

## Research Paper

**Cite this article:** González-Moreno A, Bordera S, Ballina-Gómez H, Leirana-Alcocer J (2023). Age matters: variations in parasitoid diversity along a successional gradient in a dry semi-deciduous tropical forest. *Bulletin of Entomological Research* **113**, 604–614. <https://doi.org/10.1017/S0007485323000287>

Received: 24 February 2023  
Revised: 17 May 2023  
Accepted: 19 June 2023  
First published online: 29 August 2023




### Keywords:

Diversity; guilds; Ichneumonidae; neotropic; successional stages

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# Age matters: variations in parasitoid diversity along a successional gradient in a dry semi-deciduous tropical forest

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## Abstract

Parasitoids are an important group of insects because their species number is among the highest. Multiple studies have addressed the relationships between forest successional age and insect diversity by focusing on herbivorous organisms, but changes in diversity of parasitoids are still poorly known. This work analyses the diversity of parasitoids in tropical forests representing three successional stages. A total of 30 traps were placed, ten in each forest successional stages. We estimated true diversity of Ichneumonidae species and guilds and explored the relationship between their diversity and the abundance of plant species using an Indicator Species Analysis; the relationship between parasitoid species and plant richness and abundance was tested using a Redundancy Analysis. A total of 1522 individuals and 168 morpho-species were captured in four months. Species richness showed no differences; however, parasitoid abundance was higher in young forest, while intermediate forest had the highest true diversity values ( ${}^1D$ ) with 71.6 effective species. According to insect guilds, richness, abundance, and diversity were similar in the three vegetation successional stages. This finding may be explained based on the intermediate disturbance hypothesis, which postulates that moderate disturbance levels favor the highest diversity. In conclusion, successional age matters, i.e., diversity is the highest in intermediate stages, while the old forests harbors guilds unique to that successional stage, such as parasitoids of melitophagous larvae of bees. Other successional stages were characterized by a single species of parasitoid, belonging to the genera *Eiphosoma* and *Anomalon*, which may indicate altered and preserved forests, respectively.

## Introduction

Parasitoids are insects belonging mostly to the Hymenoptera, an order that well could be 2.5 to 3.5 times larger than the order Coleoptera, currently the richest order in described species (Forbes *et al.*, 2018). Parasitoids have high economic and ecological relevance as their larvae feed on other insect species, killing them in the process (Godfray, 1994), so they control populations of species that could otherwise damage wild and cultivated plants (LaSalle and Gauld, 1993). In addition, parasitoid populations depend on the abundance of their hosts and are also indicators of community diversity and abundance, which ultimately depend on vegetation integrity and productivity (Sharkey, 2007).

Multiple studies explain the relationships between vegetation and parasitoids. The information reported to date is inconsistent because several authors claim that a more complex vegetation structure, with larger number of different microhabitats available, as shelters and food resources, support a higher parasitoid diversity (Price *et al.*, 1980; Russell, 1989; Hawkins *et al.*, 1992; Sääksjärvi *et al.*, 2006; Fraser *et al.*, 2007; Scherber *et al.*, 2010; Rubene *et al.*, 2015). In contrast, other authors claim that the herbivore-induced volatiles produced by different plant species are more important than plant complexity (e.g., Koricheva *et al.*, 2000) because they attract different species of parasitoids (Godfray, 1994; Wäschke *et al.*, 2014).

The structural complexity and species richness are driven mainly by forest succession (Basset *et al.*, 2001). In tropical forests, early successional stages (less than 20 years old) differ from old forests in the taxonomic and functional diversity of vegetation, as well as in litter production and vegetation structure (Lohbeck *et al.*, 2012; Nyafwono *et al.*, 2014; Souza *et al.*, 2019). Some studies have explained the inverse relationship between forest successional stage and insect diversity focused on predators and herbivorous insects (Neves *et al.*, 2014; Rubene *et al.*, 2015; Fonseca *et al.*, 2018; Rocha-Ortega *et al.*, 2018). In contrast, several authors have reported different results for tropical dry forests, where herbivory levels and herbivorous insect diversity were higher in advanced successional stages (Silva *et al.*, 2012; Neves *et al.*, 2014). Considering this, we would

expect parasitoid diversity to vary between forest successional ages, being highly sensitive to environmental changes, since parasitoids play a specialized ecological role and belong to upper trophic levels (LaSalle and Gauld, 1993; Shaw and Hochberg, 2001).

The present study is focused on sampling parasitoids of the family Ichneumonidae in a dry semi-deciduous tropical forest. This insect group comprises a high species diversity, being one of the species-rich families with over 25,000 known species (Yu *et al.*, 2016). The populations of each species tend to be small and closely related to their hosts. Parasitoids are especially vulnerable because they are scarcely represented in conservations policies, particularly in tropical subhumid and dry forests that have been disturbed by anthropogenic activities such as agriculture and cattle ranching, and are poorly represented in preserved areas (Hernández-Stefanoni *et al.*, 2010). The objective of the present study was to analyze the diversity of Ichneumonidae parasitoids in three forest successional stages. We hypothesized that parasitoid species richness and diversity would be higher in old forests but with lower abundances, consistent with their more complex structure. Also, the species composition of parasitoid assemblages may change according to forest age in terms of both species and guilds, especially regarding dominant species. This information will expand our knowledge of the diversity of parasitoids and the relationships between this insect group and vegetation structure along a successional gradient in one of the ecosystems most threatened by fragmentation.

## Materials and methods

### Study area

This study was conducted in the Kaxil-Kiuic private reserve, located at the south of Yucatan, Mexico (20°04' N–20°06' N; 89°32' W–89°34' W). The local climate is tropical warm with rainy summer and a dry season from November to April, with mean annual precipitation ranges between 1000 and 1100 mm. The landscape is dominated by seasonally dry semideciduous tropical forests (50%–75% of species shed their leaves during the dry season) of different ages after the abandonment of the traditional slash-and-burn agriculture. The canopy forest is 8–13 m high, with a few prominent old trees 15 to 18 m high. The most abundant tree species are *Neomillspaughia emarginata*, *Gymnopodium floribundum*, *Bursera simaruba*, *Piscidia piscipula*, and *Lysiloma latisiliquum* (Hernández-Stefanoni *et al.*, 2014).

Inside the tropical dry forest, we selected thirty sites belonging to three different types of land-cover and landscape structure (ten plots for each successional age), corresponding to different successional stages: early successional forest (hereafter young forest), six to nine years post-disturbance; intermediate successional forest (hereafter intermediate forest), 10 to 15 years post-disturbance; mature forest (hereafter old forest), +60 years post-disturbance (Hernández-Stefanoni *et al.*, 2010, 2014). The three successional ages have tree and shrubs as dominant growth forms. The young forest has a low relative low canopy stature (8–13 m) with a few prominent trees; in general have fewer species and less biomass than the older successional stages. The old forest has trees with 15–18 m of height (Hernández-Stefanoni, 2014).

### Parasitoid sampling

Ichneumonid insects were sampled using Malaise traps, which is the usual method in monitoring programs (e.g., Gauld, 1991;

Longino, 1994) and produces large captures of parasitic Hymenoptera (Sääksjärvi *et al.*, 2006; Fraser *et al.*, 2007; Chan-Canché *et al.*, 2020). A total of 30 traps were placed with a north-south orientation to maximize sampling efficiency (Darling and Packer, 1988), ten in each of the three forest successional stages, during the rainy season (August to November) of 2016. Every 15 days, samples were collected and preserved in 70% alcohol. All Ichneumonidae specimens collected were dry-pinned for taxonomic identification. Keys to the Neotropical fauna (e.g., Gauld, 1991, 1997, 2000; Gauld *et al.*, 1998, 2002), Mexican fauna (e.g., Kasparyan and Ruiz-Cancino, 2005, 2008) and Nearctic fauna (e.g., Townes and Townes, 1962; Townes, 1969, 1970a, 1970b, 1971), were used to identify Ichneumonidae to the genus level and morphospecies. All specimens were deposited in the Colección Entomológica de Referencia (Reference Insect Collection) at Instituto Tecnológico de Conkal (Yucatan, Mexico).

### Data analysis

The vegetation data used in this work (species richness, abundance, and species composition in each conglomerate) were evaluated previously by Hernández-Stefanoni *et al.* (2010; 2014); this evaluation was repeated in 2018 and 2021, and no changes were noted in the vegetation structure (Hernández-Stefanoni, personal communication). The diversity of Ichneumonidae was analyzed related to species richness, abundance, community structure, and true diversity of species and guilds. Trophic guilds followed the classification of Mazón and Bordera (2014):

**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.

**gPh:** parasitoids of exposed phytophagous larvae feeding on 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 of wasp larvae living in nests.

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

**Sap:** parasitoids of saprophagous larvae.

**Unkn:** parasitoids whose hosts remain unknown.

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

**Zoo:** parasitoids of zoophagous larvae and spiders.

**Hyp:** hyperparasitoids whose host range includes many species of primary parasitoids.

We used accumulation curves to visualize the completeness of sampling and extrapolate the species richness predicted by the nonparametric estimator Chao 1. We assessed differences in species richness between vegetation stages considering 95% confidence intervals (CI), generated by 1000 bootstrap resamplings (Colwell and Elsensohn, 2014) and using the software Estimates 9.0. To test for abundance differences between successional stages (SS), a Generalized Linear Mixed Model (GLMM) was run, in which SS was treated as the fixed factor and malaise traps as the random factor. A Poisson distribution and a Log link function were used. In addition, we used a Bonferroni test to identify

differences between SS. This analysis was run in The jamovi project (2022).

The structure of ichneumonid assemblages was compared using rank-abundance curves (Feinsinger, 2001). Ichneumonidae species diversity was calculated by means of true diversity measures, using the software SPADE (Chao and Shen, 2010). These measures consider three diversity levels, based in Hill numbers  ${}^qD$  (Jost, 2006):  ${}^0D$ , which refers to species richness only;  ${}^1D$ , which is the ecological diversity if all species had the same relative importance, counting individuals equally and weighing species in proportion to their abundance, uses the inverse of the exponential of Shannon's entropy (Jost, 2006); and order  ${}^2D$ , which considers only the dominant species, uses the inverse of Simpson index (Moreno *et al.*, 2011); with 95% CI to determine whether there were significant differences between forest stages.

We ran a cluster analysis (CA) and two-way cluster analysis (TWCA) to explore the similarity of successional age classes (SAC) and identify patterns of similarity in parasitoid species, parasitoid diversity variables (species richness, abundance, alpha diversity index), and indicator species of each SAC, using Euclidean measures based on quantitative data. These diversity variables (Appendix 1) were built in order to generate a dendrogram and to determine which values (abundance, Shannon's  $H'$  or species richness and other alpha indices) were more correlated with plant diversity. To link plant community and abundance data with SAC, we used an Indicator Species Analysis (ISA) (Ter Braak and Prentice, 1988; Dufrene and Legendre, 1997). Altogether, this information provided knowledge of the concentration of species abundance in a particular SAC and the fidelity of occurrence of a given species in that SAC. Indicator values for each species in each SAC were obtained and tested for statistical significance using the Monte Carlo test. ISA evaluated each species in terms of the strength of its response to the SAC, from the SAC matrix (3 conglomerates, belonging to the same sites selected to parasitoids sampling  $\times 3$  SAC). A threshold level of 60% with 95% significance ( $p$ -value  $\leq 0.05$ ) was selected as the cut-off value for identifying indicator species. These analyses were carried out with PC-Ord Ver.7 (McCune and Mefford, 2016).

The relationship between parasitoid species and plant richness, plant abundance, and SAC was tested through Redundancy Analysis (RDA; Legendre and Legendre, 1998). Before running the analyses, we calculated the length of the gradient (Braak and Smilauer, 2002) with a Detrended Correspondence Analysis (DCA; Hill, 1979). The statistical significance of each forest characteristic (plant richness, plant abundance, and SAC), as well as of the four axes, was tested within the forward selection procedure using a Monte Carlo random permutation test (999 permutations,  $P \leq 0.05$ ). These analyses were run using the software Canoco 4.5.

## Results

A total of 1522 individuals representing 18 subfamilies, 74 genera, and 168 morpho-species were captured during the studied period. The Chao richness estimator predicted a maximum of 199.5 species, so the species inventory from field sampling was approximately 84% complete. When the individual numbers from all sites were considered, Cryptinae and Cremastinae accounted for 60% of all individuals (464 and 445 individuals, respectively). *Diapetimorpha*, *Xiphosomella*, and *Acerastes* were the most abundant genera, with more than 100 individuals each (Appendix 2). Concealed phytophagous and cocoon parasitoids were the most abundant of the ten guilds defined in this work, with 511 and

364 individuals (34% and 24%, respectively) (fig. 1). The Ichneumonidae species and composition of community guilds are described below in terms of species richness, abundance, and true diversity across successional stages of vegetation in the tropical forest studied.

### *Ichneumonidae* community composition

Species richness showed no differences according to the Chao 1 estimator with 95% CI (fig. 2), with 177 species in the young forest, 170 species in the intermediate forest, and 111 species in the old forest; sampling efficiency from each vegetation stage was 80, 60, and 71% from the total species, respectively.

Abundance differed between vegetation stages according to the GLMM ( $\chi^2$  Wald = 1635;  $P < 0.001$ ; Deviance = 4.31, AIC = 285.2); the number of individuals was higher in young forest (798 individuals) than intermediate and old forests, with 372 and 352 individuals, respectively (fig. 3).

Diversity, defined as the effective number of species, i.e., considering species richness  ${}^0D$ , showed no differences between vegetation stages because there is overlap at the 95% CI. These results are consistent with the accumulation curves. However, for ecological diversity  ${}^1D$ , the intermediate forest shows the highest diversity, with 71.6 species. This successional stage surpasses the old forest by 15.9 effective species and the young forest by 12.46 effective species (Table 1). Finally, based on the diversity  ${}^2D$ , all sites yield a lower number of effective species because this value focuses on the most common species. Thus, intermediate and old forests show non-random differences in diversity with 95% CI, reaching more than twice the number of effective species relative to the young forest (Table 1).

The higher diversity of  ${}^2D$ , in intermediate and old forests may be due to the higher evenness of the ichneumonid assemblage in both successional stages (fig. 4). In the young forest, the parasitoid assemblage was dominated by a single species, *Eiphosoma* sp. 1, with 22% of the total number of individuals, almost twice the proportion of the dominant species in the other stages, resulting in lower evenness and less diverse communities. To note, this same species was the most abundant in the intermediate forest, but the most abundant species in the old forest was *Anomalon* sp. (fig. 4).

### *Ichneumonidae* guild composition

Guild richness was the same in the three different forest successional ages, with ten guilds (fig. 5). Abundance did not differ between vegetation stages according to the GLMM ( $\chi^2$  Wald = 4.96;  $P = 0.08$ ; Deviance = 5.26, AIC = 271.5).

True diversity  ${}^0D$  was higher in the old forest, but only by three additional guilds. However,  ${}^1D$  and  ${}^2D$  showed the same diversity at 95% CI (Table 1, fig. 6). It is worth mentioning that parasitoids of melitophagous larvae of bees were observed only in the old forest (fig. 6).

### Plant communities, parasitoids, and guild species

A total of 106 plant species were recorded (Appendix 3). Cluster and two-way cluster analyses broadly divided the SAC of plant species into five communities (at 75% similarity), regardless of their previously established SAC. Community 1 included the three conglomerates of young forest (YF) and one intermediate forest (IF); Community 2 included two conglomerates of the

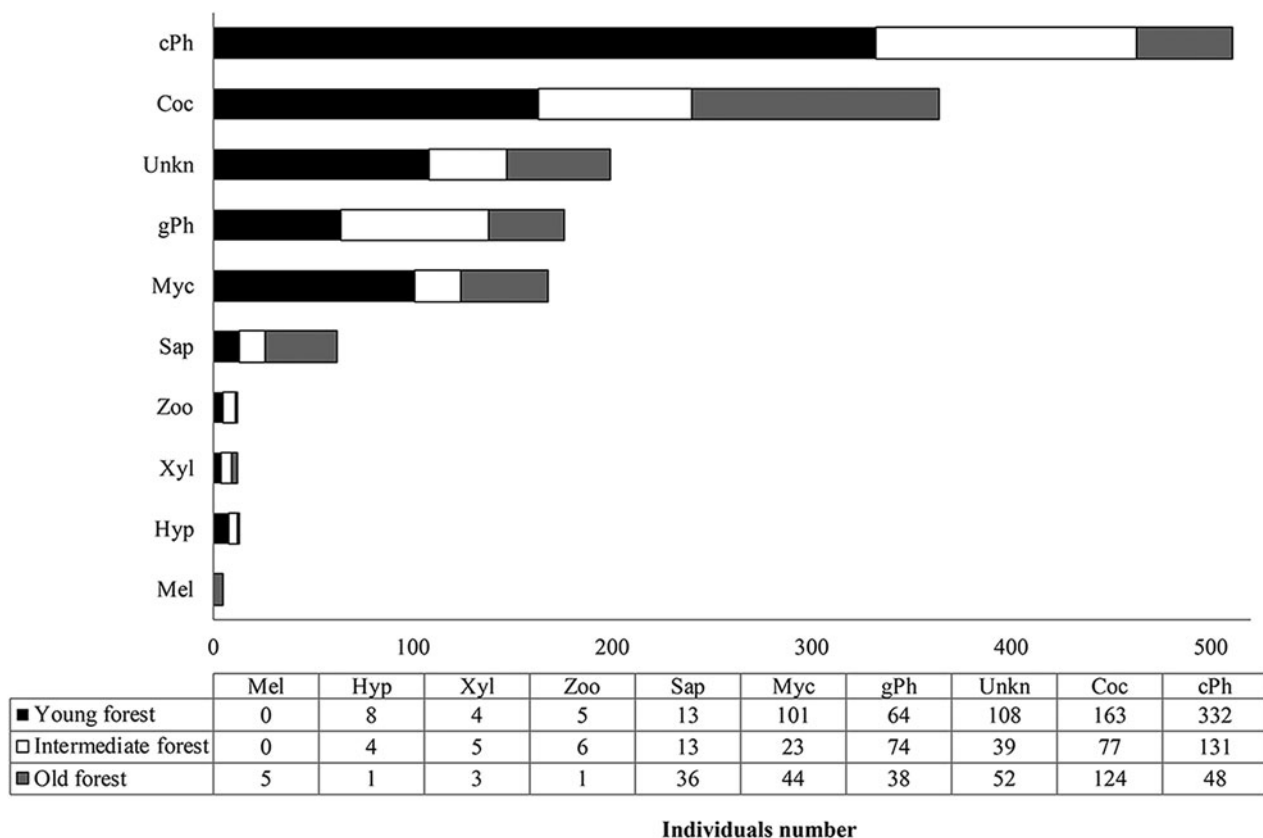


Figure 1. Guilds of parasitoids founded in different ages of abandonment after traditional slash and burn agriculture.

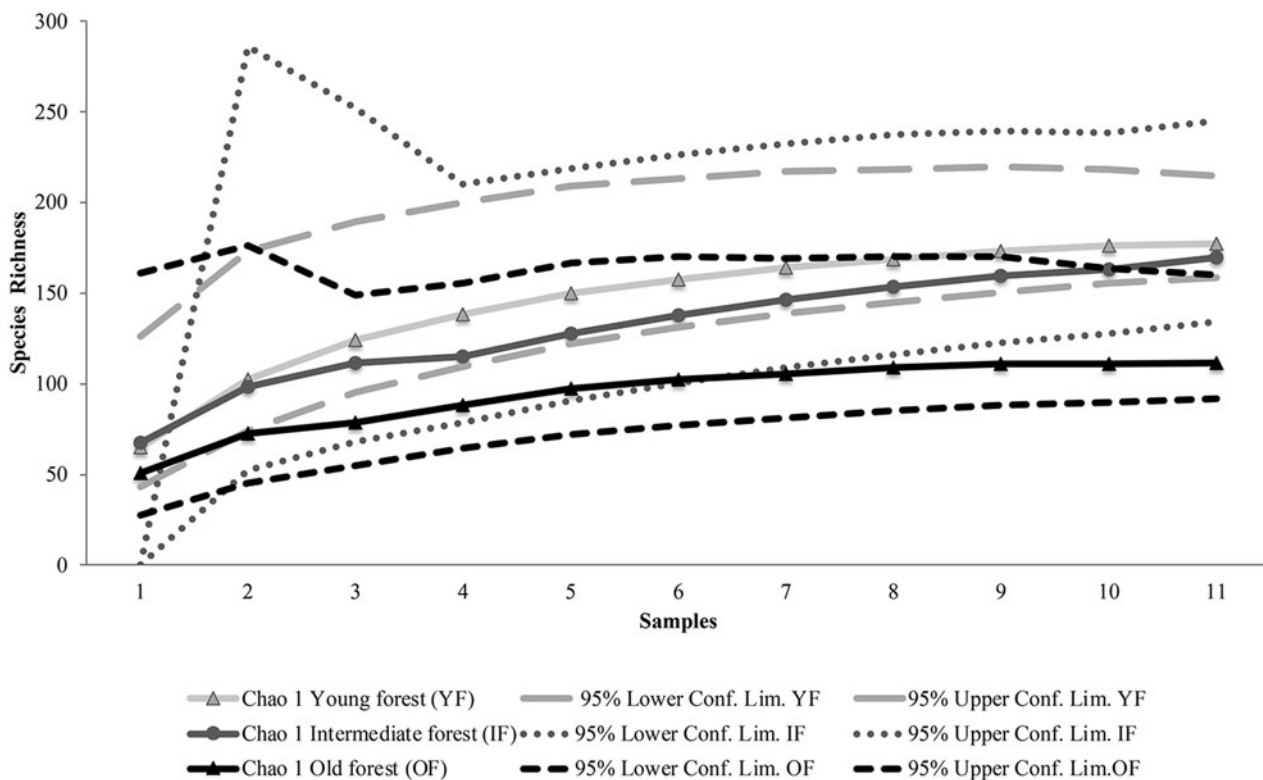
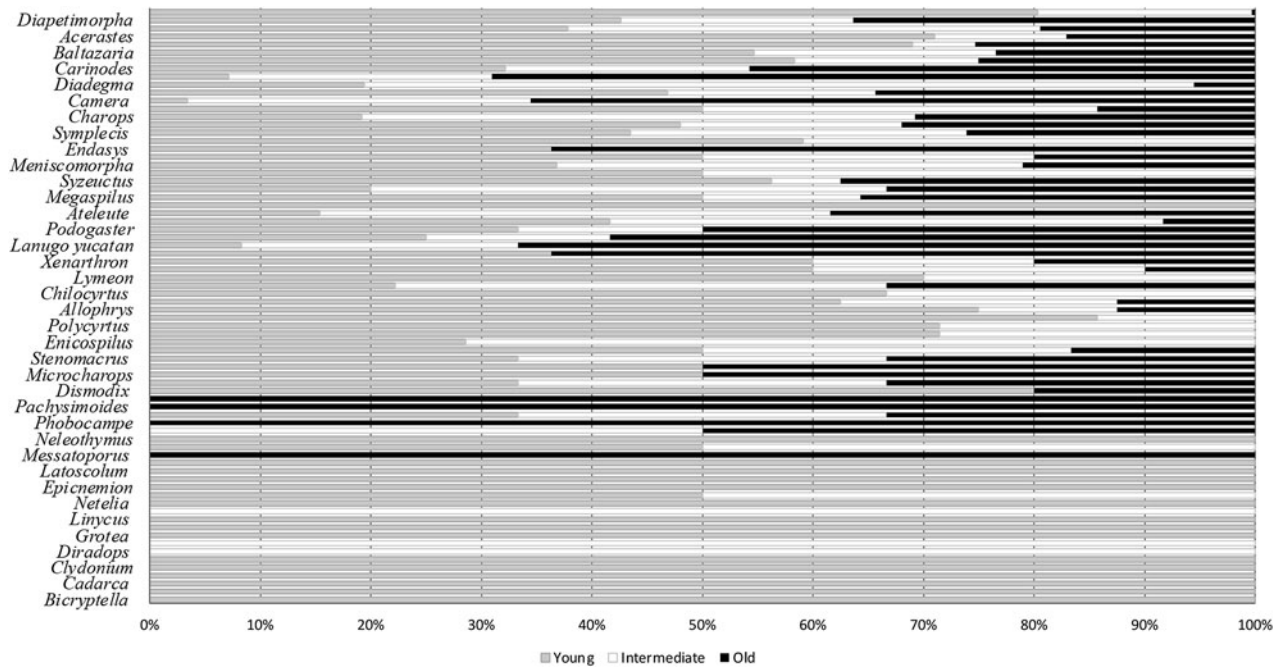


Figure 2. Accumulation curves of the Ichneumonidae in the three vegetation ages in dry semideciduos forest for species collected in the Malaise traps.





**Figure 3.** Proportional abundance of Ichneumonidae genera in different ages of dry semideciduous forest.

**Table 1.** True diversity of Ichneumonidae as effective number of species and guilds for estimating species richness ( ${}^0D$ ), exponential of the Shannon index ( ${}^1D$ ), and inverse of the Simpson index ( ${}^2D$ ), of three different stages in the dry semi-deciduous forest

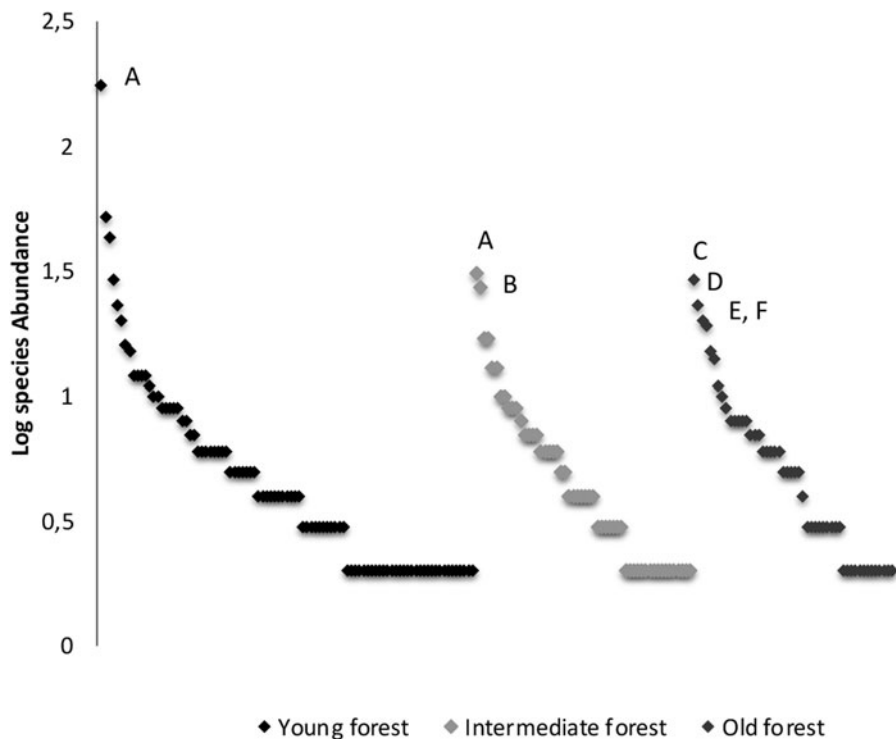
| Vegetation            | Species true diversity |                         |         |                         |         |                         |
|-----------------------|------------------------|-------------------------|---------|-------------------------|---------|-------------------------|
|                       | ${}^0D$                | 95% Confidence interval | ${}^1D$ | 95% Confidence interval | ${}^2D$ | 95% Confidence interval |
| Young forest          | 177                    | (158.6, 214.6)          | 59.14   | (52.05, 66.23)          | 16.42   | (15.69, 17.16)          |
| Intermediate forest   | 169.8                  | (134.1, 245.2)          | 71.6    | (60.64, 82.54)          | 39.91   | (39.59, 40.23)          |
| Old forest            | 111.3                  | (91.9, 160.1)           | 55.7    | (47.85, 63.53)          | 35.79   | (35.53, 36.05)          |
| Guilds true diversity |                        |                         |         |                         |         |                         |
| Young forest          | 9                      | (9, 9)                  | 4.96    | (4.67, 5.24)            | 3.90    | (3.40, 4.43)            |
| Intermediate forest   | 9                      | (9, 9)                  | 5.61    | (5.15, 6.07)            | 4.53    | (4.04, 5.01)            |
| Old forest            | 12.1                   | (10.2, 29.5)            | 6.08    | (5.60, 6.57)            | 4.48    | (4.03, 4.93)            |

two old forest (OF); Communities 3, 4, and 5, included only one conglomerate per SAC (two belonging to intermediate forest (IF) and one to old forest (OF) (fig. 7a, b).

The ISA identified species for each SAC (threshold level  $\geq 60\%$  or  $P \leq 0.05$ ). YF showed two indicator plant species: *Diphysa carthagenensis* and *Senna atomaria*; in IF, there were seven indicator plant species: *Arrabidaea floribunda*, *Bursera simaruba*, *Croton glabellus*, *Mimosa bahamensis*, *Neomillspaughia emarginata*, *Thevetia gaumeri*, and *Zapoteca formosa*; OF included 22 indicator plant species: *Acacia gaumeri*, *Bunchosia glandulosa*, *Bunchosia swartziana*, *Caesalpinia gaumeri*, *Coccoloba acapulcensis*, *Diospyros veraecrucis*, *Erythroxylum rotundifolium*, *Guettarda elliptica*, *Guettarda gaumeri*, *G. floribundum*, *Heteropterys laurifolia*, *Hippocratea excelsa*, *Jatropha gaumeri*, *Karwinskia humboldtiana*, *Machaonia lindeniana*, *Malpighia glabra*, *Melicoccus oliviformis*, *Neea psychotrioides*, *Platymiscium yucatanum*, *Sideroxylon obtusifolium*, *Tabebuia chrysantha*, and *Thouinia paucidentata* (fig. 7a, b).

The parasitoid species more associated to YF were *Eiphosoma* sp. 8 and *Eiphosoma* sp. 7; in IF, *Eiphosoma* sp. 8 and *Diadegma* sp.; and in OF, *Anomalon* sp. 3 and *Diapetimorpha* sp. 1 (fig. 7c). As regards the parasitoids diversity variables in the Ichneumonidae guilds community, the better associated to YF were Coc, Unkn spp, Myc, cPh, Xyl, Zoo, and Hyp; in IF, gPh, Xyl, cPh, and Zoo; and in OF, Coc, Sap, and Mel (fig. 7d).

We analyzed the relationship of parasitoid species with plant species richness, plant abundance, and SAC. The RDA triplot showed a narrow separation along the axes, and the Monte Carlo permutation test was not significant for any of the four axes (Table 2). Nonetheless, plant species richness, plant abundance, and SAC were significant ( $F = 1.47$ ,  $P = 0.02$ ;  $F = 1.56$ ,  $P = 0.01$ ; and  $F = 1.33$ ,  $P = 0.04$ , respectively) (fig. 8). However, the influence of each forest characteristic showed a differential response of parasitoid species. We identified seven groups of parasitoid species and three response patterns: (1) Neutral response: parasitoid species in groups A and E showed no association



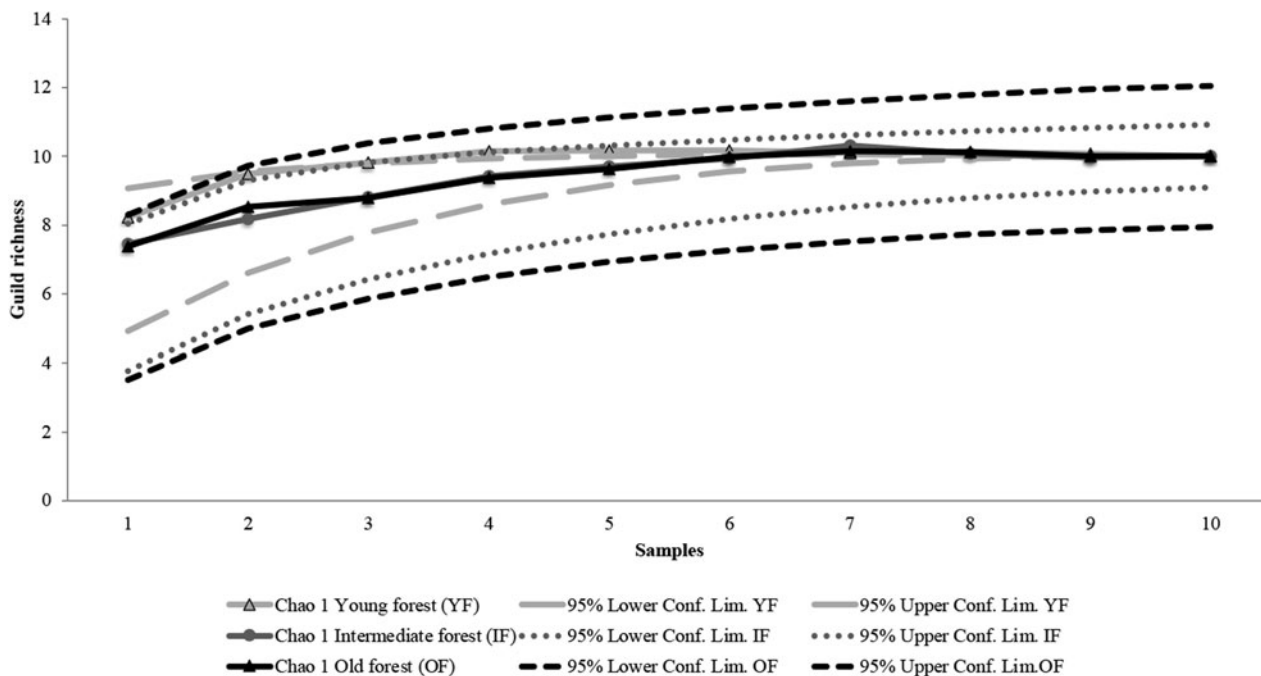
**Figure 4.** Rank-abundance plots of ichneumonid ensembles collected from the three vegetation ages in a dry semideciduous forest. A logarithmic scale of abundance was plotted against the species-rank ordered by species, from those with the most abundant individuals to those with the fewest. The species codes were as follows (only the most abundant for every age): A, *Eiphosoma* sp.; B, *Diadegma* sp.; C, *Anomalon* sp. D, *Diapetimorpha* sp.; E, *Carinodes* sp.; F, *Camera euryaspis*.

with forest characteristics; (2) Positive response: parasitoid species in groups F and G showed a positive association with three forest characteristics; (3) Negative response: parasitoid species in groups B, C, and D showed a negative association with forest characteristics (fig. 8).

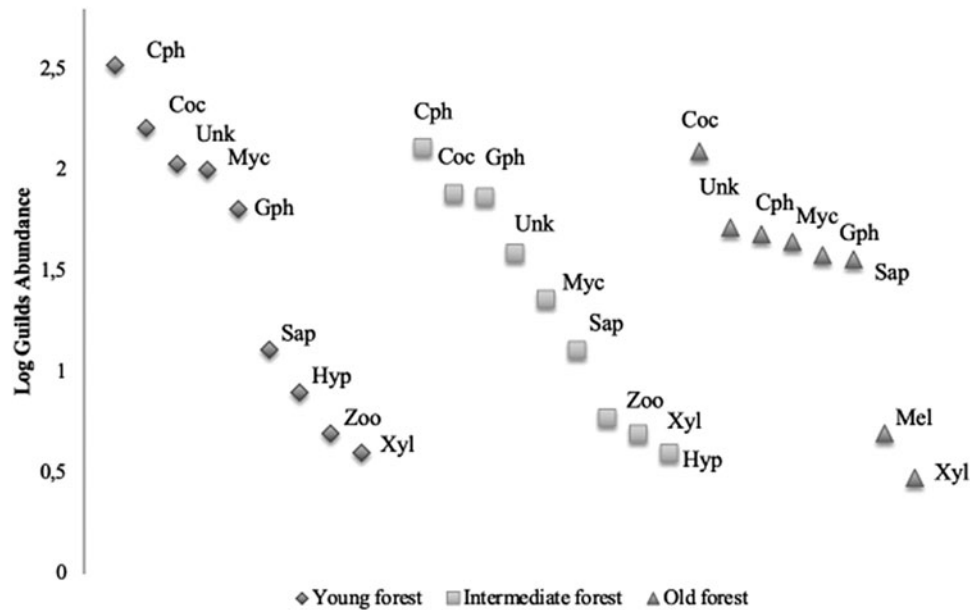
**Discussion**

This study provides a better understanding of the changes in parasitoid communities inhabiting forests of different

successional ages. The estimated value of Ichneumonidae species richness of 84% was adequate for comparative studies of parasitoid diversity, according to other studies providing results ranging between 70 and 80% of the expected number of species (Skillen *et al.*, 2000; Sääksjärvi *et al.*, 2004; Fraser *et al.*, 2007; Mazón and Bordera, 2008; González-Moreno *et al.*, 2018). Besides, an intensive malaise-trapping regime is better for sampling over short periods of time (Saunders and Ward, 2018). In this case, we used a total sampling effort of approximately 4500 malaise trap-days considering all sites



**Figure 5.** Accumulation curves of the Ichneumonidae guilds in the three vegetation ages in dry semideciduous forest for species collected in the Malaise traps.



**Figure 6.** Rank–abundance plots of ichneumonid guilds ensembles collected from the three vegetation ages in a dry semideciduous forest. A logarithmic scale of abundance was plotted against the species-rank ordered by guilds, from those with the most abundant individuals to those with the fewest.

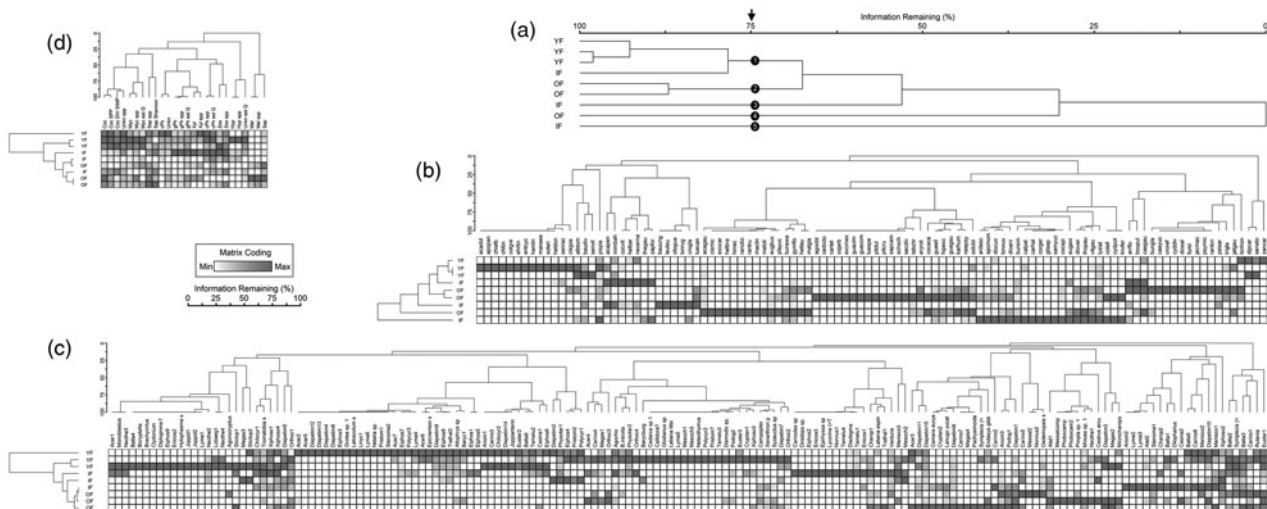
sampled over four months (1200 trap-days in each forest successional stage).

### *Ichneumonidae* community composition

Several studies have shown that structural complexity, high plant diversity, or forest successional stage favor the species richness of herbivores (Wäschke *et al.*, 2014; Li *et al.*, 2017; Valtonen *et al.*, 2017; Rocha-Ortega *et al.*, 2018; Sánchez-Reyes *et al.*, 2019) and their predators and parasitoids (Scherber *et al.*, 2010; Zhang and Adams, 2011; Borer *et al.*, 2012; Zou *et al.*, 2013; Rubene *et al.*, 2015; Li *et al.*, 2017; González-Moreno *et al.*, 2018). However, these results were contrary to our expectations, as *Ichneumonidae* species richness was the same in all areas; this

may indicate the capacity of these areas to maintain viable communities of parasitoids due to the connectivity between forest patches (Li *et al.*, 2017). These findings are similar to those reported in other studies that have shown no differences in species richness between habitats in the *Ichneumonidae* (Cryptinae) (González-Moreno *et al.*, 2015) and in butterflies (Valtonen *et al.*, 2017). Some studies demonstrated that in areas of intermediate successional age, insect species richness is similar to values recorded in mature or undisturbed habitats (Winfree *et al.*, 2007; Neves *et al.*, 2014; Nyafwono *et al.*, 2014) or in secondary forests (Li *et al.*, 2017).

Arthropod abundance is occasionally affected by habitat succession or changes in land use (Teodoro *et al.*, 2011; Valtonen *et al.*, 2017). Nevertheless, some studies state that the abundance



**Figure 7.** Cluster and Two-Way Cluster Dendrogram based on Euclidean measures, showing distribution of 106 plant species (a, b), 168 parasitoid species (c) and 26 parasitoid diversity variables (d), named in Appendix 1; in Successional Age Classes (SAC). The SAC are named by their indicator plant species. Colors are scaled from highest (deep gray) to lowest (faint gray) values within squares. The three conglomerate replicates for vegetation and sites for parasitoids, are shown as young forest (YF), intermediate forest (IF) and old forest (OF).

**Table 2.** Eigenvalues and Monte Carlo results for the Redundancy Analysis (RDA) of parasitoid species associated with plant species richness and abundance, and Successional Age Classes (forest characteristics, FC) in a tropical forest in southeast Mexico

| Axes   | 1               | 2     | 3               | 4     |
|--|-----------------|-------|-----------------|-------|
| Eigenvalues  | 0.195           | 0.132 | 0.076           | 0.195 |
| Parasitoid species (PS)-Forest characteristic (FC) | 0.955           | 0.944 | 0.980           | 0.000 |
| Cumulative variance of PS data (%):                | 19.5            | 32.7  | 40.2            | 59.8  |
| Cumulative variance of PS-FC (%):                  | 48.4            | 81.2  | 100             | 0.0   |
| Significance of first canonical axis:              | F ratio = 1.210 |       | P value = 0.184 |       |
| Significance of all canonical axes:                | F ratio = 1.122 |       | P value = 0.273 |       |

of parasitoids was independent of plant diversity and was best explained by the abundance of their hosts (Wäschke *et al.*, 2014): habitats with higher tree density and plant richness showed higher herbivore diversity and density (Leal *et al.*, 2016); accordingly, we expected a higher diversity of parasitoids, which means less abundance.

The highest Ichneumonidae abundance in the young forest may reflect the ability of specialist ichneumonids to colonize new areas in this successional stage. In fact, 66% of all individuals

were koinobionts, which have a higher searching ability and were more mobile. Furthermore, this stage was dominated by species like *Eiphosoma*, which is more common in open habitats (González-Moreno *et al.*, 2018). This pattern was observed in other studies about bees (Winfree *et al.*, 2007) and wasps (Rubene *et al.*, 2015), where species abundance and richness in young forest habitats were higher than in later successional stages because flowering plants are major resources for bees and wasps in these successional stages.

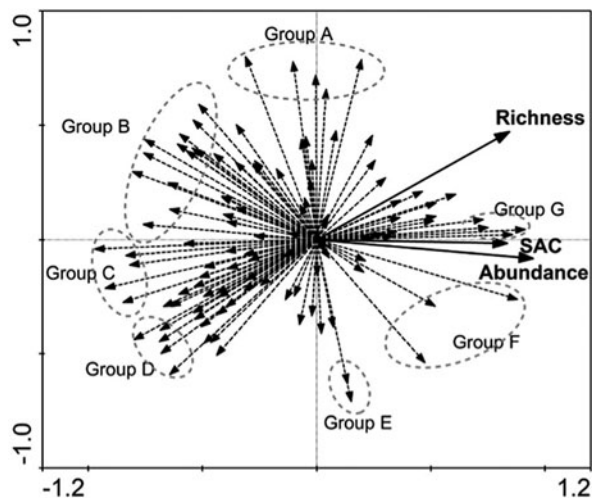
Some studies reported that habitats at intermediate successional stages are more diverse than old forests based on several taxa, like ants (Rocha-Ortega *et al.*, 2018), cerambycid Coleoptera (Li *et al.*, 2017), free-feeding species of herbivores (Neves *et al.*, 2014), and butterflies (Nyafwono *et al.*, 2014). This finding may be explained by the intermediate disturbance hypothesis (Connell, 1978), which postulates that early successional stages with high disturbance favor opportunistic disturbance-adapted species only, and thus diversity decreases. Moderate disturbance levels show the highest diversity, whereas late successional stages with low disturbance levels lead to competitive exclusion and loss of biodiversity. Besides, high forest cover has adverse effects on wasp diversity (Rubene *et al.*, 2015), likely because some species are associated with open habitats, as is the case of *Eiphosoma* (González-Moreno *et al.*, 2018), or because early stages have more clearcuts with flower-rich patches, which is particularly important for bee and wasp abundance (Rubene *et al.*, 2015). Considering the common species, old and intermediate forests are equally diverse, maybe because some species depend on late successional stages (Winfree *et al.*, 2007; Rubene *et al.*, 2015).

One species of *Anomalon* attained the highest abundance in the old forest. This finding may be because this genus includes specialized endoparasitoids (koinobionts), and insects with narrow niches are more susceptible to rapid changes in microhabitats, such as forest fragmentation (Stork *et al.*, 2009). *Anomalon* species are endoparasitoids mainly of Lepidoptera and Coleoptera (Tenebrionidae), the latter associated with trees (Cifuentes-Ruiz and Zaragoza-Caballero, 2014). They are also parasitoids of saprophagous larvae, so this result may be associated with the fact that decaying material is more abundant in old forests.

**Ichneumonidae guild composition**

The guilds observed in this study are consistent with those found in previous investigations in the region (González-Moreno *et al.*, 2018); no significant differences were found in either richness or diversity between the three forest successional stages. Some studies conducted in tropical dry forests have reported a higher percentage of leaf herbivory in trees growing in forests of advanced successional stages (Silva *et al.*, 2012; Neves *et al.*, 2014); this may foster the diversity of parasitoids belonging to different guilds.

The presence of parasitoids of melitophagous larvae of bees (**Mel**) in old forest patches suggests that this successional stage has enough hosts for the establishment of these guilds. Studies conducted in temperate forests confirm higher abundance and species richness of social bees in naturally regenerated forests observed as the successional stages progressed (Taki *et al.*, 2013). Although several studies confirm that old forests with closed canopies are less favorable to bees than younger forests (Taki *et al.*, 2007), these studies were performed in temperate



**Figure 8.** Redundancy Analysis (RDA) scatterplot illustrating the relationships of parasitoid species (represented by groups) to richness and abundance of plant species and SAC (Successional Age Classes) in a tropical forest in Southeast Mexico. **Group A:** *Baltazaria* sp. 4, *Bicyrtella* sp. 1, *Brachycirtus* sp. 1, *Clydonium* sp. 1, *Diapetimorpha* sp. 6, *Diplognina fulvithorax*, *Eiphosoma* sp. 9, *Enicospilus* sp. 2, *Hylophasma* sp. 1, *Joppidium* sp. 1, *J.* sp. 2, *Lymeon* sp. 1, *Megaspilus* sp. 2, *Microcharops* sp., *Mnioes* sp. 1. **Group B:** *Allophrys* sp. 1, *Anomalon* sp. 1, *Baltazaria* sp. 6, *Carinodes* sp. 3, *Chilocyrtus* sp. 2, *Diapetimorpha* sp. 4, *Diapetimorpha* sp. 5, *Eusterinx* sp. 2, *Joppidium* sp. 1, *Lobaegis* sp. 1, *Neotheronia* sp. 2, *Neotheronia* sp. 4, *Temelucha* sp. 2. **Group C:** *Diapetimorpha* sp. 9, *Eiphosoma* sp. 7, *Eiphosoma* sp. 8, *Physotarsus* sp. 2, *Trathala* sp. 2, *Xiphosomella* sp. 1. **Group D:** *Eiphosoma* sp. 4, *Lymeon* sp. 4, *Physotarsus* sp. 1, *Polycirtus* sp. 1, *Pristomerus* sp. 2. **Group E:** *Venturia* sp. 1, *Xiphosomella* sp. 2. **Group F:** *Anomalon* sp. 3, *Carinodes* sp. 5, *Nonnus* sp. 2. **Group G:** *Ateleute* sp. 1, *Camera euryaspis*, *Diapetimorpha* sp. 1, *Lanugo yucatan*, *Podogaster* sp. 1. We show only parasitoid species with best fit (based on longest length of the arrows).



zones. Therefore, further studies on these aspects are required for tropical forests.

The group of parasitoids of concealed phytophagous larvae (cPh) was the most abundant guild in young and intermediate forests. This result was expected because this parasitoid type needs visual cues to find the host, such as damage by leaf miners (Quicke, 2015), which may be difficult to detect in old forests with a complex canopy cover (De Rijk, 2016). Besides, Neves *et al.* (2014) reported a higher frequency of leaf miners in the early and intermediate successional stages in a tropical dry forest relative to the late stage.

To note, the guild of parasitoids of exposed phytophagous larvae (gPh) was similar in young and intermediate successional forests, likely because these stages harbor similar hosts that show no preference between these successional stages (Fonseca *et al.*, 2018).

On the other hand, we expected a higher diversity of cocoon parasitoids (Coc) in mature vegetation since generalist parasitoids (idiobionts) are favored in complex types of vegetation with high richness of potential hosts and non-host species (De Rijk, 2016). 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). Other studies support this finding, with specialist herbivores decreasing along a successional gradient (Sánchez-Reyes *et al.*, 2019); the same pattern probably occurs for parasitoids. A study has reported that idiobionts dominated clearcuts rather than closed forests, and koinobionts were more common in mature managed forests and old reserves (Stenbacka *et al.*, 2010); however, this study was conducted in a boreal forest. The study suggests that latitude may be important because, contrary to the statements of several authors, idiobionts are more diverse in conserved tropical dry forests (González-Moreno *et al.*, 2018).

### Plant communities, parasitoids and guild species

Species belonging to higher trophic levels, like parasitoids, might serve as indicators of ecosystem changes (Stenbacka *et al.*, 2010). Our results suggest that some tree and parasitoid species inhabiting tropical forests can be used as indicators of successional stages. In the young forest, *D. carthagenensis* and *S. atomaria* are representative Fabaceae trees found in the most arid zone of the peninsula of Yucatan (Hanan and Sousa, 2009). Parasitoids of the genus *Eiphosoma* may be indicative of young and intermediate forests because these parasitoids are associated with open habitats (González-Moreno *et al.*, 2018). In mature dry forests, *Anomalon* and *Diapetimorpha* are well-represented. *Anomalon* is a specialized endoparasitoid mainly of Lepidoptera and Coleoptera (Tenebrionidae) larvae (Gauld, 1991); unfortunately, most of the hosts of *Diapetimorpha* are still unknown (Kasparyan and Ruíz-Cancino, 2005); but some species like *Diapetimorpha introita* and *D. macula*, are parasitoids of important pest such as *Spodoptera frugiperda* and *Lygropia tripunctata*, respectively (Townes, 1970a).

All the parasitoid guilds were observed in old forest, being Coc, the most representative guild. In tropical dry forests, some authors have found that leaf nitrogen content and specific leaf mass decreased as secondary succession progresses (Fonseca *et al.*, 2018); which may reduce folivore populations, probably making their parasitoids less abundant in old forests compared to young ones.

Besides, the species *Anomalon* sp. 3, *Carinodes* sp. 5, *Nonnus* sp. 2., *Ateleute* sp. 1, *Camera euryaspis*, *Diapetimorpha* sp. 1, *Lanugo yucatan*, and *Podogaster* sp. 1 showed a positive association with plant species richness, plant abundance, and SAC. This can be explained by tree richness and density that represent high heterogeneity and availability of resources for herbivorous insects, allowing the coexistence of a large number of species (Neves *et al.*, 2014). In general, all genera are endo- and ectoparasitoids mainly of Lepidoptera (Gauld, 1991; Kasparyan and Ruíz-Cancino, 2005). Butterfly species richness, abundance, and diversity did not show an increasing trend along the successional gradient, but species richness and abundance peaked at intermediate stages (Nyafwono *et al.*, 2014).

### Conclusion

The present study indicates that the successional age matters. Our results showed that forests in different successional stages harbor parasitoid communities that are similar in terms of species richness and types of guilds. However, we found differences in abundance, diversity, and predominance of parasitoid guilds, with diversity being highest in intermediate successional ages. A finding worth noting is that the old forest is characterized by the unique presence of parasitoids of melitophagous larvae of bees. The young forest harbors specialist parasitoids that are common in open areas, such as *Eiphosoma*, a genus that may be used in the future as an indicator of disturbance. On the other side, the genus *Anomalon* may indicate forests preservation. These parasitoid assemblages associated with young forests were partly replaced by generalist species in older forests. The results derived from this study demonstrate the importance of habitat maintenance to conserve the diversity of parasitoid insects, which are essential elements in food webs.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0007485323000287>.

**Acknowledgements.** We are grateful to the staff of the Kaxil-Kiuc Asocacion Civil (Yucatán, Mexico), specially to Ruby Capetillo and James Callaghan for providing authorization for allow access in this protected area. We also want to thank to María Virginia Solis Montero and Santos Armin Uc for their help with fieldwork and we greatly acknowledge to Dr José Luis Hernández-Stefanoni and Dr Juan Manuel Dupuy for their help with vegetation data. This study was supported by Project CONACyT titled 'Diversidad de parasitoides y su relación con la complejidad estructural de la vegetación: modelos predictivos a nivel climático y de paisaje'. Reference: CB-2014-01, 241138.

**Competing interests.** None.

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