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CHANGES IN THE INSECT HERBIVORE FAUNA AFTER THE FIRST RAINS IN A TROPICAL DRY FOREST

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Abstract: Tropical dry forests are characterized by a pronounced dry season, when most trees shed their leaves, and a rainy season characterized by the production of new leaves. This study aimed to determine the effect of the first rains at the beginning of the rainy season on the insect herbivore fauna. We sampled 90 trees at the end of the dry season and 60 trees six days after the first rains using an entomological umbrella. Species richness and abundance of insect herbivores per tree was higher after the first rains. The results suggest a high synchrony between leaf production at the onset of the rainy season and the increase in insect herbivore diversity. Because young leaves are rich in nutrients and have a lower concentration of carbon-based defenses, many herbivore species in seasonal environments have their life cycles highly adjusted to the phenology of their host trees.

Keywords: dry-wet transition; insect seasonality; phenological synchrony.

Tropical insect diversity varies over time with changes in climate conditions and availability of food resources (Wolda 1978, Wolda 1988). This seasonal pattern is more evident when comparing insect diversity between dry and rainy seasons (Wolda 1988, Pinheiro *et al.* 2002, Neves *et al.* 2010, Silva *et al.* 2011, Neves *et al.* 2014, Kishimoto-Yamada & Itioka 2015, Novais *et al.* 2018). In tropical dry forests (TDF), the pronounced dry season, when up to 90% of all trees lose their leaves, is a critical period for most insect herbivores (Murphy & Lugo 1986, Pezzini *et al.* 2014). Thus, insect activity is usually limited to the rainy season, when leaves are abundant (Janzen 1981, Nunes *et al.* 2012, Pezzini *et al.* 2014).

The first rains at the beginning of the rainy season in TDF trigger synchronous leaf flushing (Nunes *et al.* 2012, Pezzini *et al.* 2014). This synchronous flushing represents not only an adaptation to environmental conditions, but it has also been suggested to serve to satiate herbivores at the beginning of the rainy season (Lieberman & Lieberman 1984, Aide 1992, van Schaik *et al.* 1993). New leaves are restricted to the start of the rainy season and represent a short-time resource of high nutritional quality for these insects, with small amounts of defensive compounds (Filip *et al.* 1995, Boege 2005). Thus, the synchronicity between their life cycles and the phenology of their host plants is crucial for the insect herbivores (Van Asch & Visser 2007). Previous studies comparing herbivorous insect communities (e.g., folivorous and sap-suckers) between dry and rainy seasons in TDFs have shown that the richness and abundance of these insects are lower in the dry season (Janzen 1973, Vasconcellos *et al.* 2010, Novais *et al.* 2018). However, the response of insect herbivores to the immediate changes in forest microclimate and structure caused by first rains at the beginning of the rainy season in a TDF, such as the increase of humidity and the availability of new leaves, remains unknown. This study aimed to determine if there is a synchronism between the first rains, consequently the regrowth of new leaves, and an increase in the richness and abundance of herbivorous insects.

The study was conducted in the Mata Seca State Park (MSSP), located in the municipality of Manga, northern of Minas Gerais state, Brazil (14°48'36" - 14°56'59"S and 43°55'12" - 44°04'12"W. The total area of the park is 15,466.44 ha and the dominant vegetation type is TDF. The climate is Aw according to the Köppen classification system, with a pronounced dry season (Peel *et al.* 2007). The dry season is characterized by 90–95% leaf fall and extends from May to October (Pezzini *et al.* 2014). The annual average temperature is 24.4 °C and the annual average rainfall is 871 mm (Antunes 1994).

Sampling was conducted before and after the onset of the 2011 rainy season. Relative humidity and rainfall data were acquired from an on-site weather station (Supplementary Material 1, Figure 1a and b, respectively). Ten 20 x 50 m permanent plots (0.1 ha each) established along a 7 km transect and spaced at least 100 m from each other were used in this study (see Madeira *et al.* 2009). Five points were selected in each plot, one at each corner and one at the center of the plot. In order to ensure the sampling of insects in established adult trees, we selected at each point three trees with circumference at breast height (CBH) ≥ 15 cm, totaling 150 trees. Ninety trees were sampled at the end of the dry season, between September 7–11 (pre-rains period), and other 60 trees were sampled at the beginning of the rainy season, between October 4–13 (post-rains period; accumulated rainfall: 33.1 mm). The sampled trees were not the same between seasons and several plant species were sampled with the aim of increase the sampling range. Sampling in the post-rains period started six days after the first rains, which was enough time to cause significant changes in vegetation cover (Figure 2).

Canopy insects were sampled by beating the foliage using a modified entomological umbrella (Neves *et al.* 2014). Beating was performed on three branches per tree with 10 beatings per branch. The canopy of trees < 7 m in height was reached using a

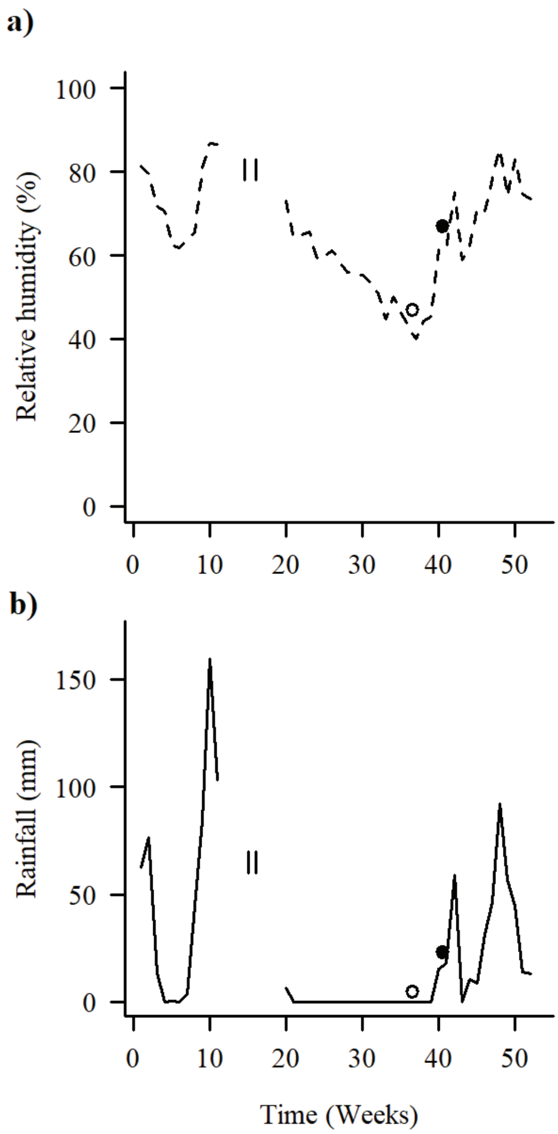

Figure 1: Relative humidity (a) and rainfall (b) in 2011 at Mata Seca State Park, Minas Gerais, Brazil. Vertical bars indicate missing data. The highlighted circles indicate the beginning of the two sampling periods (white: dry season; black: rainy season).

Figure 2: Vegetation cover at the end of the dry season (left) and six days after the first rains at the beginning of the rainy season (right) in a tropical dry forest, Minas Gerais, Brazil. Photos by C. F. Silva and S. Novais, respectively.

ladder, whereas trees > 7 m were reached using the single-rope climbing technique. All herbivorous insects belonging to families with prevailing herbivorous habits were identified to family level and morphotyped based on external morphological characters (Rafael *et al.* 2012). Next, the abundance and richness (number of morphospecies) of insect herbivores per tree were determined.

Generalized linear models (GLMs) were constructed to determine the effect of the dry season/rainy season transition on the abundance and species richness of insect herbivores, using the species richness and abundance of insect herbivores per tree as response variables and season as the explanatory variable. The complete models were submitted to residual analysis to evaluate adequacy of error distribution (Crawley 2007). The analyses were performed using R software (R Development Core Team 2018).

A total of 93 insect herbivores belonging to eight families and 32 morphospecies were collected in the two sampling periods. Of these, 20 individuals (nine morphospecies) were sampled at the end of the dry season and 73 (29 morphospecies) at the beginning of the rainy season (Table 1). The families Chrysomelidae (16) and Curculionidae (6) had the highest morphospecies richness. Both the abundance ($p < 0.001$, d.f. = 1, Deviance = 57.38) and morphospecies richness ($p < 0.001$, d.f. = 1, Deviance = 25.37) of insect herbivores were higher at the beginning of the rainy season (Figure 3a and b). The models followed a Poisson error distribution. This is the first study in a TDF to demonstrate the change in insect herbivore diversity in response to the onset of the rainy season. Mean abundance and morphospecies richness of insect herbivores per tree were higher six days after the first rains of the 2011 rainy season than at the end of the dry season. In addition, the total number of morphospecies and individuals was more than three times higher after the first rains, despite the lower sampling effort in the rainy season (90 trees sampled in the dry season vs. 60 trees in the rainy season). Synchronous leaf flushing in response to rainfall is the most common phenological pattern in TDFs (Nunes *et al.* 2012, Pezzini *et al.* 2014).

Table 1. Morphospecies richness and abundance of insect herbivores sampled at the end of the dry season (pre-rains period) and beginning of the rainy season (post-rains period) in a tropical dry forest at Mata Seca State Park, Minas Gerais, Brazil.

Families	Dry season		Rainy season	
	Richness	Abundance	Richness	Abundance
Hemiptera				
Cicadellidae	1	1		
Cixiidae			1	1
Lygaeidae			3	4
Scutelleridae	1	7	1	4
Tingidae	1	1	3	14
Coleoptera				
Chrysomelidae	5	9	14	39
Curculionidae			6	10
Mordelidae	1	2	1	1
Total	9	20	29	73

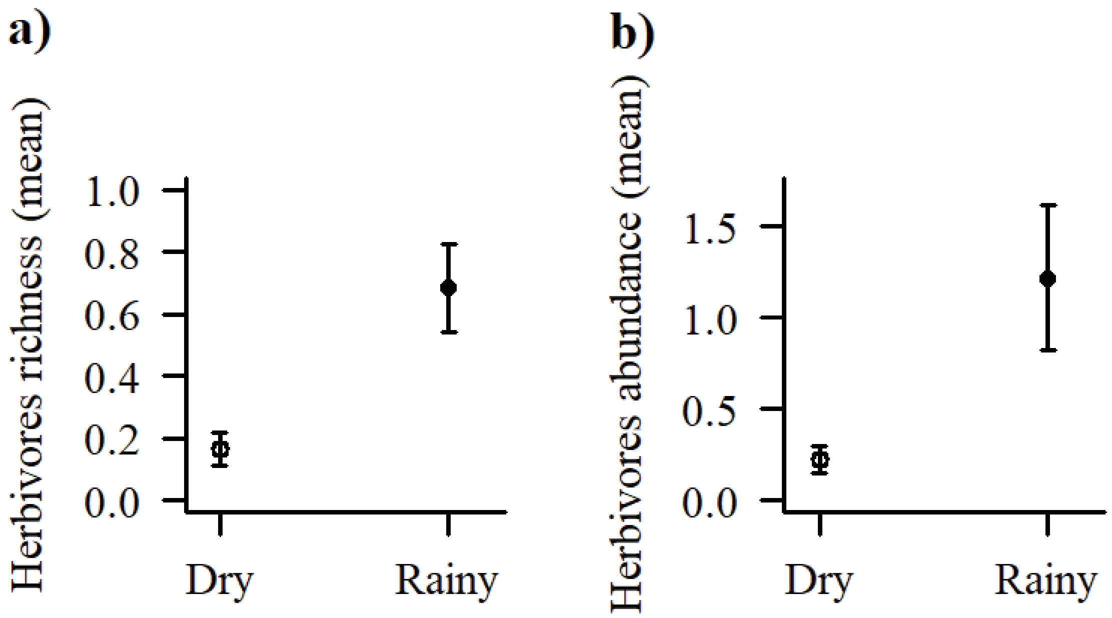

Figure 3: Morphospecies richness (a) and abundance (b) of insect herbivores per tree (means ± SE) at the end of the dry season and beginning of the rainy season in a tropical dry forest, Minas Gerais, Brazil.

Despite the occurrence of different tree phenological types in TDFs (Medina 1995), the results suggest a high synchrony between rainy season and the increase in insect herbivore diversity at the onset of the rainy season, after 19 dry weeks. This is probably influenced by the production of new leaves, which usually happens in this time of the year. Studies reported that some insect herbivore species are synchronized with the phenology of their hosts (Yukawa 2000, Ivashov *et al.* 2002, Van Asch & Visser 2007). Silva *et al.* (2011) found that the density of insects (including herbivores) correlated positively with temperature and humidity, which were greater in the dry/rainy season transition and coincide with the peak production of leaves in the Brazilian Cerrado. Insect herbivores feed on young leaves due to their high nutritional quality (e.g., nitrogen and water) and lower concentration of carbon-based defenses such as tannins (Coley & Barone 1996). In fact, most herbivores in seasonal environments are probably "early-season feeders", with life cycles highly adjusted to the availability of new leaves (Silva *et al.* 2012, Neves *et al.* 2014).

Nevertheless, we highlight the presence of some species at the end of the dry season, which also could be caused by the production of new leaves. Succulent deciduous trees produce leaves before the onset of the rainy season (Nunes *et al.* 2012). This mechanism is triggered by abiotic changes such as increased air humidity, photoperiod, and temperature at the end of the dry season (Murphy & Lugo 1986, Bullock & Solís-Magallanes 1990, Rivera *et al.* 2002). On one hand, this contributes to escape from herbivory in time (Aide 1992, van Schaik *et al.* 1993) and, on the other, it probably favored the specialization of certain insect herbivores that use the same abiotic cues to benefit from this phenomenon at a time when competition is low, at the end of dry season in tropical dry forests. Thus, our results show that the first rains at the beginning of the rainy season are an important seasonal cue for many insect herbivores in tropical dry forests, enabling them to access the new leaves.

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Supplementary Material 1. Precipitation and humidity data during 2011 from a meteorological station located in the Mata Seca State Park.

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