




Effect of forest disturbance on ant (Hymenoptera: Formicidae) diversity in a Mexican tropical dry forest canopy

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Abstract. 1. Ants are the dominant insects in tropical forest canopies. The α and β diversities of ants change in response to forest disturbance. Understanding the response of ants to forest disturbance will help to guide ant conservation and forest management plans, especially in endangered ecosystems such as the tropical dry forest.

2. We analysed ant α and β diversities in 15 fragments (5 mature, 5 disturbed, and 5 secondary) of a tropical dry forest in central Mexico. We identified and measured all of the trees in two transects (10 × 50 m) established within each fragment. Pit-fall traps were used to sample ants in all of the trees.

3. We identified 52 ant species (from a total of 11,524 individuals). The mature forest presented the greatest quantity of exclusive species and the highest α diversity. Ant composition differed among the mature forest but not between disturbed and secondary forest, and was related to tree size and richness. The β diversity was lower in the disturbed forest, reflecting the cost of biotic homogenization (15%). Among the β diversity components in all three forest types, this diversity was mainly influenced by turnover, while nestedness diminished in the disturbed forest.

4. In the tropical dry forest studied, anthropogenic disturbance homogenises the ant community, probably because the availability of resources is also homogenised, decreasing the α diversities of the canopy ants. Our results show the importance of the conservation of mature forests in terms of maintaining the diversity of canopy ants.

Key words. Alpha diversity, beta diversity, habitat fragmentation, nesting habits.

Introduction

Habitat loss and fragmentation by human activities exert a negative impact on biodiversity (Fischer & Lindenmayer, 2007). Significant biodiversity can persist in fragments of mature forest (Gibson *et al.*, 2011), but this remnant diversity is endangered by chronic anthropogenic disturbance (e.g., firewood extraction and livestock production; Martorell & Peters, 2005). Chronic

anthropogenic disturbance causes biodiversity loss (i.e., loss of forest specialist species) and increases the presence of generalist species, causing increased similarity among forest fragments over time and space (i.e., biotic homogenization; Olden *et al.*, 2004; Flores-Palacios *et al.*, 2008).

Recently, a different outcome of chronic anthropogenic disturbance has been noted: biotic differentiation (Arroyo-Rodríguez *et al.*, 2013). This is when β diversity increases between fragments because different species are selected among the fragments, probably because disturbance creates differences among the fragments (Solar *et al.*, 2015; Souza *et al.*, 2018). At the landscape level, the hypothesis of β diversity dominance (Tscharntke

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et al., 2012) predicts that the β diversity among fragments will determine the landscape diversity, which can be obscured by the effects that disturbance causes within each fragment. Since disturbance in the landscape will act to increase habitat heterogeneity, the probability of biotic differentiation could also be increased (Socolar *et al.*, 2016). The α and β diversities are therefore expected to be higher in heterogeneous landscapes than in simpler landscapes (Tschamtko *et al.*, 2012).

The previous perspectives consider β diversity as a single black-box value. However, β diversity can be decomposed in turnover and nestedness, this process allows inference of which of the components mainly causes a given β diversity value and which component is affected by environmental factors (e.g., disturbance). The turnover component measures the compositional differentiation between communities or samples, and nestedness is caused by the loss of species throughout the communities or samples, being a subset of an assemblage with higher species richness (Baselga, 2010; Baselga & Orme, 2012). If β diversity diminishes between forest fragments, and this is mainly caused by nestedness, biotic homogenization could be caused by the progressive substitution of specialist species for generalist species (Solar *et al.*, 2015).

Biotic homogenization/differentiation among plants can cause cascade effects that impact the fauna (Tabarelli *et al.*, 2012). If plant resources are less diverse for the animal species, then the local animal diversity could diminish (lower α diversity) while the animal similarity between forest fragments could increase (lower β diversity). Ants are one of the most abundant insect groups in tropical ecosystems (Rico-Gray & Oliveira, 2007). Different studies have reported that ant communities are extremely sensitive to environmental changes brought about by anthropogenic disturbance (Andersen *et al.*, 2002; Hoffmann & Andersen, 2003; Hoffman, 2010). Ant species richness is lower in secondary forests and agroforestry systems than in the mature forest (Bihn *et al.*, 2010; Fayle *et al.*, 2010; Martello *et al.*, 2018) and ant species composition also changes (Widodo *et al.*, 2004; Neves *et al.*, 2010). For example, in disturbed forests of Brazil, it has been found that ant species richness diminishes with perturbation, but β diversity buffers this species loss as a result of the increased habitat heterogeneity (Solar *et al.*, 2015). However, there is no pattern to the response of the ants to habitat disturbance, making it necessary to conduct more studies.

Ants represent 20% to 60% of the total biomass of canopy arthropods (Davidson *et al.*, 2003). The canopy offers the ants a great variety of plant resources (e.g., seeds, extrafloral nectar, and nesting sites; Armbrrecht *et al.*, 2004; Yanoviak *et al.*, 2011; Morales-Linares *et al.*, 2017, 2018; Vergara-Torres *et al.*, 2018) and the structure of the canopy ant community can be regulated by the availability of these resources, as well as by tree size and canopy connectivity (Blüthgen *et al.*, 2004; Philpott & Foster, 2005; Klimes *et al.*, 2012; Yusah & Foster, 2016; Vergara-Torres *et al.*, 2018; Adams *et al.*, 2019a). However, anthropogenic disturbance could reduce the physical structure and diversity of the plant community, negatively affecting both habitat heterogeneity and resource availability for the canopy ants (Andersen, 2018) and for the ground ant species that forage in the canopy (Marques *et al.*, 2017; Da Silva *et al.*, 2019). Habitat homogenization could result in fewer resources for canopy

ants, eliminating forest specialist ant species (Fayle *et al.*, 2010), and facilitating the dominance of aggressive generalist ants (Dejean *et al.*, 2015).

The tropical dry forests (TDF) of Mesoamerica provide an important scenario in which to study the effects of disturbance on faunal diversity, since these are among the most threatened of the tropical forests (Miles *et al.*, 2006). This threat is due mainly to logging of the forest, which transforms it into a heterogeneous landscape composed of fragments of mature, disturbed, and secondary forest. The TDF are highly seasonal, and plant activity changes between the dry and rainy seasons. During the dry season, most plants flower and disperse their seeds while, during the rainy season, the plants grow, and the fruits mature (Orozco-Ibarrola *et al.*, 2015). Insect diversity varies according to plant phenological patterns, and insect richness is high in the TDF during the rainy season (Toledo-Hernández *et al.*, 2015; Martínez-Hernández *et al.*, 2019; Ramos-Robles *et al.*, 2020). Disturbance and seasonality therefore influence the availability and abundance of resources and can affect ant diversity (Neves *et al.*, 2010).

The objective of this study was to evaluate the α and β diversities of the canopy ant community in TDF fragments with different degrees of disturbance (mature, disturbed, and secondary), as well as the TDF characteristics (richness, density, and size of the woody plants), that determine ant diversity and composition. We hypothesized that:

- 1 Both the α and β diversities of canopy ants will decline along the gradient of forest disturbance due to the fact that anthropogenic disturbance leads to processes of biotic homogenization. However, if the disturbance in the landscape increases the heterogeneity of the habitat and leads to β dominance, the β diversity among forest fragments, and the α diversity will increase along the gradient of disturbance.
- 2 The β diversity will mainly be caused by nestedness along the gradient of disturbance.
- 3 Since greater richness and size of woody plants are associated with resource availability, these will positively influence the composition of canopy ants.

Materials and methods

Study area

This study was conducted in the TDF of the Apatlaco River sub-basin (between 19°13'24" and 18°36'00"N and 99°09'55" and 99°21'11"W) in the south of the state of Morelos, Mexico (Sotelo-Caro *et al.*, 2015). The climate is semi-warm, with a mean annual temperature of 23 °C and mean annual precipitation of 850 mm, in which ~90% of the rainfall occurs between May and October (Comisión Nacional del Agua, 2008; Sotelo-Caro *et al.*, 2015) and most of the trees lose their leaves during the dry season (November–April). The landscape of the sub-basin of the Apatlaco River comprises 1,375 TDF fragments of different sizes (1–315 ha) that together cover an area of 4,576.5 ha, and are immersed in a matrix of different land covers (e.g., cultivated land and urban areas; Sotelo-Caro *et al.*, 2015). The TDF fragments vary in terms of degree of disturbance,

Table 1. Woody plants traits in a tropical dry forest in central Mexico. Mean (\pm SD). Lower-case letters indicate significant differences among forest types (multiple comparisons Kruskal–Wallis test $P < 0.05$).

Traits	Mature ($n = 10$)	Disturbed ($n = 10$)	Secondary ($n = 10$)
Richness	10.5 \pm 2.8 ^a	10.9 \pm 4.8 ^a	5.4 \pm 1.9 ^b
Accumulated basal area (cm ² /0.05 ha)	8,931.2 \pm 4,742.6 ^a	5,496.9 \pm 2,629.5 ^{ab}	4,597.6 \pm 2917.7 ^b
Density	42 \pm 12.7 ^a	29.7 \pm 10.8 ^{ab}	17 \pm 10.9 ^b

floristic composition and predominance of woody plant species, but can be broadly categorised into three forest types: mature, disturbed, and secondary (Table S1; Sotelo-Caro *et al.*, 2015).

In our study site, the mature and disturbed forests present a greater richness of woody plants than the secondary forest (Kruskal–Wallis test, $H_2 = 12.2$, $P < 0.05$; Table 1). Moreover, the mature forest harbours the largest trees and a higher density of woody plants compared to the secondary forest ($H_2 = 6.3$, $P < 0.05$; $H_2 = 12.5$, $P < 0.05$; respectively; Table 1).

Sampling design

The study was conducted from the 26th of March to the 7th of April (dry season) and from the 23rd of July to the 6th of August (rainy season) of 2018. Fieldwork was conducted in five fragments of different sizes in each forest type (mean \pm SD, mature: 41 \pm 47 ha, disturbed: 37.5 \pm 34.3 ha and secondary: 34.2 \pm 11.8 ha). Two permanent transects (0.05 ha, 50 \times 10 m) were established in each fragment at a distance of 50 m apart and more than 50 m in distance from the forest edge.

Forest characterisation

All woody plants with diameter at breast height (DBH) ≥ 5 cm along each transect were quantified and identified. To estimate tree size, we measured the DBH (at 1.3 m) and then calculated the basal area ($BA = \pi(DBH/2)^2$) of each tree. Plant species that could not be identified in the field were collected for identification in the herbarium HUMO of the Centro de Investigación en Biodiversidad y la Conservación (CIBYC) of the Universidad Autónoma del Estado de Morelos (UAEM). Average tree size, density and richness of the woody plants were calculated for each transects (Table 1). These parameters are related to the availability of resources (e.g., nesting and feeding sites) for the ants.

Sampling of ants

In each transect, ants were collected from all of the trees, using one baited arboreal pitfall trap per tree (Ribas *et al.*, 2003; Fig. S1). We used a ladder to set these traps in trees of height >2 m. All of the traps were installed on the same day in one fragment of each of the three forest types (mature, disturbed, and secondary) and left for a period of 7 days, following the proposal of Lasmar *et al.* (2017). Sampling was carried out twice on the same

individual trees (once in the rainy season and once in the dry season). In total, 890 baited pitfall traps were set per season (420, 295, and 175 traps in mature, disturbed, and secondary forest, respectively).

Ant species were classified based on their nesting habits (ground, arboreal, or both), according to the specialised literature and web pages (Adams *et al.*, 2019b; AntWeb, 2020; AntWiki, 2020). Collected material was deposited in the Entomological Collections of the Universidad Autónoma del Estado de Morelos (CIUM) and the Universidad de Guadalajara (CZUG).

Data analysis

In the initial analyses, we tested whether there were differences in the richness and abundance of the ants between forest types, considering the intrinsic variations of these variables within the fragments using generalised linear mixed models (GLMM). As a measure of ant abundance, we recorded the species occurrence in each sampled tree for each transect. Species richness was taken as the number of ant species recorded in each transect, which is equivalent to the ⁰D true diversity (Jost, 2007). In each model (richness and abundance), the fixed factors were forest type (three levels = mature, disturbed, and secondary) and season, while the random factor was the fragment (five levels for forest type) and the unit of replication was the transect (two units). Both models were generated with Poisson error and logarithmic link function (Crawley, 1993) using the package *lme4* (Bates *et al.*, 2015). Multiple comparisons were conducted in the package *multcomp* (contrast method; Bretz *et al.*, 2010).

Coverage, α and β diversity

In the subsequent analyses, we tested diversity at the forest type level, pooling the data between transects and fragments. To evaluate the completeness of the species richness in each forest type, a comparison was made among forest types using the sample coverage (Hsieh *et al.*, 2016). Sample coverage allows comparison of species censuses, standardising the richness of the communities at the same level of completeness (Chao & Jost, 2012).

For each forest type, we calculated true α -diversities (⁰D, ¹D, and ²D). Alpha diversities were calculated with the effective number of species (^qD; Jost, 2007). The order q determines the sensitivity of the metric to the relative abundance of the species (Jost, 2007). When $q = 0$, the diversity is equal to the species richness; when $q = 1$, it measures the number of equivalent

species, i.e., those that would have the same abundance (Jost, 2007); when $q = 2$, 2D measures the number of “equally dominant” species (Jost, 2010). For 4D we used data of incidence of the ant species along the transects per forest type. The sample coverage and true diversities (0D , 1D , and 2D) with their 95% confidence intervals were analysed with the package *iNEXT* (Hsieh *et al.*, 2016). To illustrate the number of shared and non-shared species between the three forest types, we produce a Venn diagram using the package *eulerr* (Larsson, 2020).

The β diversity was calculated as compositional similarity, using the Sorensen index for presence/absence data (Jost *et al.*, 2011). We calculated all Sorensen index values between all the pairs of transects (Baselga, 2010). We used the Sorensen index because this is directly linked to true β diversity (Jost *et al.*, 2011) and this β diversity (β_{Sorensen}) can be separated into two components: one component (species turnover, β_{Simpson}) measures the differentiation caused by unique species presence between samples, while the other (nestedness, $\beta_{\text{nestedness}}$) measures how species are shared along a richness gradient. The package *betapart* (Baselga *et al.*, 2020) was used to generate square matrices of β dissimilarities (β_{Sorensen}) and its components (β_{Simpson} , $\beta_{\text{nestedness}}$) between the transects of each forest type.

We tested whether the β diversity (β_{Sorensen}) and its components (β_{Simpson} , $\beta_{\text{nestedness}}$) differed between forest types with generalised linear mixed models. To test β diversity within the forest types, we compared the mean β value of each transect inside each forest type ($n = 10$) with the mean β values observed in the other forest types. In this way, we obtained a single value of β for each transect and avoided pseudoreplication (Flores-Palacios *et al.* 2008).

Species composition and its relationship with forest variables

Ant species community composition was analysed among forest types with a non-metric multi-dimensional scaling (NMDS) analysis followed by an analysis of similarities (ANOSIM). For these analyses, a squared matrix of Bray-Curtis dissimilarities was constructed. The r values of ANOSIM ranged from 0 to 1, in which values close to 0 indicate similar communities and those close to 1 indicate distinct communities (Clarke, 1993). In addition, the function *envfit* of the package *vegan* was used (Oksanen *et al.*, 2018) to evaluate whether the forest variables (i.e., mean tree size, density, and richness of woody plants) are related to the ant species composition. The significance of these variables was determined with a test of 999 permutations. NMDS and ANOSIM analyses were performed using the package *vegan* (Oksanen *et al.*, 2018). The graphs were generated using the package *ggplot2* (Wickham, 2016). All analyses were performed in the program R (R Core Team 2017).

Results

Over the two seasons, a total of 11,524 individual ants, belonging to 7 subfamilies, 23 genera, and 52 species (Table S2), were collected in the 15 fragments from three forest types. The subfamilies Myrmicinae and Formicinae represented 71% of all of

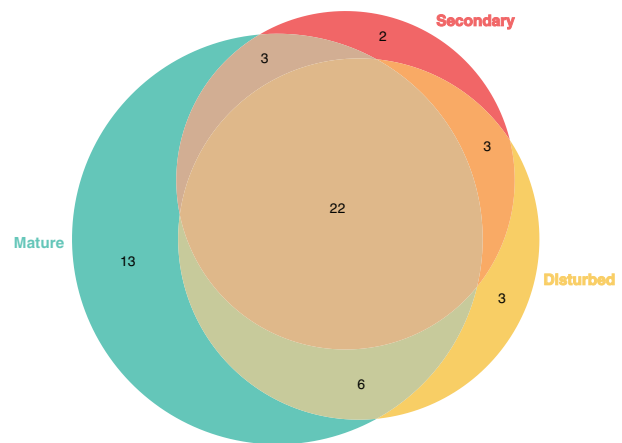


Fig. 1. Venn diagram illustrating proportional size of richness of each forest type, the number of shared and unique ant species and the overlap between three forest types in a tropical dry forest of central Mexico. [Color figure can be viewed at wileyonlinelibrary.com]

the species sampled. The mature forest presented the majority (44 species), followed by the disturbed (34 species), and the secondary (30 species) forests. Of the total number of species, 13 (25%) were exclusive to the mature, three (5.7%) to the disturbed, and two (3.8%) to the secondary forest (Fig. 1).

When comparing the abundance and richness of ants considering the variation within fragments, ant abundance was affected by forest type ($\chi^2 = 237.5$, d.f. = 2, $P < 0.001$) and by season ($\chi^2 = 19.2$, d.f. = 1, $P < 0.001$; Table 2). The abundance of ants per transect differed between the mature and secondary forest ($P < 0.05$, contrast method), while the disturbed forest did not differ from the other two forest types (Table 2). Ant abundance increased slightly during the dry season (Table 2).

The richness of ant species was affected by forest type ($\chi^2 = 21.5$, d.f. = 2, $P < 0.001$) but not by season ($\chi^2 = 1.9$, d.f. = 1, $P = 0.166$). However, neither the contrast method nor the 95% confidence intervals enabled detection of which mean richness values differed between forest types (Table 2).

α and β diversity

Sample coverage was similar in all forest types (mature = 94%, disturbed = 98%, and secondary = 93%). The α diversity was significantly greater in the mature forest, with no differences found between the disturbed and secondary forest (Fig. 2). Although the species *Camponotus atriceps* (Smith) was found to dominate all three forest types, its presence was higher in the secondary forest (25.2%), which presents a greater degree of habitat disturbance (Fig. 3; Table 3).

The β_{Sorensen} diversity was significantly greater in the mature and secondary than in the disturbed (Table 4) forest. In all forest types, turnover (β_{Simpson}) was the main component of β (Table 4) and β_{Simpson} was between 3 and 9 times more important than the nestedness component ($\beta_{\text{nestedness}}$). However, β_{Simpson} did not

Table 2. Mean abundance and mean species richness of the ants found in a disturbance gradient (forest type), in two sampling seasons in a tropical dry forest of the central Mexico. For each mean, we show the lower and upper limit of the 95% confidence interval for a *Poisson* variable. Means with a different letter inside the same factor significantly differ (contrast method, $P < 0.05$). n.s. = not significant differences, un = indeterminate differences.

Factor level	Ant abundance			Richness of ant species		
	Mean	Lower	Upper	Mean	Lower	Upper
Forest type						
Disturbed	32.0 ^{bc}	21.8	45.1	10.4 ^{un}	5.0	18.8
Mature	51.0 ^a	38.0	67.1	12.2	6.3	21.2
Secondary	22.4 ^b	14.1	33.8	7.6	3.2	15.2
Season						
Dry	38.5 ^a	27.3	52.7	10.6 ^{ns}	5.2	19.2
Rainy	31.7 ^b	21.7	44.9	9.0	4.4	17.7

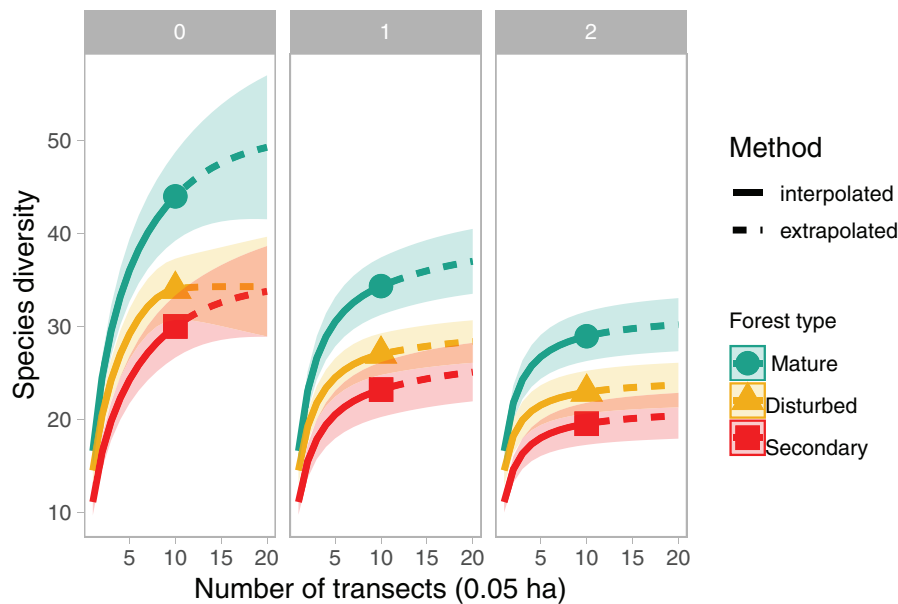


Fig. 2. Diversity of ants based on Hill numbers ($q = 0, 1, \text{ and } 2$) in three forest types in a tropical dry forest of central Mexico. The 95% confidence intervals (shaded area) are indicated. [Color figure can be viewed at wileyonlinelibrary.com]

differ between forest types. The $\beta_{\text{nestedness}}$ followed the same pattern as β_{Sorensen} , and was lower in the disturbed forest, but similar between the mature and secondary forests.

Species composition and its relationship with the forest variables

The NMDS ordination analysis indicated that the square matrix of Bray-Curtis similarities could be reduced in two dimensions, with an error of $<25\%$ (stress = 0.22; Fig. 4). The fit of the forest variables to the ordination of the NMDS indicates that increased basal area and woody plant richness are both associated with a change in species composition (*envfit*: $r^2 = 0.25, 0.29$; $P < 0.01$; Fig. 4).

The ANOSIM analysis showed that species composition differs among the forest types (Global $R = 0.26, P < 0.01$; Fig 4).

The paired comparisons between forest types showed significant differences between the mature and disturbed and secondary forests (Mature vs. Disturbed, ANOSIM statistics, $R = 0.21, P < 0.01$; Mature vs. Secondary, $R = 0.42, P < 0.01$), but not between the disturbed and secondary forest types (Disturbed vs. Secondary, $R = 0.12, P > 0.05$).

Discussion

Our evaluation of diversity and composition of canopy ants in the dry tropical forest showed that anthropogenic disturbances affect the ant assemblages by increasing the similarity of species composition, decreasing the number of exclusive species, and reducing α diversity. Our results do not support the biotic differentiation hypothesis, which has been reported in other studies for other taxa such as trees and dung beetles, and in insect galls

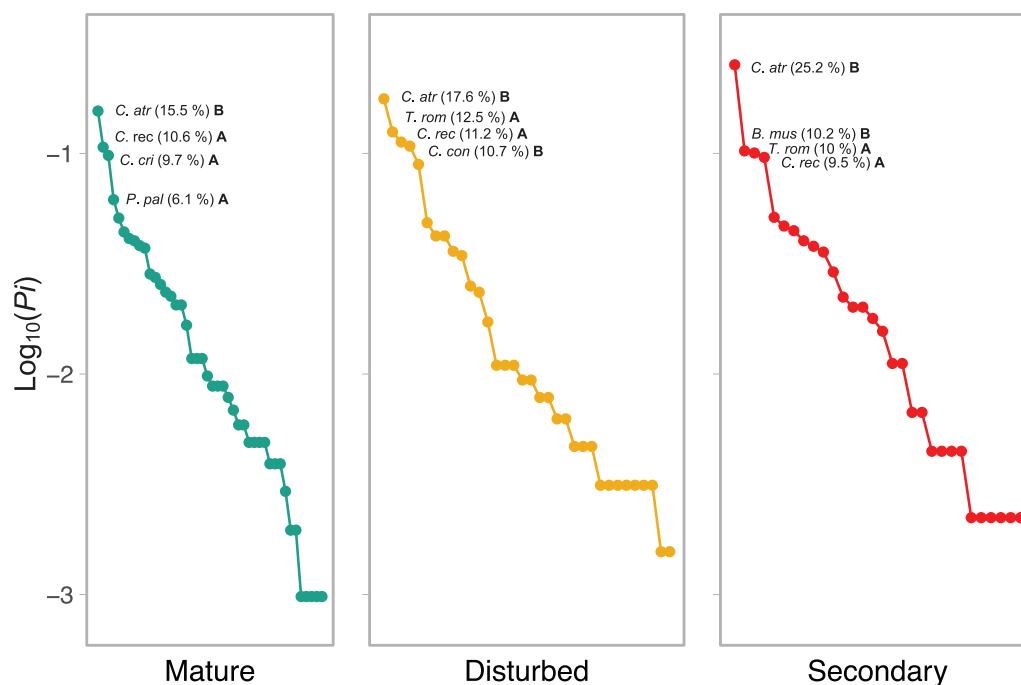


Fig. 3. Rank-abundance curves of ant species in three forest types in a tropical dry forest of central Mexico. Nesting habits: A: Arboreal, G: Ground, B: Both. The four most abundant species are named. Ant species: *C. atr*, *Camponotus atriceps*; *B. mus*, *Brachymyrmex musculus*; *T. rom*, *Tapinoma romularum*; *C. rec*, *Camponotus rectangularis*; *C. con*, *Camponotus conspicuus zonatus*; *C. cri*, *Crematogaster crinosa*, and *P. pal*, *Pseudomyrmex pallidus*. [Color figure can be viewed at wileyonlinelibrary.com]

(Arrollo-Rodríguez *et al.*, 2013; Filgueiras *et al.*, 2016; Souza *et al.*, 2018). The pattern observed in this study was consistent with the hypothesis of β dominance (*sensu* Tschamtker *et al.*, 2012), since greater β diversity could cancel out the adverse local

effects of secondary forest. The α diversity of ants decreased in habitats with anthropogenic disturbance of the forest, as has been demonstrated in other studies (Ribeiro-Neto *et al.*, 2016; Oliveira *et al.*, 2017). Since habitats without anthropogenic disturbance are more complex and heterogeneous, they offer greater availability of resources (e.g., food and nesting sites) for the ants, which could allow the coexistence of a high number of species (Philpott & Foster, 2005; Fayle *et al.*, 2010; Klimes *et al.*, 2012).

In all of the forest types, β diversity was caused mainly by the turnover component, which was in accordance with the observed high number of exclusive species and the high β diversity of the TDF (Trejo & Dirzo, 2000). However, β diversity was lower in the disturbed forest, with 15% lower β than that of the mature

Table 3. Nesting habits of ants in a tropical dry forest in central Mexico.

Nesting habits	Mature (%)	Disturbed (%)	Secondary (%)
Arboreal	47.7	41.2	43.3
Ground	27.3	32.3	33.3
Both	25.0	26.5	23.3

Table 4. Mean (\pm SD) of total β -diversity (β_{Sorensen}) and its components: Nestedness ($\beta_{\text{nestedness}}$) and turnover (β_{Simpson}) by forest type in a tropical dry forest of central Mexico. Means with a different letter inside the same factor significantly differ (contrast method, $P < 0.05$). n.s. = not significant differences.

Level of comparison in each model	β diversity		
	β_{Sorensen}	β_{Simpson}	$\beta_{\text{nestedness}}$
Disturbed	0.41 ^b \pm 0.04	0.36 ^{ns} \pm 0.04	0.04 ^b \pm 0.01
Mature	0.48 ^a \pm 0.07	0.40 \pm 0.08	0.08 ^a \pm 0.02
Secondary	0.49 ^a \pm 0.08	0.38 \pm 0.10	0.11 ^a \pm 0.05
χ^2	15.4	1.7	27.4
d.f.	2.0	2.0	2.0
P	<0.001	0.431	<0.001

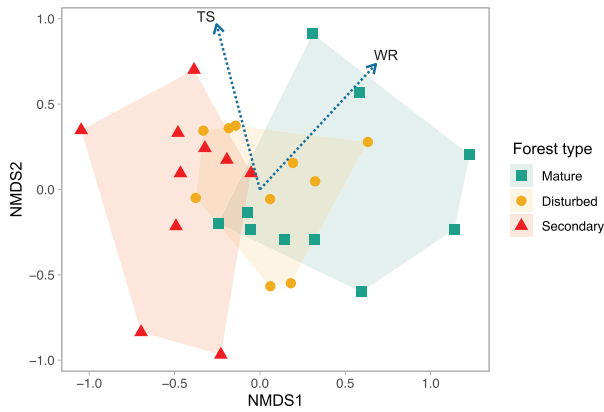


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination for ant composition between three forest types, based on Bray–Curtis index with fitted vectors (WR: Richness; WD: density; TS: Tree size of woody plants). Vector length is proportional to the correlation between habitat variables and the ordination of ant species composition. Vectors were only plotted for variables with significance of $P < 0.05$. [Color figure can be viewed at wileyonlinelibrary.com]

forest (i.e., the cost of habitat homogenization). Although the nestedness component was of less importance to β , this component differed between forests, following the same β pattern. This pattern may be a result of the fact that the disturbance could act to benefit some species, expanding their distribution among the fragments (decreasing nestedness; Socolar *et al.*, 2016). In the secondary forest, we find β diversity that is similar to that of the mature forest (but with a tendency towards lower α). This was counterintuitive, because there is a greater simplification of plant diversity in these forests. These results suggest that, in the secondary forest, β could compensate for the loss of diversity at the α level.

Determination of the composition of species of the ant community is appropriate for evaluation of disturbance of the forest (Solar *et al.*, 2016). The gradient of disturbance analysed showed that the composition of species of the canopy ant community differs between the mature forest and the forest types that present greater disturbance. The composition of exclusive species was responsible for the greater diversity of ants in the mature forest (25%), while this was low in the disturbed and secondary forests (5.7% and 3.8%, respectively). In this context, the loss of species with specific ecological requirements could have negative consequences for the ecosystem (e.g., seed dispersion, insect predation, or nutrient cycling; Folgarait, 1998; Philpott & Armbrrecht, 2006; Peters *et al.*, 2016). In this study, two of the species that are shared among the three forest types display a high dominance: *C. atriceps*, and *Camponotus rectangularis*. Both of these species have general feeding habits; *C. atriceps* has opportunistic nesting habits (nesting both in the ground and in trees) while *C. rectangularis* is arboreal (Brown Jr, 2000; Rios-Casanova *et al.*, 2004) and both have been reported as dominant in nearby TDF (Vergara-Torres *et al.*, 2018). However, *C. atriceps* increased its dominance in forests with a higher degree of disturbance. Competition among ants increases in

habitats that offer lower diversity of resources, promoting antagonistic interactions between the ants. Thus, the dominant ant species will be aggressive, such as *C. atriceps* (Dejean *et al.*, 2015).

Loss of resources is an important filter that produces changes in ant communities (Solar *et al.*, 2015). The assemblage of ants was related to the tree size and richness of the woody plants, probably because larger trees are associated with increased availability of nesting sites (Klimes *et al.*, 2012; de Queiroz *et al.*, 2017). Thus, the richness of trees can increase the heterogeneity of the habitat, since each tree species can offer different resources to the canopy ants (Ribas *et al.*, 2003) and thus determine their composition (Yanoviak & Kaspari, 2000; Dejean *et al.*, 2015). Moreover, large trees can host a greater diversity of epiphytic plants (Flores-Palacios & García-Franco, 2006) that provide food and nesting sites to the ants, as has been found in a tropical lowland forest of Panama, where the presence of the epiphyte *Caularthron bilamellatum* increased the species richness of ants in the crowns of *Annona glabra* (Yanoviak *et al.*, 2011).

Seasonal changes in the TDF did not affect canopy ant richness, but did affect their abundance. This pattern of species richness coincides with that found in a TDF in Brazil (Neves *et al.*, 2010; but see Sousa-Souto *et al.*, 2016; Marques *et al.*, 2017). Plant phenology affects the availability of resources for canopy ants (Rico-Gray *et al.*, 2012; Lange *et al.*, 2013); in this case, the high abundance of ants in the dry season could be related to seed and nectar availability. In a TDF close to the forest studied, seed removal by ants and the flowering of epiphytes both occur mainly during the dry season (Orozco-Ibarrola *et al.*, 2015; Vergara-Torres *et al.*, 2018).

Canopy resources can be used by ants with different nesting habits (Rico-Gray & Oliveira, 2007). In this study, we found ant species that nest in the ground and forage in the canopy, a pattern that is probably more frequent in forests where the trees are relatively short (<15 m in height), such as the TDF. However, stratification between ants of the ground and those of the canopy could change in forests with trees of greater height (Antoniazzi *et al.*, 2020), where connectivity between tree crowns via lianas could be more important for the canopy ants (Adams *et al.*, 2017). In the mature forest, we found more dominant species with arboreal nesting habits, which could be due to the greater variety of microhabitats and resources available in this habitat type (Armbrrecht *et al.*, 2004). Anthropogenic disturbance reduces the number of available nesting sites due to reduced tree size (Walter *et al.*, 2018). For this reason, a greater presence of dominant ants as a result of the available nesting sites, and those with opportunistic nesting habits, could indicate a reduced availability of resources.

Overall, our study suggests that ants are a biological group that is highly sensitive to environmental changes brought about by anthropogenic disturbance (Oliveira *et al.*, 2017; Ribeiro-Neto *et al.*, 2016). Nevertheless, some ant species could benefit from disturbance (e.g. *C. atriceps*). It is likely that, if anthropogenic disturbance occurs in mature forests, the similarity in species composition will increase, causing the loss of exclusive species and becoming more similar to that of the disturbed and secondary forests, which present a higher degree of disturbance. This study therefore contributes to the knowledge of the influence of anthropogenic disturbance on the community of canopy

ants in anthropised landscapes and highlights the importance of conservation of mature forests.

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Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix: Supporting information

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