

Ferns and Lycophytes as new challenges The effect of tropical dry forest seasonality on the diversity of insects associated with ferns

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Abstract

Seasonality is one of the main characteristics of a tropical dry forest that affects the structure of ecological communities. In this context, we evaluated the seasonal diversity of ferns and insects in the tropical dry forest of Morelos, Mexico, to determine whether a relationship exists between the presence of each of these two groups. Hill's numbers indicated differences in the diversity of both groups according to season. In the rainy season, we recorded the highest diversity of ferns, with 6,471 individuals. In contrast, in the dry season, we recorded only 293 individuals. Regarding the insects, we collected 723 individuals in the rainy season and 171 individuals in the dry season. The order Orthoptera was the most abundant (50%). The best-represented functional group according to feeding guild was that of chewing herbivores. Correlation analysis revealed a positive relationship between insect and fern abundances since, for both groups, the minimum abundance was presented in the dry season and the maximum abundance in the rainy season. We recorded 12 orders of insects associated with eight ferns in the rainy season. Seasonal studies that consider different biological groups are necessary to understand how changes in resource availability shape temporal patterns of species diversity.

Key words: alpha diversity, functional groups, herbivorous insects, tropical forest.

Resumen

La estacionalidad es una de las principales características de los bosques tropicales secos que afectan la estructura de las comunidades ecológicas. En este contexto, evaluamos la diversidad estacional de helechos e insectos en el bosque tropical seco de Morelos, México, para determinar si existe una relación entre la presencia de estos dos grupos. Los números de Hill indicaron diferencias en la diversidad de ambos grupos según la temporada. En la época de lluvias registramos la mayor diversidad de helechos, con 6,471 individuos. En contraste, en la estación seca registramos solo 293 individuos. Con respecto a los insectos, colectamos 723 individuos en la época de lluvias y 171 individuos en la época seca. El orden Orthoptera fue el más abundante (50%). El grupo funcional mejor representado según el gremio alimenticio fue el de los herbívoros masticadores. El análisis de correlación reveló una relación positiva entre las abundancias de insectos y helechos ya que, para ambos grupos, la menor abundancia se presentó en la época seca y la abundancia mayor en la época lluviosa. Registramos 12 órdenes de insectos asociados a ocho helechos en la temporada de lluvias. Se necesitan estudios estacionales que consideren diferentes grupos biológicos para comprender cómo los cambios en la disponibilidad de recursos dan forma a los patrones temporales de la diversidad de especies.

Palabras clave: diversidad alfa, grupos funcionales, insectos herbívoros, bosque tropical.

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Introduction

Seasonality is one of the main characteristics of a tropical dry forest (TDF) and it affects the structure of ecological communities through changes in different abiotic resources, such as water, temperature, and photoperiod (García & Cabrera-Reyes 2008; van Schaik *et al.* 1993). Mexican TDF presents a marked seasonality, with only four months of rain and five to eight months of drought per year (Rzedowski 2006; Lopezaraiza-Mikel *et al.* 2014). This causes plant growth, reproduction, and establishment to be largely limited by the particular climatic conditions of the site (Murphy & Lugo 1986; Castrejón-Alfaro *et al.* 2022). In addition, TDF is a highly diverse ecosystem comprising vertebrates, insects, and plants (Janzen 1987; Ceballos & Valenzuela 2010; Aguilar-Pérez *et al.* 2019), mainly as a result of its structure and the physiological properties of the individuals that are determined by seasonality. In plants, for example, the dry season can trigger flowering (van Schaik *et al.* 1993; Lopezaraiza-Mikel *et al.* 2014) or may accelerate leaf loss as a mechanism to resist drought, whereas the rainy season favors the production of new leaves (Sánchez-Azofeifa *et al.* 2013; Lopezaraiza-Mikel *et al.* 2014).

The main abiotic factors that affect the population dynamics of ferns are rainfall and temperature. These factors trigger the production of new and fertile leaves, as well as the release of spores (Mehlreter & García-Franco 2008; Lee *et al.* 2018; Castrejón-Alfaro *et al.* 2022) since this season presents favorable conditions for their germination and establishment (Sharpe & Mehlreter 2010). Temporal dynamics such as seasonality can therefore affect species abundance (López-Carretero *et al.* 2015). For example, in the seasonal ecosystems of Mexico, Bolivia, and Costa Rica, higher abundance and diversity of vascular plants are reported in the rainy season (Acebey *et al.* 2003; Gradstein *et al.* 2003; Cardelús *et al.* 2006) because of the generalized influence of humidity and precipitation that to a large extent dictates the richness and abundance of vascular plants (Kessler *et al.* 2011).

The same is true for the insect group, which varies seasonally according to changes in climatic conditions and food resource availability that act to favor the development and reproduction of these organisms (Wolda 1988; Danks 2007; Kishimoto-Yamada K & Itioka 2015). Seasonal patterns become more evident when comparing

insect abundance and diversity between wet and dry seasons in ecosystems such as the TDF (Kishimoto-Yamada & Itioka 2015). The dry season brings a reduction in insect diversity and abundance, which is largely due to the duration of the phenological leafing events that regulate plant-insect interactions (Janzen 1973; van Schaik *et al.* 1993; Borchert 1994). In this sense, insects of the chewing and sap-sucking food guild present reduced abundance and diversity in the dry season (Janzen 1973; Creão-Duarte *et al.* 2016), mainly as a result of habitat restriction, food shortage, or the presence of unsuitable conditions for their development (Pinheiro *et al.* 2002).

The interaction between insects and ferns has been widely studied (Balick *et al.* 1978; Auerbach & Hendrix 1980; Mehlreter & Tolome 2003; Chaves & de Gois 2006; Mehlreter *et al.* 2006; Mehlreter 2010; Fuentes-Jacques *et al.* 2022a, b). Studies of ferns have reported foliar herbivory damage of between 5–15% (Auerbach & Hendrix 1980; Mehlreter & Tolome 2003; Chaves & de Gois 2006; Mehlreter *et al.* 2006), with similar values reported in herbivory studies in angiosperms (Dirzo & Domínguez 1995; Williams-Linera & Baltazar 2001). It should be noted that, although the study of interactions such as herbivory in ferns has received increasing attention, the existing information is focused mainly on studies in ecosystems with low seasonality (Fuentes-Jacques *et al.* 2022a, b). In this sense, Mehlreter (2010) suggests that the proportion of 98 herbivorous insects could be 3 to 7 times lower than in seed plants and that there could be between 1,500 and 3,500 species of insects that feed on the ferns.

It is therefore necessary to determine how the temporal seasonality of tropical dry forests affects the presence and/or absence of different groups of species. In this regard, the fern group can indicate changes in precipitation and temperature patterns since these plants are susceptible to environmental change. Consequently, they can be considered bioindicators (Zotz & Bader 2009; Pouteau *et al.* 2016). The objectives of the present study were 1) to determine the diversity of ferns and insects in the rainy and dry seasons; 2) to determine the richness of the functional groups of insects associated with ferns, considering their feeding guild; 3) to analyze the relationship between the diversities of ferns and insects.

We hypothesized that 1) there will be a greater diversity of ferns during the rainy season because of the high precipitation, and the insect

diversity will increase due to the availability of a greater quantity of resources (*e.g.*, food and shelter); and 2) the chewing herbivores functional groups will be the best represented.

Material and Methods

Study area

This study was conducted in a tropical dry forest (TDF) established on lava fields near the community of San Andres de la Cal, Tepoztlan, in Morelos, Mexico (18°57'22.2"N, 99°06'50.2"W). The local climate is semi-warm (A) C (w2) (w) ig, with rainfall during summer and winter (May to October). The average annual precipitation is approximately 1,200 mm and the average annual temperature is around 20 °C (Ruíz-Rivera 2001). The maximum and minimum temperatures are around 32 °C in April and 11 °C in January. The highest rainfall occurs from June to October, ranging from 113 to 242.3 mm per month (CONAGUA 2016).

In Morelos, the TDF harbors about 39 species of woody plants, including *Sapium macrocarpum* Müll. Arg. (Euphorbiaceae), *Ipomoea pauciflora* M. Martens and Galeotti (Convolvulaceae), and *Quercus obtusata* Humb. & Bonpl. (Fagaceae) (Cortés-Anzures 2015). In the case of the Pteridoflora, 22 species have been reported, the most abundant of which are *Cheilanthes kaulfussii* Kunze, *Bommeria elegans* (Davenp.) Ranker and Haufler, *B. pedata* (Sw.) Fourn, *Dryopteris maxonii* Underw. & C. Chr., *Notholaena candida* (M. Martens & Galeotti) Hook., and *Pleopeltis polypodioides* (L.) E.G. Andrews & Windham. Likewise, lycophytes such as *Selaginella lepidophylla* (Hook. & Grev.) Spring and *S. pallescens* (C. Presl) Spring (Selaginellaceae) have been reported (Castrejón-Alfaro *et al.* 2022).

Sampling

To determine the diversity of ferns and insects of the TDF, observations were made during 2019 and 2020 in the dry and rainy seasons (from 26 field samples). A total of 17 quadrats of 2.5 × 2.5 m were randomly established at a distance of 50 m apart. Sampling was conducted every 15 days from 9:00 am to 5:00 pm (eight hours per day). Each quadrat was checked for the presence of insects associated with ferns, through an active search for each individual of each fern species conducted for approximately 30 minutes, the time of the insect-fern sample effort was 3,536 hours in total.

In addition, in each quadrat, insects associated with the ferns were collected directly by sweeping the plants with an entomological net and then quantified. The collected insects were taken to the laboratory where the insects were identified to morphospecies level with the help of a specialist (Dr. Armando Burgos) in the plant parasitology laboratory of the Center for Biological Research of the Autonomous University of the State of Morelos and using specialized identification guides (Triplehorn & Johnson 2005; Fontana & Buztetti 2007; Fontana *et al.* 2008). The collected insects were deposited in the Morelos University Entomological Collection (CEUM) of the Center for Biological Research of the Autonomous University of the State of Morelos, Mexico (CIB-UAEM). The species were identified using floral listings, keys, and descriptions (Mickel & Smith 2004), while the taxonomic classification was conducted according to the PPG I (2016). The collected fern specimens were deposited in the herbarium (HUMO) of the Center for Biodiversity and Conservation Research of the Autonomous University of the State of Mexico (CIByC-UAEM).

The collected insects were classified according to the functional group (FG) to which they belong according to feeding guild (McGavin 2000): 1) chewing herbivores; 2) sucking herbivores; 3) predators; 4) decomposers and 5) xylophages.

Data analysis

We obtained the average number of individuals per month for each fern species to calculate the abundance. We then determined the proportion in percentage as a proxy for the relative abundance of each species. To determine the sampling effort, rarefaction and extrapolation curves were generated, which allowed us to estimate the number of species based on the number of samples (Chao *et al.* 2014). To determine whether there were differences in the diversity of both groups according to season, Hill numbers, or the effective number of species, were used where the estimates of each order and their confidence intervals are shown. The order $q = 0$ refers to the richness or number of species and does not consider the abundance of species; order $q = 1$ indicates the effective number of equally frequent (or common) species, in which all species are included with a weight proportional to their abundance (exponential of the Shannon index) and

its calculation is not biased by the presence of rare or abundant species in the sample; and order $q = 2$ indicates the effective number of very abundant or dominant species, the inverse of Simpson's index (Moreno *et al.* 2011). These analyses were performed using the iNEXT package (Hsieh *et al.* 2016). In addition, to define the relationship between fern and insect abundance, a Spearman correlation analysis was performed to determine the degree of correlation of different variables. All analyses were performed in R software (R Development Core Team 2017).

Results

Diversity of ferns

A total of 6,764 individual ferns belonging to two orders, five families, and 13 species were recorded (Tab. 1). Regarding the seasons, the highest abundance was recorded in the rainy season, with a total of 6,471 individual ferns. The most abundant species were *Bommeria pedata* (24%; Fig. 1a), *Bommeria elegans* (22%; Fig. 1b), and *Asplenium pumilum* (17%; Fig. 1c) (Tab. 1). In contrast, in the dry season, a total of 293 individuals were recorded and the most abundant species were *Bommeria pedata* (28%) and *Notholaena candida* (16%) (Tab. 1).

The sample coverage values for ferns during the rainy and dry seasons were 95% and 99%,

respectively. Regarding fern diversity, it was found that the fern richness (q_0) was significantly higher in the rainy season. In contrast, the common species (q_1) were significantly lower in the rainy season, and the dominant species (q_2) did not differ between seasons (Fig. 2a).

Diversity of insects

A total of 899 insect individuals, belonging to ten orders, 17 families, and 75 morphospecies, were recorded (Tab. 2). The highest abundance was found in the rainy season, with 723 individual insects and 71 morphospecies belonging to 17 families and 10 orders. The families with the highest number of individuals were Acrididae (50%; Fig. 3a-f, dorsal and side) and Pentatomidae (10%). In contrast, in the dry season, 176 individual insects and 18 morphospecies belonging to eight families and ten orders were recorded. The families with the highest number of individuals were Acrididae (46%) and Lygaeidae (10%) (Tab. 2).

The sample coverage for insects was 97% in both the rainy and dry seasons. Regarding diversity, we found the same pattern as in the ferns where the observed richness of insects (q_0) and common species (q_1) was significantly lower in the dry season; however, the dominant species (q_2) did not present significant differences between seasons (Fig. 2b).

Table 1 – The abundance of ferns in the rainy and dry seasons in the tropical dry forest of Morelos.

Family	Genera	Species	Abundance Wet	Abundance Dry
Aspleniaceae	<i>Asplenium</i>	<i>pumilum</i> Sw.	1 100	37
Dryopteridaceae	<i>Dryopteris</i>	<i>karwinskyana</i> (Mett.) Kuntze	653	38
Dryopteridaceae	<i>Dryopteris</i>	<i>rossii</i> C. Chr.	7	0
Nephrolepidaceae	<i>Nephrolepis</i>	<i>undulata</i> (Afzel. ex Sw.) J.Sm.	800	5
Pteridaceae	<i>Bommeria</i>	<i>pedata</i> (Sw.) Fourn.	1 568	81
Pteridaceae	<i>Bommeria</i>	<i>elegans</i> (Davenp.) Ranker & Haufler	1 416	26
Pteridaceae	<i>Notholaena</i>	<i>candida</i> (M. Martens & Galeotti) Gancho.	330	46
Pteridaceae	<i>Cheilanthes</i>	<i>lozanoii</i> (Maxon) R.M. Tryon & A.F. Tryon	353	9
Pteridaceae	<i>Adiantum</i>	<i>andicola</i> Liebm.	105	20
Pteridaceae	<i>Adiantum</i>	<i>concinnum</i> Humb. & Bonpl. ex Willd.	64	12
Pteridaceae	<i>Myriopteris</i>	<i>aurea</i> (Poir.) Grusz & Windham	33	10
Pteridaceae	<i>Cheilanthes</i>	<i>kaulfussii</i> Kunze	17	9
Polypodiaceae	<i>Phlebodium</i>	<i>areolatum</i> (Willd.) J.Sm.	25	0

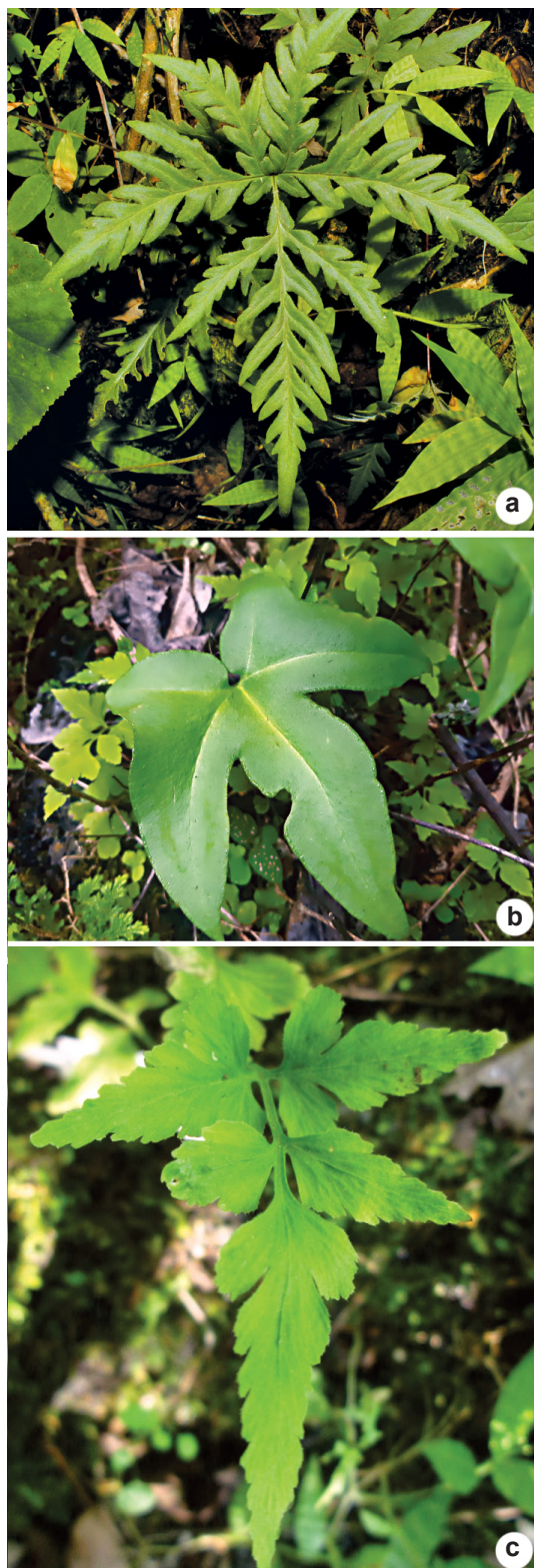


Figure 1 – a. *Bommeria pedata*, b. *Bommeria elegans*, c. *Asplenium pumilum*. Photos by David Tenango and Clara Hernández.

Functional groups of insects

In general, five functional groups according to feeding guild were found in both seasons. In the rainy season, a total of 480 chewing herbivores, 162 predators, 38 decomposers, 15 sucking herbivores, seven xylophages, and 21 unidentified individuals were recorded. During the dry season, 88 chewing herbivores, 51 sucking herbivores, 22 predators, 14 decomposers, one xylophage, and one unidentified individual were collected (Fig. 4).

Seasonal relationship between abundances of ferns and insects

Correlation analysis showed a positive relationship between insect and fern abundances ($r = 0.85$; $P = 0.007$) since the minimum abundance was presented in the dry season and the maximum abundance in the rainy season for both groups.

Diversity of insects associated with ferns

We found 12 insect orders associated with eight fern species in the rainy season. The most associated species of ferns were *Bommeria elegans*, *Dryopteris karwinskyana* and *B. pedata*. The insect orders with the most associations were Hemiptera (9/9) followed by Orthoptera (6/9) (Fig. 5).

Discussion

This study is the first to provide information about seasonal patterns among ferns and their associated insects in tropical dry forests. The hypotheses proposed were fulfilled since we found that both ferns and insects showed greater diversity in the rainy season. Regarding the functional group, herbivorous insects were the most commonly represented in this study, while we evidenced a positive correlation between the abundance of ferns and insects.

Effect of seasonality on fern diversity

Temporal habitat dynamics, such as seasonality, can affect species abundance (López-Carretero *et al.* 2015). In the present study, we found a greater diversity of ferns in the rainy season. This coincides with other studies in seasonal ecosystems in Mexico, Bolivia, and Costa Rica that also report the highest diversity of vascular plants in this season (Acebey *et al.* 2003; Gradstein *et al.* 2003; Cardelús *et al.* 2006; Jiménez-López *et al.* 2020; Castrejón-Alfaro *et al.* 2022). This is likely to be because the rainy season presents optimal microenvironmental conditions of

Table 2 – Taxonomic determination at morphospecies and functional group level of the insects collected in the tropical dry forest of Morelos.

Order	Family	Functional group	Morphospecies	No. of individuals
Orthoptera	Acrididae	Chewing herbivore	1	446
	Gryllidae	Chewing herbivore	1	26
Hemiptera	Lygaeidae	Sap sucker	4	65
	Reduviidae	Predator	6	40
	Pentatomidae	Predator	13	91
	Membracidae	Sap sucker	1	1
	Cicadellidae	Chewing herbivore	1	22
	Unidentified	Unidentified	1	2
Coleoptera	Chrysomelidae	Chewing herbivore	12	43
	Coccinellidae	Predator	3	3
	Cerambycidae	Xylophage	5	7
	Carabidae	Predator	8	15
	Curculionidae	Chewing herbivore	2	11
	Leiodidae	Decomposer	1	9
	Tenebrionidae	Decomposer	5	43
Mantodea	Mantidae	Predator	1	32
Phasmida	Phasmatidae	Chewing herbivore	2	20
	Unidentified		1	4
Hymenoptera	Formicidae	Predator	1	3
	Unidentified		1	4
Dermaptera	Unidentified	Unidentified	1	6
Lepidoptera	Unidentified	Unidentified	2	4
Diptera	Unidentified	Unidentified	1	1
Psocoptera	Unidentified	Unidentified	1	1

precipitation and humidity for the establishment and development of these plants (Kessler *et al.* 2011; Castrejón-Alfaro *et al.* 2022).

The Pteridaceae family was the best represented, with *Bommeria pedata* and *B. elegans* contributing most to the abundance. These species have been reported to be associated with a wide variety of habitats, including those with xeric conditions (Mickel & Smith 2004; Schuettpelz *et al.* 2007). In this sense, the TDF of our study site is characterized by a mainly rocky soil type. In addition, some species of this family present unique adaptations that enable them to establish under

contrasting environmental conditions due to the presence of indumentum, leaf rolling, and deciduous leaves (Schuettpelz *et al.* 2007; Hietz 2010), which generally allow them to cope with adverse microenvironmental conditions (Hietz 2010).

It has been shown, mainly through changes in the availability of different abiotic resources such as water and temperature, that the structure of ecological communities can affect the diversity of species (García & Cabrera-Reyes 2008; Lopezariza-Mikel *et al.* 2014), limiting their growth, reproduction, and establishment (Murphy & Lugo 1986). In this sense, in some fern species, the presence or absence of

water provokes leaf loss by causing them to dry up and fall, with new leaves produced when conditions are optimal (van Shaik *et al.* 1993; Castrejón-Alfaro *et al.* 2022).

This difference in seasonal patterns of fern diversity could be explained as a synchronization that reflects a direct influence of climate. Ferns have low control of evaporative potential during

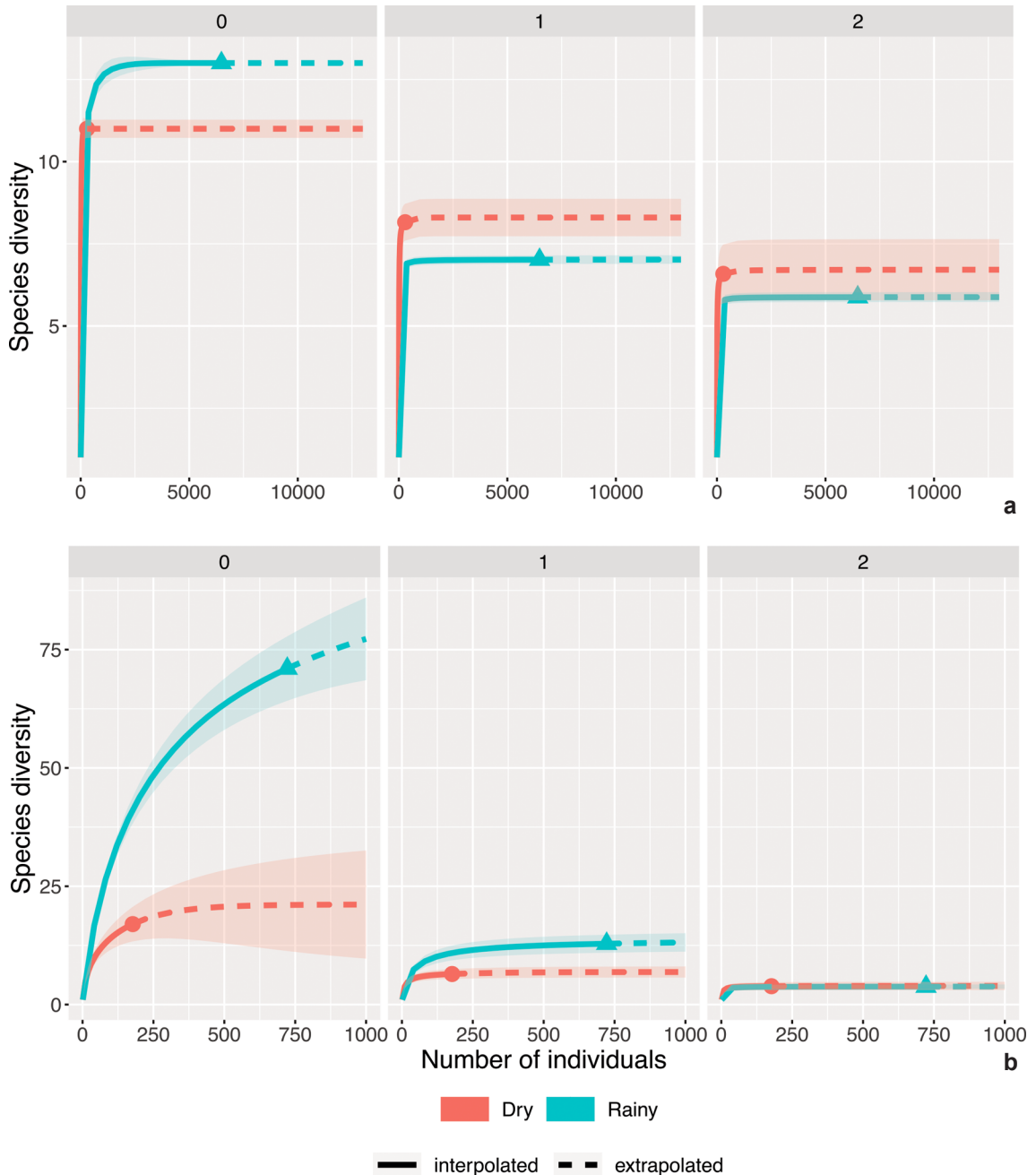


Figure 2 – a. Alpha diversity of ferns (q_0 , q_1 , and q_2) during the two seasons of the year in the tropical dry forest of Morelos, Mexico. Solid lines indicate individual rarefaction; dashed lines indicate extrapolation to the sample size of 6,764 individuals; shading denotes 95% confidence intervals. b. Alpha diversity of insects (q_0 , q_1 , and q_2) during the two seasons of the year in the tropical dry forest of Morelos. Solid lines indicate individual rarefaction; dashed lines indicate extrapolation to the sample size of 899 individuals; shading denotes 97% confidence intervals.

most of their life cycle and are thus dependent on water availability and relative humidity (Page 2002; Hietz 2010). Moreover, our study site presents low ambient humidity values of around 20% (CONAGUA 2016), which could be related to changes in the diversity and abundance of the group. Likewise, the relative homogeneity of microenvironments and low availability of suitable niches for ferns in tropical forests could be another limiting factor for the occurrence of greater fern richness (Kluge & Kessler 2011).

Effect of seasonality on insect diversity

In the insect group, we found the same pattern as in the ferns, since the insects presented greater diversity and abundance in the rainy season. A strong reduction in the abundance of insects has been documented during the dry season, which may

be due to habitat restriction, food shortage, or the presence of unsuitable conditions for development (Pinheiro *et al.* 2002). This could indicate that the insect diapause (*i.e.*, the mechanism through which the annual life history rhythm is manifested) is synchronized with the presence of appropriate seasonal conditions (Janzen 1973; van Schaik *et al.* 1993; Rodríguez-Porras 2012).

The most abundant family in both seasons was Acrididae (locusts, grasshoppers). Another study conducted in a tropical dry forest in Mexico reports this as the most abundant and dominant family that contributes greatly to the biomass of herbivorous insects (Arya *et al.* 2015). This group of generalist herbivores is characterized by folivores and has a wide distribution ranging from sea level to high elevations and including different habitat types from scrubland to temperate forest. They also

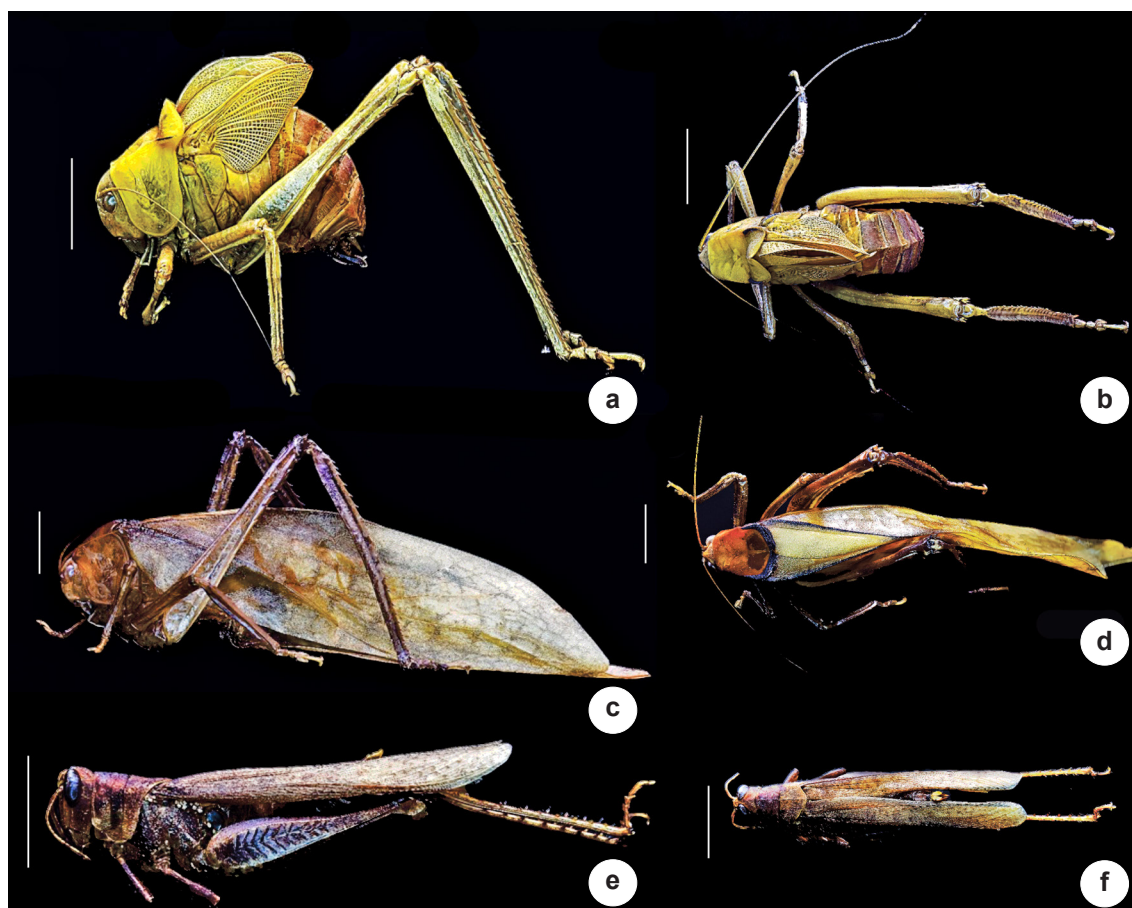


Figure 3 – a-f. Specimens of the order Orthoptera of the Tettigoniidae family in different stages – Nymph, habitus, lateral a) and dorsal view b); Female, habitus, lateral c) and dorsal view d); Male, habitus, lateral e) and dorsal view f) associated with ferns in the tropical dry forest of Morelos, Mexico. Scale bar = 10 mm.

possess a great capacity for migration and can infest economically important crops (Rusconi 2017). The family includes the order Orthoptera, which was the most abundant in this study, contrasting thus with findings from other tropical regions, which show a high abundance of the order Coleoptera during the rainy season (Tanaka & Tanaka 1982; Boinski & Fowler 1989; Smythe 1990; Pinheiro *et al.* 2002; Andresen 2005; Nyeko 2009; Rodríguez-Porras 2012). This could be because this order contains 22,400 phytophagous species, but only 1.1% of all fern-insect interactions and 1.5% of all fern-feeding insect species (Fuentes-Jacques *et al.* 2022a).

In contrast, the order Hemiptera (cicadas, aphids, or woodlice) was the least abundant, probably because this group presents very varied forms, including sessile organisms that are difficult to recognize as insects, for which reason we consider that this group may have been under-represented in this study. This result contrasts with Wolda (1996), who reports that the order Hemiptera is the most abundant at the beginning of the rainy season in a tropical forest in Panama, while

Pinheiro *et al.* (2002) documents that the orders Hemiptera, Lepidoptera, and Orthoptera present a clustered distribution, with greater abundance during the transition from the end of the dry season to the beginning of the rainy season.

It is therefore possible that the difference in order is due to the vegetation type and the stable climatic conditions, which could mean that many tropical insects may have their greatest diversity in this type of ecosystem (Pinheiro *et al.* 2002). It is possible that ferns provide microhabitats for other groups such as insects and that this acts to promote their abundance and diversity. However, the facilitation effect that ferns may have on insects or other groups in TDF remains to be studied, in addition to considering temporal habitat dynamics such as seasonality and resource abundance (López-Carretero *et al.* 2015).

Functional groups of insects

In this study, we found five functional groups, the most abundant feeding guild being chewing herbivores, followed by predators and,

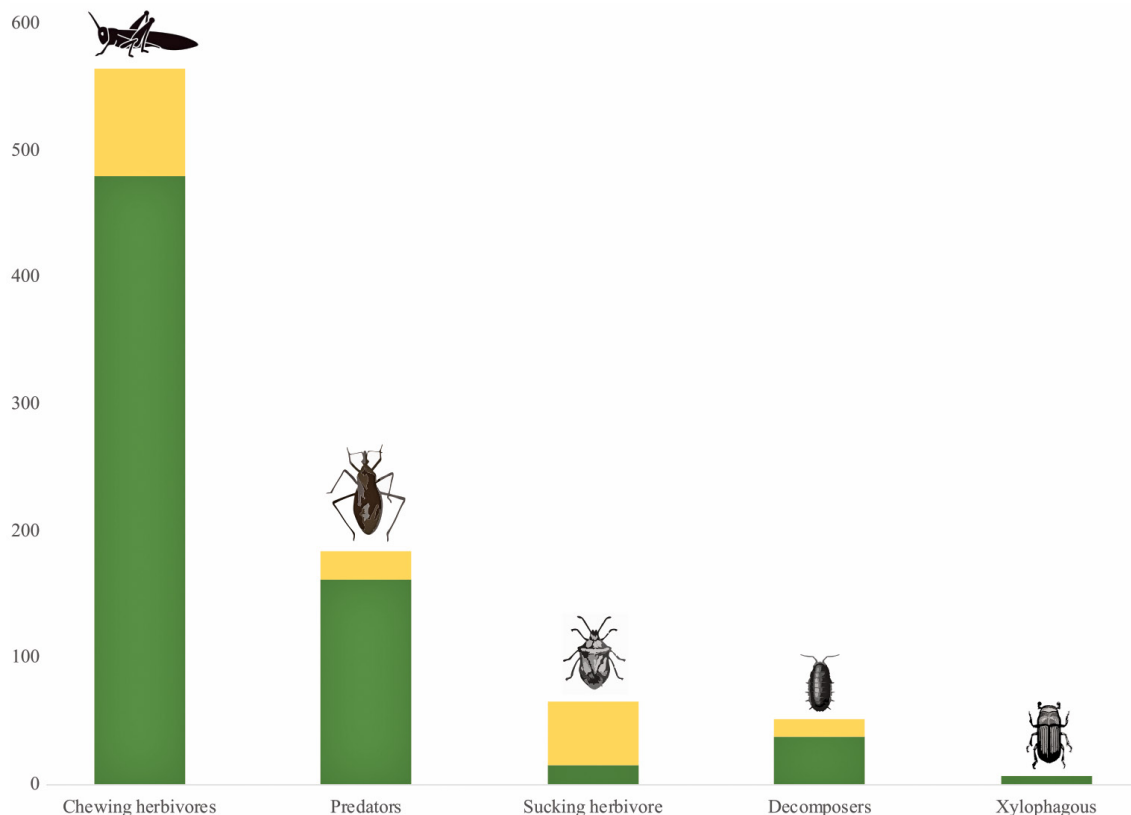


Figure 4 – Abundance of insect functional groups according to feeding guild in a tropical dry forest of Morelos, Mexico. Green and yellow colors indicate the rainy and dry seasons, respectively.

in lower proportion, by sucking and xylophagous herbivores. However, this pattern may vary among insect guilds, which depend mainly on the abiotic conditions of the site (Novais *et al.* 2018). This result supports that reported by Fuentes-Jacques *et al.* (2022a), who state that the most common feeding guild is that of the leaf chewers and it usually comes from generalist insect groups. In this sense, it was the order Orthoptera that contributed the largest number of species for this feeding guild. This order has a worldwide distribution, with a preference for warm and temperate regions (Aguirre-Segura & Barranco 2015) and with a very varied feeding regime, from omnivorous, phytophagous species to those that feed on material of animal origin (McGavin 2000). However, it should be noted that the order Orthoptera could be overrepresented in this study since only 1.1% of all the species in this order interact with any fern species (Fuentes-Jacques *et al.* 2022a).

The second most common feeding guild found was that of predators, where the order Hemiptera, specifically the reduvids and pentatomids, contributed 131 individuals to the guild. This order is among the most abundant insect groups in tropical forests, comprising more than 23,500 known species, many of which are highly specialized to particular host plants or habitats (Hamilton & Whitcomb 2010). In the same sense, Fuentes-Jacques *et al.* (2022a) state that the order Hemiptera is overrepresented for ferns since they found that this group accounted for 36.6% of all interactions between ferns and insects.

In contrast, the feeding guild with the lowest number of morphospecies (15) was that of the sap-sucking herbivores, belonging to the order Hemiptera. This finding was surprising because the guild of the sap-sucking herbivores is the most abundant in seasonal ecosystems (Novais *et al.* 2018; Fuentes-Jacques *et al.* 2022a).

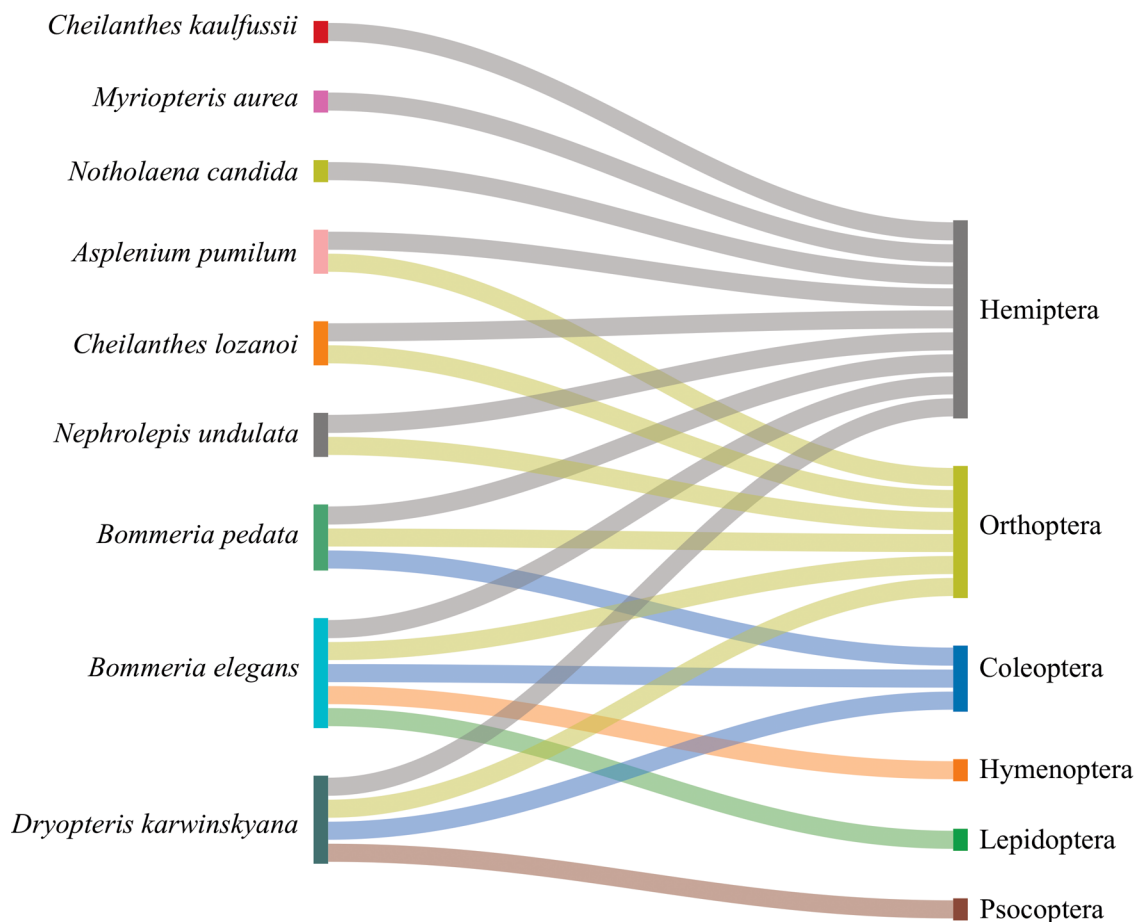


Figure 5 – Diversity of insects associated with ferns in the rainy season in a tropical dry forest of Morelos, Mexico. Sankey diagram created using the open-source, online tool SankeyMATIC (sankeymatic.com).

It is worth mentioning that, in the case of the xylophagous feeding guild, we found the presence of five morphospecies that belong to the cerambycid family. In this sense, it could be that the ferns are providing oviposition sites for this group of insects, as suggested by Vargas-Cardoso *et al.* (2018) since they mention that cerambycids have specific relationships with certain plant taxa, such that the time of emergence of these individuals could be dictated by the phenology of the host plants. Moreover, it has been reported that xylophagous beetles show greater activity in the transition between the rainy and dry seasons (Macedo-Reis 2016; Martínez-Hernández *et al.* 2019). The temporal patterns of the insect feeding guilds present a wide range (Fuentes-Jacques *et al.* (2022a) but they are often unknown in tropical dry forests.

This type of approach can help to understand the effect of seasonality and how it affects the associations between ferns and insects. It also facilitates the identification of groups that are vulnerable to the effects of global climate change, due to the possible decoupling between the two groups. In this sense, it has been suggested that ferns will present modifications to their distribution range as a result of changes in weather patterns (Reyes-Chávez *et al.* 2021; Pie *et al.* 2022). This could affect the species that are related to the presence of ferns (Pie *et al.* 2022), such as the different groups of insects (12 orders in this study) that we found associated with this group and which could be affected by the changes in distribution or the extinction of certain fern species that cannot adapt to the new climatic conditions. However, these studies have been conducted in various vegetation types, finding general patterns (Pie *et al.* 2022; Murakami *et al.* 2023) and have not explored highly seasonal tropical forests such as the TDF, which could yield different results from those previously reported. These studies can provide the basis for proposing strategies for the conservation and appropriate management of the TDF, which faces significant anthropic pressure.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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