






ARTICLE

Rapid ant community reassembly in a Neotropical forest: Recovery dynamics and land-use legacy

Philipp O. Hoenle¹  | David A. Donoso^{2,3}  | Adriana Argoti⁴ |
 Michael Staab¹  | Christoph von Beeren¹  | Nico Blüthgen¹ 

¹Ecological Networks, Department of Biology, Technical University of Darmstadt, Darmstadt, Germany

²Departamento de Biología, Escuela Politécnica Nacional, Quito, Ecuador

³Centro de Investigación de la Biodiversidad y Cambio Climático, Universidad Tecnológica Indoamérica, Quito, Ecuador

⁴Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador

Correspondence

Philipp O. Hoenle

Email: philipp.hoenle92@gmail.com

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Abstract

Regrowing secondary forests dominate tropical regions today, and a mechanistic understanding of their recovery dynamics provides important insights for conservation. In particular, land-use legacy effects on the fauna have rarely been investigated. One of the most ecologically dominant and functionally important animal groups in tropical forests are the ants. Here, we investigated the recovery of ant communities in a forest–agricultural habitat mosaic in the Ecuadorian Chocó region. We used a replicated chronosequence of previously used cacao plantations and pastures with 1–34 years of regeneration time to study the recovery dynamics of species communities and functional diversity across the two land-use legacies. We compared two independent components of responses on these community properties: resistance, which is measured as the proportion of an initial property that remains following the disturbance; and resilience, which is the rate of recovery relative to its loss. We found that compositional and trait structure similarity to old-growth forest communities increased with regeneration age, whereas ant species richness remained always at a high level along the chronosequence. Land-use legacies influenced species composition, with former cacao plantations showing higher resemblance to old-growth forests than former pastures along the chronosequence. While resistance was low for species composition and high for species richness and traits, all community properties had similarly high resilience. In essence, our results show that ant communities of the Chocó recovery rapidly, with former cacao reaching predicted old-growth forest community levels after 21 years and pastures after 29 years. Recovery in this community was faster than reported from other ecosystems and was likely facilitated by the low-intensity farming in agricultural sites and their proximity to old-growth forest remnants. Our study indicates the great recovery potential for this otherwise highly threatened biodiversity hotspot.

KEYWORDS

ant diversity, chronosequence, Ecuador, forest regeneration, Formicidae, functional traits, land-use history, tropical forest

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INTRODUCTION

The global cover of natural landscapes continues to decline in the 21st century, almost exclusively caused by human land-use (Curtis et al., 2018; Hansen et al., 2013; Potapov et al., 2017). A substantial portion of these natural landscapes are forests, which are converted into agricultural areas, leading to habitat loss for forest-adapted species (Curtis et al., 2018). Loss is especially prevalent in the Neotropics, which are particularly vulnerable to commodity-driven deforestation (Curtis et al., 2018; Newbold et al., 2020). However, partly facilitated by rural exodus because of urbanization, a fraction of global forests with previous anthropogenic disturbances are increasingly undergoing natural succession (Benayas et al., 2007; Chazdon et al., 2020; Chazdon & Guariguata, 2016; Meli et al., 2017).

Understanding the dynamics of recovering forests plays a pivotal role for future conservation efforts and management strategies (Curran et al., 2014; Moreno-Mateos et al., 2017). Indeed, a pressing issue in modern ecology is to determine ecosystem regeneration dynamics, for instance, whether a disturbed forest is capable of reaching old-growth conditions, and how long this would take (Chazdon, 2003; Gibson et al., 2011; Lennox et al., 2018). Human-induced conversion of forest is generally understood as a disturbance event, and its recovery dynamics to pre-disturbance levels are characterized by ecological concepts such as resistance, resilience and variability (Chazdon, 2014; Donohue et al., 2016; Pimm, 1984). These concepts are the means to understand and to predict how fast a system can return to its original state.

Previous work showed that forest recovery time is highly variable and mainly influenced by factors such as climate and distance to nearest forest fragments (Bowen et al., 2007; Crouzeilles et al., 2016, 2019; Dent & Wright, 2009; Lawton et al., 1998; Meli et al., 2017). Further, the extent of previous disturbance influences recovery as, e.g., selectively logged forests recover faster than former agricultural areas (Bowen et al., 2007; Chazdon, 2003; Meli et al., 2017). Land-use legacy effects are multi-faceted and can, for example, delay natural plant recovery through deprivation of ground nutrients by crops (Holl & Zahawi, 2014; Pascarella et al., 2000).

Studying recovery is challenging because the necessary long-term monitoring data is rarely available (but see Norden et al., 2015). To overcome this, sites with different regeneration age in a similar environment can be studied to represent a chronosequence. However, this approach comes with its own challenges and, while several studies have investigated recovery using chronosequences, important questions remain

unanswered, as shortcomings such as low replication are common and recovery is hard to predict (Bowen et al., 2007; Chazdon et al., 2007; Norden et al., 2015). In particular, comparisons of faunistic recovery between sites with differing land-use legacies are rare, even for well-studied faunal taxa such as birds and ants (Bowen et al., 2007; Crouzeilles et al., 2016). Ants are an exceptionally abundant group of insects and well-established, representative indicator taxa for environmental gradients and disturbance (Alonso & Agosti, 2000; Arnan et al., 2014; Gibb, Sanders, et al., 2015; Gibb, Stoklosa, et al., 2015; Majer, 1983; Schmidt et al., 2013; Tiede et al., 2017). Understanding their recovery patterns thus allows for a better understanding of general community recovery, as they contribute in many ways to ecosystem functioning (Dunn, 2004). While numerous studies have described ant recovery, research on the comparative effects of past land-use is sparse (Stuhler & Orrock, 2016; Williams et al., 2012). For example, Debinski et al. (2011) showed that ant communities were affected by past land management in the United States, while in tropical forests this topic remains, to the best of our knowledge, largely unexplored (but see Vasconcelos, 1999).

To study community recovery dynamics, we sampled ant communities in a secondary tropical forest originating from former cacao plantations and pastures. We investigated the effects of land-use legacy, through a chronosequence approach, for regenerating areas of cacao plantations and livestock pastures. We assessed different emergent properties of communities (species composition, taxonomic diversity, functional trait diversity, and trait structure), which are characteristics not identifiable from individual organisms alone but arise from higher perspectives of community organization (Konopka, 2009). We expected that all properties show a gradual recovery response towards pre-disturbance conditions, meaning their similarity to an old-growth forest reference increases with recovery time (Figure 1). As cacao plantations have been shown to harbor a high diversity of ants, which is mediated through their structural similarity to forest such as leaf litter and a small canopy layer (Belshaw & Bolton, 1993; Delabie et al., 2007), we expected to find a comparatively faster recovery for all properties in cacao compared to pastures, indicating a higher resistance and/or resilience in cacao.

Our aim was to explicitly compare recovery times of related community properties. Because species richness and trait structure are aggregate properties emerging from species composition but can obtain similar values with entirely different sets of species, we expected that species richness and traits could only be equal or faster than species composition in their recovery. Previous studies indicate that species composition takes often several

decades longer than species diversity to recover (Curran et al., 2014; Dunn, 2004; Moreno-Mateos et al., 2017), while the recovery of other community properties, such as trait structure, are less explored (Aubin et al., 2013; Barber et al., 2017; Edwards et al., 2021). In line with other studies, we expected that trait structure in agricultural environments is profoundly different from those in old-growth forest, thus resulting in a slower recovery than species richness (Bihn et al., 2010; Rocha-Ortega et al., 2018) (Figure 1). Here, we investigate recovery after disturbance by breaking it into two measurable and statistically independent components: resistance and resilience (sensu Pimm, 1984, Pimm et al., 2019). Resistance is measured as the proportion of an initial property that remains following the disturbance. Resilience on the other hand is a measurement of the recovery rate. We set out to understand how recovery times are influenced by the dynamics of the systems; that is, if different outcomes are primarily driven by effects of resistance or resilience, or a combination of both. As an example, in Figure 1, diversity is conceptualized with a higher resistance in comparison to the other community properties, and thus recovered quicker. We expected resistance to be similar in community composition to traits, as both are tightly linked to each other.

MATERIAL AND METHODS

Study site and plot design

Our study was conducted at the Reserva Río Canandé (0.5263° N, 79.2129° W) in Ecuador (Esmeraldas Province) during the rainy season in April–June 2018 and February–May 2019. The reserve and surrounding areas contained old-growth rainforests, regenerating secondary forests that used to be either pastures or cacao plantations (henceforth referred to as regeneration areas), and currently used pastures and cacao plantations (Figure 2a, b). The current land-use in this area is relatively recent, and although we do not have specific dates, interviews with farmers showed that the majority of agricultural use has been within the last 50 years. The land-use is not intensive, but mostly small-scale farming in a forest mosaic landscape. We selected a total of 61 plots, each encompassing an area of 40 × 40 m. Our plot design included the following habitat categories: eight cacao plots, eight pasture plots, 12 cacao regeneration plots, 17 pasture regeneration plots, and 16 old-growth forest plots. Spatial dependence was minimized by haphazardly selecting locations and by keeping a minimum distance of at least 200 m among plots of the same type. Plots were

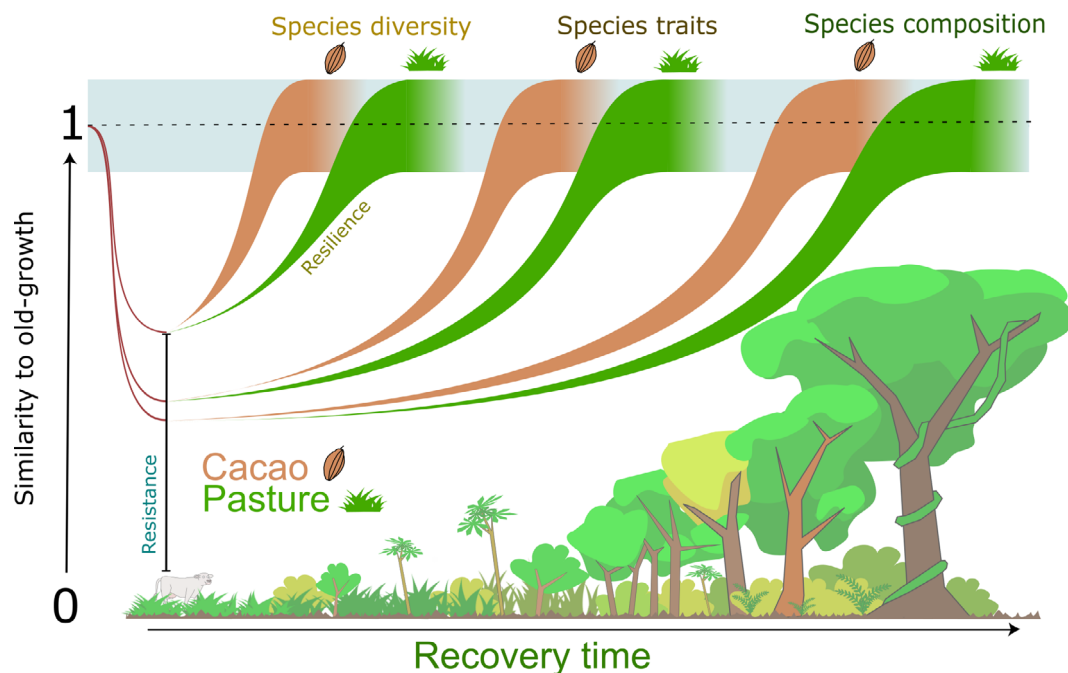


FIGURE 1 Framework of hypothesized recovery trajectories. Disturbance is represented by deforestation and subsequent agriculture (cacao or pasture), and resistance describes the remaining similarity to old-growth forest after disturbance. Resilience, in turn, refers to the recovery rate. Old-growth forest represents the reference state (blue top layer). The y-axis therefore defines the similarity to the reference state. We expected to find different recovery times for the three community properties species diversity (here assessed as species richness), species traits, and species composition, as well as faster recovery time for former cacao plantations (brown trajectories) than pastures (green trajectories). This figure was inspired by Moreno-Mateos et al. (2017)

located at elevations between 127 and 615 m and showed substantial overlap in elevation (Appendix S1: Figure S1). Old-growth forests had on average the highest elevation (374 ± 30 m), followed by cacao regeneration (319 ± 35 m), pasture regeneration (308 ± 31 m), pasture (205 ± 39 m), and cacao (205 ± 58 m). To account for potential influences of elevation, we incorporated elevation as fixed effect in all our models (see subsection “*Statistical analysis*”). The agricultural plots were located close to the forest edge, the approximate distance of which was assessed with Google Earth (Version 7.3.3.7786) satellite data (mean 60 ± 17 m; range 0 to 233 m). All other plots were embedded within the forest.

The regenerating areas are under natural succession with negligible human interference. Belonging to former smallholder farms, they are distributed patchily throughout the reserve and embedded in a matrix of surrounding forest. The Fundación Jocotoco bought most of the farms and integrated them into the reserve Río Canandé. A few plots were already abandoned before the installation of the reserve. We determined regeneration age by interviewing local park rangers and farmers and incorporated information of land purchase provided by the Fundación Jocotoco. Each plot was assigned the number of years it has been in succession (starting as year of abandonment, range 1–34 years). The age distribution and replication is approximately equal among recovery plots: cacao recovery had seven plots that were younger and five older than 15 years, while pasture recovery had 10 plots younger and seven older than 15 years. There were no obvious differences in the plot structure between older recovery plots of pasture and cacao, except for interspersed cacao trees on former cacao plantations. Agricultural areas, i.e., cacao plantations and pastures, were selected from adjacent active farms. The cacao plantations are typically monocultures and lack shade trees (sun-tolerant type). Cacao trees reached a height of ~ 4 m and a distance of 4 m between trees in a row; herbicide application was common. Pasture plots were extensively grazed by cattle, horses or donkeys. While the vegetation consisted mainly of grasses, there are typically sparse trees providing shade for livestock. The regeneration time of plots currently used as agricultural fields was defined as zero years. The two different time trajectories of cacao and pasture, which each consist of year 0 and all following regeneration ages, are referred to as land-use legacies. To facilitate comparisons, we identified 16 plots as old-growth forest that have, to the best of our knowledge, experienced no logging in recent times. These served as reference state and consequently received no regeneration age. Further information on the age and spatial distribution of the plots are given in the Appendix S1: Figure S1.

Ant sampling and identification

On each plot, ants were collected with three standardized methods to cover ant diversity from different strata: leaf litter, epigeal, and tree trunk (modified from Agosti et al., 2000). To capture the leaf litter ant community, we used Winkler extraction. We established a 20 m transect line parallel to one side of the plot. A leaf litter sample (including topsoil) of approximately 20×20 cm was collected every 5 m along the transect. We sifted the leaf litter (1 cm^2 mesh size) for approximately 5 min to remove larger twigs and leaves before transferring it into a Winkler bag. We pooled these samples per plot resulting in a total area of 0.2 m^2 . Because pastures had no leaf litter, we used a spade to cut out the first 5 cm of the grass turf with the same dimensions and pooled the samples per plot. The samples were subsequently transferred to Winkler bags for 48 h.

The ground ant community was collected by hand sampling. We used another 20-m transect parallel to the Winkler transect and placed a sampling subplot every 5 m. In each subplot, we collected ants with forceps within an area of 1 m^2 for 5 min. The five samples were pooled per plot. We focused on maximizing species numbers by collecting only a few individuals per species (e.g., close to a nest). While collecting, we carefully removed leaf litter and opened small twigs to look for ant nests.

For tree trunk sampling, we located the five largest trees in each plot and collected ants at trunks for 5 min per tree. Collecting was restricted to reachable heights (0–2 m). We focused on collecting ants from the trunk, but also looked under epiphytes and tree bark. Because of the lack of trees on some pastures, we collected from trees directly adjacent to the plot in the same pasture, when necessary. Three of the pastures had fewer than five trees but at least one tree per pasture was sampled (total of $n = 10$ missing trees).

To avoid a collector bias, the same person carried out leaf litter sampling (A. Argoti), hand sampling (P. O. Hoenle), and tree trunk sampling (P. O. Hoenle). Specimens were sorted into morphospecies and identified to species level whenever possible. Detailed information on the ant identification process can be found in the Appendix S1: Section S1. Voucher specimens are deposited in the MEPN museum collection at Escuela Politécnica Nacional in Quito. The Ministerio de Ambiente de Ecuador issued the permits for collection (MAE-DNB-CM-2017-0068) and exportation (41-2018-EXPCM-FAU-DNB/MA and 144-2019-EXP-CM-FAU-DNB/MA).

Traits

We measured a subset of morphological traits following Parr et al. (2017). The 10 traits used have repeatedly been

shown to be related to ecological attributes of ants (Gibb, Sanders, et al., 2015; Gibb, Stoklosa, et al., 2015; Parr et al., 2017; Sosiak & Barden, 2020; Weiser & Kaspari, 2006). A table of all functional traits used in this study together with a short description of their proposed functional significance can be found in the Appendix S1: Table S1. For instance, mandible length correlates to feeding mode, with longer-mandibled ants having a more predatory lifestyle, while femur length is positively correlated with structurally more complex environments (Weiser & Kaspari, 2006).

We used a Keyence VHX-5000 (Keyence Deutschland BmH, Neu-Isenburg, Germany) for taking high-resolution images and trait measurements. In total, the traits of 653 specimens belonging to 242 species were recorded (Data S1). Due to the high number of species (284 in total) and high number of uniques (99 species) in our data set, we aimed for measurements of at least three specimens per species for more common species (>10 occurrence) and at least two specimens for rare species (>2 incidences) except for *Paraponera clavata* ($n = 1$ specimen measured). On average, we measured traits on 2.7 specimens per species/morphospecies (range 1–12).

We measured minor workers in the polymorphic genera *Azteca*, *Pheidole*, *Tranopelta*, *Camponotus*, and *Solenopsis*, because other castes were often not available. To assess the ants' color lightness, we assigned each specimen a main color, which was based on the color wheel of Parr et al. (2017). We then used the software GIMP Version 2.10.22 to extract the lightness value for each color coding using the protocol of Law et al. (2020).

All length and width measurements scale with body size. Because we were interested in trait change independent of body size, we regressed all length-measured traits with Weber's length (a surrogate of body size regularly used in ants) in linear models. Each trait was then expressed as the residuals of this model. Trait values of all specimens were averaged on the species level.

Analysis overview

The main objective of our analysis was to compare the recovery trajectories of three elemental community properties, and to break these properties down into recovery components of resistance and resilience. All measures were based on unweighted incidence (presence/absence) of each ant species per plot. The three community properties were species richness, species composition and traits (Figure 1). To facilitate comparisons, all community properties were expressed as a similarity to old-growth forest.

From these similarity metrics, we assessed the resistance as the intercept value (recovery year 0) relative to

the old-growth forest mean, which we predicted from linear mixed-effects models in a regression against recovery time. This was done separately for each community property, and for each legacy type (cacao and pasture subsets).

For comparing resilience, we first unified scales by standardizing between the intercept as 0, and mean old-growth forest value as 1, which was necessary to compare slope values independent of the intercept. Again, we used linear mixed-effects models on the standardized data, and extracted their slopes for regeneration time, i.e., the resilience. Resistance and resilience could then be directly compared among each community property and each independent land-use legacy type (see Figure 1). All analyses were performed with the software R (R Core Team, 2018; Version 3.5.1).

Species richness

As a measure of species diversity, we calculated the species richness for each plot based on the species incidence. Species richness similarity was calculated as the richness value of each plot relative to the mean richness value across 16 old-growth forest plots as a reference.

Species composition

For species composition, we created a nonmetric multi-dimensional scaling plot (NMDS) using the Jaccard similarity with the R package *vegan* (Oksanen et al., 2010). We tested for differences in composition between the habitat categories with the function *adonis* from *vegan*.

To assess species composition similarity, we summarized all 16 old-growth forest plots by the proportional occurrence p_i of each ant species i across all plots as a reference for a mean expected ant community composition in old-growth forests. This proportion p_i is defined as the number of plots in which species i was recorded, divided by the total number of old-growth plots ($n = 16$). For each plot (including each old-growth plot itself), we then calculated the Bray-Curtis Similarity ($1 - \text{Bray-Curtis Dissimilarity}$) to this reference community. Hence, the absence of an ant species in a secondary forest plot that was widespread across all old-growth forests contributes to a larger dissimilarity than the absence of a rare species only found in a single plot.

Traits

As trait measures, we distinguished between the functional diversity (FD indices) and trait structure

(community weighted means). Community weighted means (CWMs) are trait averages of plots and are representative of the trait structure. Functional diversity was expressed by a variety of indices that aim to depict multiple aspects of trait diversity: Functional Richness (FRic) is a volume measurement of the amount of functional space filled by the community, Functional Evenness (FEve) quantifies the regularity with which the functional space is filled by species, Functional Divergence (FDiv) measures the average distance of species to the centroid of the functional trait space, and Functional Dispersion (FDis) is an estimator of the dispersion of the species in the trait-dimensional space (Laliberté & Legendre, 2010; Villéger et al., 2008).

Based on the averaged species traits and a species incidence matrix that excluded species without trait measurements (excluded ~3% of species incidences), we calculated the above-mentioned functional indices (FRic, FEve, FDiv, FDis) as well as the trait structure (CWMs) with the R package *FD* (Laliberté et al., 2014). Each of the FD indices, were subsequently expressed as relative values to the average old-growth forest value. We recognize that due to the limitation of using only incidence data our analysis is conservative and the actual functional diversity is potentially underestimated.

As for species richness, trait diversity similarity based on each of the FD indices (one value per plot) was expressed as proportion of the mean old-growth forest value. CWMs were computed for each of the 10 traits in each plot. The trait structural similarity to old-growth forests was then calculated as Gower similarity to the mean old-growth forest trait values.

Statistical analysis

We used linear mixed-effects models with the obtained similarity values as responses, elevation, land-use legacy (pasture or cacao plantation), and regeneration time as fixed effects, and collection year as a random effect (R packages *lme4*; Bates et al., 2007 and *lmerTest*; Kuznetsova et al., 2017). Regeneration time was square root transformed to approximately linearize the slope, a commonly used geometric average method for obtaining annual growth rates. As old-growth forest plots did not have a regeneration age, they were not part of the models. We tested for interaction between regeneration time and land-use legacy but, since these were never significant, we excluded them from the final models. Residuals of all models met assumptions of normality and homogeneity of variances. We are aware that since similarity values are constrained between 0 and 1, they might in theory violate two assumptions of linear models, the

normal distribution of residuals and the homoscedasticity of variances (Douma & Weedon, 2019). We therefore applied an alternative beta regression (R package *glmmTB*; Brooks et al., 2017) to the similarity values of composition and trait structure (with otherwise identical random and fixed effects structure), and compared the model results and residuals to our LMM approach. Since the residuals showed similar distributions (Appendix S1: Figures S2, S3) and model results (Appendix S1: Table S2), we used the LMM for the analysis.

For the similarities of each property, we used the function *predict* to estimate the regeneration time for complete recovery based on the previous linear-mixed effects model, with the average elevation (300.3 m) and the old-growth forest mean. We obtained confidence intervals through bootstrapping with the function *bootmer* (*lme4*). Potential spatial autocorrelation of model residuals was assessed with Moran's I test from the R package *ape* (Paradis et al., 2004). We also tested whether the distance to the forest edge was correlated with any of the similarities with a Spearman correlation test. This test only included agricultural sites, as all other plots were embedded within the forest. For graphical representation, we used the package *ggplot2* (Wickham et al., 2016) to plot linear models with 95% confidence intervals for the regeneration types cacao and pasture, containing only regeneration time as fixed effect.

Comparison of recovery time

We were interested whether the recovery trajectories differ among functional traits, species richness and species composition (Figure 1). However, claiming that property *A* fully recovers in half of the time as property *B* may imply three scenarios: (1) that *A* and *B* have dropped to a similar amount during disturbance, but *A* recovers twice as fast as *B*, (2) that *A* has dropped only half as far as *B* and both recover at a similar rate, or (3) a combination of level dropped and recovery rate. Consistent with independent concepts and measurements of resistance versus resilience (Pimm, 1984; Pimm et al., 2019), we interpret the level to which property *A* dropped in agricultural plots compared to the reference forest as its resistance and the relative rate of recovery towards the reference level as resilience.

Assuming a linear recovery of property *A* against square-root-transformed time in our linear-mixed effects models, we defined its resistance as the proportion of the intercept (which is the prediction of the level for zero years) in relation to the mean old-growth forests value. To predict the intercept, we used the function *predict* and average elevation as covariate. We obtained confidence intervals through bootstrapping with the function *bootmer*. To test whether there was a significant disturbance

effect compared to the references (i.e., *resistance* < 1), we used a Welch *t* test on the property values of agriculture and old-growth forest.

To calculate resilience, each community property *A* was normalized between the intercept defined as zero and the mean old-growth forest value defined as 1, in order to make slopes comparable across properties and independent of the intercept. The resulting slope β for recovery time depicts the proportional change from 0 (defined minimum) to 1 (reference stage) per square-root year.

RESULTS

Ant species richness

The Canandé hosted an extremely diverse ant fauna. We recorded a total of 284 species and morphospecies

across all plots (Data S1). We found several new country records for ant species and detected several undescribed species (e.g., Figure 2c,d). Species richness was unrelated to regeneration age ($p = 0.09$; Table 1), but increased with elevation ($p = 0.006$; Table 1). There was no difference between cacao and pasture recovery ($p = 0.41$, Table 1; Figure 3a). The model predicted a regeneration time to complete recovery of 7.0 years (CI: 2.3–14.4) for cacao and 7.9 years (CI: 2.9–15.4) for pasture. We detected no spatial autocorrelation (Moran's *I*, $p = 0.39$, $I_{(exp)} = -0.02$, $I_{(obs)} = 0.03$). Old-growth plots contained 30 species on average, while agricultural plots harbored 19 species on average, i.e., a relative richness of 63%. The resistance was significantly lower than the Null expectation (Welch *t* test $t = -4.23$, $df = 29.96$, $p < 0.001$). The relative ant species richness was unrelated to the distance to forest edge (Spearman correlation, $\rho = 0.01$, $p = 0.96$).



FIGURE 2 (a) A typical extensively used pasture in the study area of Río Canandé. Picture: K. Mody. (b) Former pasture after 12 years in natural recovery. Picture: K. Mody. (c) Undescribed species of *Acanthoponera* (R. Feitosa, personal communication). This genus is relatively rare, and no new species has been described for half a century. Picture: P. Hoenle. (d) The queen of an undescribed species of *Tapinoma* (F. J. Guerro, personal communication). Picture: P. Hoenle

TABLE 1 Linear mixed-effects model results, with elevation, land-use legacy, and square-root-transformed (sqrt) regeneration time as fixed factors, and collection year as random factor

Parameter	Estimates	95% CI	<i>p</i>
Species richness similarity			
Intercept	51.204	32.083–70.325	0.003
Elevation (km)	78.371	25.228–131.513	0.006
Land-use legacy, pasture	−4.874	−16.800 to 7.051	0.413
Regeneration time (years, sqrt transformed)	2.952	−0.503 to 6.408	0.092
Marginal R^2 /Conditional R^2	0.286/0.385		
Resistance (%)	72	58–87	<0.001
Resilience	0.106	−0.014 to 0.225	0.084
Species composition similarity			
Intercept	0.100	0.066–0.134	<0.001
Elevation (km)	0.206	0.092–0.321	0.001
Land-use legacy, pasture	−0.038	−0.063 to −0.013	0.005
Regeneration time (years, sqrt transformed)	0.025	0.018–0.032	<0.001
Marginal R^2 /Conditional R^2	0.721/0.721		
Resistance (%)	43	37–51	<0.001
Resilience	0.140	0.101–0.178	<0.001
Trait (CWMs) similarity			
Intercept	0.748	0.710–0.786	<0.001
Elevation (km)	0.179	0.052–0.306	0.009
Land-use legacy, pasture	−0.025	−0.053 to 0.003	0.086
Regeneration time (years, sqrt transformed)	0.015	0.007–0.022	<0.001
Marginal R^2 /Conditional R^2	0.477/0.481		
Resistance (%)	93	90–96	<0.001
Resilience	0.241	0.113–0.368	<0.001

Note: Resistance is the predicted intercept relative to average old-growth forest mean and resilience is the slope from a separate model that was standardized with intercept as 0 and old-growth forest mean as 1. Land-use legacy indicates the trajectory of pastures relative to cacao. CI shows 95% confidence intervals. Significant *p* values are highlighted in boldface type.

Ant species composition

Species composition was significantly different among old-growth forests, recovery plots, and agriculture (Appendix S1: Figure S4; ADONIS, $F_{2,60} = 3.71$, $R^2 = 0.11$, $p < 0.001$). With increasing age, ant composition of regenerating forests converged towards old-growth forests (Table 1, Figure 4). Land-use legacy affected the regeneration trajectory: as expected, communities in current and previous cacao plantations at a given age were more similar to those found in old-growth forests than communities in pastures ($p = 0.005$; Table 1, Figure 4). The compositional species similarity was well predicted by a combination of regeneration time, elevation and land-use legacy ($R^2 = 0.72$, Table 1). We found a significant difference between agriculture and old-growth forest in compositional species similarity (Welch

$t = -16.15$, $df = 15.0$, $p < 0.001$). We predicted a regeneration time of 20.6 years (CI: 13.6–29.1) for cacao, and 28.9 years (CI: 19.2–40.6) for pastures until full recovery. No signs of spatial autocorrelation were detected (Moran's I , $p = 0.17$, $I_{(exp)} = -0.02$, $I_{(obs)} = 0.06$), and there was no correlation with distance to forest edge (Spearman correlation test, $\rho = -0.004$, $p = 0.98$).

Functional traits

The CWM similarity increased significantly with regeneration time ($p < 0.001$; Table 1, Figure 3b), and was not influenced by legacy ($p = 0.09$, Table 1, Figure 3b). The model predicted a regeneration time of 6.2 years (CI: 2.5–11.3) for cacao and 8.5 years (CI: 4.0–14.6) for pasture until complete recovery. No spatial autocorrelation was found

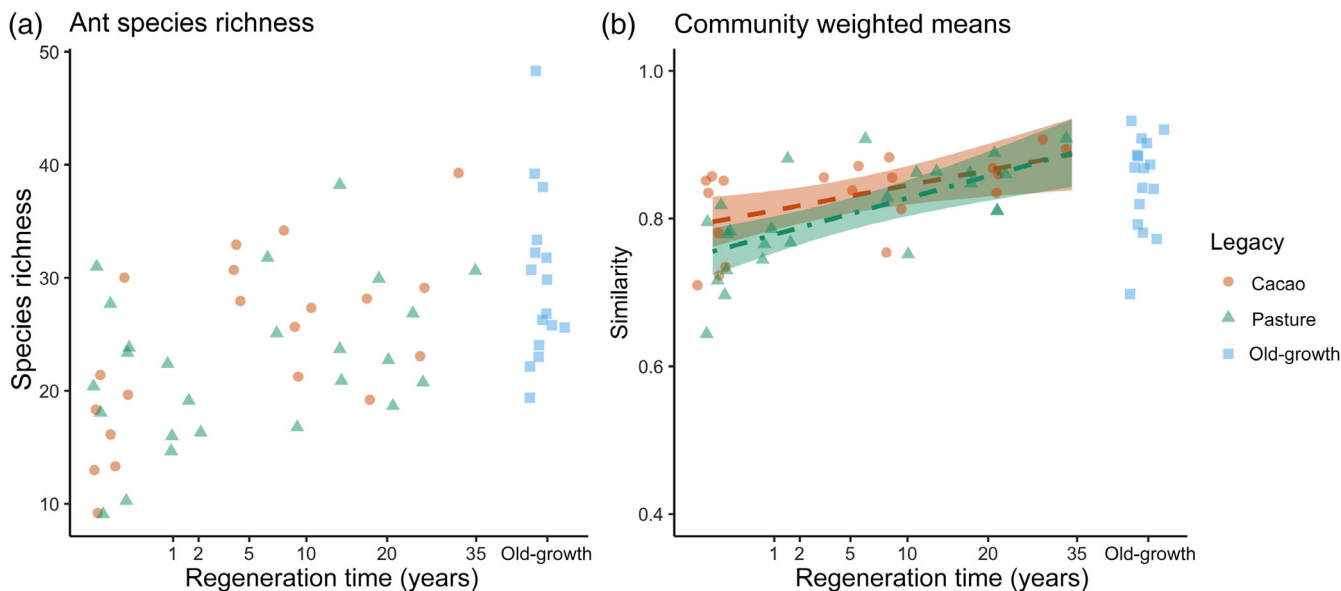


FIGURE 3 Recovery trajectories illustrating (a) ant species richness along the forest regeneration chronosequence and (b) the standardized similarity of trait means of each plot to the average old-growth forest level. Land-use legacy differences are highlighted with green (pasture) and red (cacao), their trajectories are predicted from a linear model with 95% CI. If no dashed lines are shown, there was no significant effect of regeneration time on the similarity (see Table 1)

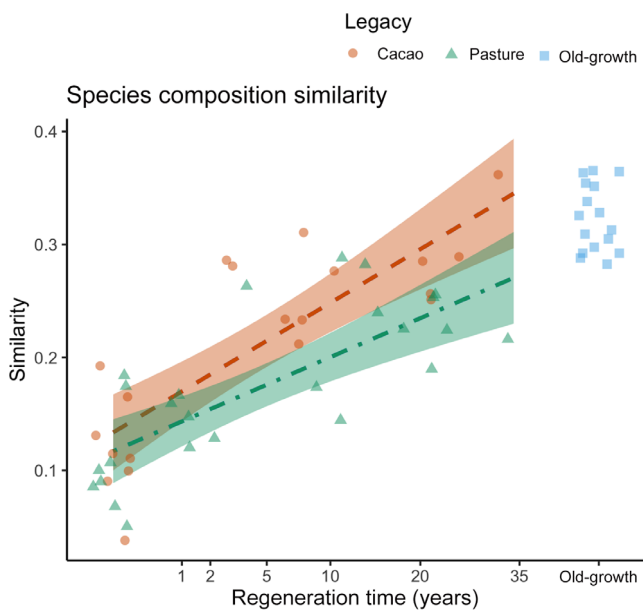


FIGURE 4 Species composition recovery of ant communities along the chronosequence, measured as the similarity to old-growth forests. Land-use legacy differences are highlighted with green (pasture) and red (cacao); their trajectories are predicted from a linear model with 95% CI

(Moran's I , $p = 0.75$, $I_{(exp)} = -0.02$, $I_{(obs)} = -0.04$), and there was no correlation with distance to the forest edge (Spearman correlation test, $\rho = -0.169$, $p = 0.53$). All the other functional diversity indices (FRic, FEve, FDiv, FDis) remained relatively constant in agricultural plots and over the entire chronosequence, with no detectable differences

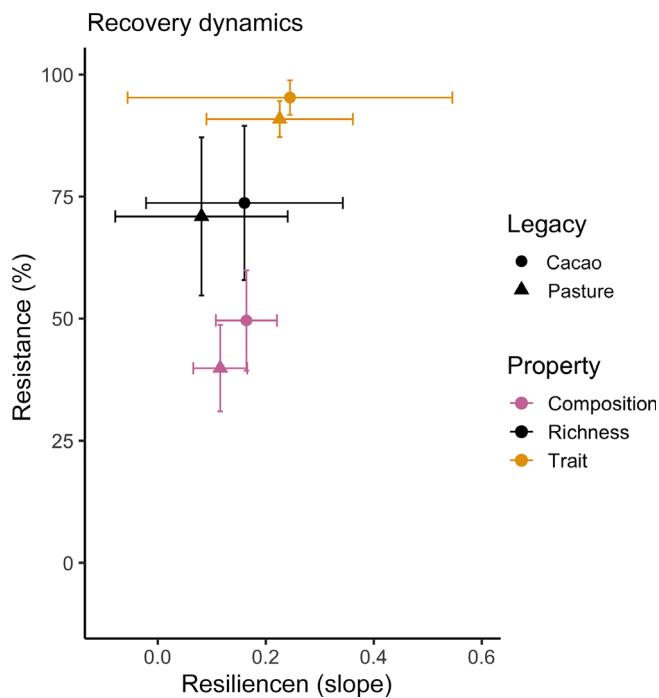


FIGURE 5 Recovery dynamics of the three studied community properties (species richness similarity, species composition similarity, trait structure similarity), partitioned into resistance and resilience. Resistance is the predicted intercept relative to average old-growth forest mean and resilience is the slope (i.e., relative recovery per sqrt-year) from a separate model that was standardized with intercept as 0 and old-growth forest mean as 1. A property needs less regeneration time the more it is situated towards the upper right, and more regeneration time the more it is situated towards the lower left

in land-use legacy (all $p > 0.10$). However, relative FRic values differed between agriculture versus old-growth forest values, having lower values in agriculture (FRic: Welch $t = 3.76$, $df = 28.78$, $p < 0.001$; Appendix S1: Table S3, Figure S3).

Comparative recovery dynamics

Among the assessed community properties, resistance was by far lowest in species composition with 43% (CI: 38%–51%). Traits (CWMs) and species richness showed high resistance values with 93% (CI: 90%–95%) and 72% (CI: 58%–87%), respectively (Figure 5). The two legacy subsets of cacao and pasture were very similar.

In contrast, differences for resilience were less clear: traits (CWM) recovered fastest with 0.24 (CI: 0.11–0.37), followed by species composition with 0.13 (CI: 0.10–0.18), and finally species richness with 0.11 (CI: –0.01 to 0.23), but the CIs of the metrics were overlapping (Table 1; Figure 5). The cacao and pasture legacy subsets were similar, although the resilience CI of cacao traits overlapped with 0 (i.e., nonsignificant resilience) while that of pasture traits did not.

DISCUSSION

We found a rapid recovery of ant communities and their functional traits in the Ecuadorian Chocó and provided evidence that all studied community properties will reach old-growth forest levels within less than four decades. Rapid and complete recovery was facilitated by a high resistance of species richness, trait structure and trait diversity (high similarity to old-growth forest remaining in the disturbed stage) and a similar resilience of all parameters (return rate to predisturbance stage). Hence, high levels of species richness occurred along the entire chronosequence, from ongoing agriculture and young secondary forests to mature forests. Whereas agricultural sites had dissimilar ant assemblages compared to old-growth and gradually approached old-growth forests with recovery, species with similar functional traits replaced one another, thus buffering overall changes in the functional trait space. The high resistance of ant communities found in agricultural sites was likely promoted by site conditions: land use was rather small in scale and relatively low in intensity and had occurred over relatively short time periods (few decades). The resilience was likely accelerated by the mosaic of secondary, selectively used and old-growth forests, promoting rapid dispersal of forest animals and plants into early recovery sites, as forest proximity generally aids natural or close-to-natural

forest succession (Chazdon et al., 2009; Dent & Wright, 2009; Wijdeven & Kuzee, 2000).

Ant species richness

Species diversity is one of the most frequently assessed community properties. In line with the few other studies, we recorded comparatively many ant species within the Chocó area (Donoso, 2017; Donoso & Ramón, 2009). Several studies have linked species diversity to higher ecosystem stability, however, outcomes are mixed among studies (e.g., Oliver et al., 2015; Pennekamp et al., 2018). We found that ant species richness was remarkably constant across the chronosequence, conveying a high resistance to disturbance. However, ant richness has been reported to have idiosyncratic responses to chronosequences in the majority of studies, as some report an increase of species richness or diversity with regeneration time (Bihn et al., 2008; Rocha-Ortega et al., 2018), while others found no such relationship (Belshaw & Bolton, 1993; Estrada & Fernández, 1999; Hethcoat et al., 2019; Schmidt et al., 2013; Staab et al., 2014). Ultimately, species richness changes depend on the species pool that is specialized to disturbed areas, which replace forest species during disturbance. In some regions, open areas have similar species richness levels to forested areas, and thus a disturbance does not result in a decline of ant species richness (Andersen, 2019).

Even though our study design aimed to reduce confounding effects of elevation, we found elevation to be moderately related to all community properties. In particular, elevation seems to be a more influential driver to species richness patterns than recovery time. Elevation increased species richness, which was expected as ant species diversity often peaks at mid-elevations in the Neotropics at around 500 m, which is within our upper boundary (Longino & Branstetter, 2019; Szewczyk & McCain, 2016).

Species composition

In contrast to species richness, composition accounts for a shift in species identities and often provides a stronger indication of environmental changes. As predicted, ant assemblages showed strong, consistent, and gradual changes towards the conditions found in old-growth forests, with high species turnover across sites and with forest recovery time. From highly dissimilar ant communities in agricultural areas, communities gradually converged to those found at old-growth forest level, and recovery was completed within the timeframe covered by the chronosequence, which is uncommon in chronosequence studies (Bowen et al., 2007; Crouzeilles

et al., 2016; Dunn, 2004). For instance, ant assemblages in the Atlantic rainforest were not recovered after 50 years of natural recovery (Bihn et al., 2008). Nevertheless, similarities of ant assemblages to old-growth forest assemblages were typically reported to be higher in older than in younger successional stages, suggesting that succession shapes ant assemblages in similar ways across ecosystems all around the globe (Dent & Wright, 2009; Dunn, 2004; Estrada & Fernández, 1999; Gomes et al., 2014; Hethcoat et al., 2019; Neves et al., 2010; Schmidt et al., 2013; Staab et al., 2014).

In our case, abiotic conditions were probably an important driver of the high community similarity of cacao and pasture, and their low similarity to old-growth forest. In particular, early recovery stages and agricultural areas have a warmer, drier, and more fluctuating microclimate due to the lack of canopy cover compared to old-growth forests (Gregory et al., 2019; Meijide et al., 2018). We found that differences shaped by land-use start to emerge only in the successional stages. Communities from recovering cacao had a consistently higher similarity to old-growth forest than those derived from pastures throughout the chronosequence, which lead to faster recovery rates for previous cacao sites (~21 years) than for former pastures (~29 years). Our findings are consistent with studies in cacao agriculture, in particular agroforestry, which showed particularly rich ant communities, especially in the leaf litter (Belshaw & Bolton, 1993; Delabie et al., 2007), representing an advantage of recovering cacao over non-woody crops.

Functional traits

Functional traits link species to their assumed functions (Wong et al., 2019). Given that species composition showed a strong response to disturbance and thus substantial changes with recovery, it is surprising that this response is not nearly as strongly reflected in their functional diversity. While trait structure (community-weighted means) gradually approached levels of old-growth forest with increasing recovery time, they had a high resistance to disturbance. The functional diversity indices, frequently applied to describe the trait space of communities, showed no change across the chronosequence, further highlighting a high functional redundancy of ant communities. This was unexpected since several studies on ant recovery found pronounced effects of environmental change on trait functional diversity and trait structure (e.g., Mexico [Rocha-Ortega et al., 2018], Brazil [Bihn et al., 2010], Argentina [Santoandré et al., 2019], Australia [Gibb & Cunningham, 2013; Lomov et al., 2009]).

However, in line with our findings, there are also several studies which showed that environmental degradation does not need to be associated with reductions in functional trait diversity. For instance, ant species functional dispersion of plots with low tree species diversity was similar to plots with high tree species diversity in China (Skarbek et al., 2020). Further, dung beetles and birds have also been shown to retain high levels of functional diversity even in young secondary forests in the Colombian Chocó (Edwards et al., 2021).

The influence of legacy effects on the trait structure (CWM similarity) is notable. Although only marginally significant, there appears to be a trend for environmentally selected traits that are different between the open areas of the pasture and the understory of cacao. Habitat openness can be a major environmental variable shaping the trait structure of ant assemblages (Andersen, 2019; Guilherme et al., 2019). We find that with forest growth during succession, the functional similarity to old-growth forests is quickly restored.

Recovery comparison of community properties

Forest recovery outcomes are predictable by the synergistic effects of resistance and resilience of community properties (Nimmo et al., 2015). Among chronosequence studies, our study is one of few to explicitly distinguish between resistance and resilience for several community properties according to Pimm's (1984) definition. This enabled us to disentangle the separate components of the recovery. We expected different recovery times for all community properties, and that community composition would be slowest to recover, followed by trait structure and then species richness. Our data confirm the slow relative recovery of community composition, which was mediated through a much lower resistance, but similar resilience compared to the other properties. These patterns are consistent with most findings from community recovery studies as well as with theoretical expectations (Curran et al., 2014; Dunn, 2004; Moreno-Mateos et al., 2017; Pimm et al., 2019). However, we did not find clear differences in recovery outcome for trait structure and species richness, which both showed high resistance and resilience in the face of disturbance. Interestingly, for all tested community properties, only resistance, but not resilience, drove differences in total recovery time. An explanation could be that community properties are biologically nested and thus computationally not independent of each other. Since species richness and trait structure are calculated from species composition, their turnover rates might be coupled, which would be worth

investigating through simulations. Our result that resilience was similar among properties confirms findings on forest recovery in the Amazon, where recovery rates (resilience) of species richness in comparison to community composition of birds, plants and dung beetles were surprisingly similar (Lennox et al., 2018). While resistance and resilience are conceptually independent, it is hard to untangle how much they are interdependent in the biological context, i.e., whether the same biological attributes that reduce impact to disturbance (resistance) are also beneficial to the recovery rates (resilience) (Nimmo et al., 2015). For instance, species attributes that correlate more to reproduction and re-colonization should increase resilience, while those that infer high physiological or behavioral plasticity should increase resistance (Nimmo et al., 2015; Shade et al., 2012). Further, resistance and resilience of the whole ecosystem is likely to be influenced by landscape configuration, with forest remnants acting as refuges (Shackelford et al., 2018). In the landscape mosaic of our study site, the community properties resistance and resilience were likely positively affected by the surrounding forest matrix. However, the distance of the plot to the forest edge was never correlated with any of the community properties. Since all plots were located rather close to forests, future experiments in more isolated forest patches are desirable. They could shed light on the question if similar, fast recovery happens also in more fragmented areas. The two concepts of resistance and resilience could also be differentially targeted with conservation and land-use strategies. For instance, we would expect that the use of agroforestry instead of monoculture would increase resistance, as communities are more similar to forests during disturbance. Likewise, the proximity to forest remnants or active re-planting of trees during early succession should lead to an increase of resilience. Manipulative ecological experiments, which try to explicitly alter resistance independent of resilience, could greatly improve our understanding of these recovery mechanisms. While the Ecuadorian Chocó is one of the most threatened biodiversity hotspots, our study confirms a strong recovery potential for recently deforested areas, particularly since intact forests are still abundant. This knowledge is important for future development in such regions, where deforestation by logging and small-scale farming is still common. Conservation action should thus target both old-growth forests remnants as well as recovering forests, including young stages on abandoned agricultural land.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

R code and raw data (Hoenle et al., 2021) are available in Dryad at <https://doi.org/10.5061/dryad.83bk3j9sk>.

ORCID

Philipp O. Hoenle  <https://orcid.org/0000-0001-8160-8859>

David A. Donoso  <https://orcid.org/0000-0002-3408-1457>

Michael Staab  <https://orcid.org/0000-0003-0894-7576>

Christoph von Beeren  <https://orcid.org/0000-0002-0072-5795>

Nico Blüthgen  <https://orcid.org/0000-0001-6349-4528>

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