

Explaining variations in the diversity of parasitoid assemblages in a biosphere reserve of Mexico: evidence from vegetation, land management and seasonality

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Abstract

Insect fauna biodiversity in natural protected areas has not been thoroughly studied. Therefore, the aim of this work was to assess whether and how vegetation types, land management and seasonality influence the diversity of Ichneumonidae (Hymenoptera) in the Ría Lagartos Biosphere Reserve (Mexico). A sampling programme was conducted using Malaise traps from 2008 to 2009 in three vegetation types, each with two conservation zones (core and buffer zones). Three seasons were considered: rainy, dry and north-winds (isolated storms from November to February). A total of 336 species were identified. Rarefaction and Generalized Linear Model indicated higher species richness and abundance, respectively, in the buffer zone of the dry forest; possible explanations for this finding include the intermediate disturbance hypothesis, wherein diversity can be higher in sites where disturbance is not very frequent or very intense, and the ‘enemies hypothesis’, wherein structural complexity and high plant diversity favour increased predators or, in this case, parasitoids. Diversity was higher during the rainy season, which may have been due to the higher availability of resources. Vegetation and management had a positive impact on the Coc (attack cocoons and pupae) and Myc (attack concealed larvae living in the fruiting bodies of mushrooms) parasitoid guilds. Members of the Coc guild are generalist parasitoids, which may be favoured in complex vegetation with a high richness of potential hosts and non-hosts. The Myc guild requires certain environmental conditions that promote fungal growth, such as humidity, that is absent in the other vegetation types of savannah and coastal dune scrubland.

Keywords: Ichneumonidae, protected area, species richness, parasitoid diversity, conservation, Neotropic

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Introduction

In natural protected areas, monitoring programmes, management and conservation strategies are commonly designed for plants and vertebrates, but the effectiveness of these plans in the conservation of invertebrates is not well known (Haslett,

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2001; Carignan & Villard, 2002). Among insects, parasitoids are a promising model for diversity studies. These species represent a large proportion of global species richness (LaSalle & Gauld, 1993); for instance, it has been estimated that there are five to six parasitoid species for every herbivorous insect species (Askew & Shaw, 1986; Hawkins & Lawton, 1987). Parasitoid insects also provide essential ecological services for ecosystems by regulating insect populations, especially those of phytophagous species (LaSalle & Gauld, 1993). This regulatory role makes parasitoids key bioindicators of the conservation status of disturbed environments (Chay-Hernández *et al.*, 2006; Sharkey, 2007; Anderson & Purvis, 2008).

For conservation purposes, parasitoids are relevant because they have highly sensitive life cycles, which increases their vulnerability to drastic population reductions and sometimes leads to local extinctions of some species (Hochberg & Ives, 2000). These reductions and extinctions can have unpredictable effects on prey population dynamics and may unleash cascade effects in ecosystems (LaSalle & Gauld, 1993). The effective conservation of parasitoids requires a basic species inventory, research on parasitoid diversity and distribution, and the development of monitoring programmes that allow the evaluation of species' conservation status (Fraser *et al.*, 2008a).

Given their ecological importance and the limited coverage of parasitoids in management plans for biodiversity conservation, our study focused on the Ichneumonidae (Hymenoptera) in a biosphere reserve in the seasonal tropics of south-eastern Mexico (Yucatan Peninsula). Ichneumonidae species richness is highest among parasitoids. Parasitoids are present in almost all natural and managed ecosystems but are among the least represented organisms in management and conservation plans (Gauld, 1991; Hochberg & Ives, 2000; Dolphin & Quicke, 2001).

Studies on the Ichneumonidae of Mexico have mainly focused on faunistic, taxonomic or biogeographical patterns (e.g., Ruíz-Cancino & Tejada, 1986; Ruíz-Cancino *et al.*, 2002; Kasparyan & Ruíz-Cancino, 2004a, b, c, d; Kasparyan, 2007a, b, c; Khalaim & Ruíz-Cancino, 2009; Bordera *et al.*, 2010; González-Moreno *et al.*, 2010; Ruíz-Cancino, 2010; Ruíz-Cancino *et al.*, 2010; González-Moreno & Bordera, 2011, 2012), but few studies have evaluated the spatial and/or temporal diversity of Ichneumonidae in Mexico (Chay-Hernández *et al.*, 2006; Pérez-Urbina *et al.*, 2010; González-Moreno *et al.*, 2010; González-Moreno *et al.*, 2015).

The aim of the present paper is to assess whether and how vegetation type, land management of conservation areas and seasonality influence the diversity of Ichneumonidae in a protected area of Mexico. To this end, the following three hypotheses were tested:

- 1) The 'enemies hypothesis' (EH) (Root, 1973) argues that structural complexity and high plant diversity favour increased prey or phytophagous hosts and, consequently, predators or parasitoids; therefore, the dry forest should have higher species richness and diversity indices than other vegetation types.
- 2) The second hypothesis proposes that the conservation status of vegetation affects ichneumonid species richness; zones with a higher conservation level (core zones) should have higher richness and diversity than zones with a low conservation level (buffer zones) because, in buffer zones, agriculture, construction and other activities are allowed, and these activities have been reported as the main causes

of insect habitat loss, leading to population decreases or even extinction (Samways, 2007).

- 3) The third hypothesis proposes that abundance and species richness will be higher during the rainy season because of the increase in productivity and vegetation complexity (Andrade *et al.*, 2007), offering more resources for herbivores and parasitoids (Gauld, 1991; Shapiro & Pickering, 2000).

Materials and methods

Study area

The Ría Lagartos Biosphere Reserve (Reserva de la Biósfera Ría Lagartos, RBRL) is located at approximately 21°36'N, 88°10'W in north-eastern Yucatan, Mexico. The average annual temperature is 26°C; the temperature of the coldest month averages 18°C. The average annual rainfall is 670 mm, most of which (48%) occurs during the summer months (July–October). During the dry season (March–June), 27% of the precipitation occurs, while during the north-winds season (November–February), 25% of the precipitation occurs (CONANP, 2000). The three most common vegetation types are coastal dune scrubland, savannah and tropical dry forest (González-Moreno & Bordera, 2011). Every vegetation type has two conservation status areas, a core, and a buffer zone, which have a total area of 23,681 ha and 36,666 ha, respectively.

In the core zones, only research and habitat restoration activities are permitted; any other kind of activity, such as agriculture, hunting or plant collection, is forbidden. In the buffer zones, some activities that are considered 'low impact' are allowed by law, such as wood collection for fuel and traditional slash and burn agriculture or the maintenance of the artificial grasslands that existed before the reserve was established.

The pressure on the buffer zones differs by vegetation type; for instance, the coastal scrubland is subject to destruction for construction and trails. The savannah is sometimes destroyed for grassland establishment but then abandoned, as this ecosystem is not very productive; it is also affected by highway and dumping site establishment. The dry forest is subject to several uses, such as slash and burn agriculture, the establishment of artificial grasslands and cattle grazing, the establishment of orchards for fruit production, maintenance of honeybee hives and forestry exploitation.

The tropical dry forest is dominated by trees that lose their leaves during the driest months of the year (Rzedowski, 2006), which lasts between 5 and 6 months in the reserve; the canopy height ranges between 8 and 12 m. Stem diameters rarely reach 50 cm, and the branches develop at low heights. The shrub cover is sparse, except in gaps where the tree canopy is open from damage to branches or tree falls. Some of the dominant tree species, either by size or by density, include the naked Indian tree *Bursera simaruba* (Burseraceae), black poisonwood *Metopium brownei* (Anacardiaceae) and *Caesalpinia gaumeri* (Fabaceae). Other conspicuous elements of this forest include the presence of columnar and shrubby cacti, the existence of epiphytic plants such as bromeliads and orchids, and some palm-like trees such as *Beaucarnea philibilis* (Asparagaceae).

The savannah consists of isolated patches dominated by low trees (8 m or less) that are surrounded by a matrix of bare rocky soil with abundant herbs and grasses during the rainy season. Some species are shared between this vegetation type and the dry forest type, such as the naked Indian tree;

however, individuals here are smaller due to the shallow soils. In some sections, the drainage is poor, and since its terrain is flat, with almost non-existent slope, it can be flooded during part of the rainy season.

The coastal scrubland exhibits a structure typical of dry regions, which may be due to the combination of high temperatures and sandy soil, which reduce the water stored in the soil and increase the evaporation rates. This vegetation type is dominated by small palm trees and shrubs, which do not reach 6 m in height and produce branches less than 1 m from the soil. Several shrub species are thorny or spiny; Cactaceae such as *Opuntia stricta*, *Acanthocereus pentagonus* and *Selenicereus grandiflorus* are very abundant, together with other succulent plants, such as *Agave angustifolia*. Epiphytic bromeliads and orchids are common and, in some patches, can be very abundant.

In each vegetation type, two sites were selected, each representing the two land management types: the core and the buffer zones of the reserve. Sites were a minimum of 2 ha. Malaise traps were used for ichneumonid sampling, which is the method most often used in monitoring programmes (e.g., Gauld, 1991; Longino, 1994) and which produce large captures of hymenopteran parasitoids (Sääksjärvi *et al.*, 2004, 2006; Fraser *et al.*, 2007). Twelve traps in total (two traps per site) were used. At each site, the traps were separated by 2 km and were placed at the centre of the vegetation type to avoid edge effects. The sampling programme was carried out for 14 months, from June 2008 to September 2009, with samples collected every 15 days.

Neotropical fauna keys were used to identify Ichneumonidae, (e.g., Townes & Townes, 1966; Dasch, 1974; Gauld, 1988, 1991, 1997, 2000; Gauld *et al.*, 1998, 2002), Mexican fauna (e.g., Kasparyan & Ruiz-Cancino, 2005, 2008) and Nearctic fauna (e.g., Townes & Townes, 1959, 1962; Townes, 1969, 1970a, b, 1971; Dasch, 1979). Due to a lack of keys, some subfamilies, such as Ichneumoninae, Campopleginae and Orthocentrinae, were only identified to the genus level and separated as morphospecies using the keys by Townes & Townes (1966), Townes (1970b) and Townes (1971).

Some of the collected materials were compared with type and non-type specimens from the following institutions: Instituto Nacional de Biodiversidad (INBio), currently MNCR (Costa Rica), the American Entomological Institute and the Florida State Collection of Arthropods (Florida, USA), the Museo de Insectos of the Universidad Autónoma de Tamaulipas (México) and the Természettudományi Múzeum Állattára (Budapest, Hungary).

The collected material was deposited at the Colección Entomológica de la Universidad de Alicante (Spain) and the Colección Entomológica Regional at the Universidad Autónoma de Yucatán (México).

Data analysis

To assess whether all species at each site were represented in the sample, nonparametric richness estimators were calculated using EstimateS 8.2 (Colwell, 2009); the estimators included ICE (Incidence-based Coverage Estimator), Jackknife 1 and ACE (Abundance-based Coverage Estimator), which are well fitted for small samples (Magurran, 2004). The rarefaction curves were built to compare species richness using EcoSim700 (Gotelli & Entsminger, 2004) with confidence limits of 95%. Then, to test for differences in species composition among seasons, we performed a nonparametric one-way

analysis of similarity (ANOSIM), wherein shared species are shown using Venn diagrams.

We ran a Generalized Linear Model (GLM) (McCullagh & Nelder, 1989) to determine the influence of vegetation type, land management and season on species richness and abundance. Three variables were analyzed under the structure of repeated measures: factor 1 (inter-subject) included vegetation type (three levels), factor 2 (inter-subject) included land management (two levels) and factor 3 (intra-subject) included seasons (three levels). Each dependent variable was individually analyzed with a Poisson probabilistic model and a log link function. Differences among levels of factors were analyzed with a Bonferroni pairwise estimation (<0.05). A Wald statistical test, using the maximum likelihood method, was used to evaluate the effects of covariates (vegetation types, land management and seasons) on species abundance and richness. The statistical analysis was run in SPSS 22 for Mac.

The α diversity was measured using the Simpson diversity and Pielou evenness indexes (Zar, 1984), which were calculated with 95% confidence intervals obtained by bootstrap resampling using the Species Diversity and Richness software (Henderson & Seaby, 2002); the β diversity was described using the Jaccard index of similarity (Magurran, 2004).

The γ spatial diversity of the reserve was calculated according to the partition model of diversity. This analysis calculates the contribution of alpha and beta diversities to the gamma or landscape diversity. The relative importance of local species diversity and turnover in each vegetation type and its contribution to the total γ diversity of RBRL were analyzed using the additive partition model of diversity, which permits the evaluation of significant differences between diversity levels and identification of the principal components of diversity contributing to the total diversity. We estimated the partition of γ diversity (Crist *et al.*, 2003) as follows: $\gamma = \alpha_s + \beta_s + \beta_z + \beta_v$, where γ is the total species richness recorded in the RBRL, partitioned in average richness within sites (α_s), among sites within management zones (β_s), among management zones (β_z) and among vegetation types (β_v). We evaluated whether the observed partitions could have been obtained by a random allocation of individuals using 10,000 individual-based randomizations with PARTITION software (Veech & Crist, 2009).

To analyze the relationship among ten guilds of parasitoids and vegetation type and seasons, we ran a Redundancy analysis (RDA, Legendre & Legendre, 1998), which was selected over Canonical Correspondence Analysis because of the reduced length of the gradient of our variables (Ter Braak & Smilauer, 2002). The length of gradients was calculated using detrended correspondence analysis (Hill, 1979). The significances of each guild of parasitoid and seasonality were treated as dummy variables, as well as the first axis and all axes, which were tested within the forward selection procedure using a Monte Carlo random permutation test (499 permutations, $P \leq 0.05$). The analysis was performed using Canoco 4.5 (Ter Braak & Smilauer, 2002). The trophic guilds followed the classification of Mazon & Bordera (2014), who recognized ten guilds of parasitoids belonging to Ichneumonidae family, and based on the classification criteria from Garbarczyk & Sawoniewicz (1984), to define the trophic level membership of their hosts and food specialization:

Coc: parasitoids of cocoons and pupae.

cPh: parasitoids of concealed phytophagous larvae feeding inside above-ground plant parts, such as leaf rollers, leaf folders, gall formers and leaf miners.

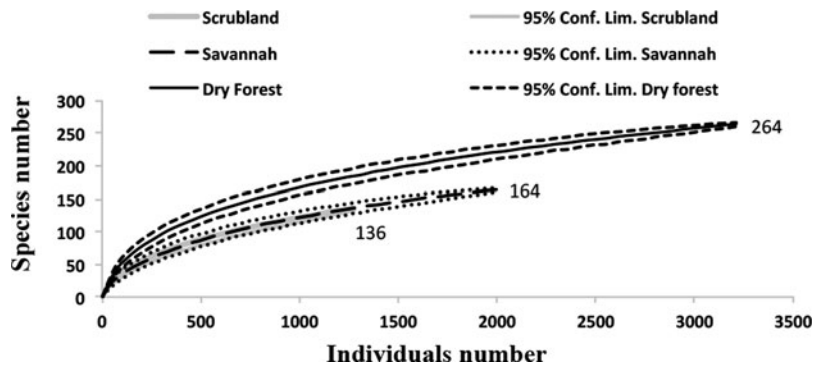


Fig. 1. Rarefaction curves of the Ichneumonidae in the three vegetation types in the RBRL for species collected in the Malaise traps. The richness is indicated at the end of each line. The standardized sampling effort was 1321, which the smallest number of individuals found in any vegetation type. The rarefaction curves exhibited higher species richness in the dry forest (264 species) compared to the savannah (164 species) and coastal dune scrubland (136 species).

gPh: parasitoids of exposed phytophagous larvae feeding on the external parts of plants, such as leaves, stems, flowers and buds.

Mel: parasitoids of melitophagous larvae of bees that feed on stores of honeydew, nectar and pollen and wasp larvae living in nests.

Myc: parasitoids of larvae living in the fruiting bodies of mushrooms and bracket fungi.

Poly: polyphagous parasitoids whose host range include two or more arthropod orders with different trophic habits.

Sap: parasitoids of saprophagous larvae.

Unkn: unknown parasitoids whose hosts remain unknown.

Xyl: parasitoids of xylophagous larvae, excluding those feeding in dead but not decomposing wood.

Zoo: parasitoids of zoophagous larvae and spiders.

Results

A total of 6686 individuals representing 18 subfamilies, 113 genera and 336 species were captured during the study period. The ICE richness estimator predicted a higher maximum number of species of 475 in the RBRL, while the ACE estimator predicted 473 species. Thus, according to both estimators, the species inventory was approximately 71% complete. Below, we describe the influence of vegetation type, land management and seasonality on Ichneumonidae diversity.

Evidence from vegetation type

The rarefaction expected richness of 1321 individuals per vegetation type indicated a significantly higher cumulative richness in the dry forest (with 264 species) than in the savannah and coastal dune scrubland (with 164 and 136 species, respectively) (fig. 1). The species composition changed among vegetation types (fig. 2); in the savannah and in the coastal dune scrubland, the most abundant species was *Microcharops anticarsiae*, and in the dry forest, two species were dominant, *Agonocryptus chichimecus* and *Camera euryaspis*. We found the highest α diversity in the dry forest, followed by scrubland and savannah (Table 1). Few species were shared among all vegetation types (Table 2), reflecting high β diversity in the RBRL; the scrubland and savannah were the vegetation types with the highest similarity.

Evidence from land management

A comparison of species richness among management policies for each vegetation type revealed differences only in the dry forest; scrublands and savannahs exhibited no differences between the buffer and core zones (fig. 3). However, species composition differed according to land management only in the dry forest; the dominant species was *Agonocryptus chichimecus* in the buffer zone and *Camera euryaspis* in core zone (fig. 3). In the savannah and dry forests, the α diversity was different between the conservation status zones (Table 1). The highest species shift was observed between the buffer and core zones in the scrubland (Table 2).

Partition diversity at the landscape level

The gamma diversity in the RBRL was 336. This regional diversity was more influenced by species turnover among management zones ($\beta_z = 102.17$ species) and among vegetation types ($\beta_v = 100$ species) than among sites ($\beta_s = 39.91$ species) and species richness within sites ($\alpha_s = 93.92$ species); all of these values (β_z , β_v , β_s , α_s) were equivalent to 30, 30, 12 and 28% of the contribution to the total richness (336), respectively. However, the only turnover among management zones (β_z) and among vegetation types (β_v) exhibited higher diversity than expected for a random distribution ($P < 0.001$). The other values, (α_s) and (β_s) did not differ significantly from the random distribution (fig. 4).

Evidence from seasonality

The species richness was similar among the three sampled seasons (fig. 5). During the rainy season, the ensembles were more 'heterogeneous', with several species having similar abundance; in contrast, during the north-winds and dry seasons, only two and one dominant species were found, respectively (fig. 6). The α diversity differed among seasons, with greater diversity in the north-winds and rainy seasons than in the dry season (Table 3). The species composition was different among seasons (ANOSIM: $R = 0.7124$; $P = < 0.0001$), with only approximately 1/3 of species shared among all three seasons (fig. 7).

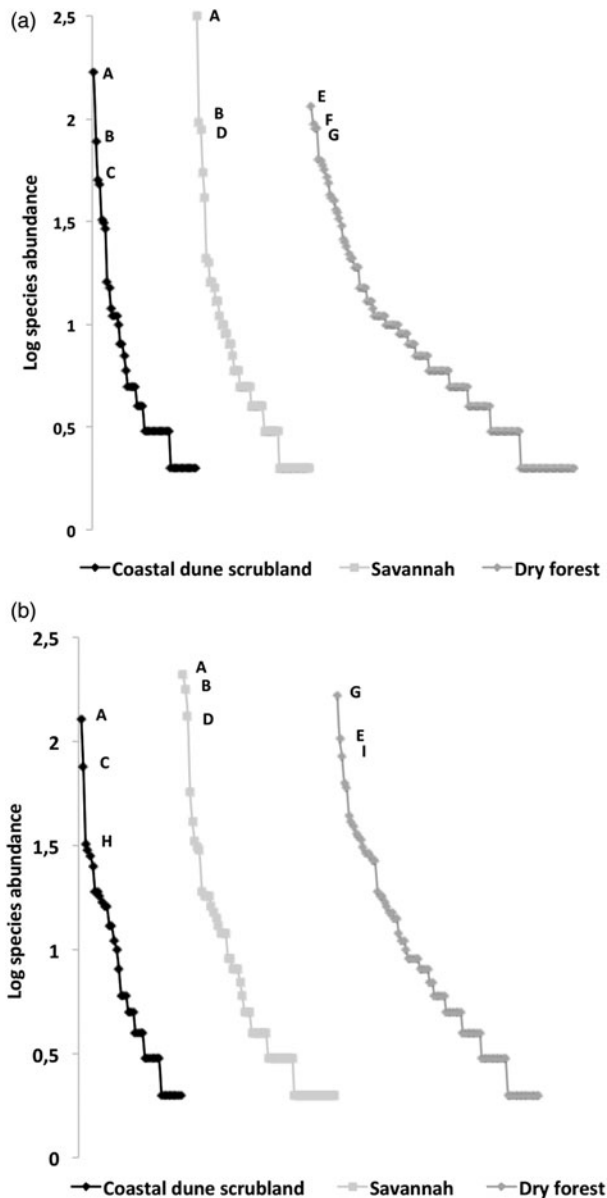


Fig. 2. Rank-abundance plots of ichneumonid ensembles collected from the three vegetation types in the RBRL: (a) buffer zone and (b) core zone. A logarithmic scale of abundance was plotted against the species-rank ordered by species, from those with the most abundant individuals to those with the fewest. The species codes were as follows (only the three most abundant): A, *Microcharops anticarsiae*; B, *Eiphosoma dentator*; C, *Xiphosomella roxana* D, *X. ozne*; E, *Agonocryptus chichimecus*; F, *Baltazaria crassicornis*; G, *Camera euryaspis*; H, *Casinaria* sp.; I, *Baltazaria rufonotata*.

Interactive effects of vegetation type, land management and seasonality

We found significant influences of vegetation type, land management and season on the abundance of parasitoids, including almost all of the interaction effects (Table 4). Of the three vegetation types, the dry forest had the highest abundance. Furthermore, in terms of land management, the

parasitoid abundance was higher in the buffer zone than in the core zone. Finally, we found a higher parasitoid abundance during the rainy season than during the north-winds and dry seasons. We observed that the species abundance was higher in the buffer zone than in the core zone. Surprisingly, when we analyzed the interaction types of vegetation \times season, we uncovered a different pattern; parasitoid abundance was higher in the rainy season in the coastal dune scrubland and the dry forest, but was the lowest in savannah vegetation. The interaction of vegetation type \times land management \times season was statistically significant, reflecting a cross-effect of factors and a differential magnitude of effects relative to the three factors. In other words, parasitoid abundance increased in almost only one direction: higher abundance in the dry forest, buffer zone and rainy season.

Guilds of parasitoids, vegetation type and seasonality

Among the 9 guilds defined in this work, exposed and concealed phytophagous were the most abundant, which together represented 56% of the collected individuals; the third most abundant guild was the cocoon parasitoid (Table 5). Possible relationships between the guilds of parasitoids with the vegetation types and seasonality were analyzed. The RDA tri-plot indicated a reduced separation of the guilds of parasitoids on the axes (sum of eigenvalues axes 1–4 = 0.21; and the guilds and type of vegetation – seasonality correlations = 0.631 (axis 1) and 0.378 (axis 2)); however, Monte Carlo permutation tests were significant for the first canonical axis (F -ratio = 28.4, $P \leq 0.005$) and for all canonical axes ($F = 5.89$, $P \leq 0.05$). Only vegetation type, such as dry forest buffer (DFB; $F = 13.65$, $P = 0.002$), dry forest core (DFC; $F = 12.55$, $P = 0.002$) and rainy season ($F = 12.34$, $P = 0.002$) were significant in the model. For example, DFB and DFC had strong positive relationships with the Coc and Myc parasitoid guilds, while only DFC had a strong negative relationship with the cPh parasitoid guild. Although the rainy season had a significant effect on the model, only weak positive relationships were detected with the cPh and gPh parasitoid guilds (fig. 8).

Discussion

The estimated values of species richness suggest that approximately 71–74% of Ichneumonidae species were sampled at the study sites in the RBRL. These results were adequate for comparative studies of parasitoid diversity according to other studies providing results ranging between 70 and 80% of the expected species (Skillen *et al.*, 2000; Sääksjärvi *et al.*, 2004; Fraser *et al.*, 2007; Mazon & Bordera, 2008).

Vegetation

In our study, as in others (e.g., Sääksjärvi *et al.*, 2006; Fraser *et al.*, 2008b), vegetation had a strong influence on species richness, which is in keeping with the EH, which predicts that structural complexity and high plant diversity favour increased predators or parasitoids (Price *et al.*, 1980; Sheehan, 1986; Letourneau, 1987; Russell, 1989; Mulder *et al.*, 1999; Jactel & Brockerhoff, 2007; Vehviläinen *et al.*, 2007, 2008; Scherber *et al.*, 2010; Zhang & Adams, 2011; Borer *et al.*, 2012; Zou *et al.*, 2013). In the RBRL, the tropical dry forest was the vegetation type with the highest richness and

Table 1. Simpson Diversity (1/D) and Pielou evenness (J') according to the 95% confidence limits obtained by bootstrapping.

Habitat	1/D	Inferior limit	Superior limit	J'	Inferior limit	Superior limit
Scrubland total	13.45	11.85	15.07	0.71	0.72	0.75
Savannah total	9.939	9.086	10.81	0.65	0.65	0.68
Forest total	40.56	37.53	42.74	0.78	0.78	0.81
Scrubland buffer	11.79	9.995	13.58	0.71	0.71	0.76
Scrubland core	13.54	11.36	15.73	0.74	0.74	0.79
Savannah buffer	7.512	6.618	8.392	0.65	0.65	0.69
Savannah core	11.83	10.66	13.01	0.68	0.69	0.72
Forest buffer	48.66	44.01	51.47	0.82	0.83	0.85
Forest core	27.37	24.24	29.94	0.79	0.79	0.82

Table 2. Qualitative similarity species index.

Vegetation type		Shared species (observed)	Shared species (estimated)	Jaccard
Scrubland	Savannah	95	147	0.45
Scrubland	Forest	109	156	0.37
Savannah	Forest	114	172	0.36
Scrubland Buffer	Core	54	109.78	0.39
Savannah Buffer	Core	68	180.68	0.41
Dry forest Buffer	Core	111	176.89	0.42

diversity. The dry forest had the most structured complex vegetation (Noyes, 1989), offering a greater variety of resources such as food, refuge and mating sites; these conditions facilitate a higher diversity of herbivorous insects and, as a consequence, of parasitoids (Hawkins & Lawton, 1987; Hawkins *et al.*, 1992; Jervis *et al.*, 1993 in Idris & Hainidah, 2003; Sääksjärvi *et al.*, 2006; Fraser *et al.*, 2008b); furthermore, it has been reported that many herbivorous insects produce volatile compounds from different plant species that can attract different species of parasitoids (Godfray, 1994).

The similar richness observed between the scrubland and the savannah may be due to their similar vegetation structures (Flores & Espejel, 1994), which may produce a similar diversity of herbivorous insects and associated parasitoid diversity (Hawkins & Lawton, 1987; Hawkins, 1988). Furthermore, the lower diversity in the savannah could be explained by the simpler vegetation structure, which may lead to a lower host diversity and, as a consequence, lower parasitoid diversity.

These results largely agree with those obtained previously in the RBRL by Gonzalez-Moreno *et al.* (2010) in a study on Cremastinae and Labeninae (Ichneumonidae), who reported the highest species richness in the dry forest, and by González-Moreno *et al.* (2015) on Cryptinae (Ichneumonidae), who also found the highest values of abundance and diversity in the dry forest. However, our results appear to contradict those reported by Chay-Hernández *et al.* (2006) and Mazon & Bordera (2014), who identified the highest diversity of ichneumonids in open areas surrounded by natural forest, which may be favoured because these areas allow them to pass from one habitat to another, acting as biological corridors (Haddad *et al.*, 2003). However, in this case, a more open savannah is also a harsh environment with higher temperature and humidity fluctuations, leading to further reductions in insect

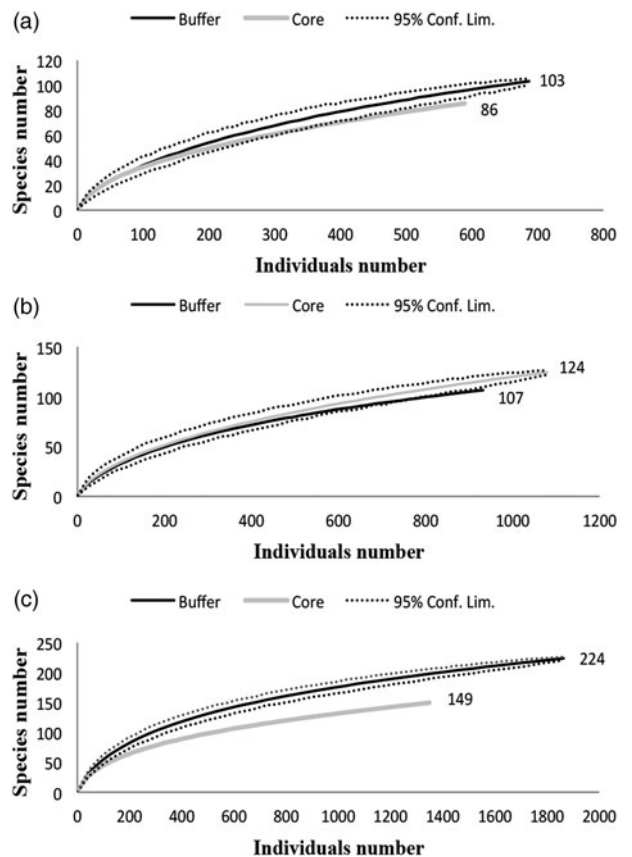


Fig. 3. Rarefaction curves of both conservation status types under three vegetation types: (a) Scrubland, (b) Savannah and (c) Dry forest.

biodiversity (Gauld, 1987; Shapiro & Pickering, 2000). The savannah was also the most fragmented vegetation type, surrounded by roads and urban areas, especially in the buffer zone. Furthermore, the disturbance intensity is not the only factor that affects diversity (Idris *et al.*, 2001; Chay-Hernández *et al.*, 2006); the surrounding landscape also has an effect (Chay-Hernández *et al.*, 2006). Therefore, it is necessary to maintain as much quality landscape heterogeneity as possible because many insects require a variety of structural vegetation types, fields and forest boundaries (Samways, 2007), and many studies conclude that landscape diversity favours parasitoid diversity, especially in landscapes with crops

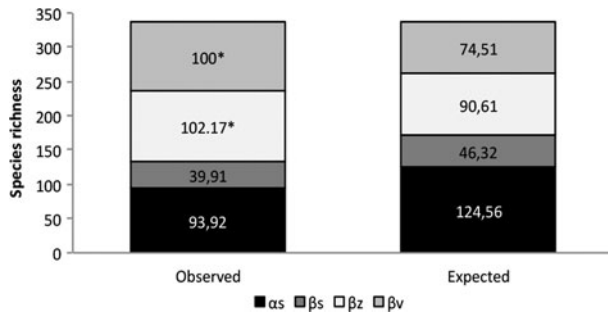


Fig. 4. Spatial additive partitioning of Ichneumonidae species richness at four levels: within sites (α_s), among sites within management zones (β_s), among management zones (β_z), and among vegetation types (β_v). Asterisks indicate statistical significance ($P = 0.001$) based on 10,000 randomizations.

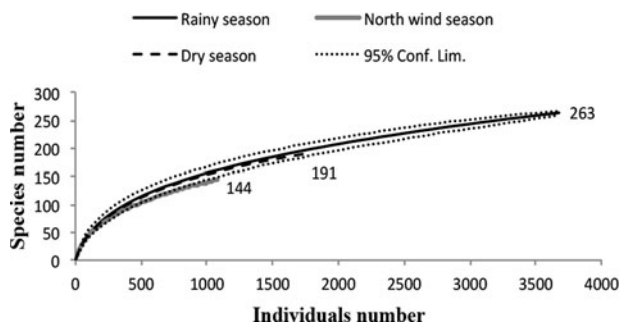


Fig. 5. Rarefaction curves for Ichneumonidae during the three seasons for the species collected in the Malaise traps, whose richness values are indicated at the end of each line. The standardized sampling effort was 1110, which is the smallest number of individuals found in any vegetation type. Rarefaction curves indicate similar species richness during the rainy season (263 species), dry season (191 species) and north-winds season (144 species).

surrounded by natural vegetation (Östman *et al.*, 2001; Roschewitz *et al.*, 2005; Tschardt *et al.*, 2005; Zhao *et al.*, 2014; Pak *et al.*, 2015; Meagher *et al.*, 2016); therefore, landscape simplification has a negative effect on the species richness of natural enemies (Inclán *et al.*, 2014). Unfortunately, the savannah in the RBRL could be considered an 'island' because it is a vegetation patch surrounded by urban areas and roads.

The dominant ichneumonid species suggest that parasitoids are exploiting different resources depending on the vegetation type. Ichneumonid species shifts were high among the vegetation types. It is possible that the low similarity between communities was due to the narrowness of the ichneumonids' niches, which allowed the coexistence of many species (Hirose, 1994) and led to specious communities.

Land management

Land management influences Ichneumonidae abundance and richness, probably by modifying resource heterogeneity and availability. A general tendency towards higher species richness in buffer zones was found in this study. A possible

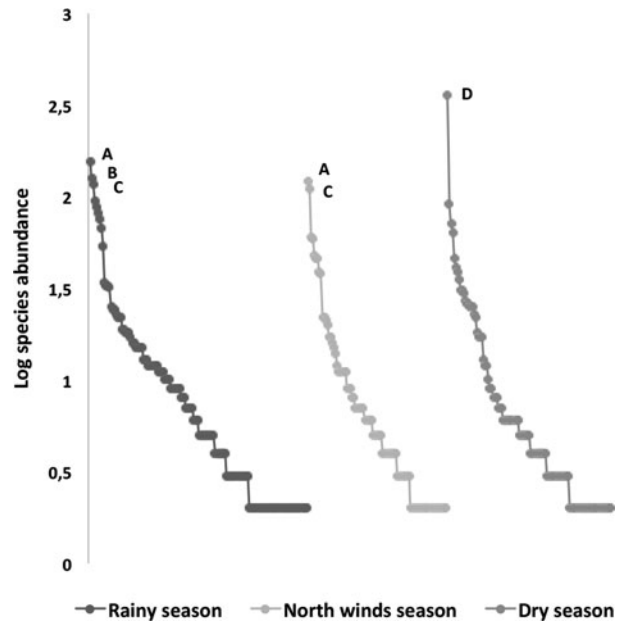


Fig. 6. Rank-abundance plots of ichneumonid ensembles collected throughout the year during three seasons (rainy, north-winds and dry); a logarithmic scale of abundance was plotted against the species-rank ordered by species with the most individuals to those with the fewest. Species codes include only the most abundant: A, *Agonocryptus chichimecus*; B, *Eiphosoma dentator*; C, *Xiphosomella ozne*; and D, *Microcharops anticarsiae*.

explanation for this is the intermediate disturbance hypothesis (IDH), which states that diversity will be higher in sites where disturbance is not very frequent or very intense than in undisturbed or very intensively or frequently disturbed sites (Connell, 1978; Speight *et al.*, 2008). Insects are no exception; several authors have supported the use of IDH for different functional groups, including specialized apple pests (Szentkirályi & Kozar, 1991), insect herbivores (Stork *et al.*, 2017) and parasitoids in agricultural systems (Landis & Menalled, 1998; Lewis & Whitfield, 1999; Menalled *et al.*, 1999; Klein *et al.*, 2002; Chay *et al.*, 2006).

In our study, the highest diversity was found in the buffer zone of the forest, which could be explained by the vegetation in the Yucatan deciduous forests; it has been reported that at intermediate disturbance levels, young trees are the dominant life form but do not yet suppress the herbaceous and shrubby vegetation (Leirana-Alcocer *et al.*, 2009), offering a variety of resources and microhabitats to herbivores and their predators (Price *et al.*, 2011). In other words, it has been suggested that on lightly disturbed land (i.e., old abandoned farms), some arthropods specializing in 'mature' forests coexist with those specializing in disturbed habitats (New, 2015), leading to a higher species richness than that observed either in mature forests or urbanized land. Furthermore, the dry forest buffer has a higher environmental heterogeneity originating from the existence of a mosaic, including small orchards, cattle grazing and subsistence agriculture, together with forests at various stages of succession; these activities are forbidden in the core zone.

Importantly, on the savannah and scrubland, in both the buffer and core zones, the dominant species employ an

Table 3. Simpson Diversity (1/D) and Pielou evenness (J') according to the 95% confidence limits obtained by bootstrapping in the three seasons.

Hábitat	1/D	Inferior limit	Superior limit	J'	Inferior limit	Superior limit
Rainy season	22.52	20.68	24.19	0.70	0.68	0.70
North-wind season	25.86	22.55	28.36	0.67	0.65	0.68
Dry season	17.43	15.35	19.51	0.67	0.65	0.68

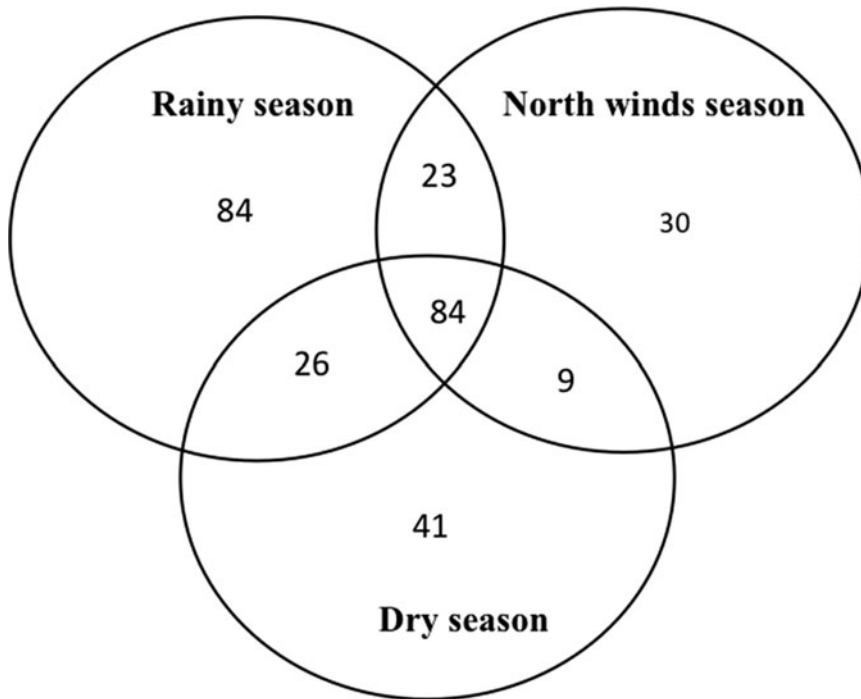


Fig. 7. Venn diagrams representing shared species of Ichneumonidae among seasons in the RBRL.

Table 4. Generalized linear model for the abundance of parasitoids among vegetation types, management zones and seasonality.

Effect	Abundance	Wald χ^2
Inter-subjects		
Vegetation types (Vt)		469***
Coastal dune scrubland	15.5 ± 0.56a	
Savannah	26.9 ± 0.72b	
Dry forest	39.2 ± 0.91c	
Land management (Lm)		54.8***
Core	22.4 ± 0.57a	
Buffer	28.8 ± 0.64b	
Intra-subjects		
Seasonality (S)		76.2***
Rainy season	30.9 ± 0.80a	
North-wind season	22.6 ± 0.69b	
Dry season	23.4 ± 0.73b	
Vt × Lm		7.8*
Vt × S		179.4***
Lm × S		1.7 ns
Vg × Lm × S		77.9***

Different letters indicate significant differences (Bonferroni < 0.05). ns, no significant; *P < 0.05; **P < 0.01; ***P < 0.001.

endoparasitoid koinobiont strategy, which is considered to be a specialist strategy for host species, mostly Lepidoptera, with low agricultural importance, such as *Spodoptera frugiperda*, *Mocis latipes*, *Euglyphis fibra*, *E. rivulosa*, *Alabama argillacea*, *Anticarsia gemmatalis* and *Autoplusia egea* (Yu et al., 2012). In forests, the two dominant species included idiobionts (ectoparasitoids with wide ranges of host species), suggesting higher herbivore diversity in the forest.

Furthermore, the other abundant Ichneumonid wasp in the forest buffer, *Agonocryptus chichimecus*, has been widely collected in different habitats in Mexico (Ruiz-Cancino 2010) and is a known predator of several species of Coleoptera, including *Aerenicopsis championi*, *Anelaphus parallelus*, *Psyrassa unicolor*, *Saperda vestita*, and *Anthonomus grandis* and of lepidopteran species, such as *Podosesia syringae*. The dominant ichneumonid species *Camera euryaspis* has unknown hosts (Yu et al., 2012). This result is similar to that reported by Stork et al. (2017), who found that disturbance affected the species composition more strongly than the species richness.

Communities were different not only among vegetation types but also between the conservation status zones (buffer or core zone) of each vegetation type; therefore, the parasitoid

Table 5. Individuals number and proportion of Ichneumonidae guilds.

Guilds	Individuals number	Percentage	Guilds	Individuals number	Percentage
cPh	2006	30.44	Myc	76	1.15
gPh	1673	25.38	Hyp	62	0.94
Coc	1390	21.09	Zoo	27	0.41
Unkn	1015	15.40	Mel	19	0.29
Xyl	166	2.52	Poly	2	0.03
Sap	155	2.35			

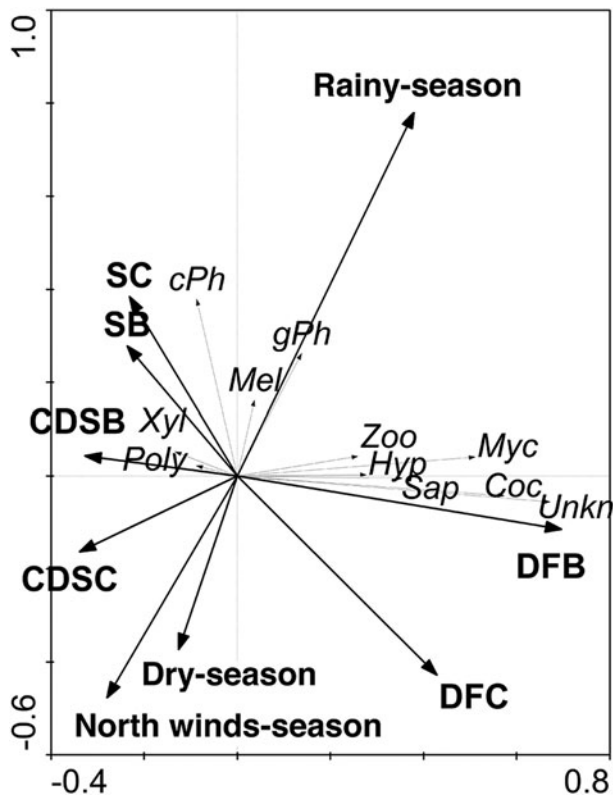


Fig. 8. Redundancy analysis (RDA) scatterplot illustrating the relationships among 9 guilds of parasitoids, types of vegetation and seasonality. The thick arrows represent the types of vegetation and seasonality. The thin arrows refer to the parasitoid guild.

community seems to be very specific to each habitat and management category.

Landscape diversity

Notably, a larger component of the regional diversity was represented by the high species turnover between vegetation types and management zones. This pattern of high turnover could be explained by the variation in structural diversity (White *et al.*, 2006), even within the same vegetation types, which is an indicator that the RBRL has great microhabitat diversity and is able to support well-defined Ichneumonidae communities. These results reinforce the importance of the exclusive species within each vegetation type. Therefore, the diversity of ichneumon assemblages depends on the

vegetation structure of a site and its surrounding landscape in the RBRL.

Seasonality

Many studies, including the present study, have found that seasonality, especially rainfall, is important to determining parasitoid ensembles (Gauld, 1991; Shapiro & Pickering, 2000). In the RBRL, the abundance and richness of the species were influenced not only by the vegetation type and management zone but also by the season; the annual maximum diversity occurred during the rainy season, perhaps due to the higher productivity of vegetation and the peak of resource abundance, such as nectar, at this time of year in the RBRL, which occurs when most plant species are in flower and a higher diversity of herbaceous plants exists (Flores & Espejel, 1994; Andrade *et al.*, 2007). Our results agree with those obtained by González-Moreno *et al.* (2015) in the RBRL; several other studies have been conducted in the Neotropics on the same family and other Hymenoptera (Shapiro & Pickering, 2000; Tylianakis *et al.*, 2005) as well as with other insect orders, such as Diptera and Coleoptera (Sobek *et al.*, 2009), as well as in temperate zones in Mediterranean climates, where two peaks are observed throughout the year (Rodríguez-Berrió, 2006; Mazon & Bordera, 2008) that are associated with maximum rainfall and mild temperatures (Mazon & Bordera, 2008).

The composition of ichneumonid species changed throughout the year, depending on the season, with only approximately 33% of species common among all seasons. These seasonal changes in species were not unusual; for instance, in Ecuadorian forest Hymenoptera, there was 30% species turnover from the rainy to the dry season (Tylianakis *et al.*, 2005). Beetles also exhibited high seasonal species turnover (Sobek *et al.*, 2009). In the RBRL, this pattern could be explained by the fact that phytophagous communities are also in constant flux throughout the year, following the vegetation phenology and species changes (Andrade *et al.*, 2007). Furthermore, as with other insects, Ichneumonoidea wasps are able to react to environmental factors, such as seasonal photoperiod, temperature, humidity (González-Moreno *et al.*, 2012) and air flow (Gullan & Cranston, 2000). It is also important to consider the ordination results that indicated opposing directions of species dissimilarity related to seasonality. However, the species composition was analyzed by guild; therefore, these differences could be marked by seasonality together with other biotic conditions such as hosts.

Guilds of parasitoids, vegetation type and seasonality

Our results coincide with those of Mazon & Bordera (2014), who found that phytophagous parasitoids are the most

abundant guild in Spanish forests. It has been estimated that there are five to six species of parasitoid for every phytophagous insect (Askew & Shaw, 1986; Hawkins & Lawton, 1987). Nevertheless, even when they were the most abundant, phytophagous parasitoids experienced no strong influence from vegetation or land management and only appeared to be weakly impacted by season. This pattern might be caused by the complexity of the tropical forests, in which abundant chemical signals may hinder a parasitoid's ability to find its host species (Portillo-Quintero & Sánchez-Azofeifa, 2010). This effect is even more evident in specialized parasitoids (De Rijk, 2016), as most of the species identified in this study were specialized koinobionts. A koinobiont abundance pattern was also found by other authors (Askew & Shaw, 1986; Hawkins, 1988; Chay-Hernández *et al.*, 2006). Therefore, it is possible that insect populations in the RBRL are very abundant and able to support viable specialized koinobiont assemblages (Hawkins & Lawton, 1987; Hawkins *et al.*, 1992).

Vegetation type and management had an important effect on the guilds, and the buffer and core zone of the dry forest had a positive impact on the Coc and Myc parasitoid guilds, which attack cocoons and pupae and the concealed larvae living in the fruit bodies of mushrooms and bracket fungi, respectively. Members of the Coc guild are generalist parasitoids (idiobionts), and their strong relationship with dry forests may be due to their search strategies; in complex vegetation with a high richness of potential hosts (Janzen, 1981) and non-hosts (De Rijk, 2016), generalist parasitoids may be favoured. Furthermore, generalist parasitoids respond with greater intensity to vegetation diversity, as they depend on a higher availability of host species and alternative resources that can be found in heterogeneous habitats (Sheehan, 1986). The Myc guild requires environmental conditions such as high humidity, which supports the growth of fungi, conditions that are absent in savannahs and coastal dune scrublands.

These findings are very different from the findings of Mazon & Bordera (2014), who reported that parasitoids with generalist habitats are dominant in oak woodland, which is a homogeneous habitat, while parasitoids of xylophages are characteristic of scrubland. In our study, xylophages were not associated with vegetation and represented only 2% of the total abundance.

In contrast, the core zone had a strong negative relationship with the cPh parasitoid guild of concealed phytophagous larvae feeding inside above-ground plant parts, such as leaf rollers, leaf folders, gall formers and leaf miners. Therefore, the explanation that the most structurally complex vegetation favours parasitoid diversity, as previously stated, was not at work in this guild, which may be because this parasitoid type needs visual cues to find the host, such as damage by leaf miners (Quicke, 2015). In a dry forest with complex vegetation (Noyes, 1989), these cues are difficult to identify (De Rijk, 2016). Other studies have found no effects from genotypic diversity or species diversity on leaf miner abundance, parasitism or parasitoid species richness (Abdala-Roberts *et al.*, 2016).

This study highlights the role of vegetation type, land management based on conservation type, and seasonality on the diversity of Ichneumonidae in a protected area of Mexico, resulting in the following findings: (1) the vegetation type influenced species richness and abundance of Ichneumonidae, with the dry forest having the highest diversity, supporting our first hypothesis in keeping with the EH, which predicts that structural complexity and high plant diversity favour increased predators or parasitoids. (2) Furthermore, land

management influences Ichneumonidae diversity but in a manner opposite what was expected; diversity was higher in the buffer zone than in the core zone, rejecting our second hypothesis. Nevertheless, these results are based on the IDH, which states that diversity can be higher at sites where disturbance is not very frequent or very intense than in undisturbed or very intensively or frequently disturbed areas. (3) The evidence supported our third hypothesis predicting the highest parasitoid abundance in the rainy season because of the increase in productivity and vegetation complexity. (4) Finally, vegetation and management had a positive impact on parasitoid guilds that attack cocoons and on the pupae and parasitoids that attack concealed larvae living in the fruiting bodies of mushrooms.

In conclusion, variations in the diversity of parasitoid assemblages in the RBRL can be explained at both local and landscape scales. At the local scale, diversity was mainly influenced by the vegetation type, followed by seasonality and management policies, resulting in different assemblages with high beta diversity, both at spatial and temporal scales. However, at the landscape scale, land management is as important as the vegetation type, each contributing 30% to the regional diversity of Ichneumonidae. Considering that the RBRL's fundamental objective is to protect and conserve biodiversity over a large area of high ecological value in south-eastern Mexico, fostering compatibility between the undisturbed vegetation conservation areas and the areas where agricultural holdings are permitted and traditional forestry use exist inside the reserve, our results provide an interesting reference for the reserve managers. These findings demonstrate that this type of environmental conservation policy contributes to the maintenance of high diversity at the landscape level, as both types of management (core and buffer) are complemented, increasing the diversity of different parasitoid assemblages.

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