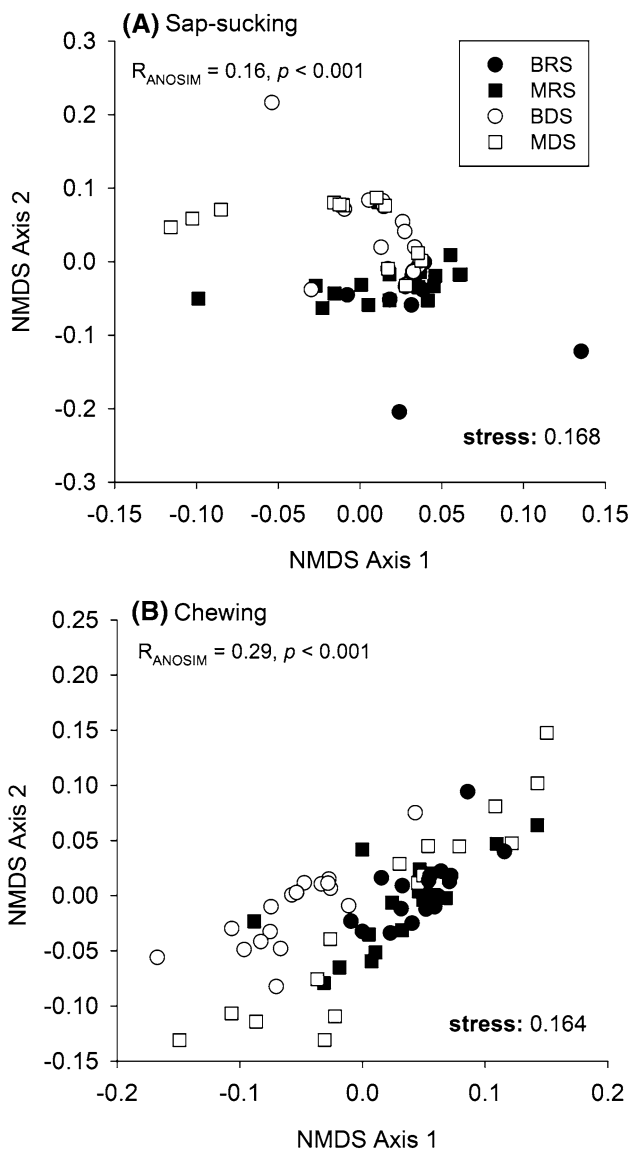
## Results

A total of 5827 free-feeding herbivorous insects were sampled during the study (3463 sucking and 2364 chewing insects), belonging to 396 morphospecies in 36 families (see Tables S1 and S2). The Cicadellidae family was the most abundant (3,405 individuals) and richest (53 morphospecies) among the sap-sucking herbivores (Table S1). Among the chewing insects, the Chrysomelidae family presented the highest abundance (411 individuals) and richness (78 morphospecies; see Table S2).

For sap-sucking insects, the community composition at the family level clearly differed between rainy and dry periods ( $R_{\text{ANOSIM}} = 0.16$ ,  $p < 0.001$ ; Fig. 1a). The community of chewing insects showed differences in composition at the family level among the four periods ( $R_{\text{ANOSIM}} = 0.29$ ,  $p < 0.001$ ; Fig. 1b).

We recorded a greater abundance of sap-sucking insects in the middle of the dry season, whereas their richness showed two peaks: in the middle of both rainy and dry seasons. A morphospecies belonging to the *Neozygina* genus (Cicadellidae: Typhlocybinae) dominated the samples with 2941 individuals (up to 50.5% of all the insects sampled in this study and 85% of all sap-sucking insects). This morphospecies occurred exclusively on *Goniorrhachis marginata* evergreen trees and was responsible for the huge discrepancy in the mean abundance and standard error observed in the middle of the dry season (Table 1; Fig. 2). We recorded the lowest abundance and richness of chewing herbivores at the beginning of the dry season (Table 1; Fig. 3).

The abundance of sap-sucking insects was higher in deciduous than evergreen trees during the rainy season, a pattern that was inverted during the dry season (Table 1; Fig. 2). In general, the insect abundance was higher in the middle of the dry season (Fig. 2a) because of the occurrence of two Cicadellidae morphospecies on *G. marginata* (see Tables S1, S2). On the other hand, the richness of sap-sucking insects on deciduous trees peaked in the middle of the rainy season, whereas the same occurred on evergreen trees in the middle of the dry season (Fig. 2b). The abundance and richness of chewing insects was significantly lower for evergreen and deciduous trees at the beginning of the dry season (Table 1; Fig. 3a). However, the abundance of this guild did not differ between phenological groups. The richness of chewing insects was significantly higher on deciduous trees during the rainy season, and the opposite occurred during the dry season (Table 1; Fig. 3b).



**Fig. 1** Ordination of 72 traps sampled in four periods (beginning and middle of both rainy and dry seasons) through a nonmetric multidimensional scaling (NMDS), using the family abundance from **a** chewing and **b** sap-sucking herbivorous insects ( $p < 0.05$ ). *BRS* beginning of rainy season, *MRS* middle of rainy season, *BDS* beginning of dry season, and *MDS* middle of dry season

Finally, diel activity for insect herbivores showed significant diurnal/nocturnal changes during the dry season, during which the abundance of both sap-sucking and chewing insects was higher during the night (Table 2). No diel differences were detected during the rainy season.

### Discussion

We detected an unexpected higher diversity of herbivorous insects during the dry season in the studied TDF, mainly

due to an increase in insect abundance and richness on evergreen tree species. To our knowledge this is the first study to show the role of evergreen trees within TDFs in maintaining insect diversity during the severe dry season. Also, the observed variations in the abundance and richness of two leaf-chewing and sap-sucking insects indicate small-scale spatial and temporal adaptations (i.e. moving to evergreen trees and shifting to nocturnal periods) to survive the harsh dry season of TDFs. Given its scarce occurrence in the TDF landscape and its importance to sustain insect herbivores (and maybe species from higher trophic levels) during the dry season, evergreen trees should receive special attention in management and conservation strategies for TDFs.

### Seasonality

We recorded pronounced seasonal changes in community composition, abundance, and richness of herbivorous insects on TDF trees. The sap-sucking insect fauna was equally distributed among families during the rainy season, but was dominated by Cicadellidae (Typhlocybinae) both at the beginning and in the middle of the dry season. The Cicadellidae family is characterized by a morpho-physiological specialization of the Malpighian tubules, with the secretion of the protein-lipid named brochosomes (Rakitov 2000). Brochosomes form a thin hydrophobic layer on the insect integument (on all ontogenetic stages), providing protection from contamination with sticky honeydew, and creating a barrier against attachment and penetration of spores of entomopathogenic fungi (Rakitov 2002). Specifically, in arid environments, the main advantages of the brochosomes could be the protection against heat by reflecting the ultraviolet rays (Rakitov 2002). Most Typhlocybinae feed on sap in the leaf mesophyll (Novotny and Wilson 1997; Novotny et al. 2003), and this would explain the high abundance of the mesophyll cell feeders *Alconeura* sp. (Typhlocybinae: Dikraneurini) and *Neozygina* sp. (Typhlocybinae: Erythroneurini) on evergreen trees in the dry season.

Changes in sap-sucking composition were observed between rainy and dry seasons, but not between periods within each season. This pattern may be possibly related to a relatively low variability in sap quality within a season (Santos et al. 2014). On the other hand, chewing herbivores were more sensitive to seasonal variations in abiotic and biotic conditions, given that changes in chewing composition were observed among the four periods. The community of chewing herbivores was characterized by prevalence, in the rainy season, of families that feed on young and highly nutritional leaves, such as Chrysomelidae and Curculionidae. The abundance of these groups decreased at the beginning and in the middle of the dry season, being replaced



**Table 1** Deviance of the generalized linear models (GLMs) to test the effects of seasonality (beginning and middle of both rainy and dry seasons), phenological group (deciduous vs. evergreen) and their interactions on abundance and richness of free-feeding herbivorous insects (sap-sucking and chewing)

Response variable	Explanatory variable	DF	Deviance	Residual DF	Residual deviance	<i>F</i>	<i>P</i>
Sap-sucking abundance	Null model			71	15862.5		
	Season	3	6211.6	68	9650.9	13.1016	<b>&lt;0.001*</b>
	Group	1	1632	67	8019	10.3265	<b>&lt;0.01*</b>
	Season × Group	3	944.6	64	7074.4	1.9378	<b>&lt;0.05*</b>
Sap-sucking richness	Null model			71	265.47		
	Season	3	73.544	68	191.93	10.9108	<b>&lt;0.001*</b>
	Group	1	20.202	67	171.72	0.0899	<b>&lt;0.01*</b>
	Season × Group	3	17.793	64	153.93	2.6398	0.061
Chewing abundance	Null model			71	1308.8		
	Season	3	184.761	68	1124.1	3.1529	<b>&lt;0.05*</b>
	Group	1	5.042	67	1119	0.2581	0.613
	Season × Group	3	17.371	64	1101.7	0.2964	0.827
Chewing richness	Null model			71	390.05		
	Season	3	62.8	68	327.25	4.5361	<b>&lt;0.01*</b>
	Group	1	12.951	67	314.3	2.8063	<b>&lt;0.05*</b>
	Season × Group	3	10.732	64	303.57	0.7752	<b>0.0412*</b>

The significant relation was bolded in the table ( $p < 0.05$ )

All models were overdispersed and we used a link-log function ( $n = 72$  for each model)

\*Explanatory variable retained in the minimum adequate model ( $p < 0.05$ )

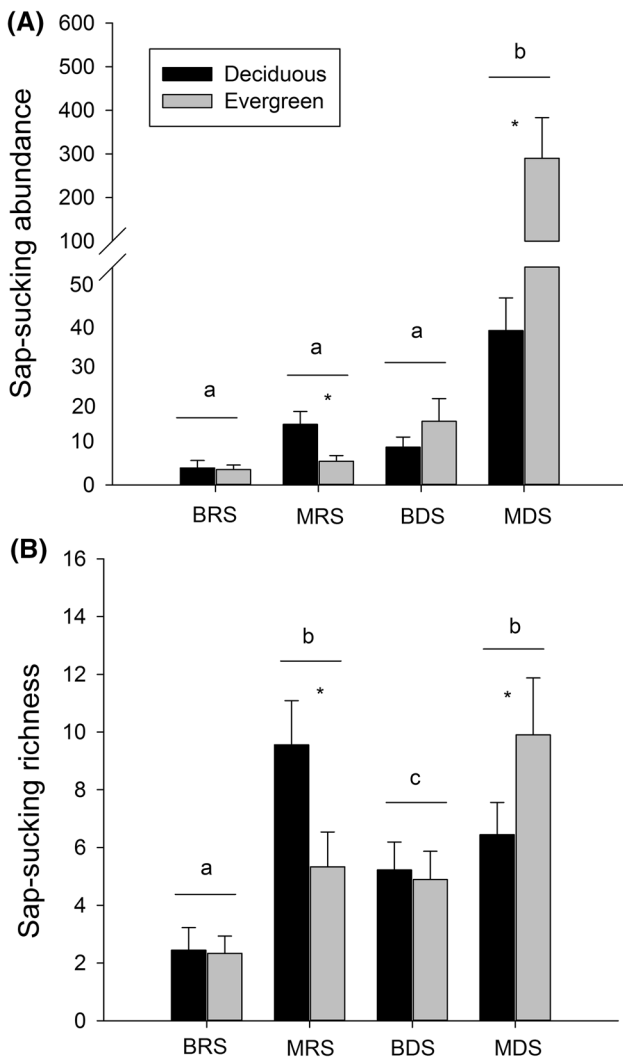
by large generalist herbivores with robust mouthparts and well-developed digestive systems (Orthopteroids: Orthoptera and Phasmida) that are able to cut relatively tough, mature leaves with low nutritional quality (Didham and Springate 2003; Novotny et al. 2003; Wardhaugh 2014). Moreover, there is an increase in the amount of recently dead wood suspended in the canopy (e.g. fallen branches) during the dry season, favoring the occurrence of generalist wood-eating or mixed-diet beetles, such as Cerambycidae, Elateridae and Dermestidae (Novotny et al. 2003; Novotny and Basset 2005; Grimbacher and Stork 2009). The presence of chewing herbivores in leafless trees during the dry season is intriguing, but it is likely that these insects are searching for food or suitable microhabitats and mates, avoiding predation and eventually dispersing or migrating.

A reduction in insect diversity during the dry season seems to be common in tropical habitats (Novotny and Basset 1998; Pinheiro et al. 2002; Freire-Jr et al. 2014; Kishimoto-Yamada and Itioka 2015), and this pattern would be even more drastic for herbivorous insects in TDFs with intense drought-deciduousness (Janzen 1973, 1981; Vasconcellos et al. 2010). Nonetheless, we recorded a higher abundance and richness of sap-sucking herbivorous insects during the dry season, an unusual pattern already detected for insects in general in other TDFs (Kishimoto-Yamada and Itioka 2015). However, our result must be interpreted in the context of the sampling design used in this study.

When the two most abundant Cicadellidae morphospecies were removed from the analyses, insect abundance peaked during the rainy season. Furthermore, we sampled the same number of evergreen and deciduous trees, but this proportion is quite different in TDFs. In general, only up to 1.7–9.7% of tree species in TDFs are evergreen (Lott and Atkinson 2002; Ragusa-Netto and Silva 2007). Thus, it is very likely that the overall insect diversity (i.e. at the landscape level) is highest during the rainy season when all deciduous species have leaves. In spite of that, it is possible that the high diversity of herbivorous insects in the dry season is related to an increased foraging activity to compensate for the resource scarcity (see Grimbacher and Stork 2009), or to an increased searching for humid refuges provided by evergreen trees (Silva and Neves 2014). Temporal and spatial replicates (i.e. more than 1 year and one site) are necessary to corroborate the unexpected higher diversity of herbivorous insects in the dry season and elucidate the mechanisms underlying such a pattern.

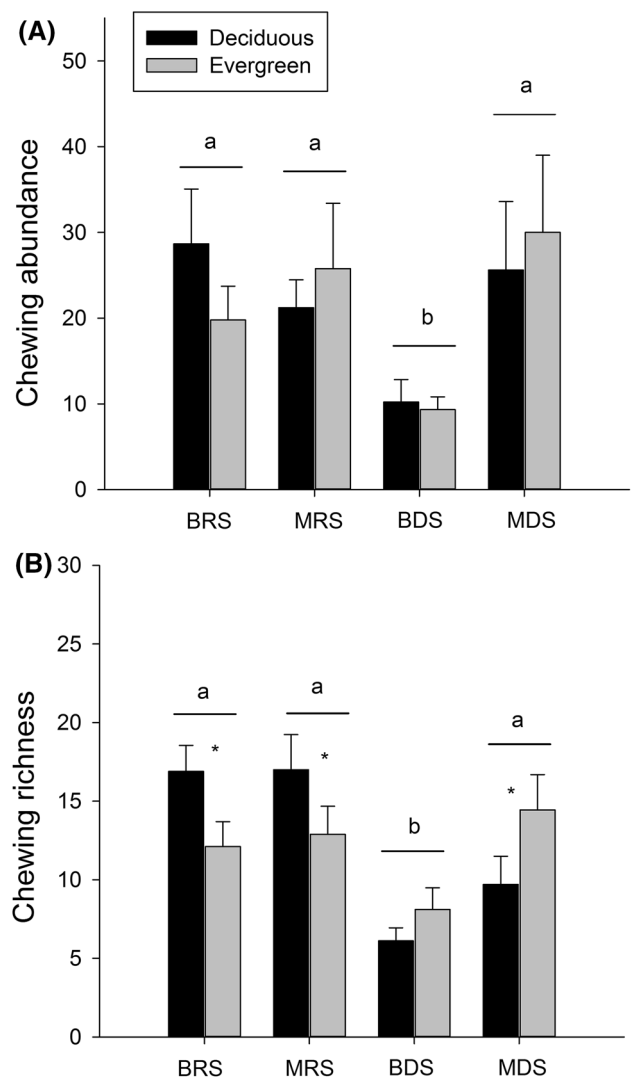
### Phenological groups

The insect diversity on plants from different phenological groups varied seasonally. In the dry season, a higher herbivore richness (for both sap-sucking and chewing insects) and abundance (only for sap-sucking) was recorded on evergreen trees. This result suggests that these different



**Fig. 2** Average **a** abundance and **b** richness of sap-sucking insect herbivores per trap on deciduous and evergreen trees sampled in four periods (beginning and middle of both the rainy and dry seasons) in a tropical dry forest (n=72). The use of *different letters* upon bars indicates differences among periods, whereas the use of *asterisk* indicates differences between phenological groups (deciduous vs. evergreen) within the same period ( $p < 0.05$ ). *Error bars* indicate one standard error. *BRS* beginning of rainy season, *MRS* middle of rainy season, *BDS* beginning of dry season, and *MDS* middle of dry season

guilds of insect herbivores show a small-scale spatial adjustment to withstand the harsh dry season by moving to trees with leaves. The greater abundance of sap-sucking herbivores (e.g. *Neozygina* sp.; Cicadellidae: Typhlocybiinae) on evergreen trees in the dry season may be associated with increased availability of amino acids, nitrogen and soluble carbohydrates in the sap (Walter et al. 2012; Gonda-King et al. 2014), and reduced water potential of evergreen plants (Hasselquist et al. 2010). In addition, the phloem does not contain large concentrations of defenses during the dry season (Walter et al. 2012), which can



**Fig. 3** Average **a** abundance and **b** richness of chewing insect herbivores per trap on deciduous and evergreen trees sampled in four periods (beginning and middle of both the rainy and dry seasons) in a tropical dry forest (n=72). The use of *different letters* upon bars indicates differences among periods, whereas the use of *asterisk* indicates differences between phenological groups (deciduous vs. evergreen) within the same period ( $p < 0.05$ ). *Error bars* indicate one standard error. *BRS* beginning of rainy season, *MRS* middle of rainy season, *BDS* beginning of dry season, and *MDS* middle of dry season

increase the performance of sap-sucking herbivores in this period. Moreover, as mentioned above, Typhlocybiinae species feed on sap in the mesophyll of leaves (Novotny and Wilson 1997), which are only available on evergreen trees during the dry season.

For chewing herbivores, the availability of leaves on evergreen trees in the dry season does not necessarily constitute a food resource, since in this period the leaves are tougher and better defended (Silva and Neves 2014; Silva et al. 2015). Although leaf-chewing insects and sap-sucking mesophyll-feeders exploit the same resource, the latter

**Table 2** Effects of the diel period (diurnal vs. nocturnal) on the abundance and richness of free-feeding herbivores (sap-sucking and chewing) for each period (beginning and middle of both rainy and dry seasons)

Response variable	Beginning-rainy		Middle-rainy		Beginning-dry		Middle-dry	
	Diurnal	Nocturnal	Diurnal	Nocturnal	Diurnal	Nocturnal	Diurnal	Nocturnal
Sap-sucking insects								
Abundance	1.61 ± 0.69	2.50 ± 0.58 <sup>NS</sup>	4.28 ± 0.67	6.38 ± 1.50 <sup>NS</sup>	6.33 ± 2.47	6.50 ± 1.16 <sup>NS</sup>	48.63 ± 23.13	136.94 ± 83.04*
Richness	0.88 ± 0.27	1.58 ± 0.38 <sup>NS</sup>	3.33 ± 0.53	4.11 ± 0.70 <sup>NS</sup>	2.17 ± 0.40	2.89 ± 0.36 <sup>NS</sup>	3.47 ± 0.54	5.35 ± 1.07 <sup>NS</sup>
Chewing insects								
Abundance	12.17 ± 2.6	12.06 ± 2.46 <sup>NS</sup>	10.89 ± 2.18	12.61 ± 1.98 <sup>NS</sup>	3.05 ± 0.51	6.72 ± 1.30 <sup>NS</sup>	9.95 ± 3.75	19.83 ± 5.70*
Richness	6.0 ± 0.80	8.5 ± 0.74 <sup>NS</sup>	7.05 ± 0.68	7.88 ± 0.86 <sup>NS</sup>	2.83 ± 0.43	4.28 ± 0.53 <sup>NS</sup>	5.05 ± 1.25	7.71 ± 1.69 <sup>NS</sup>

The use of “\*” indicates  $p < 0.05$  obtained through generalized linear mixed models (GLMMs)

Non-significant statistical differences ( $p > 0.05$ ) are represented by “NS” ( $n = 18$  for each model)

guild can avoid certain leaf parts (e.g. channels of resin, latex, and trichomes), and feed on leaves that possess defensive barriers (Novotny and Wilson 1997; Novotny et al. 2003). Such differences in feeding mechanisms and limitations would explain the higher sap-sucking abundance on evergreen trees in the dry season. Alternatively, a large proportion of the chewing insect herbivore community spends the dry season as non-reproductive adults with reduced leaf consumption rates (Dirzo and Domínguez 1995). Further research is needed to understand what these insects are doing on these trees and how they complete their life cycle in the studied TDF.

Although the three evergreen species sampled in this study are leaf-exchangers, during our sampling dates in the middle of the dry season, only *A. polyneuron* and *G. marginata* had young leaves, whereas *M. scleroxylon* supported mature/old leaves. This is a possible explanation for the higher similarity in their associated insect fauna when compared to *M. scleroxylon*. At the beginning of the rainy season, the young leaves from both deciduous and evergreen tree species, were still expanding and the humid conditions probably favored the absence of differences in insect diversity between evergreen and deciduous trees. However, in the middle of the rainy season, deciduous trees with a shorter lifespan and faster leaf expansion may have accumulated fewer carbon-based defenses, being preferred by herbivores (see Silva et al. 2015). Thus, small interspecific differences in the timing of leaf exchange (i.e. like leaf flushing by evergreen species in the dry season) may affect herbivore colonization.

### Diel activity

In the dry season, the abundance of both herbivore guilds was higher during the night (see Table 2), a pattern probably driven by the interaction of abiotic and biotic factors such as suitable microclimate and reduced competition and predation (Janzen 1973; Basset and Springate 1992;

Novotny et al. 1999). According to Lebrija-Trejos et al. (2011), in the dry season, the canopy is more exposed to intense solar radiation, wind speed and extreme temperatures, and is therefore much less humid than in the rainy season. However, such harsh conditions are attenuated during the night (see Janzen 1973; Wardhaugh 2014). In a study conducted during the dry season in a tropical rainforest in New Guinea with *Ficus wassa* (Moraceae), Novotny et al. (1999) found higher insect diversity at night and related this result to a lower predation risk for herbivores (i.e. mostly Chrysomelidae, Curculionidae and Cicadellidae). The community of herbivore insects differed between seasons, but our data cannot be directly used to determine changes in species behavior between seasons (i.e. same species flying during the day in rainy season and at night during the dry season) because most morphospecies were captured only in one season. Our results suggest that insect morphospecies become more nocturnal during the dry season and not that nocturnal morphospecies were relatively more common during the dry season. Thus, we indicate the existence of seasonally-conditioned variations in diel activity of herbivorous insects in TDFs, a pattern which may be typical of these ecosystems.

### Conclusions

Our study contributes to filling the gaps in knowledge about insect seasonality patterns at the community level in TDFs. Unexpectedly, our results indicate a higher diversity of herbivorous insects during the dry season. Their activity during the dry season in TDFs is probably of importance in the maintenance of higher trophic levels and interaction networks, and certainly deserves further attention. Our results indicate that the strategies used by insect herbivores to withstand the severe climatic conditions of TDFs during the dry season include both small-scale escape in space and



time, with evergreen trees playing a key role in maintaining resident insect herbivore populations in TDFs.

Based on the fact that TDFs represent 42% of the tropical forests (Miles et al. 2006) and have been considered the most threatened tropical ecosystem (Quesada et al. 2009; Portillo-Quintero and Sánchez-Azofeifa 2010), conservation efforts must be urgently directed to the maintenance of their biodiversity and ecosystem process (Quesada et al. 2009). Evergreen species serve as dry season refuges for insect herbivores (and probably their predators) in TDFs and, due to their scarcity in the TDF landscape, these trees should be especially targeted for protection in this threatened ecosystem as key micro-habitats for insect conservation.

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