



Taxonomic and functional ant diversity along a secondary successional gradient in a tropical forest

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ABSTRACT

The taxonomic diversity (TD) of tropical flora and fauna tends to increase during secondary succession. This increase may be accompanied by changes in functional diversity (FD), although the relationship between TD and FD is not well understood. To explore this relationship, we examined the correlations between the TD and FD of ants and forest age in secondary forests at the α - and β -diversity levels using single- and multi-trait-based approaches. Our objectives were to understand ant diversity patterns and to evaluate the role of secondary forests in the conservation of biodiversity and in the resilience of tropical forests. Ant assemblages were sampled across a chronosequence in the Lacandon region, Mexico. All species were characterized according to 12 functional ecomorphological traits relevant to their feeding behavior. We found that TD and FD were related to forest age at the alpha level, but not at the beta level. α -functional richness and divergence increased linearly with species richness and diversity, respectively. Also, the relationship between taxonomic and functional turnover was linear and positive. Our results indicated that functional traits were complementary across the chronosequence. The increase in FD was mainly driven by the addition of rare species with relevant traits. The older secondary forests did not recover all of the functions of old growth forest but did show a tendency to recovery. Because older successional stages support more TD and FD, we suggest developing agriculture and forestry management practices that facilitate rapid post-agricultural succession and thereby better preserve the functionality of tropical forests.

Key words: environmental filtering; Formicidae; functional redundancy; habitat disturbance; species traits.

DURING THE LAST CENTURY, A LARGE PORTION OF OLD GROWTH TROPICAL FORESTS AROUND THE WORLD HAVE BEEN CONVERTED TO AGRICULTURE (Hansen *et al.* 2013). Several biophysical and societal factors have subsequently led to the abandonment of these agricultural lands, giving rise to secondary growth forests (Chazdon 2014). Presently, secondary forests represent more than 50 percent of all tropical forests (Chazdon 2014). Several studies have documented changing patterns in the taxonomic diversity (TD) of plant and animal assemblages during the old-field succession of tropical forests (*e.g.*, Dunn 2004, van Breugel *et al.* 2006, Chazdon *et al.* 2009, Norden *et al.* 2009, Bihn *et al.* 2010, Lobo *et al.* 2011), yet changes in functional diversity (FD) have been scarcely documented (see Bihn *et al.* 2010, Lohbeck *et al.* 2012). Filling in this gap in knowledge will improve our understanding of the effects of environmental changes on functional diversity, the

response of species to environmental changes and the role of species in ecosystem functions and services during successional processes (Lohbeck *et al.* 2012, Díaz *et al.* 2013, Chazdon 2014). In addition, as the cover of tropical secondary forests increases worldwide, a better understanding of the FD-TD relationship is necessary to identify mechanisms of community assembly (Bihn *et al.* 2010). This knowledge can improve the conservation and restoration of biological communities in the currently burgeoning epoch of the Anthropocene (Micheli & Halpern 2005).

Changes in the FD of a particular site may be related to species richness, the successional age of vegetation and the proportion of rare species that are functionally unique (Bihn *et al.* 2010, Lohbeck *et al.* 2012). Moreover, during secondary succession, changes in species composition may affect ecosystem processes and services if the composition of functional traits that deliver an ecosystem service is also modified (Cardinale *et al.* 2012, Butterfield & Suding 2013). Animals can additionally influence ecosystem processes (*e.g.*, productivity) via trophic cascades (Kagata &

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Ohgushi 2006), and the feeding habits of animals are usually related to the ecosystem services that they supply (e.g., pest control; Cardinale *et al.* 2012). However, animals in secondary forests exhibit a lower number and variety of feeding behaviors both within and among trophic levels in comparison to those in old growth forests (see Duffy *et al.* 2007).

The modulation of ecosystem functions by environmental changes may be analyzed from a mechanistic perspective through exploring the relationship of FD to TD along different environmental gradients (Mayfield *et al.* 2010, Mouillot *et al.* 2013a). The level of functional redundancy (or, conversely, functional complementarity) in a community is especially relevant for the FD-TD relationship (Díaz & Cabido 2001, Petchey & Gaston 2002). For instance, the functional niche complementarity hypothesis states that ecosystem processes depend on the varied functional traits of species (Díaz *et al.* 2011) and that each species contributes to an ecosystem function (Blüthgen & Klein 2011). Thus, if species' traits are complementary (*i.e.*, functionally complementary) across a successional gradient, the addition of a new species would contribute a set of traits not yet present in the community; in this case, the TD-FD relationship would be positive and linear (Petchey & Gaston 2002, Schmid *et al.* 2002). However, if species' traits are redundant (*i.e.*, functionally redundant), the addition of a new species would provide some functional attributes that are already present in the community; in this case, a logarithmic TD-FD relationship would be expected (Petchey & Gaston 2002, Schmid *et al.* 2002). Finally, the TD-FD relationship would be exponential if functional performance depends on both the complementarity of species' traits and the degree of specialization of the particular functional attributes of each species (Blüthgen & Klein 2011), regardless of whether species are rare in abundance (e.g., psychoactive agent of *Lophobora williamsii*, Díaz *et al.* 2011) or common (e.g., higher root:shoot ratio in all plants, Mokany *et al.* 2008). Different TD-FD patterns have been found, yet most of the literature analyzing this relationship to date supports a positive and linear relationship between the two (e.g., Bihn *et al.* 2010, Lohbeck *et al.* 2012) resulting from the link between species-level traits and diet and habitat preferences (Gibb *et al.* 2015).

The analysis of diversity patterns at different scales (e.g., alpha and beta diversity) can also improve our understanding of the processes that shape the structure of communities (Whittaker *et al.* 2001). For instance, the role of environmental filtering in the assembly of species is more prominent at the regional scale (*i.e.*, beta diversity), while the role of species interactions is more important at the local scale (*i.e.*, alpha diversity; Loreau 2000). Analyzing diversity patterns at only one of these scales can result in misleading or incomplete interpretations (Whittaker *et al.* 2001). For example, if strong niche filtering (*i.e.*, environmental determinism) is the main driver of changes in diversity (via trait-based species sorting) along an environmental gradient, significant turnover in TD and FD would be found (Meynard *et al.* 2011). However, this does not necessarily indicate the existence of a relationship between alpha TD and FD, as local TD and FD may remain unchanged despite significant species and species-trait

turnover (Mouchet *et al.* 2010). Alternatively, if other processes besides environmental determinism are involved (e.g., historical differences in the species pool), functional turnover might be consistently low in spite of substantial species turnover; for example, new species may be replacing others with similar trait attributes (Fukami *et al.* 2005). In this scenario, no relationship between turnover and TD or FD would be expected.

Ants are considered in the present study as they are one of the most diverse, abundant and ecologically relevant group of organisms on Earth and also support a large variety of ecological functions in different ecosystems (Underwood & Fisher 2006). Ants have multiple lifestyles that range from sessile herbivory (e.g., leaf cutting Attini) to highly mobile carnivory (e.g., Dorylinae army ants). The foraging and resource use strategies of ants are also involved in the supply of ecosystem services. For example, ants may act as pest regulators or pollinators and may contribute toward soil formation (del Toro *et al.* 2012). In tropical forests, ant species form part of different functional groups according to their feeding behavior or their trophic position (Philpott & Armbricht 2006, Leal *et al.* 2012), wherein the latter is usually influenced by their morphology (Gibb *et al.* 2015).

The present study aims to analyze the relationship between the alpha and beta components of TD and FD in ant assemblages along a secondary successional chronosequence of Neotropical rainforest. Because the species richness of ants increases as secondary forests age (Rocha-Ortega & Favila 2013), we hypothesize that the addition of new ant species during succession will contribute sets of traits not yet present in the ant community. Based on the three above-mentioned theoretical relationships between TD and FD, we expect a positive, linear relationship between TD and FD along the successional gradient for both the alpha (α) and beta (β) components of diversity.

MATERIAL AND METHODS

STUDY AREA.—The present study was conducted in the Lacandon region near the village of Loma Bonita in the municipality of Marqués de Comillas (16°04'N, 90°45'W), located to the south of the Montes Azules Biosphere Reserve (Reserva de la Biosfera Montes Azules; RBMA) in south-eastern Mexico. The mean annual precipitation of the study area is approximately 3000 mm, and the average temperature is 24°C. A marked dry season is present from February to April (Martínez-Ramos *et al.* 2009). The geomorphology of the region is irregular in soil type and topography (Siebe *et al.* 1996). Our study sites were located at 115–300 m asl on small hills and valleys with sandy and limestone soils of low pH (<5.5). The dominant vegetation is lowland tropical rain forest (Ibarra-Manríquez & Martínez-Ramos 2002). In the area surrounding Loma Bonita, 65 percent is used for agricultural activity, while 13 percent is composed of old growth forest fragments and 22 percent of secondary forests (Zermeño-Hernández *et al.* 2016).

We selected eight permanent plots (0.5 ha) of secondary forest regenerating from abandoned cornfields with successional ages ranging from 6 to 27 yr. These plots represented a gradient,

or chronosequence, of forest recovery. For comparison purposes, we then selected four plots of old growth forest within the RBMA. Site selection was in accordance with an earlier study that considered environmentally homogeneous sites with respect to soil type, topography and management history within the Low-Hill geomorphological unit (van Breugel *et al.* 2006).

ANT INVENTORY.—Ants were sampled during the wet season (July and August) in 2010 and 2011. In each plot, two parallel 100-m transects separated by 20 m were established. Along the two transects, two complementary samplings were conducted per year. First, twenty 1-m² samples of leaf litter were collected: one sample every 10 m per plot. Ants were collected following the ALL (Ants of the Leaf Litter) protocol established by Agosti and Alonso (2000). Second, six pitfall traps were placed at intervals of 20 m and were maintained active for 120 h per plot. To obtain the average abundance values, we first calculated p_i for each sampling method (*i.e.*, leaf litter or pitfall) as $p_i = A_i / \sum A_i$, where A_i is the number of individuals of each species divided by the total number of individuals within each plot. The resulting p_i values of both sampling methods were then averaged. A reference collection of species from the study plots is maintained at the Instituto de Ecología, A.C., Xalapa, Mexico.

ALPHA TAXONOMIC DIVERSITY.—We constructed rank-abundance curves to assess changes in local relative species abundance (p_i) across the chronosequence. Then, we used exponential regression models to determine changes in the homogeneity of relative species abundance in each secondary forest and in the four old growth forest through evaluating the slopes of the models. Next, we quantified the α -taxonomic diversity of ants using the following three indices: (1) species richness (*i.e.*, the number of species, S), which was transformed to the natural logarithm; (2) species evenness, which was calculated as the Simpson's evenness index, or $E_D = (1/D)/S$, where D is the Simpson's diversity index calculated as $D = \sum_{i=1}^S p_i^2$; and (3) species diversity, which was calculated as the Gini-Simpson index with the Jost (2007) correction, or $GS = 1 - D$, where D was the Simpson's index computed in R (R Development Core Team 2013) using the script from de Bello *et al.* (2010).

ANT TRAIT DATA.—To characterize the functional diversity of ant assemblages, we selected 12 ecomorphological traits that reflect different dimensions of ants' ecological niches. Castes were absent in the monomorphic ant species considered in the present study, so only minor workers were measured. We used a Leica MZ 9 stereo-microscope (Leica Microsystems, Heerbrugg, Switzerland) fitted with an ocular micrometer to record digital pictures to the nearest 0.01 mm. Then, we measured 13 morphoanatomical traits (*i.e.*, Weber's length, distance of compound eye to mandible insertion, clypeus length, etc.; Fig. S1) from the recorded digital pictures (Olympus, 7-million-pixel resolution) in the Image J software v1. (Schneider *et al.* 2012) at a precision of 0.1 mm. Each morphoanatomical trait was measured for two to five specimens per species to obtain an average value. For the

species with only one specimen, we obtained the average of the measures of one image from AntWeb and the measures of the collected specimen. In morphospecies with one specimen, we only used measures from the collected specimen. Morphoanatomical traits values can often be highly correlated; therefore, 12 ecomorphological traits at the species level were calculated as the proportional measurements of 13 morphoanatomical trait values (see Table 1 and Fig. S1 for more details on trait selection and assessment). Ecomorphological traits have been used to assess the relationships between morphoanatomical traits and the environment (Villéger *et al.* 2008) and, in our case, are used to quantify three key functions performed by ants: the acquisition of food resources, the amount of acquired resources and the type of resources consumed (Weiser & Kaspari 2006, Bihn *et al.* 2010, Silva & Brandão 2010). In this study, we assumed that functional traits were species-specific and that intra-specific variation was lower than inter-specific variation. Although intra-specific trait variation may exist, it was omitted from the analyses. The inclusion of intra-specific trait variation would likely result in a bias toward weaker trait-disturbance relationships. However, future research should focus on exploring the intra-specific variability of traits and/or modeling its potential significance. The pairwise correlations among all 12 ecomorphological trait values were globally weak (mean \pm SD, Pearson $r = 0.12 \pm 0.16$, $P > 0.05$), supporting the independence of these traits and the absence of collinearity (see Table S1). Hence, we used the 12 considered ecomorphological traits to posteriorly calculate functional diversity indices.

ALPHA FUNCTIONAL DIVERSITY.—To assess effects of functional trait diversity on ecosystem processes and to avoid multi-collinearity, we computed three indices that reflect three independent facets of functional diversity. These indices, which are equivalent to the previously mentioned indices for calculating alpha taxonomic diversity, are the most suitable for obtaining functional measures at the community level (Mason *et al.* 2005, de Bello *et al.* 2010, Mouchet *et al.* 2010) and are listed as follows: (1) functional richness (FRic), which represents the amount of functional space occupied by a species or the volume filled by an assemblage in a trait space; (2) functional evenness (FEve), which measures the regularity of species distributions in a trait space; and (3) functional divergence (Rao Q), which measures the amount of trait variation considering mean trait values and reflects the probability that two species randomly picked from an assemblage will be functionally different. Before calculating the three functional indices, the mean values of each trait were standardized so that the mean would be equal to 0 and the standard deviation would be equal to 1 to ensure the equal contribution of each trait to each index. To calculate the FEve and Rao Q indices, functional distances between pairs of ant species were estimated for the standardized functional trait values according to Euclidean distance. The resulting raw functional distance matrix was then standardized through dividing its resulting values by its maximum value to obtain an operational distance matrix d_{ij} with a normalized range from 0 to 1. The three functional diversity

TABLE 1. The 12 ecomorphological traits of ants considered in the present study. The abbreviations, associated equations and ecological significance of traits are also shown.

Functional trait	Abbreviation	Equation	Ecological significance
Mandibular ratio	MR	ML/HL	Linked to prey size (Kaspari 1993)
Clypeus ratio	CR	CL/HL	Linked to trophic level (Hawkins <i>et al.</i> 2007)
Eye size	ES	$AE/(P_i * (0.5 HW * 0.5 HL))$	Important for prey detection and activity times (Weiser & Kaspari 2006)
Eye position	EP	IOD/HW	Linked to hunting method (Fowler <i>et al.</i> 1991) or the component of the habitat occupied (Gibb <i>et al.</i> 2015), particularly for predatory species
Head shape	HS	HW/HL	Correlated with food size (Kaspari 1993)
Petiole shape	PS	PW/PH	Correlated with predaceous species' behavior and performance (Silva & Brandão 2010, 2014)
Femur ratio	FR	FL/WL	Associated with locomotion and search area (Feener <i>et al.</i> 1988, Kaspari & Weiser 1999)
Antennal ratio	AR	AL/WL	Linked with behavior and capacity to follow pheromone trails, especially for eyeless workers (Weiser & Kaspari 2006)
Mandibular position	MP	DEM/HL	Helpful for fighting and ingesting food, particularly seeds (Molet <i>et al.</i> 2012)
Petiole ratio	PR	PW/WL	Correlated with predaceous species' behavior and performance (Silva & Brandão 2010, 2014)
Mass	M	$(PrW * WL + 1)\log$	Biomass-associated nutrient supply rates to ecosystems
Thorax shape	TS	PrW/WL	Associated with metabolic reserves (Peeters & Ito 2001)

indices were computed with R using the *dbFD* function in the FD library. We individually calculated each index for each ecomorphological trait and for all 12 traits combined. Both single- and multi-trait indices may similarly reflect certain aspects of functional composition, although each analysis provides unique information about variations in ecosystem functions and services (Butterfield & Suding 2013).

BETA TAXONOMIC (TAXONOMIC TURNOVER) AND FUNCTIONAL (FUNCTIONAL TURNOVER) DIVERSITY.—To compute β taxonomic and functional diversity, we used the Rao's quadratic entropy index (Rao 1982) with the correction proposed by Jost (2007). This index allows for diversity to be partitioned into its different facets (*e.g.*, TD and FD) using the same mathematical framework (Ricotta & Szeidl 2009, de Bello *et al.* 2010). This index incorporates data on the relative abundances of species and is thus highly suitable for detecting changes in the taxonomic or functional composition of species assemblages across environmental gradients. Multiplicative partitioning was then used to separate regional species diversity (γ) into its α and β components. The formula used to calculate α -diversity and γ -diversity was as follows: $Rao Q = \sum_{i=1}^S \sum_{j=1}^S d_{ij} P_i P_j$, where d_{ij} is the distance (taxonomic or functional) between species i and j . The regional relative abundances of species i and j are P_i and P_j , respectively. The values of P_i and P_j were used to obtain the ever-positive functional β Rao values, which were calculated as follows: $P = (\sum_{i=1}^n p) / n$, where p is local relative species abundance of species i or j and n is the number of plots (1 to n) in the region.

To calculate pairwise β -diversity between plots, α and γ were previously calculated for the whole set of plots. Pairwise β -diversity was then multiplicatively partitioned as follows: $\beta = (\hat{\gamma} - \hat{\alpha}) / \hat{\gamma}$, where $\hat{\alpha} = 1/(1 - \bar{\alpha})$ and $\hat{\gamma} = 1/(1 - \gamma)$. Rao Q (γ) was also calculated for each plot pair. The abundance of each species is given by the average of its regional relative abundance

in two plots. Finally, $\bar{\alpha}$ is equivalent to Rao Q , which was calculated for each of the two plots and then averaged.

The taxonomic distances between species were measured as $d_{ij} = 1$, where $i \neq j$ and $d_{ij} = 0$ when $i = j$. The standardized functional distance matrix between pairs of ant species was obtained as described in the above section for alpha Rao Q . For both taxonomic and functional β -diversities, d_{ij} should be constrained from 0 (species i and j are identical) to 1 (maximum distance) to ensure that $Q \leq D$ and $\hat{Q} = 1/(1 - Q) \leq \hat{D} = 1/(1 - D)$, where \hat{D} is the Gini-Simpson diversity index corrected according to Jost (2007) and is identical to Rao's Q when all functional dissimilarity distances (d_{ij}) are equal to 1 (Ricotta & Szeidl 2009). This step allows β -diversity at the functional level to be directly compared to β -diversity at the taxonomic level. Henceforth, the Gini-Simpson's turnover index is the measure of taxonomic turnover, and the β -Rao index is the measure of functional turnover. Both taxonomic and functional turnover indices were computed in R using the script from de Bello *et al.* (2010). Both β -diversity indices were calculated individually for each trait and also for all 12 traits combined in a multi-trait index.

STATISTICAL ANALYSES.—We used linear, logarithmic and exponential regression models to assess differences in α -TD (quantified with the S , E_D and GS indices) and α -FD (quantified with the FRic, FEve and Rao Q indices) as a function of forest age. Later, we analyzed the pairwise relationships among the three α -FD indices and the three α -TD indices. Analyses were conducted for each trait separately and for the multi-trait index. The best-fit model was selected based on the highest R^2 value (Lohbeck *et al.* 2012) and the smallest AIC value. In all cases, when differences between models were not >5 percent, we chose the linear model. Secondary forests display a large difference in structure and composition with respect to nearby old growth forest (*sensu* FAO 2010). Fallow age *per se* is a variable that reflects community

organization at a certain point in time along a successional trajectory (van Breugel *et al.* 2006), although secondary forests do not necessarily increasingly resemble old growth forest over time (Melo *et al.* 2013). For this reason, we calculated all models using the eight secondary forests and only visually compared these with the means \pm SD of the four plots of old growth forest. All analyses were performed in the R statistical software using the *nls* function (Pinheiro & Bates 2000) in the *nmle* package.

To assess changes in taxonomic and functional turnover between pairs of eight secondary forests (SF-SF) as a function of dissimilarity in forest age, we used multiple matrix regression analyses (Anderson *et al.* 2011). The dissimilarity between secondary forests was measured in terms of years since

abandonment (according to Euclidean distance). We plotted the relationships between taxonomic and functional turnover for eight paired secondary forests (SF-SF) considering the single- and multi-trait indices and visually compared the relationships between taxonomic and functional turnover among the eight secondary forests and the four old growth forest (SF-OGF). To assess the recovery of taxonomic turnover and functional turnover between the eight paired secondary forests (SF-SF), we used multiple matrix regression analyses considering both the single- and multi-trait indices. Analyses were conducted with 5000 permutations using the function *multi.mantel* in the *phytools* package of the R statistical software.

RESULTS

ANT ASSEMBLAGE.—Overall, our analyses were based on 104 ant species (Table S2). The six most abundant species in all plots were *Wasmannia auropunctata* (Roger 1863; 9% of total ant abundance), *Pachycondyla harpax* (Fabricius 1804; 9%), *Nylanderia guatemalensis* (Forel 1885; 8.8%), *Odontomachus laticeps* (Roger 1861; 4.7%), *Camponotus atriceps* (Smith 1858; 4.1%), *Pheidole* sp. A (3.7%) and *Pheidole* sp. B (3.7%). The genera with the most species were *Strumigenys* (10), *Pheidole* (9 species), *Solenopsis* (7), *Camponotus* (6) and *Hypoponera* (5). The rank-abundance plots showed that most species had a low relative abundance across the studied chronosequence (Fig. 1). The percentage of ant species with at least 5 percent relative abundance per plot gradually increased from the youngest plot, SF1 (70%), to the oldest plot, SF8 (90%), and in comparison, to the old growth forest (96%), demonstrating an increase in rare species with advancing forest succession. Exponential regression analyses showed that with increasing forest age, the slopes of the models were shallower and the curves were longer, suggesting that the species richness and abundance of ant assemblages becomes more homogenous in older forests (Table 2).

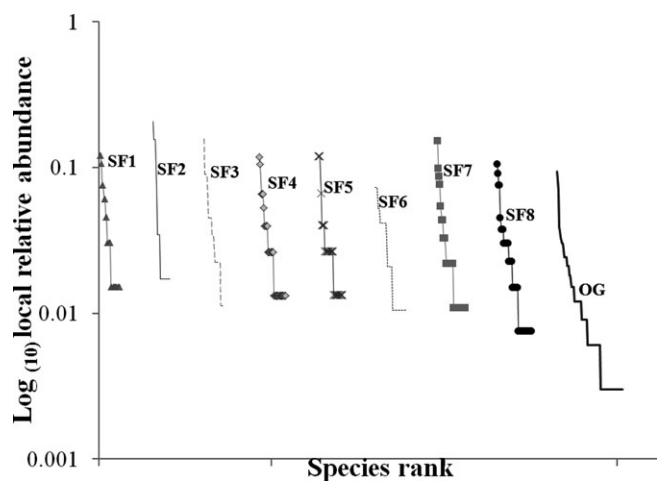


FIGURE 1. Rank-abundance curves for each of the eight secondary forests and mean species abundance of the four old growth forests studied in the Lacandon region of Chiapas, Mexico. The curves illustrate the change in local relative species abundances across the successional chronosequence.

TABLE 2. Exponential regression models of relative ant species abundance across eight secondary forests (SF) abandoned at different times and an old growth forest (OGF) in the Lacandon region, Mexico.

Forests	Time since abandonment (yr)	Plot area (ha)	Number of observed species	Number of species with <5% relative abundance	Model
SF1	6	2.8	24	17	$y = 0.1115e^{-0.103x}$
SF2	9	3	20	15	$y = 346.28e^{-0.128x}$
SF3	11	1.1	25	20	$y = 24781e^{-0.102x}$
SF4	12	4	31	25	$y = 40697e^{-0.071x}$
SF5	13	10	29	25	$y = 1E + 07e^{-0.074x}$
SF6	14	1	37	34	$y = 4E + 07e^{-0.063x}$
SF7	18	2.8	33	29	$y = 2E + 11e^{-0.072x}$
SF8	27	5.5	41	37	$y = 5E + 11e^{-0.065x}$
OGF1			36	31	$y = 4.33e^{-0.051x}$
OGF2			32	28	$y = 4.99e^{-0.066x}$
OGF3			49	42	$y = 4.76e^{-0.043x}$
OGF4			43	36	$y = 3.65e^{-0.04x}$
OGF (mean)			80 (38 \pm 7.8)	77 (35 \pm 5.7)	$y = 4E + 07e^{-0.039x}$

RELATIONSHIPS BETWEEN FOREST AGE AND ALPHA TD AND FD.—At the α -diversity level, species richness and diversity increased linearly with forest age (Figs. 2A and C; Table 3). Functional richness and divergence showed the same relationship with forest age (Figs. 2D and F; Table 3), although functional and species evenness were not related with forest age (Figs. 2B and E; Table 3). Functional richness and divergence increased linearly with species richness (Fig. 3A) and diversity (Fig. 3C), respectively (Table 3). Nonetheless, species evenness was not related to functional evenness (Table 3).

When analyzing each trait separately, only the functional richness of the femur ratio was exponential and positively related to forest age, while thorax shape was logarithmic and positively related to forest age (Table S3). Meanwhile, only the functional evenness of the antennal ratio was logarithmic and positively related with forest age (Table S3). Functional divergence of all single traits increased linearly with forest age (Table S3). Functional richness of the clypeus ratio and the thorax shape increased linearly with species richness, while the petiole ratio increased exponentially (Table S3). The functional divergence of all traits increased linearly with species diversity (Table S3). The femur ratio and the mandibular position increased linearly with species evenness (Table S3).

RELATIONSHIPS BETWEEN FOREST AGE DISSIMILARITY AND TAXONOMIC AND FUNCTIONAL TURNOVER.—The relationship between taxonomic (Pseudo- $F = 0.55$, $P = 0.51$) or functional (Pseudo- $F < 0.00$, $P = 0.99$) turnover and dissimilarity in forest age was not significant (Figs. 4A and B). Also, the functional turnover of each single trait was not related with dissimilarity in forest age (Table S4).

For the multi-trait analysis, a positive and linear relationship was found between taxonomic and functional turnover for the eight paired secondary forests. However, taxonomic and functional turnover values between the eight secondary forests and the old growth forest (SF-OGF) were greater than between the paired secondary forests (SF-SF; Fig. 4C). For the single-trait analysis, we also found a linear and positive relationship between the functional turnover of several morphological traits (clypeus ratio, mandibular ratio, eye size, head shape, femur ratio, antennal ratio and mandibular position) and the taxonomic turnover (Table S4). In these cases, taxonomic and functional turnover values between SF-SF were more similar than between SF-OGF, except for the femur and antennal ratios, whose SF-SF values were lower than those between SF-OGF (Fig. S2). Moreover, the functional turnover of eye position, mass and

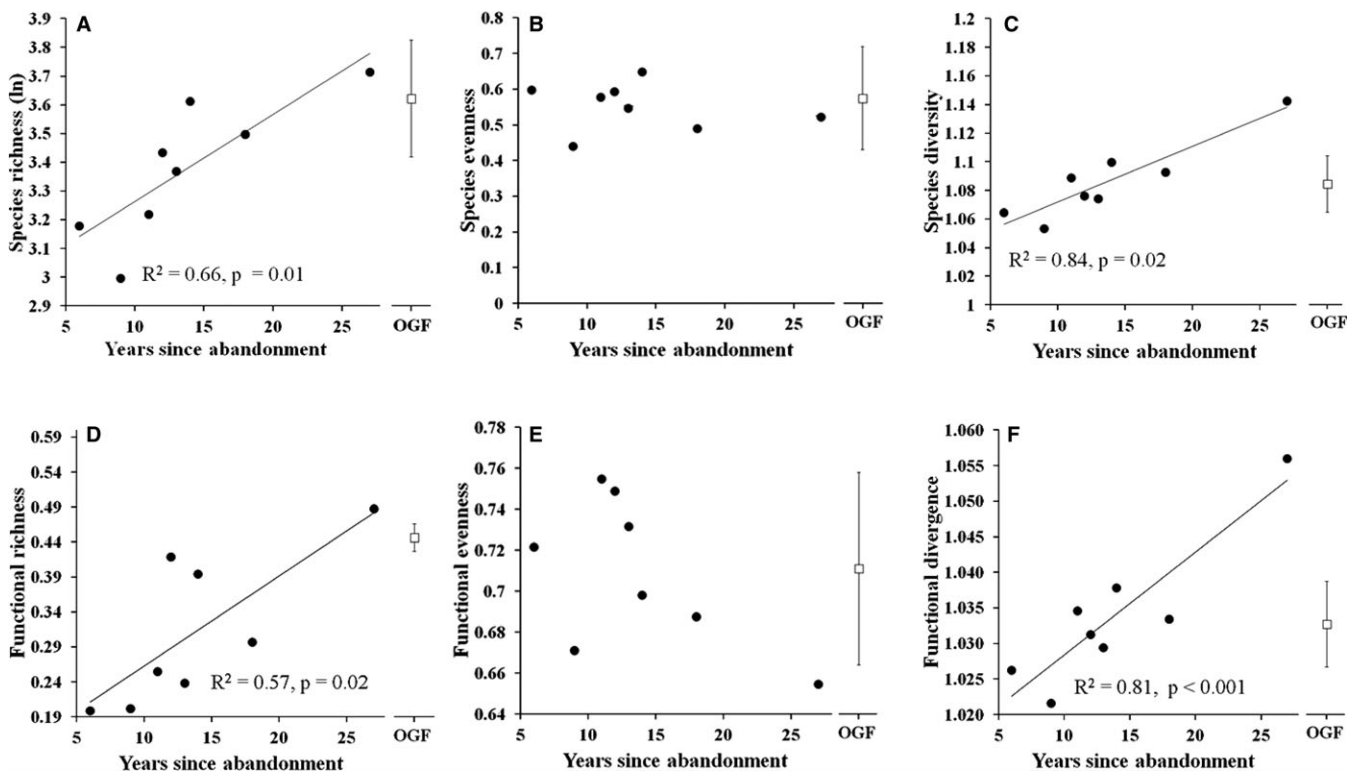


FIGURE 2. Changes in alpha taxonomic and functional diversity for multiple traits as a function of forest age in secondary forests of the Lacandon region of Chiapas, Mexico. The panels show the relationships between (A) species richness (natural logarithm-transformed, \ln), (B) species evenness (Simpson's evenness index), (C) species diversity (Gini-Simpson index), (D) functional richness ($\text{FRic}_{\text{multi-traits}}$), (E) functional evenness ($\text{FEve}_{\text{multi-traits}}$) and (F) functional divergence ($\text{Rao}_{\text{multi-traits}}$) and forest age across the studied successional chronosequence. In all cases, the white squares illustrate the means \pm SDs of the four plots of old growth forest.

TABLE 3. Results of linear, logarithmic and exponential regression models for evaluating the predictive power of forest age (FA, years since abandonment) on the taxonomic diversity (TD) and functional diversity (FD) of ant assemblages in the Lacandon region, Mexico. The results of regression models for assessing the predictability of TD and FD are also shown. TD was included in the models as species richness (natural logarithm-transformed, \ln), species evenness (Simpson evenness index), and species diversity (Gini-Simpson index); FD was included as functional richness ($Fric_{multi-traits}$), functional evenness ($FEve_{multi-traits}$), and functional divergence ($Rao_{multi-traits}$). Values in bold show the best-fit model.

Composition Index	Model	df	R ²	P	AIC
TD ~ FA					
Species richness	Linear	6	0.66	0.01	-4.19
	Logarithmic	6	0.68	0.01	-4.65
	Exponential	6	0.65	0.01	-3.94
Species evenness	Linear	6	0.04	0.63	-16.03
	Logarithmic	6	0.3	0.07	-15.96
	Exponential	6	0.35	0.07	-16.03
Species diversity	Linear	6	0.84	<0.001	-44.8
	Logarithmic	6	0.74	<0.001	-40.92
	Exponential	6	0.84	<0.001	-44.92
FD multi-traits ~ FA					
FRic	Linear	6	0.57	0.02	-14.76
	Logarithmic	6	0.57	0.38	-14.69
	Exponential	6	0.56	0.03	-14.45
FEve	Linear	6	0.33	0.13	-28.53
	Logarithmic	6	0.22	<0.001	-27.34
	Exponential	6	0.32	<0.001	-28.47
Rao	Linear	6	0.81	<0.001	-58.92
	Logarithmic	6	0.69	<0.001	-54.98
	Exponential	6	0.81	<0.001	-58.98
FD multi-traits ~ TD					
FRic ~ species richness	Linear	6	0.75	<0.001	-18.99
	Logarithmic	6	0.73	0.01	-18.98
	Exponential	6	0.75	<0.001	-18.58
FEve ~ species evenness	Linear	6	0.30	0.15	-28.22
	Logarithmic	6	0.32	<0.001	-28.46
	Exponential	6	0.30	<0.001	-28.16
Rao ~ species diversity	Linear	6	0.98	<0.001	-78.60
	Logarithmic	6	0.98	<0.001	-77.59
	Exponential	6	0.98	<0.001	-79.98

thorax shape did not show any relationship with taxonomic turnover, and the SF-OGF values were higher than the SF-SF values (Fig. S2).

DISCUSSION

Changes in the taxonomic diversity of tropical flora and fauna during secondary forest succession have been extensively documented (e.g., Dunn 2004, Chazdon et al. 2009, Melo et al. 2013, Arroyo-Rodríguez et al. 2015). However, in spite of the importance of FD

as a bridge that links species diversity and ecosystem functions and services (Díaz & Cabido 2001), previous studies have rarely paid attention to changes in FD during succession (see Bihn et al. 2010, Lohbeck et al. 2012). In particular, several studies have documented successional changes in the TD of ant assemblages in abandoned fields (e.g., Dunn 2004, Bihn et al. 2008, Rocha-Ortega & Favila 2013), although only one study has evaluated changes in the FD of such assemblages (Bihn et al. 2010). Our study is the first to report the relationships between ant TD and FD during old-field tropical forest succession considering both single- and multi-trait-based approaches at the α - and β -diversity levels. This approach enables the description of TD and FD patterns in ant assemblages during secondary succession and also allows for the identification of the mechanisms underlying such patterns.

The linear relationship between TD and FD along the successional gradient was supported by our results, as predicted, for both the alpha (α) and beta (β) components of diversity. Regarding α -diversity, changes in the species richness and diversity of ant assemblages across successional stages were accompanied by an increase in ant functional richness and divergence. This implies an increasing amount of and variation in feeding behaviors among species (i.e., niche complementarity) as forest succession advances, resulting in a more complete utilization of resources. Also, as predicted, we found low levels of functional redundancy among coexisting ant species along a secondary successional gradient, and the complementarity of ant species traits was stronger in species-rich assemblages (Petchey & Gaston 2002, Schmid et al. 2002).

These results have some important applied implications. Our findings suggest that functional space and functional divergence as well as a broad array of functions supported by ant assemblages (e.g., predation, seed removal, seed dispersion and herbivory) are systematically recovered at a local scale during forest succession (Bihn et al. 2010). Our results also showed that secondary forest at 27 yr since abandonment resembled old growth forest in both the amount and variation of functional traits. Thus, we propose that land management programmes promote natural forest regeneration and succession in abandoned fields and also conserve the diversity of ant species, as ant diversity is a key component of the functionality of secondary forests.

In addition, our results agree with those of Bihn et al. (2010), who reported strong relationships between TD and FD and showed that TD is a good surrogate for the FD of ant assemblages in secondary tropical forests. Interestingly, Lohbeck et al. (2012) also found strong relationships between TD and FD in tree assemblages in the same secondary forests of the present study. The close association between TD and TF is particularly important for the study of functional diversity in hyper-diverse tropical ecosystems where ecosystem functionality may depend on biotic communities composed of several taxa. Using TD as a surrogate for FD would save the time and resources necessary for properly quantifying functional diversity.

In contrast with the strong relationship found between α -diversity and forest age, our results did not support the relationship of β -taxonomic and functional diversity with dissimilar secondary forest age as expected. Environmental filtering is

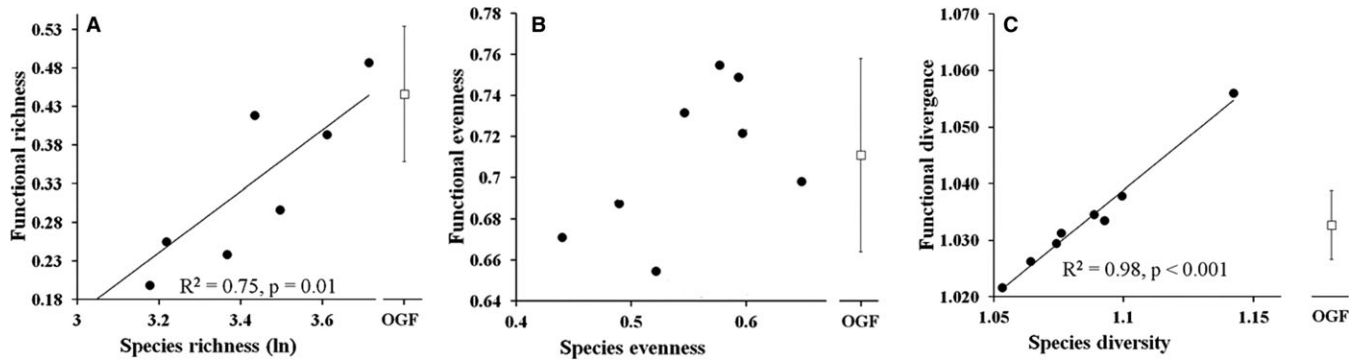


FIGURE 3. Changes in alpha functional diversity for multiple traits as a function of taxonomic diversity in secondary forests of the Lacandon region of Chiapas, Mexico. The panels show (A) the relationship between species richness (\ln) and functional richness ($FRic_{\text{multi-traits}}$), (B) the relationship between species evenness (Simpson's evenness index) and functional evenness ($FEve_{\text{multi-traits}}$) and (C) the relationship between species diversity (Gini-Simpson index) and functional divergence ($Rao_{\text{multi-traits}}$).

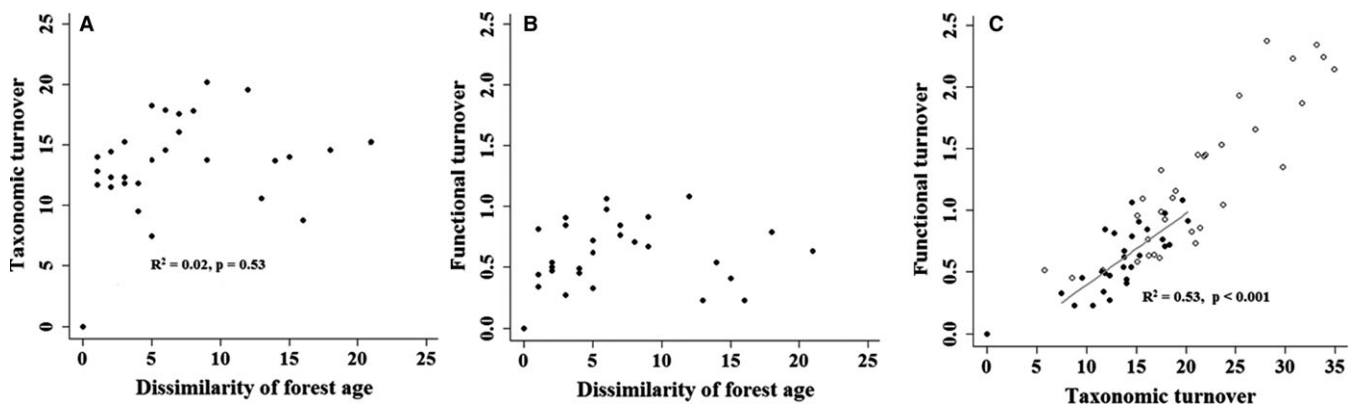


FIGURE 4. Changes in taxonomic turnover and functional divergence turnover for multiple traits across a chronosequence in the Lacandon region of Chiapas, Mexico. The panels show the relationship of (A) taxonomic turnover (Gini-Simpson's turnover index) and (B) functional divergence turnover ($\beta\text{-}Rao_{\text{multi-traits}}$) with dissimilar forest age across the studied successional chronosequence and the relationship between (C) taxonomic turnover (Gini-Simpson's turnover index) and functional divergence turnover ($\beta\text{-}Rao_{\text{multi-traits}}$), wherein the dark circles represent the functional divergence turnover between eight paired secondary forests (SF-SF) and the white circles represent turnover between the eight secondary forests and the four old growth forests (SF-OGF). The dark gray line shows the multiple matrix regression analysis between taxonomic and functional turnover among pairs of eight secondary forests (SF-SF).

purportedly stronger at the regional level, while species interactions (e.g., competition, predation) drive local-level assembly patterns (Cavender-Bares *et al.* 2009). In this context, the lack of an association between β -diversity and forest age indicates that other mechanisms may be determining β -diversity patterns in our ant assemblages across secondary forests. For example, changes in biotic interactions along the successional gradient might be responsible for the observed β -diversity patterns for TD and FD. Some additional evidence may support this idea. First, we mostly selected functional species traits that were widely accepted as representative of a variety of life-history traits relevant to the feeding behavior of ant species (Bihn *et al.* 2010, Silva & Brandão 2010). In other words, our trait selection was largely based on the way species influence ecosystem processes through trophic interactions rather than their response to environmental changes (Devicor *et al.* 2010). Although traits linked to feeding behaviors might be relevant in the response of species to environmental changes,

traits directly related to the tolerance of species to environmental changes might be more appropriate for assessing such responses (Wiescher *et al.* 2012, Arnan *et al.* 2013).

Alternatively, evidence also exists that changes in biotic interactions across secondary forests may not be the only mechanism involved in increasing FD during succession. In fact, several studies have demonstrated that changes in functional diversity along disturbance gradients are primarily driven by the addition of rare species that are functionally unique (Bihn *et al.* 2010, Arnan *et al.* 2013, Mouillot *et al.* 2013b). Our study concurs with this observation. Most ant species had low abundances, although few were numerically dominant, which is a common pattern in natural ant assemblages (Leponce *et al.* 2004). Thus, along successional gradients, the addition of new and rare (low abundance) species in addition to increasing species richness and diversity may be one of the drivers of the observed increases in functional diversity.

At the alpha-scale, we found that the functional richness inside of old growth forest is similar to that of the oldest secondary forests and that the functional divergence was lower. These patterns support the intermediate disturbance hypothesis (IDH) that predicts that competitive interactions and species filtering as a result of disturbance are, at least partially, driven by species' functional traits, so trait differences between species likely lead to distinct inter-specific reactions to disturbances (Mouillot *et al.* 2012). Indices based on both species traits and abundances (*e.g.*, functional divergence or specialization) cannot provide evidence of species extirpations or local extinctions along disturbance gradients (Mouillot *et al.* 2012). However, our results showed that secondary succession affects the patterns of niche differentiation of the species forming the functional space of secondary forests (see Maeshiro *et al.* 2013). In addition, in secondary forests with intermediate levels of disturbance, species with combinations of traits that are vulnerable to disturbance could coexist with disturbance-tolerant species. Our results showed a linear and positive TD-FD turnover relationship between secondary forests (SF-SF), although we found that turnover between secondary and old growth forest (SF-OGF) was greater. These results suggest that species replacement is associated with functional traits, which are important for ecosystem functionality from a conservation perspective. Hence, our results indicate that even though ant species may cover the same functional space in old growth forest and oldest secondary forest, that their functions may be very different. Finally, our results suggest that the oldest secondary forest abandoned 27 yr ago recovered the niche spaces of old growth forest but not all of ants' ecosystem functions. However, a tendency toward the recovery of ecological functions was notable.

Furthermore, our results showed that functional richness, evenness and functional divergence values (at the α scale) for most single and multiple traits were mostly linear and positively related to forest age and TD. This implies that our multi-trait space of functional diversity is representative of the patterns that most of the single functional traits independently follow. However, we found some exceptions (*i.e.*, femur ratio, thorax shape, petiole ratio and antennal ratio) that highlight the importance of analyzing single traits, especially if we are interested in exploring particular ecosystem functions via functional traits. Single-trait indices of functional composition are linked to a greater extent to variation in environmental gradients and ecosystem services than multi-trait indices (Butterfield & Suding 2013). In using single-trait FD indices, effective functional dimensionality is reduced; consequently, an increase in FD strongly depends on species identity and the particular trait values of newly added species (Petchey & Gaston 2002). In this context, one remarkable result was that the functional richness of the ants' femur ratio and petiole ratio were exponentially related to forest age since abandonment and species richness, respectively. Such patterns are only possible if the trait values provided by newly added species are complementary and very distinct (Díaz *et al.* 2011) in comparison to those at the initial stages of forest succession. Thus, the increasing functional space in the oldest secondary forests is

more likely due to the addition of rare species with particular attributes (Díaz *et al.* 2011) than to the presence of abundant species that likely share trait values. Meanwhile, the functional richness of ants' thorax shape and the functional evenness of the antennal ratio were logarithmically related to time since abandonment and species evenness, respectively. This pattern shows redundancy in the amount and evenness of some trait values at a particular age threshold across secondary forests.

CONCLUSION

Ants are important for the maintenance and functioning of ecosystems as well as the supply of ecosystem services in most terrestrial ecosystems around the world (del Toro *et al.* 2012). In the present study, we report a parallel and linear increase in ant taxonomic and functional diversity (related to ant feeding behaviors) during tropical forest succession. Also, we propose that the addition of rare species (that perform unique functions) and that the increase in inter-specific competition as forests age may explain the corresponding rise in functional diversity. Whilst tropical regions hold most of the world's biodiversity, secondary forests represent the principal forest cover in most tropical regions (Melo *et al.* 2013, Chazdon 2014, Arroyo-Rodríguez *et al.* 2015). Therefore, understanding the biodiversity value of secondary forests is of paramount importance for biodiversity conservation (Melo *et al.* 2013). In this regard, our study has several important implications. We showed that tropical secondary forests have the potential to recover high levels of the alpha TD and FD of ant assemblages in <30 yr, including rare species with unique combinations of traits that are important for ecosystem functions and services. Nonetheless, at 30 yr, secondary forests had still not completely recovered all functions performed by ants in old growth forest. Notably, the landscape of the present study area forms part of the recent agricultural frontier (inhabited by humans <50 yr ago) yet still maintains some old growth forest cover (*ca.* 13%; Zermeno-Hernández *et al.* 2016), which may favor the persistence of high levels of ant diversity. More studies are needed to assess the extent to which TD and FD recover in landscapes with differing proportions of old growth forest cover. Despite this previous finding, we found that the older secondary forests retained the highest levels of TD and FD and resembled old growth forest. This implies that older secondary forests, similar to old growth forests, could retain tropical biodiversity in the long run. Therefore, specific policies directed to promote and to protect the development of old secondary forests are of great importance for biodiversity conservation efforts in human-modified landscapes.

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DATA AVAILABILITY

Data available from the Dryad Repository: <https://doi.org/10.5061/dryad.53q1v> (Rocha-Ortega *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. *Graphic description of 13 morphoanatomical traits of ant species used in this study and their abbreviations.*

FIGURE S2. *Relationship between taxonomic turnover, and functional divergence turnover on single traits.*

TABLE S1. *Pairwise Correlations among the 12 ant functional traits sampled in the Lacandon region of Chiapas, Mexico.*

TABLE S2. *Occurrences of 104 ant species across eight secondary forests and four plots of old growth forests in Lacandon region.*

TABLE S3. *Results of linear, logarithmic, and exponential regression models applied to assess the predictive power of forest age and taxonomic diversity on functional diversity based on single traits of ant assemblages in the Lacandon region, Mexico.*

TABLE S4. *Results of multiple matrix regression models used to assess the predictive power of inter-plot dissimilarity in forest age and taxonomic turnover on β Rao single-trait of ant assemblages in the Lacandon region, Mexico.*

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