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Research Article

Taxonomic, species and functional group diversity of ants in a tropical anthropogenic landscape

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Abstract

In tropical dry landscapes, biodiversity conservation is dependent upon both the protection of natural areas and the sustainable management of the agricultural matrix. We analyzed the taxonomic, species and functional group diversity of ants in three neighboring habitats with different degrees of anthropic disturbance in Veracruz, Mexico. A total of 34,957 ant workers belonging to 89 species, 34 genera, 19 tribes and 7 subfamilies were recorded. Primary forest had the highest species richness and most even distribution of species among the taxonomic levels, followed by secondary forest and active pasture. Because high species turnover among habitats increased species richness at the landscape level, the three neighboring habitats that we sampled are important for conservation biodiversity and together have a high conservation value for ants and probably for other invertebrates as well. Species of specialized functional groups were more frequent in primary forest, while those belonging to generalist and opportunistic groups were more frequent in active pasture. Human-disturbed areas in the vicinity of protected areas have an important role as reservoirs of biodiversity and should be included in landscape management practices designed to improve arthropod conservation in the tropics.

Key words: ants, tropical dry forest, regeneration, taxonomic distinctness, guilds, turnover

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Introduction

Tropical dry forests originally covered more than 40% of tropical areas worldwide, but during the last few decades a large proportion of their geographical range has been lost due to agricultural expansion [1]. In Mexico, vast areas of tropical forest have been converted to different types of non-irrigated crop fields or pastures for animal husbandry [2]. The current tropical dry forest in Mexico includes 0.42 million ha of primary forest and 4.2 million ha of secondary forest [3].

Along with the accelerated transformation of tropical ecosystems, there has been an increase in the number of studies concerning biodiversity conservation in anthropic landscapes [4-7]. The active management of different landscape elements could have either positive or negative effects on native biodiversity and its functional role in these landscapes [8]. Particularly in dry tropical landscapes, biodiversity is affected by the existence of natural areas and the management of the landscape matrix, and both are key to biodiversity conservation [4].

To fully understand the current status of conservation in anthropogenic landscapes and to predict future trends, a deeper study of biodiversity in actively managed rural landscapes is needed [5]. The most practical way to examine how assemblages are structured is by measuring diversity [9], but estimating species diversity with a single index is a very crude calculation of richness, composition and the assemblage structure [9]. Consequently, responses of assemblages to habitat transformation are better understood when taxonomic diversity (*i.e.*, the entire taxonomical arrangement/hierarchy of species) and functional group (*i.e.*, a group of species that utilize similar resources, usually food) diversity are considered [9, 10].

Among the insects of tropical forests worldwide, ants are highly diverse and stand out because of their abundance and high relative biomass [11]. Ants have been widely used as bio-indicators, because their responses to habitat transformations are relatively fast, predictable, and easy to detect and analyze [7, 12]. They are useful in the evaluation of management practices for conservation, because changes in ant assemblages are usually related to changes in other invertebrate assemblages [7, 12, 13].

Few studies compare the taxonomic, species, and functional group diversity of ant assemblages among habitats that differ in the intensity of anthropic disturbance in a given landscape [9]. Most studies only focus on species diversity, commonly reporting that human disturbance reduces ant species richness, increases ant abundance of some species favored by environmental disturbance, and provokes high species turnover at the landscape level [4, 9, 6, 14]. However, it is still not clear how taxonomic and functional group diversity is affected [6, 14-17]. In this study, we analyzed and compared the taxonomic, species, and functional group diversity of ant assemblages among habitats with different levels of structural complexity in a tropical anthropized landscape. Taxonomic diversity was measured as average and variation in taxonomic distinctness. Species diversity was measured as richness, abundance, and similarity among assemblages. Finally, functional group diversity was measured as the frequency of functional groups following the classifications of Neotropical ants by Groc et al. [9].

Methods

Study site

Field work was conducted at Centro de Investigaciones Costeras La Mancha (CICOLMA) and outlying areas on the central coastal plain of the Gulf of Mexico in Actopan, Veracruz, Mexico (Fig. 1). The climate is warm and sub-humid with a mean annual temperature of 25 °C and a mean annual precipitation of 1,500 mm. There are three distinct seasons in the area: a wet, warm season (June to September), a relatively dry, cool

season (October to January) and a dry, warm season (February to May). Soils are unstructured luvic and calcareous arenosols [18, 19].

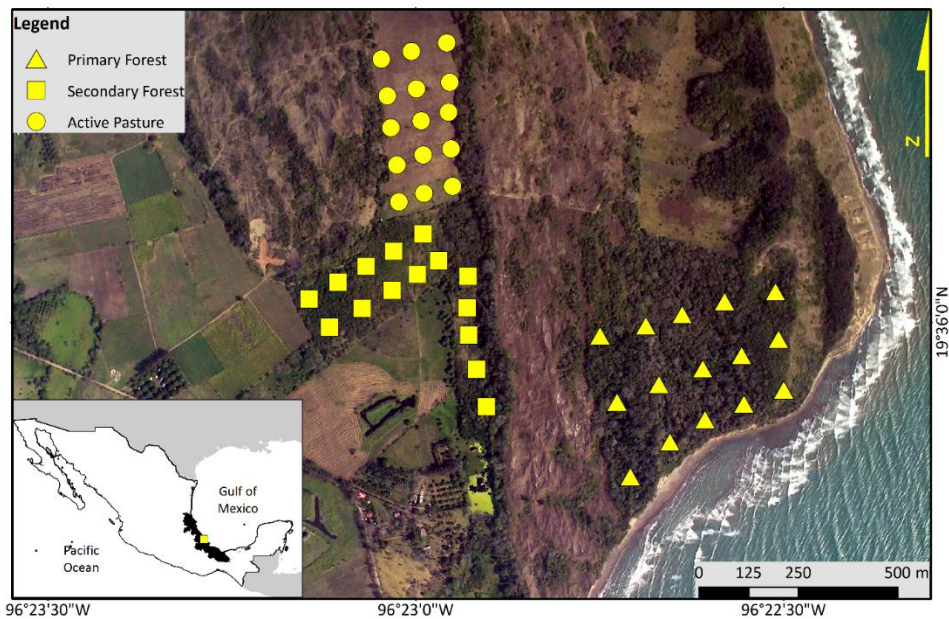


Fig. 1: Study sites location in La Mancha region, municipality of Actopan, Veracruz, Mexico.

Originally the most common vegetation type in the area was tropical dry forest, or tropical semi-deciduous forest, growing on sandy soils [20]. The last remnants of the original tropical forest in the region are presently surrounded by different vegetation types, mainly by man-made pastures, but also by coastal scrub on sand dunes and secondary woody vegetation in different phases of succession [19].

We selected three habitats with different floristic composition and vegetation structure representing different stages of succession (Fig. 1, Table 1, Appendix 1): 1) a fragment of tropical, semi-deciduous forest considered to be primary forest (PF), which is one of the last remnants of tropical dry forest on sand dunes in the coastal plain of the Gulf of Mexico; 2) a secondary forest (SF) adjacent to CICOLMA that was used for over 20 years as a cattle pasture until 1995, when cattle were excluded as part of a long term study of vegetation succession in this plot; and 3) an active pasture (AP), neighboring the SF, which is used for grazing cattle during the dry season.

Ant sampling

Sampling was conducted during the rainy (August-September 2011) and dry seasons (March-April 2012). For sampling, three parallel transects 220 m long were used in each habitat. These transects were placed at least 100 m apart and more than 20 m away from any habitat edge. Along each transect, five sampling stations were placed, each with a 10 m radius and located 30 m apart from each other (Fig. 1). Several complementary sampling techniques were used at each station in order to include the different microhabitats used by ants. Each sampling station was considered to be a complex sample, composed of a subterranean trap, two pitfall traps (one with tuna bait and another without bait), and two traps placed on trees at 2 m from the ground (one baited with tuna and the other with honey) [6]. They were recovered after 72 h of exposure in the field. Additionally, a 1 m² sample of leaf-litter was collected from the ground

at each sampling station and processed with Winkler sacks to extract the ants [21]. The Winkler sack consists of a metal box frame that supports a covering made of cotton, which is suspended from a nail in a wall or some other kind of hanger. Litter from each sample is separated into a 4-mm mesh inlet sack which is suspended inside the Winkler sack. Ants in the litter migrate out of the inlet sack and are collected in a cup, partially filled with ethanol, tied to the bottom [21]. The key of Mackay and Mackay [22] was used to identify ant genera, in addition to several other keys for species identification depending on the genus involved. Voucher specimens were deposited in the Entomological Collection of the Instituto de Ecología, A.C. in Xalapa, Veracruz, Mexico (IEXA; Reg. SEMARNAT: Ver. IN.048.0198).

Habitat characterization

At each sampling station tree canopy height was estimated by averaging the height of the tallest tree near the station and its four nearest tree neighbors using a Haga altimeter (Table 1). Canopy cover was estimated with a spherical convex densiometer (Model A; Forestry Suppliers Inc.). Additionally, four 1 m² quadrats were randomly placed for measuring soil compaction using a pocket penetrometer (JDBlab), and within each of these quadrats the percentage of area covered by grasses, herbs, leaf-litter and woody seedlings was estimated.

Table 1. Characteristics of the Primary Forest (PF), Secondary Forest (SF), and Active Pasture (AP) sampled in Actopan, Veracruz, Mexico. Average values and standard errors are given (n = 30). * Different letters denote significant differences among habitats (Mann–Whitney U test, P < 0.05).

| | PF | SF | AP |
|--|-------------------------|-------------------------|--------------------------|
| Longitude N | 19°35'58" | 19°36'03" | 19°36'10" |
| Latitude W | 96°22'36" | 96°23'03" | 96°22'59" |
| Elevation (m a.s.l.) | 25 | 27 | 29 |
| Area (ha) | 32 | 7 | 9 |
| Canopy cover (%)* | 88.4 ±0.56 ^a | 79.3 ±1.86 ^b | 19.7 ±2.39 ^c |
| Average canopy height (m)* | 12.2 ±0.33 ^a | 7.3 ±0.05 ^b | 1.7 ±0.13 ^c |
| Soil compaction (Kg/cm ²)* | 5.16 ±0.92 ^a | 8.13 ±0.87 ^b | 18.11 ±0.91 ^c |
| Soil cover (%)* | 43.3 ±3.31 ^a | 92.8 ±0.64 ^b | 96.3 ±0.68 ^c |

Data analysis

Taxonomic diversity. The names of ant subfamilies, tribes, genera, and species were assigned according to AntCat classification, which is an online catalog containing the current taxonomy and phylogeny of the world's ants [23]. As estimators of taxonomic diversity we used the average taxonomic distinctness ($\Delta+$) as well as the variation in taxonomic distinctness index ($\Lambda+$) *sensu* Clarke and Gorley [10]. Average taxonomic distinctness ($\Delta+$) is calculated from node-based phylogenetic trees and is expressed by the following equation:

$$\Delta+ = \frac{2 \sum_{i=1}^{S-1} \sum_{j=i+1}^S \omega_{ij}}{S(S-1)}$$

where S is the number of species present, and ω_{ij} the "distinctness weight" according to the length of the path linking species i and j in the phylogenetic tree [10]. We used a simple linear scaling whereby the largest number of steps in the tree is set to $\omega = 100$. Average taxonomic distinctness takes into account the taxonomic level at which any two species are related and can be thought of as the average length between any two randomly chosen species present in the sample [10]. Thus, $\Delta+$ is a direct measure of taxonomic diversity: a high value of $\Delta+$ reflects high taxonomic diversity (low relatedness among species). On the other hand, variation in taxonomic distinctness ($\Lambda+$) reflects the degree to which certain taxa are over- or under-represented in the samples and is expressed by the following equation:

$$\Lambda+ = \frac{2 \sum_{i=1}^{S-1} \sum_{j=i+1}^S (\omega_{ij} - \bar{\omega})^2}{S(S-1)}$$

where variables are the same as those used for average taxonomic distinctness. The presence of some genera with many species would tend to increase $\Lambda+$, but this would be counterbalanced by the presence of subfamilies represented by only one (or very few) species [10]. Therefore, $\Lambda+$ measures the unevenness in the taxonomic tree, and is thus the inverse of taxonomic diversity: high taxonomic diversity would be expected for a community with an even distribution of species among the taxonomic levels and units, a situation that would result in a low value of $\Lambda+$. To assess whether significant differences exist among sites, we used the TAXDTEST procedure in the software PRIMER v6 for both taxonomic indices [10].

Species diversity. Species \times sample presence/absence matrices, one for each habitat, were analyzed and compared among the habitats. Species occurrences (*i.e.*, the number of times that a given species was collected at a sampling station during dry and wet seasons) were taken into account as a proxy for ant relative abundance [9]. The observed species richness (Sobs) was randomized 1,000 times and rarefied to a minimum cut-off level of abundance, based on the habitat with the lowest abundance, at a 95% confidence interval. The incidence-based coverage estimator (ICE) calculated in EstimateS 8.2® [24] was used to measure the inventory completeness (the percentage of observed species with respect to the number of species predicted by the estimator). Rank-abundance curves were plotted to compare the assemblage structure among habitats, using the paired non-parametric Kolmogorov-Smirnov test in the software PAST to test for differences among habitats [25].

To assess beta diversity, we created an incidence matrix with all species collected from all sampling stations (30 per habitat) to compute a non-metric multidimensional scaling (NMDS) ordination and a one-way similarity analysis (ANOSIM) among habitats. In all of these analyses the Bray-Curtis index was used as a similarity metric, computed in the software PAST [25].

Functional group diversity. Species were assigned to one out of nine functional groups based on the Neotropical ant classification used by Groc et al. [9]. Functional groups included two groups of fungus-growers (*i.e.*, leaf-cutter ants and cryptobiotic attines), three groups of omnivores (*i.e.*, ground-nesting, generalist-nesting, and arboreal omnivorous ants) and four groups of predators (*i.e.*, ground-dwelling generalist, ground-dwelling specialist, raid-hunting, and arboreal predators) (Appendix 2). G tests with Williams's correction were performed to compare functional group abundance among habitats [26].

Results

Taxonomic diversity

In total, 34,957 ant workers belonging to 89 species, 36 genera, 12 tribes, and seven subfamilies were collected (Appendix 2). Subfamily Myrmicinae had the highest number of tribes, genera, and species. The richest genus was *Camponotus* (12 spp.), followed by *Pheidole* (9), *Pseudomyrmex* and *Solenopsis* (7 spp. each) and *Brachymyrmex* and *Trachymyrmex* (5 spp. each).

Taxonomic composition recorded per habitat, included 32 genera, 11 tribes and six subfamilies in the PF; 20 genera, 9 tribes and six subfamilies in the SF; and 13 genera, seven tribes and four subfamilies in the AP. The highest average taxonomic distinctness ($\Delta+$) was found in SF (87.82), followed by PF (85.47) and AP (85.46, Fig. 2a). The highest variation in taxonomic distinctness ($\Lambda+$) was found in AP ($\Lambda+$ =568.75), followed by PF (506.71) and SF (482.23, Fig. 2b). There were no significant differences among habitats in $\Delta+$ and $\Lambda+$, as shown by the 95% C.I. overlap in the randomization model ($P > 0.05$, Fig. 2a and 2b).

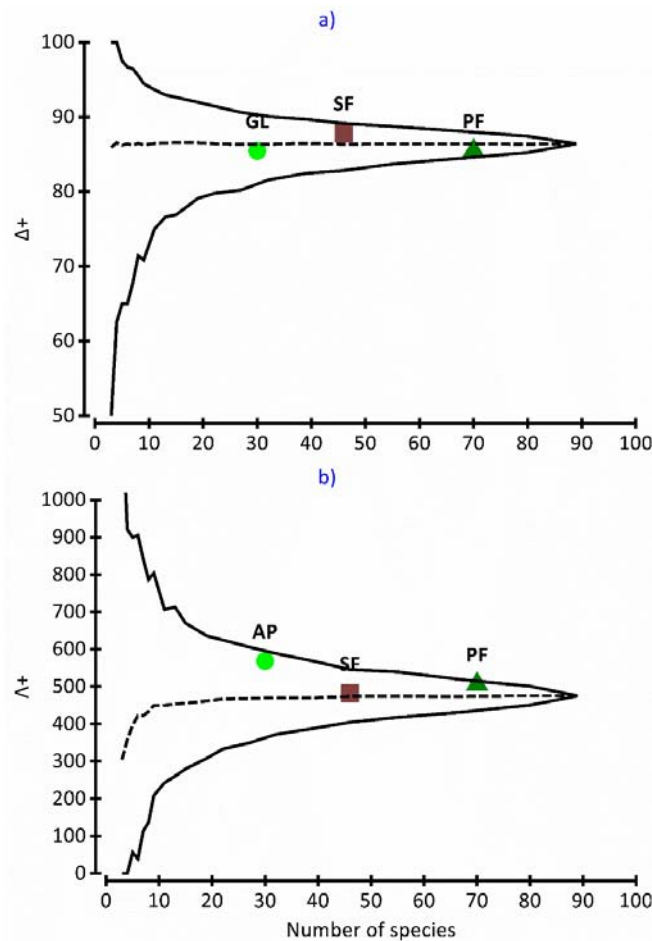


Fig. 2. Average taxonomic distinctness index ($\Delta+$) and the variation in taxonomic distinctness index ($\Lambda+$) in Primary Forest (PF), Secondary Forest (SF) and Active Pasture (AP). In both graphs the global average is shown as a dotted line and the 95% confidence interval as a continuous curve with 999 permutations of randomized species pairings from the whole species list.

Species diversity

The richest habitat was the PF (70 spp.), followed by the SF (46) and the AP (30). Rarefied species richness at the lowest abundance value (163 captures in AP), was significantly different among habitats, as shown by the non-overlapping 95% confidence intervals of the three species accumulation curves (Fig. 3). Inventory completeness was 88% in PF, 86% in SF and 83% in AP. When data from the three habitats were pooled, the inventory completeness was 94%. The highest number of species occurrences was recorded for PF (343), followed by SF (231) and lastly AP (163). Ant abundance per habitat differed significantly between PF and SF ($D = 0.26$, $P < 0.001$) as well as between PF and AP ($D = 0.44$, $P < 0.0001$), but not between SF and AP (Fig. 4).

Regarding beta diversity, the NMDS ordination showed a clear separation among the three habitats (stress = 0.04, Fig. 5), and the ANOSIM confirmed significant differences (Global $R = 0.91$, $R < 0.0001$) among habitats. Paired comparisons showed significant differences between all ant assemblages: PF and SF ($R = 0.80$, $P < 0.0001$), PF and AP ($R = 0.96$, $P < 0.0001$), and SF and AP ($R = 0.69$, $P < 0.0001$). Regarding species turnover, 49% of the recorded species were unique to a single habitat, and 13% were shared by all habitats (Appendix 2). The PF had 34 unique species, while the SF and the AP only had 5 exclusive species each.

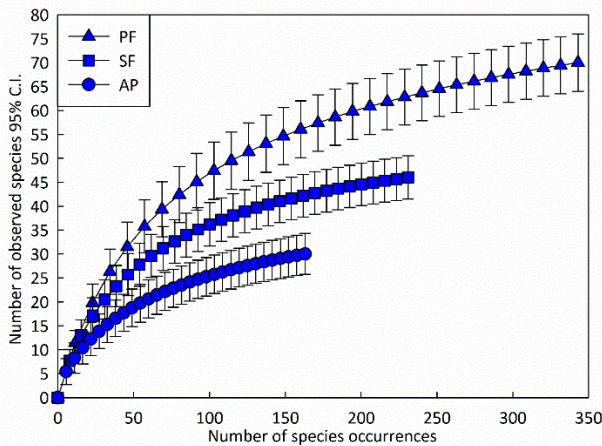


Fig. 3. Observed species richness for Primary Forest (PF), Secondary Forest (SF) and Active Pasture (AP) rarefied at 163 captures. Differences are considered to be statistically significant when 95% confidence intervals (C.I.) do not overlap ($\alpha = 0.05$).

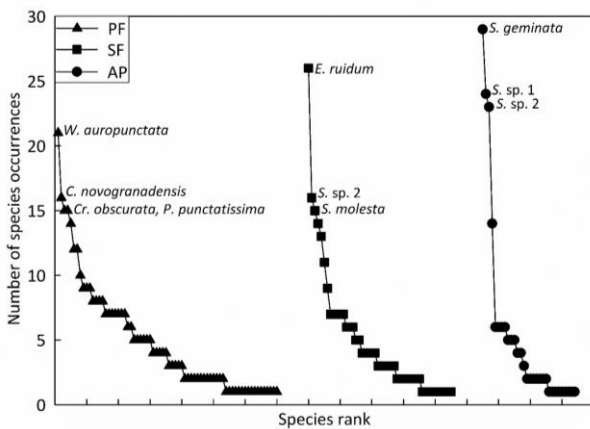


Fig. 4. Rank-abundance curves for ant species captured in Primary Forest (PF), Secondary Forest (SF) and Active Pasture (AP). Only those species with a relative abundance equal or higher than 50% in a given habitat are shown (W.: *Wasmannia*, C.: *Camponotus*, Cr.: *Crematogaster*, P.: *Pheidole* E.: *Ectatomma*, S.: *Solenopsis*).

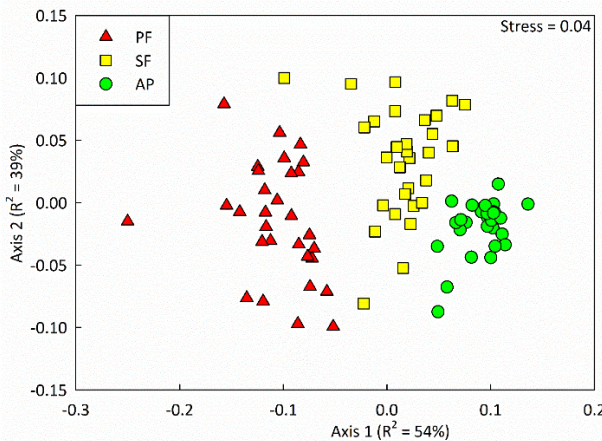


Fig. 5. Non-metric multidimensional scaling ordination of the ant assemblages in Primary Forest (PF), Secondary Forest (SF) and Active Pasture (AP) in La Mancha, Actopan, Veracruz, Mexico.

Functional group diversity

Generalist omnivores was the richest functional group with 26 species, followed by arboreal omnivores with 22, arboreal predators, cryptobiotic attines, and ground-dwelling omnivores each with eight, ground-dwelling generalist predators and leaf-cutters with six, ground-dwelling specialist predators with three, and finally, the raid-hunting predators with two (Appendix 2).

The highest number of functional groups was recorded in PF (9), followed by SF (7) and AP (5). Functional groups found in all three habitats were arboreal omnivores, generalist omnivores, ground-dwelling omnivores, cryptobiotic attines and arboreal predators (Fig. 6). The ground-dwelling generalist predators and ground-dwelling specialist predators were absent from the AP but present in both the PF and the SF. The leaf-cutters and the raid-hunting predators were found exclusively in the PF.

Relative abundance of each functional group varied significantly among habitats ($G = 195.63$, $DF = 16$, $P < 0.0001$). Leaf-cutters ($G = 59.13$, $DF = 2$, $P < 0.0001$), cryptobiotic attines ($G = 11.5$, $DF = 2$, $P < 0.001$), ground-dwelling generalist predators ($G = 23.47$, $DF = 2$, $P < 0.0001$), raid-hunting predators ($G = 20.04$, $DF = 2$, $P < 0.0001$) and ground-dwelling specialist predators ($G = 7.59$, $DF = 2$, $P < 0.0001$) decreased significantly in relative abundance from PF to AP. The ground-dwelling omnivores ($G = 56.03$, $DF = 2$, $P < 0.0001$) increased significantly in abundance from PF to AP.

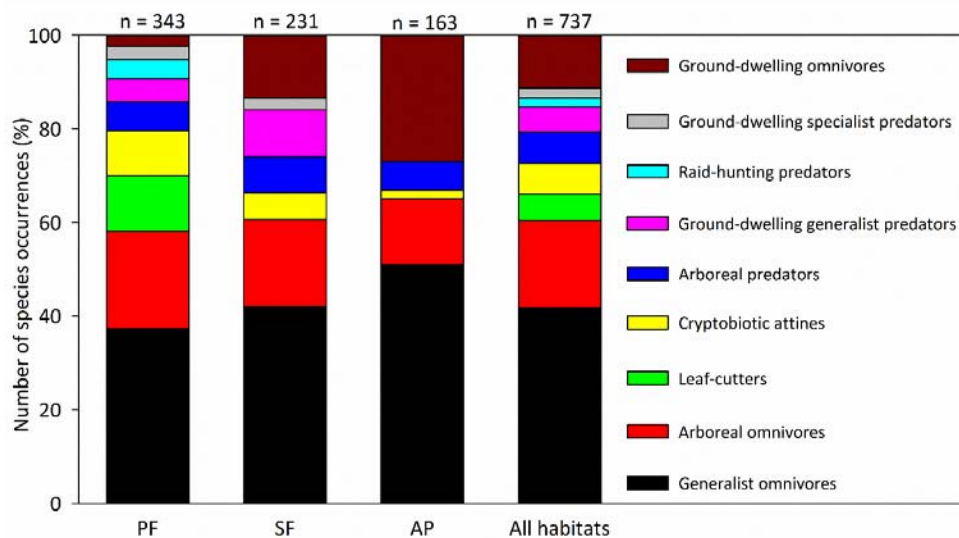


Fig. 6. Proportional distribution of accumulated occurrence of ant species in Primary Forest (PF), Secondary Forest (SF) and Active Pasture (AP) by functional group.

Discussion

The 89 ant species (including morpho-species) collected represent 10% of the Mexican myrmecofauna, and 32% of that reported for the state of Veracruz [27]. Other studies conducted in the central coastal plain of the Gulf of Mexico recorded 81 species [31], 92 [4] and 121 [29]. However, such studies vary widely in sampling efforts, collection methods, objectives, and levels of identification, making meaningful comparisons difficult. Additionally, new ant records for Mexico and Veracruz were found in this anthropized landscape [28]. These findings suggest that man-modified landscapes could serve as important refuges for myrmecofauna, considering the relatively small area (*ca.* 1 ha per habitat) sampled in this study.

Taxonomic diversity

Average taxonomic distinctness ($\Delta+$) was not significantly different among habitats, which could be explained by a high similarity at the supra-generic level. Of the seven subfamilies collected, four were shared among the three habitats (Dolichoderinae, Formicinae, Myrmicinae and Pseudomyrmicinae), and

about 50% of the recorded tribes were also shared (Attini, Camponotini, Crematogastrini, Leptomyrmecini, Plagiolepidini, Pseudomyrmecini, and Solenopsidini).

The highest variation in taxonomic distinctness (Λ^+), recorded in AP in comparison with the other two habitats, is related to an over-representation of some taxonomic groups and the under-representation of others, particularly at the genus level. *Camponotus*, *Brachymyrmex*, *Nylanderia*, *Cyphomyrmex*, *Crematogaster*, *Pheidole*, *Monomorium*, *Solenopsis* and *Pseudomyrmex* were present in all habitats and over-represented, while *Azteca*, *Atta*, *Cardiocondyla*, *Dolichoderus*, *Dorymyrmex*, *Eciton*, *Ectatomma*, *Forelius*, *Labidus*, *Leptothorax*, *Mycetosoritis*, *Temnothorax* and *Tetramorium* were under-represented in this study.

Additionally, the representation of these genera increased from the PF and SF (48.6 and 67.4%, respectively), to 86.7% in the AP. Given the low relatedness among species and the uniformity of their distribution across the classification, we interpret the composition of PF and SF to be more diverse in taxonomic diversity than AP. Although we focus on taxonomy, if we assume that it is a rudimentary approximation of phylogeny [10], we could say that the PF and the SF include more evolutionary diversity because their myrmecofauna is more diversified; while the AP showed lower phylogenetic diversification.

Another factor that could influence the results for taxonomic diversity was the presence in the PF of species belonging to genera not found in the other habitats, specifically some exotic/invasive species, such as *Tapinoma melanocephalum*, *Paratrechina longicornis*, *Monomorium floricola* and *Wasmannia auropunctata*. The presence of these open/disturbed habitat species in PF is consistent with other studies conducted in tropical dry forest fragments in the same study area [4, 29, 31], and in the Pacific coast of Mexico [34].

Species diversity

Our results show that ant species richness is inversely related to the intensity of the disturbance, the highest richness was recorded in the PF (*i.e.*, the less disturbed site), followed by the SF (*i.e.*, intermediate disturbance) and finally the AP (*i.e.*, the most disturbed site). This pattern coincides with several studies carried out in the tropics where species richness has been found to be positively related to disturbance and structural complexity of the site [6, 7, 15-17]. The highest values for richness were recorded in the PF and could be due to greater complexity in vegetation structure. It has been demonstrated that more complex vegetation structure results in a much higher availability of micro-habitats for different ant groups, particularly when there are large trees present [6, 7, 14, 29]. The SF showed an intermediate ant richness, which is also related to its intermediate structural complexity, which in turn is more complex than that of the AP. The studied SF is currently in a state of secondary succession of 16 years (*i.e.*, the time since the site was abandoned), and it has a distinct ant species composition with marked differences from the ant assemblages in the PF and in the AP.

The structure of the ant communities, in particular regarding relative abundance, also changed with the degree of human disturbance per habitat. The habitats with lower complexity in vegetation structure (AP and SF) and highest disturbance intensity showed a marked dominance by few ant species, while in the PF species evenness was highest.

Ant abundance in the three habitats showed a trend opposite to that described for ant richness. The high abundance in the AP was related to the presence of *Solenopsis geminata*, representing 74% captured ants in this habitat. This species is both generalist and opportunistic, belonging to the fire ant group, which is found in open habitats with direct and high sunlight [30].

Regarding beta-diversity, we found significant differences and high dissimilarity values among habitats. These results demonstrate that each habitat contributes different assemblages to the species composition of the regional myrmecofauna. This finding could be due to the relatively high proportion of ant species that were unique to a single habitat and the minor proportion collected in all three habitats. When the identity of the ant species shared by the three habitats was analyzed, it became clear that the presence of trees in pastures (*i.e.*, isolated shade trees) and in secondary forests was crucial. Trees provide microhabitats or refuges for some nectarivorous and predator ant species, such as *Camponotus* spp.; *Pseudomyrmex* spp. and *Monomorium ebeninum*, which are unable to survive in areas completely devoid of trees [4, 31]. Species shared among habitats, such as *Crematogaster torosa*, *Cyphomyrmex rimosus*, *Nylanderia steinheili*, *Pheidole punctatissima* and *Solenopsis molesta*, are species with a wide geographic distribution and a high tolerance of different environmental conditions [17]. These results are consistent with similar studies suggesting that some landscape elements, such as isolated trees within pastures or crop-fields, provide favorable sites for certain arthropod species [4, 14, 31, 32]. Therefore, those arboreal elements might increase the conservation value of anthropic landscapes.

Functional group diversity

The variation in functional groups found among habitats indicates that there is a turnover of predator and fungi grower ants that are replaced by soil omnivore ants. This turnover of functional groups was consistent with the degree of human transformation and the reduced structural complexity of the habitats. The composition and structure of functional groups in each studied habitat showed that the detected species turnover was mainly due to the replacement of habitat specialists by generalists. These results agree with other studies in the Neotropics that found similar replacement of functional groups among habitats [9, 33]. These results also confirm that each habitat holds a particular assemblage of ants with different resource requirements and optimal environmental conditions. The reduction of habitat complexity by human activities greatly affects the abundance of resources as well as microclimatic and abiotic conditions for ants [9]. The myrmecofauna of the PF, characterized in large part by ant assemblages with very specific ecological requirements, are replaced by groups of omnivore and generalist ants that are favored by human disturbances.

Implications for conservation

Results of this study showed that the transformation of the original tropical dry forest has an important effect on the ant assemblages, expressed as differences in species richness, composition, and relative abundance. Even though the creation of a more heterogeneous landscape by human activities favors ant species that were absent in the non-transformed forest, preservation of the few forest fragments that still exist along the coastal plain of the state of Veracruz is crucial for the long-term maintenance of regional ant diversity. Our results show that the conservation of the tropical dry forest, which was the richest habitat sampled, will greatly help to avoid the local extinction of those ant species that are restricted to this type of habitat. Species that are favored by the agricultural transformation of the original forest are habitat generalists and opportunistic species that thrive in simplified ecosystems. With accelerated landscape transformation, some specialized species or functional groups would be drastically reduced in population size or would even disappear from the area. Since they perform specialized ecosystem services, such as the degradation of organic matter or insect predation, their local extinction will have non-desirable effects on other organisms and ecosystem processes. Our results also showed that if we are able to preserve some habitats and landscape elements within agricultural areas that have great conservation value, we then could keep a high total richness in the landscape. Since the agricultural matrix that surrounds the few forest fragments has a prominent role, management practices that explicitly take into

account their effects on biodiversity would maximize arthropod conservation in human-transformed landscapes.

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Appendix 1: Floristic composition of the study sites.

Primary Forest. The forest canopy reaches 20 m in height, among the tallest canopy trees the most common species are: breadnut (*Brosimum alicastrum* Sw.), gumbo limbo (*Bursera simaruba* (L.) Sarg.), cigar-box wood (*Cedrela odorata* L.), roble (*Ehretia tinifolia* L.), elephant ear (*Enterolobium cyclocarpum* (Jacq.)), fig (*Ficus cotinifolia* Kunth) and pink trumpet-tree (*Tabebuia rosea* (Bertol.)). Most characteristic sub-canopy tree species, reaching between 6 and 15 m in height, are: *Nectandra salicifolia* (Kunth), gia verde (*Casearia corymbosa* Kunth), *Coccoloba humboldtii* Meins, *Elaeodendron trichotomum* (Turcz.), *Diospyros verae-crucis* (Standl.) and *Erythroxylum havanense* Jacq. The understory is characterized by shrub or shrub-like species such as: *Crossopetalum uragoga* (Jacq.), spider brake (*Hippocratea celastroides* Kunth), cudjoe-wood (*Jacquinia macrocarpa* Cav.), rough-leaved pepper (*Piper amalago* L.), Florida boxwood (*Schaefferia frutescens* Jacq.) and *Xylosoma panamensis* Turcz. Lianas and vines of different species are also common, while epiphytes are present but scarce.

Secondary Forest. Currently the site is covered by a 16 year old secondary forest with a dense woody canopy 6 to 8 m tall, where several tree species of Leguminosae are very abundant like the white leadtree (*Leucaena leucocephala* Lam.), palo amarillo (*Diphysa robinoides* Benth.), *E. cyclocarpum* Jacq. and quickstick (*Gliricidia sepium* Jacq.). Other abundant species include the trees *C. odorata*, pigeon wood (*Guazuma ulmifolia* Lam.), *B. simaruba* and yellow trumpet flower (*Tecoma stans* (L.)), as well as the coyol palm (*Acrocomia aculeata* (Jacq.)) and palmetto (*Sabal mexicana* Mart). In some patches of this plot (<10% of area) the African grass *Panicum maximum* Jacq. still persists with relatively high cover but is being shaded by woody plants.

Active Pasture. Dominant grasses include: bluestem (*Andropogon* sp.), *P. maximum* and crowngrass (*Paspalum* spp.). Within this pasture few isolated small trees are present, including *A. aculeata* and *S. mexicana* and the trees *G. sepium* Jacq., citrus (*Citrus* sp.) and java plum (*Spondias mombin* L.).

Appendix 2: Ant species collected at a primary tropical dry forest (PF), a secondary forest (SF) and in an active pasture (AP) in the coastal plain in the central part of the state of Veracruz, Mexico. Frequency of capture (values above diagonal) and number of individuals captured (values below diagonal) are shown. Functional groups are: generalist omnivores (GO); arboreal omnivores (AO), leaf-cutters (LC), cryptobiotic attines (CA), arboreal predators (AP), ground-dwelling generalist predators (GGP), raid-hunting predators (RHP), ground-dwelling specialist predators (GSP) and ground-dwelling omnivores (GDO).

| Species | Functional group | PF | SF | AP |
|--|------------------|--------|--------|--------|
| Dolichoderinae Forel | | | | |
| Dolichoderini Forel | | | | |
| <i>Dolichoderus lutosus</i> (Smith) | AO | 3/5 | | |
| Leptomyrmecini Emery | | | | |
| <i>Azteca velox</i> Forel | AO | 8/82 | 3/5 | |
| <i>Dorymyrmex bicolor</i> Wheeler | GDO | 2/10 | | 14/428 |
| <i>Forelius damiani</i> Guerrero & Fernández | GDO | | 1/12 | 5/23 |
| Tapinomini Emery | | | | |
| <i>Tapinoma cf. litorale</i> Wheeler | AO | 2/6 | | |
| <i>T. melanocephalum</i> (Fabricius) | AO | 2/8 | | |
| Dorylinae Leach | | | | |
| Dorylini Leach | | | | |
| <i>Eciton burchellii</i> (Westwood) | RHP | 9/45 | | |
| <i>Labidus coecus</i> (Latreille) | RHP | 5/7 | | |
| Ectatomminae Emery | | | | |
| Ectatommini Emery | | | | |
| <i>Ectatomma ruidum</i> (Roger) | GO | | 26/505 | |
| Formicinae Latreille | | | | |
| Camponotini Forel | | | | |
| <i>Camponotus atriceps</i> (Smith) | AO | | | 6/19 |
| <i>C. claviscapus</i> Forel | AO | 3/3 | | 1/13 |
| <i>C. fasciatellus</i> Dalla-Torre | AO | | 7/27 | 1/1 |
| <i>C. mucronatus hirsutinasus</i> Wheeler | AO | 7/28 | 1/5 | 1/64 |
| <i>C. nitidior</i> (Santschi) | AO | | 2/2 | |
| <i>C. novogranadensis</i> Mayr | AO | 16/100 | 3/17 | |
| <i>C. planatus</i> Roger | AO | 4/5 | 1/1 | 6/31 |
| <i>C. sericeiventris</i> (Guérin-Méneville) | AO | 5/17 | | |
| <i>Camponotus</i> sp. 1 | AO | 1/1 | | |
| <i>Camponotus</i> sp. 2 | AO | 4/9 | 4/30 | 1/1 |
| <i>C. striatus</i> (Smith) | AO | 1/1 | | |
| <i>C. cf. textor</i> Forel | AO | 3/7 | 3/4 | |
| Plagiolepidini Forel | | | | |
| <i>Brachymyrmex depilis</i> Emery | GO | 1/1 | | 3/3 |

| | | | | |
|---|-----|---------|--------|--------|
| <i>B. musculus</i> Forel | GO | | 7/2188 | 4/24 |
| <i>Brachymyrmex</i> sp. 1 | GO | | | 4/60 |
| <i>Brachymyrmex</i> sp. 2 | GO | | | 1/1 |
| <i>Brachymyrmex</i> sp. 3 | GO | 1/28 | 7/20 | |
| <i>Nylanderia steinheili</i> (Forel) | GO | 9/82 | 1/1 | 1/85 |
| <i>Paratrechina longicornis</i> (Latreille) | GO | 7/294 | | |
| Myrmicinae Lepeletier | | | | |
| Attini Smith | | | | |
| <i>Atta mexicana</i> (Smith) | LC | 3/11 | | |
| <i>Cyphomyrmex costatus</i> Mann | CA | 4/9 | | |
| <i>C. rimosus</i> (Spinola) | CA | 12/72 | 11/28 | 2/2 |
| <i>Cyphomyrmex</i> sp. | CA | 1/1 | 1/1 | |
| <i>Mycetosoritis hartmanni</i> (Wheeler) | CA | | 1/1 | 1/1 |
| <i>Mycocepurus curvispinosus</i> Mackay | CA | 5/9 | | |
| <i>M. smithii</i> (Forel) | CA | 4/7 | | |
| <i>Sericomyrmex</i> sp 1 | CA | 4/13 | | |
| <i>Sericomyrmex</i> sp 2 | CA | 3/3 | | |
| <i>Trachymyrmex intermedius</i> (Forel) | LC | 10/17 | | |
| <i>Trachymyrmex</i> sp. 1 | LC | 8/14 | | |
| <i>Trachymyrmex</i> sp. 2 | LC | 8/16 | | |
| <i>Trachymyrmex</i> sp. 3 | LC | 5/5 | | |
| <i>Trachymyrmex</i> sp. 4 | LC | 7/7 | | |
| <i>Wasmannia auropunctata</i> (Roger) | GO | 21/2507 | | |
| <i>Cephalotes minutus</i> (Fabricius) | AO | 1/1 | 6/37 | |
| <i>C. scutulatus</i> (Smith) | AO | 1/1 | | |
| <i>Strumigenys ludia</i> Mann | GSP | 7/35 | 4/9 | |
| <i>S. cf. oconitrilloae</i> (Longino) | GSP | 2/2 | 2/2 | |
| <i>S. schulzi</i> Emery | GSP | 1/1 | | |
| <i>Pheidole absurda</i> Forel | GO | 1/2 | | 2/30 |
| <i>P. cf. mackayi</i> Wilson | GO | 12/606 | 2/16 | |
| <i>P. nubicola</i> Wilson | GO | 6/16 | | |
| <i>P. punctatissima</i> Mayr | GO | 15/315 | 3/32 | 2/27 |
| <i>Pheidole</i> sp. 1 | GO | 1/4 | 6/25 | |
| <i>Pheidole</i> sp. 2 | GO | | | 1/2 |
| <i>Pheidole</i> sp. 3 | GO | 9/345 | | |
| <i>P. susannae</i> Forel | GO | 14/182 | 3/5 | |
| <i>P. tepicana</i> Pergande | GO | 5/6 | | |
| Crematogastrini Forel | | | | |
| <i>Crematogaster curvispinosa</i> Mayr | GO | 1/1 | | |
| <i>C. obscurata</i> Emery | GO | 15/126 | 5/15 | |
| <i>C. torosa</i> Mayr | GO | 1/8 | 2/2 | 6/1042 |

| | | | | |
|---|-----|------|--------|----------|
| <i>Cardiocondyla emeryi</i> Forel | GO | | | 1/3 |
| <i>Leptothorax</i> sp. | GDO | 2/3 | 3/5 | |
| <i>Temnothorax subditivus</i> (Wheeler) | GDO | 2/2 | | |
| <i>Tetramorium spinosum</i> (Pergande) | GO | 2/3 | | |
| <i>Xenomyrmex panamanus</i> (Wheeler) | AO | 1/1 | | |
| Solenopsidini Forel | | | | |
| <i>Monomorium ebeninum</i> Forel | AO | 7/84 | 9/496 | 2/5 |
| <i>M. floricola</i> (Jerdon) | AO | 2/23 | | |
| <i>Solenopsis geminata</i> (Fabricius) | GO | | 7/3920 | 29/15302 |
| <i>S. globularia</i> (Smith) | GDO | | 7/89 | |
| <i>S. molesta</i> (Say) | GO | 7/88 | 15/576 | 5/131 |
| <i>Solenopsis</i> sp. 1 | GO | | 13/241 | 24/2178 |
| <i>Solenopsis</i> sp. 2 | GDO | | 16/506 | 23/874 |
| <i>Solenopsis</i> sp. 3 | AO | | 4/61 | 5/125 |
| <i>Solenopsis</i> sp. 4 | GDO | | 2/2 | 2/19 |
| <i>Rogeria belti</i> Mann | GDO | 2/3 | 2/8 | |
| Ponerinae Lepeletier | | | | |
| Ponerini Lepeletier | | | | |
| <i>Hypoponera</i> sp. 1 | GGP | 5/18 | 5/12 | |
| <i>Hypoponera</i> sp. 2 | GGP | 1/1 | 1/2 | |
| <i>Hypoponera</i> sp. 3 | GGP | 2/3 | 1/1 | |
| <i>Hypoponera</i> sp. 4 | GGP | 1/1 | 2/10 | |
| <i>Odontomachus laticeps</i> Roger | GGP | 2/2 | | |
| <i>Pachycondyla harpax</i> (Fabricius) | GGP | 6/15 | 14/25 | |
| <i>Neoponera villosa</i> (Fabricius) | AP | 7/8 | 4/4 | |
| Pseudomyrmecinae Smith | | | | |
| Pseudomyrmecini Smith | | | | |
| <i>Pseudomyrmex cubaensis</i> (Forel) | AP | | 1/1 | |
| <i>P. ejectus</i> (Smith) | AP | | 1/1 | |
| <i>P. ferrugineus</i> (Smith) | AP | 1/1 | 6/41 | 2/89 |
| <i>P. gracilis</i> (Fabricius) | AP | 2/2 | 4/4 | 6/10 |
| <i>P. oculatus</i> (Smith) | AP | 8/12 | | |
| <i>P. pallidus</i> (Smith) | AP | 2/2 | 2/6 | 2/4 |
| <i>P. peper</i> (Forel) | AP | 1/6 | | |