Habitat disturbance modifies dominance, coexistence, and competitive interactions in tropical ant communities

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Abstract. 1. Interspecific competition is a major structuring principle in ecological communities. Despite their prevalence, the outcome of competitive interactions is hard to predict, highly context-dependent, and multiple factors can modulate such interactions.

2. We tested predictions concerning how competitive interactions are modified by anthropogenic habitat disturbance in ground-foraging ant assemblages inhabiting fragmented Inter-Andean tropical dry forests in southwestern Colombia, and investigated ant assemblages recruiting to baits in 10 forest fragments exposed to varying level of human disturbance.

3. Specifically, we evaluated how different components of competitive interactions (patterns of species co-occurrence, resource partitioning, numerical dominance, and interspecific trade-offs between discovery and dominance competition) varied with level of habitat disturbance in a human-dominated ecosystem.

4. Multiple lines of evidence suggest that the role of competitive interactions in structuring ground-foraging ant communities at baits varied with respect to habitat disturbance. As disturbance increased, community structure was more likely to exhibit random co-occurrence patterns, higher levels of monopolization of food resources by dominant ants, and disproportionate dominance of a single species, the little fire ant (*Wasmannia auropunctata*). At a regional scale, we found evidence for a trade-off between dominance and discovery abilities of the 15 most common species at baits.

5. Together, these results suggest that human disturbance modifies the outcome of competitive interactions in ground-foraging ant assemblages and may promote dominant species that reduce diversity and coexistence in tropical ecosystems.

Key words. Discovery-dominance trade-offs, interspecific competition, numerical dominance, resource partitioning, tropical dry forests, *Wasmannia auropunctata*.

Introduction

Understanding the role of competition in community structure is a longstanding goal of ecology (Hairston *et al.*, 1960; Cody & Diamond, 1975; Connor & Simberloff, 1979; Roughgarden, 1983). Interspecific competition is thought to be an

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important mechanism shaping patterns of species distribution and abundance (Schoener, 1983; Denno *et al.*, 1995; Kaplan & Denno, 2007), particularly in ant communities (Savolainen & Vepsäläinen, 1988; Hölldobler & Wilson, 1990; Human & Gordon, 1996; Davidson, 1998). Evidence of the importance of interspecific competition in structuring ant assemblages comes from studies varying in focus and experimental approach, including dominance hierarchies (Cerdá *et al.*, 1997; Bestelmeyer, 2000), territoriality and agonistic interactions (Brown & Gordon, 2000), resource partitioning (Sanders & Gordon, 2003), spatial mosaics (Floren & Linsenmair, 2000;

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Blüthgen & Stork, 2007), and intra and interspecific responses to experimental removal (LeBrun *et al.*, 2007; Tschinkel & King, 2007). However, the relative importance of competition in ant community ecology is subject to debate (Andersen, 2008; Parr & Gibb, 2010; Cerdá *et al.*, 2013; Stuble *et al.*, 2013).

Ant colonies can be large, persistent, and sessile, making them good models to understand the role of interspecific competition in structuring populations and communities (Hölldobler & Wilson, 1990; Adams, 2016). Dominance in ants is considered to play a key role in the outcome of competitive interactions and the structure of local ant assemblages (Parr & Gibb, 2010). Dominance can be estimated by measuring the ability of a species to monopolize resources in a community (Cerdá et al., 2013) which may be determined by its relative biomass or abundance (of individuals or colonies) (Parr & Gibb, 2010), or by behavioral (Suarez et al., 2002; LeBrun et al., 2007), numerical (Parr et al., 2005; Ward & Beggs, 2007) or ecological mechanisms (Davidson, 1998; Holway, 1999). In addition, competitive interactions can be influenced by biotic factors such as parasitism (LeBrun & Feener, 2007) and abiotic factors such as temperature (Cerdá et al., 1998; Bestelmeyer, 2000), habitat structure (Sarty et al., 2006; Luque & Reyes, 2007), and disturbance (Gray et al., 2018). Anthropogenic disturbances may have a particularly strong influence on ant communities as they often simplify habitat structure, resulting in changes in the competitive interactions that favour dominant species (Suarez et al., 2008; Tschinkel & King, 2017).

Ant species can also be organized into ecological dominance hierarchies based on direct interactions among species at resources (interference competition) or indirectly through the ability of species to rapidly locate and exploit resources before they are found by others (exploitative competition) (Case & Gilpin, 1974; Fellers, 1987; Vepsäläinen & Savolainen, 1990; Le Bourlot et al., 2014). Dominance can, therefore, be defined based on where a species occurs in such hierarchies (Mercier & Dejean, 1996; Cerdá et al., 1998), with dominant species either discovering a resource quickly, or displacing others, and monopolizing it after a period of time (Fellers, 1987; Davidson, 1998; Parr & Gibb, 2010). Indeed, mechanisms that may promote coexistence within hierarchies include trade-offs in functional traits and foraging strategies (van Oudenhove et al., 2018). For example, ants may excel at either dominance or discovery ability, and the resulting different foraging strategies can allow many species that forage on similar resources to coexist (Holway, 1999). While it is not always clear what may prevent a species from excelling at both forms of competition, factors such as the presence of natural enemies or sensitivity to abiotic conditions (e.g. temperature dependent activity) may keep dominant species from breaking trade-offs, thereby promoting coexistence (Cerdá et al., 1997; LeBrun et al., 2007; Feener et al., 2008). However, the ecological success of some dominant invasive ant species has been attributed to breaking this trade-off in sites where they have been introduced (Human & Gordon, 1996; Holway, 1999; Sarty et al., 2006).

Despite the large number of studies evaluating the role of competitive interactions and dominance hierarchies in ant community structure (Savolainen & Vepsäläinen, 1988; Human & Gordon, 1996; Cerdá *et al.*, 1998; Holway, 1999; Cerdá

et al., 2013), relatively little research has been carried out in communities in the Neotropics (e.g. Calcaterra *et al.*, 2008; Camarota *et al.*, 2016). Neotropical habitats are among the most species-rich regions on earth (Antonelli *et al.*, 2018), but a large proportion of its biomes and habitats are threatened by human activities (Etter *et al.*, 2006). Given the role of competition on ant community structure, it is important to quantify the effects of anthropogenic disturbance on their competitive interactions (Olden *et al.*, 2004). Furthermore, the Neotropics include the native ranges of some of the most widespread and damaging invasive ant species (e.g. *Solenopsis invicta*, Buren, 1972; *Linepithema humile*, Mayr, 1868; and *Wasmannia auropunctata*, Roger, 1863), and information on the ecological and behavioural dominance of these species in their native ranges may provide insight into mechanisms of invasion success.

In this study, we tested the hypothesis that anthropogenic habitat disturbance modifies the strength of competitive interactions. Specifically, we examined four predictions derived from ecological theory in relation to the structure of ant communities that forage actively on the ground in a highly fragmented Neotropical dry forest landscape. Our first prediction is that if interspecific competition for food is important in structuring assemblages within ant communities, ant species using the same food resource should co-occur at baits less often than would be expected at random (Schoener, 1974), and assemblages inhabiting relatively less disturbed habitats will be more likely to be structured by competition (Andersen, 1995; Parr & Gibb, 2010). Second, if anthropogenic disturbance promotes the success of dominant species (Holway, 1999; Vasconcelos et al., 2000), then (i) dominant species should be more likely to monopolize baits and (ii) coexistence of species at resources should be less common in highly disturbed habitats relative to less disturbed habitats. Third, if dominant ants act as a disturbance force themselves (Gotelli & Arnett, 2000; Cerdá et al., 2013), high numerical dominance in fragments will disrupt community structure, promoting declines in the richness and abundance of species that share food resources. Finally, we predicted that in the heterogeneous environment that characterizes the study area, ant hierarchies between resource discovery and resource domination may break down as a result of dominant species being able to break trade-offs that promote species coexistence (Davidson, 1998; Holway, 1999), particularly in more disturbed fragments.

Materials and methods

Study system

The study sites were located in the Inter-Andean floodplain formed by the upper watershed of the Cauca River in the northwestern part of South America, Colombia (Fig. 1). The floodplain covers an area 230 km long by 10–20 km wide, with an altitude of 900–1100 m. The climate is typical of a tropical dry forest, with an average annual temperature of 24 °C and 1000–2000 mm of rainfall, distributed in two periods (April–May and October–November), during which 70% of the total annual rainfall occurs (Álvarez *et al.*, 1998).



Fig 1. Map of the study area representing the location of 10 fragments that maintain tropical dry forest. Sites are abbreviated in the text as follow (Abbreviation, Altitude): Alejandría (AL, 900–940 m); Miralindo (MI, 900 m); Aguas Claras (AC, 940 m); Las Pilas (LP, 1000 m); El Medio (EM, 950 m); Las Chatas (LC, 950 m); El Vínculo (EV, 980–1150 m); El Hatico (EH, 980 m); Colindres (CO, 975 m); and San Julián (SJ, 950 m). *Sites assessed for the trade-off between dominance and discovery abilities. [Colour figure can be viewed at wileyonlinelibrary.com].

The tropical dry forest in this area of Colombia has been reduced to less than 20% of its original area, and the remnants are highly fragmented and isolated (García *et al.*, 2014). The dominant vegetation is composed of species in the genera *Piper, Solanum, Ficus, Anthurium, Lantana, Passiflora* and *Philodendron* (Vargas, 2012).

We selected 10 tropical dry forest fragments spread across the three states of the study area (Fig. 1 and Table 1). The landscape that surrounds these tropical dry forest fragments is dominated by pastures for cattle-raising (36% of the area) and intensive sugarcane production (52%) (Arcila-Cardona et al., 2008). Although these fragments are similar with respect to forest structure and size, they differ in shape, the habitat forming the matrix surrounding the fragment, and their degree of isolation from other forest patches (Arcila-Cardona et al., 2008). We used seven variables previously established by Arcila-Cardona (2007) to calculate a score of disturbance for each of the 10 fragments: (i) area, (ii) percentage of canopy cover, (iii) percentage of forest surrounding the fragment, (iv) percentage of cover representing matrix surrounding the fragment, (v) distance to the nearest neighbour with the same type of cover (i.e. degree of isolation), (vi) number of nearby fragments, and (vii) irregularity (i.e. the ratio of area to perimeter for each habitat fragment). A detailed description of the procedure

for obtaining these variables is found in Arcila-Cardona (2007), see also Appendix S1.

These specific variables were chosen for the following reasons. The size (i) and irregularity (vii) of the fragment represent habitat loss and land clearing (Haddad *et al.*, 2015), and ultimately influence the internal physical and biological environment through edge effects including modifying soil and air temperature and moisture (Sousa, 1984). Percentage of canopy cover (ii), amount of forest surrounding the fragment (iii), and habitat of the surrounding matrix (iv) are measures of land-use and are mediated by the frequency of logging within the fragments, and the presence of sugarcane and pasture around the fragments (Arcila-Cardona *et al.*, 2008). Finally, distance to the nearest neighbour (v), and number of nearby fragments (vi) are factors associated with anthropogenically induced isolation which influence rates of colonisation and recruitment (Haddad *et al.*, 2015).

To calculate the disturbance score for each fragment, we ranked the fragments from 1 to 10 for each variable with a score of 1 for the lowest value (low disturbance) and 10 for the highest value (high disturbance). For example, the largest fragment is Alejandría (15.3 ha) and the smallest is San Julian (3.5 ha) (Table 1). Thus, Alejandría obtained a score of 1 and San Julian a 10. Values of highest disturbance (10) were assigned for: lowest

	Coordinates		Variables used to calculate the score of disturbance							
Sites	North	West	Area	% Cover	% Forest	% Matrix	Isolation (ENN)	Proximity (PROX)	Irregularity	Score
EV	3 °50′2.38″	76°17′19.7″	15.0 (2)	90.9 (4)	9.9 (1)	75.4 (2)	108.2 (1)	85.5 (1)	0.2 (9)	2.9
AC	4 °53′23.1″	75 °55′56.6″	13.0 (4)	91.8 (2)	6.6 (2)	90.6 (6)	258.1 (4)	2.3 (3)	0.3 (7)	4
AL*	4 °49′58.6″	75 °53′2.4″	15.3 (1)	93.7 (1)	5.6 (4)	92.0 (8)	509.9 (5)	0.6 (6)	0.4 (5)	4.3
EM	4°20′13.8″	76°5′0.1″	13.1 (3)	87.8 (9)	2.5 (7)	90.4 (5)	182.5 (3)	2.4 (2)	0.6 (2)	4.4
MI	4 °54′19.89″	75 °51′30.5″	6.7 (9)	90.7 (5)	4.8 (5)	92.9 (9)	150.0 (2)	1.8 (4)	0.4 (4)	5.5
LP	4°26′25.7″	75 °59'23.1"	12.4 (6)	89.2 (8)	6.0 (3)	89.8 (4)	1090.8 (7)	1.0 (5)	0.3 (8)	5.9
LC	3 °51′20.8″	76°20′5.35″	10.8 (7)	91.7 (3)	0.8 (10)	73.1 (1)	3107.6 (10)	0.0 (10)	0.7(1)	6
EH*	3°38'34.48"	76°19'40.52"	12.6 (5)	89.3 (7)	2.6 (6)	96.6 (10)	597.7 (6)	0.5 (7)	0.5 (3)	6.3
SJ	3 °6′38.8″	76°31′41.2″	3.5 (10)	77.4 (10)	0.9 (9)	85.9 (3)	1360.6 (8)	0.1 (9)	0.4 (6)	7.9
CO*	3°16′25.8″	76 °29′31″	10.0 (8)	90.6 (6)	1.3 (8)	91.3 (7)	1798.0 (9)	0.1 (8)	0.1 (10)	8

Table 1. Geographic location of 10 sites of tropical dry forest and variables associated to each fragment (relative disturbance rank) used to calculate the score of disturbance.

* Sites assessed for the trade-off between dominance and discovery abilities.

The score of disturbance for each forest is the average of these relative disturbance ranks.

ENN, Euclidian nearest neighbor Distance; PROX, proximity index or number of nearby fragments.

percentage of canopy, lowest percentage of forest surrounding the fragment, highest percentage of matrix surrounding the fragment, highest isolation, lowest number of nearby fragments, and highest irregularity. These ranks were averaged for each fragment to calculate the score of disturbance and used to perform the analyses of species co-occurrence (*Prediction 1*) and resource partitioning (*Prediction 2*) (Table 1). Additional analysis of these data provided evidence for a latitudinal gradient of disturbance across the study area, with sites in the south having a higher overall score of disturbance relative to sites in the north (see Appendix S2: Fig. A1).

We tested our four predictions by examining community structure and competition for resources in the actively ground-foraging ant community. In the study area, the little fire ant W. auropunctata is recognized as a dominant species (Armbrecht & Ulloa-Chacón, 1999; Achury et al., 2008; Achury et al., 2012) and has been proposed as an indicator of disturbance in tropical dry forests (Armbrecht & Ulloa-Chacón, 2003). The little fire ant is native to South and Central America, including Colombia, but is a widely established introduced species globally (Wetterer & Porter, 2003). This species has generalist food habits, is highly opportunistic in its nesting requirements, and displays extraordinary reproductive potential (Ulloa-Chacón & Cherix, 1990). In places where it has become established, such as the Galapagos Islands, Hawaii, Florida, Australia, and West Africa, its introduction is accompanied by declines in native ants and other arthropods (Wetterer & Porter, 2003). In its native range, however, W. auropunctata often occurs in low density and coexists with other ant species (Tennant, 1994), especially in mature forest habitats. Nonetheless, it can also be numerically and competitively dominant in native communities (Achury et al., 2012). The little fire ant is frequently reported in agricultural habitats and disturbed ecosystems (Armbrecht & Ulloa-Chacón, 2003), where it becomes super-abundant, an attribute that probably contributes to its success as a dominant species, even within its native range (Orivel et al., 2009).

Ant sampling

We sampled ants in two different ways. For obtaining data on patterns of species co-occurrence, resource partitioning, and numerical dominance (*Predictions* 1-3), we placed an average of 55 sample stations separated by at least 20 m inside each of the 10 forest fragments. At each station, we placed a tuna-fish bait (8-10 g of tuna fish oil) on a $4 \times 4 \text{ cm piece of white bond}$ paper. Tuna baits are used to approximate ephemeral protein and lipid resources such as carrion or large dead insects. While tuna baits may bias estimates of community composition, particularly by excluding dietary specialists (Bestelmeyer et al., 2000), they are widely used in studies of ant community ecology and interspecific competition (Holway, 1999; Feener et al., 2008; Philpott et al., 2008; Achury et al., 2012; Stuble et al., 2013). We used these baits to examine the contribution of particular ant species to community structure and to acquire information on habitat use by trophic generalist ants (Bestelmeyer et al., 2000). The baits were placed on the ground for 2 h during the morning (between 08.00 h and 10.00 h). After 2 h the ants found directly on the tuna fish were collected as was the remaining bait and the soil attached to the bait card to include small species that may have recruited to the underside of the bait (Bestelmeyer et al., 2000). The specimens were then placed in sealed bags and kept frozen until identification.

To examine species dominance and discovery ability (*Prediction 4*), we sampled using a second set of baits at three forest fragments representing a gradient for the scores of disturbance identified previously: Alejandría (low), El Hático (intermediate), and Colindres (high) (Table 1). In each of these fragments, we placed linear transects consisting of 20 sampling stations separated by at least 10 m. A tuna bait and a pitfall trap were placed at every station. The bait was checked at the beginning of the experiment for 5 min or until the first species touched the bait and at the end of a two-hour interval. Experiments were initiated during the morning between 08.00 h and 10.00 h and retrieved before 12.00 h on the same day. Ants that discovered the bait and the ones that dominated it after the 2-h interval were collected for taxonomic identification, taking special care not to disturb

the foraging of species that were active in the first 5 min of observation. After the baiting used to assess discovery and dominance was finished, a pitfall trap was placed in the vicinity of each bait station. Baiting always preceded pitfall sampling to avoid possibly influencing estimates of discovery and dominance. Pitfall traps consisted of a plastic cup (473 ml) buried in the ground, containing approximately 120 ml of 80% ethyl alcohol (approximately 25% of the cup's volume). The traps were collected after a period of 48 h. Combining baits with pitfall traps at the same location is useful for measuring general activity of ant species along with their foraging patterns (Bestelmeyer *et al.*, 2000), yielding information about the resource use independent of its density (LeBrun & Feener, 2007; Stuble *et al.*, 2013).

Sampling was performed during three periods: two periods of sampling for *Predictions 1–3* (February to May and October to December), and one period for *Prediction 4* (June–July in 2014). The average temperature and relative humidity of the soil adjacent to each bait were 23.7 ± 2.1 °C and $76.5 \pm 11.2\%$ (\pm SD). All samples were washed, sorted, and preserved in 95% ethanol in the laboratory of Biology, Ecology and Management of Ants at the Universidad del Valle (Cali – Colombia). Ants were identified to genus using Palacio and Fernández (2003), and to species using AntWeb (2017 and references within), and the collection at the Museum of Entomology at the Universidad del Valle (MEUV). A reference collection of ants from this project was deposited in MEUV.

Data analyses

All statistical tests were conducted in R 3.5.0 (R Development Core Team, 2018), and some graphs were produced with the ggplot2 package version 2.2.1 (Wickham *et al.*, 2018).

Prediction 1: Pattern of species co-occurrence segregated if competition structures communities. We tested this prediction with null models of species co-occurrence used to distinguish between communities that are structured competitively versus randomly (Ribas & Schoereder, 2002; Sanders et al., 2007). To asses this hypothesis we organized the data in 10 matrices (one per each fragment) of presence (1) and absence (0), in which the species were located in rows and the baits in columns. An approximation of null models (Gotelli & Graves, 1996) was used employing the co-occurrence module of the package EcoSimR version 0.1.0 (Gotelli et al., 2015). We used the C-score, which measures the average number of checkerboards between all possible pairs of species (Stone & Roberts, 1990). It is defined as $CU = (r_i - S)(r_i - S)$, where S is the number of baits in which two species were found in each of the sites, and r_i and r_i are the total baits where species *i* and *j* are found. The C-score is the average of all possible checkerboard pairs, calculated for the species that occur at least once in the matrix.

The algorithm, SIM9, used to analyse species co-occurrence preserves the observed row and column totals, where the frequencies of occurrence in baits (fixed columns) and the original species richness on each fragment (fixed rows) are maintained. Thus, differences among fragments are kept constant, but the species occurrences are random with respect to one another, which makes it appropriate for detecting patterns of species interactions (Gotelli, 2000). When used with the C-score, this algorithm has the best statistical properties as it is not subject to errors types 1 and 2 (Gotelli, 2001). The C-score for the matrix of original data is then compared with the simulated C-score obtained from the randomized communities generated by 5000 Monte Carlo permutations. A larger data C-score suggests lower co-occurrence, with species predominantly avoiding each other, and a segregated pattern, suggesting competition (Parr & Gibb, 2010). If the C-score is smaller with respect to the values generated by the null models, then the pattern of species co-occurrence is aggregated. To evaluate whether the C-scores differed significantly from randomness, and to compare scores across the 10 fragments, we calculated a standardised effect size (SES), which measures the number of standard deviations that the observed index is above or below the mean index using 5000 simulated communities (Sanders et al., 2003). Given the potential biases mentioned above of using bait data, we repeated these analyses of co-occurrence using the pitfall trap data from three fragments (Appendix S2: Fig. A2).

Prediction 2: Monopolisation of food resources in highly disturbed environments. The total number of ants and the frequency of capture in baits were recorded for each species across the 10 forests. The species that were on the resource at the same time and shared the resource most frequently with W. auropunctata also were identified. We evaluated the partitioning of the bait based on four categories representing monopolisation and coexistence: (a) monopolised by W. auropunctata, (b) monopolised by other species, (c) W. auropunctata sharing with other species, and (d) other species sharing. Baits dominated by workers of one species were categorised as monopolised, whereas baits in which at least a single worker of two or more species were co-occurring on the resource resulted in categorizing as sharing. We felt this was a conservative measure as it includes solitary foraging species that do not recruit nestmates to resources. To compare the proportions of categories of bait partitioning among the different fragments, and related these results with our score of disturbance, we used the Pearson's Chi-squared test, and pairwise comparisons applying the Bonferroni method (Zar, 2010). Bait partitioning was evaluated based on the standardised residuals of a log-linear model of the counts for the different categories in each fragment using a Chi-square test (Crawley, 2012). One site did not have captures of W. auropunctata (Las Chatas), and those baits were not used for the analysis of resource partitioning. Auxiliary analyses of associations between dominant species without accounting for the score of disturbance (i.e. regional scale) are presented in Appendix S3.

Prediction 3: Numerical dominance promotes declines in the diversity of ants. We used a GLM (deviance analyses) to test whether the number of ant species that use the food resource was related to the activity and numerical dominance of *W. auropunctata* on baits. We ran this analysis with a Poisson error structure and the log link function. There was no evidence

of over-dispersion in the model (*Residual deviance* = 438.1 on 552 d.f.). To evaluate numerical dominance and competitive exclusion at baits separately from the context of disturbance, all baits regardless of the fragment in which they occurred, were considered independent. The richness of species per bait was the response variable and categorical values for the activity of *W. auropunctata* served as an explanatory variable (zero, 1-10, 11-100, 101-1000, and >1000 individuals per bait). Using worker abundance as a measure of activity can be problematic due to interspecific differences in foraging patterns, worker behaviour, colony densities, and worker size (Bestelmeyer *et al.*, 2000). However, within species, bait captures are relatively unbiased when used as a measure of intraspecific recruitment, and are frequently used in studies assessing dominance and competition (Parr & Gibb, 2010).

Additionally, we calculated the proportion of baits in each fragment that captured little fire ants as a more conservative estimate of its abundance compared to worker counts. We used linear regression to evaluate the relationship between the proportion of baits in which *W. auropunctata* was present (predictor variable) and the species richness of ants at baits (response variable) in each fragment. A generalized linear model (GLM: logistic regression) was used to examine the relationship between the proportion of baits in which *W. auropunctata* was present (predictor variable), and the proportion of baits used by other ant species (response variable) in each fragment. Due to an over-dispersed model during the exploratory analyses, we used quasi-binomial errors and the logit function in the model.

Prediction 4: Breaking the discovery-dominance trade-off. We measured discovery and dominance abilities based on the information from the second set of baits and the pitfall traps (see Ant sampling). Two competitive indices whose values ranged from 0-100% were calculated for the most common species captured (>10% of baits). The Dominance Index is the percentage of baits that were monopolised (solitary occurrences) by each species after 2h out of the total number of baits in which the species was detected (Santini *et al.*, 2007; Parr & Gibb, 2012).

The Discovery Index was estimated in two ways: First, we determined the percentage of baits where a species was the first to arrive relative to the total number of baits in which that species

was observed (i.e. discovered and/or present at 2-h end point) (Fellers, 1987; Parr & Gibb, 2012). This provides an absolute measure of discovering ability that does not consider differences in colony density, numbers of foragers or forager behaviour (Feener et al., 2008; Stuble et al., 2013). Second, we estimated discovery ability by controlling for differences in colony density adjusting for species prevalence in the environment (Feener et al., 2008; Lessard et al., 2009). This estimate gives a measure of relative discovery ability, and it estimates a null expectation of the number of baits a species discovers for a given prevalence. The expected value was calculated based on the total number of baits discovered by the most common species, divided by the total number of pitfall traps in which these species were recorded (LeBrun & Feener, 2007). This value is then multiplied by the number of pitfalls in which each individual species was detected to generate the expected number of baits that would be discovered per species. Finally, this value was compared with the observed number of baits discovered by each species (residual), and used as another measure of discovery ability, independent of the prevalence of each species. A positive value means that a given species is better at discovering resources than expected, and a negative value indicates that the species is worse at finding baits than expected based on the number of occurrences (Stuble et al., 2013).

These dominance-discovery indices were used to estimate the relationship of the dominance-discovery trade-off and to construct a dominance hierarchy based on ranks to evaluate the differences in foraging strategies by dominant ants in the overall study area, and also for three fragments that vary in the level of disturbance (see *Ant sampling: Prediction 4*). Due to tied ranks in both indices, Spearman's rank correlation 'rho' coefficient was used to analyse the aforementioned ranks (Zar, 2010).

Results

Eighty ant species from 34 genera were recorded visiting the 557 baits that were placed for 2 h in the 10 fragments (Appendix S2: Table A1). Ten of these species were found at more than 30 baits and/or had at least 1000 individuals (Table 2). The most common ant at the baits was *W. auropunctata* with 101 864 workers recorded, representing 77% of the 131 866 total ant workers

Table 2. Ant species detected in tropical dry forests with the greatest abundance and occurrence in the first set of baits (experiment associated with *Predictions* 1-3).

Species	Total individuals	Occurrence in baits (%)	Number of sites
Wasmannia auropunctata	101 864	219 (39.32)	9
Crematogaster carinata	6994	52 (9.33)	5
Crematogaster sotobosque	3751	30 (5.39)	3
Solenopsis pollux	1592	91 (16.38)	10
Azteca instabilis	1324	50 (8.98)	7
Dolichoderus bispinosus	1279	37 (6.64)	5
Pheidole sp. 4	1124	38 (6.82)	5
Pheidole susannae	507	47 (8.44)	8
Pheidole ca. sabella	359	53 (9.51)	6
Camponotus novogranadensis	248	35 (6.28)	7



Fig 2. Comparison of ant communities between 10 fragments that vary in the level of disturbance in the tropical dry forest of Colombia. The standardised C-score is a measure of the extent to which species co-occur less frequently than expected by chance. The horizontal lines (SD \pm 1.96) represent the approximate level of statistical significance (P < 0.05). Blue symbols indicate fragments with significantly segregated communities, red is significantly aggregated, and white did not differ from random. Numbers associated with each point represent the number of ant species detected per fragment. The abbreviation for the names of forests are displayed in the legend of Fig. 1. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 3.	Co-occurrence	patterns at the site	e scale of ant s	species detected	l at baits in the	10 fragments of	tropical dr	y forest
		1		1		0		

Site	C-score observed	C-score expected	P (obs \leq exp)	P (obs \ge exp)	Community structure
1. El Vínculo	16.429	16.248	0.677	0.3328	Random
2. Aguas Claras	11.904	11.656	0.9724	0.0282	Segregated
3. Alejandría*	8.3387	7.9642	0.999	0.001	Segregated
4. El Medio	27.737	28.238	0.0476	0.953	Aggregated
5. Miralindo	11.152	10.876	0.975	0.0258	Segregated
6. Las Pilas	15.536	15.028	0.9972	0.0028	Segregated
7. Las Chatas	25.485	25.318	0.658	0.3544	Random
8. El Hatico*	9.1067	7.7781	0.999	0.001	Segregated
9. San Julián	2.4222	2.4468	0.4458	0.6818	Random
10. Colindres*	10.236	9.7842	0.8756	0.1548	Random

* Sites assessed for the trade-off between dominance and discovery abilities.

The observed C-score was calculated from the ant assemblage and compared with the simulated expected C-score, which is produced after 5000 randomly assembled communities. Bold values indicate statistical significance (P < 0.05).

and occupying 39.3% of the total baits. *Wasmannia auropunctata* co-occupied baits with 43 species, of which 5 (*Solenopsis pollux*, Forel, 1893; *Pheidole* ca. *sabella*, *Crematogaster carinata*, Mayr, 1862; *Camponotus novogranadensis*, Mayr, 1870; and *Pheidole synarmata*, Wilson, 2003) represented 45% of the total shared baits.

Prediction 1

To test the extent to which competition may structure the ground-foraging ant community, we used a null model approach. These analyses revealed that among fragments there was nonrandom pattern of co-occurrence along the gradient of disturbance. For six fragments that scored low in disturbance, five had nonrandom co-occurrence scores (Fig. 2): four segregated and one aggregated (Table 3). This pattern suggests competition may be an important component of community structure in fragments with low levels of disturbance in this system. Conversely, in the most disturbed fragments, co-occurrence patterns did not differ from random in three out of the four matrices (one fragment, El Hatico, displayed segregated pattern of co-occurrence) (Table 2). Estimating co-occurrence with pitfall trap data from three fragments revealed a segregated pattern with less co-occurrence than expected by chance in the fragment with a low disturbance score (Alejandría). In contrast, co-occurrence patterns were not different than expected from



Fig 3. Mosaic plot indicating the frequencies for each category of resource partitioning in fragments of tropical dry forest where *W. auropunctata* was detected. The standardised residuals of a log-linear model are drawn in shades of red and broken outlines when negative, while positive residuals are in shaded blue with solid outlines. The abbreviation for the names of forests are displayed in the legend of Fig. 1. [Colour figure can be viewed at wileyonlinelibrary.com].

the null models in the forests with intermediate (El Hático) to high levels of disturbance (Colindres) (Appendix S2: Fig. A2).

Prediction 2

Consistent with the prediction that disturbance promotes monopolization of food resources by dominant ants, there were significantly more baits categorized as monopolized by *W. auropunctata* in highly disturbed forests than expected, and fewer in fragments with lower disturbance scores (9 fragments and 4 categories of bait partitioning, n = 36, $\chi^2_{24} = 231.28$, P < 0.0001) (Fig. 3). In fragments where monopolisation of baits by the little fire ant was higher than expected (El Hatico, San Julian and Colindres) ($\chi^2 = 125.78$, P < 0.0001), this species was present at 79% and monopolised 59% of all baits. Conversely, co-occurrence of species at baits was more common in fragments with lower levels of disturbance ($\chi^2 = 30.079$, P < 0.0001) (Fig. 3). Specifically, baits shared by two or more species were observed more often than expected in fragments with low to intermediate disturbance ($\chi^2 = 38.642$, P < 0.0001) (Fig. 3). At these sites, co-occurrence was observed at 51% of the baits, and *W. auropunctata* only monopolized 6% of the resources.

Prediction 3

We found evidence that higher activity of dominant species disrupts the structure of ant communities. Considering all baits within the fragments, the activity of *W. auropunctata* was negatively correlated with the number of other ant species that exploit the food resource (GLM: $\chi^2_4 = 167.21$, n = 557, P < 0.0001; Bonferroni-adjusted testwise error: P < 0.05/6 = 0.0083) (Fig. 4). At the level of the fragments, the proportion of baits with *W. auropunctata* was negatively correlated with both ant species richness at baits (Linear regression: $F_{1,7} = 15.74$, $R^2 = 0.6481$, P < 0.01) (Fig. 5A) and ant abundance (measured as a proportion of used baits) (Logistic regression: $F_{1,7} = 18.04$, P < 0.003) (Fig. 5B). Additional analyses using the pitfall trap data showed that there was no difference in species richness between traps with or without the little fire ant in two of the



Fig 4. Relationship between the number of ant species detected at any bait and the activity of the little fire ant foraging on the food resource. Different letters indicate P < 0.05. [Colour figure can be viewed at wileyonlinelibrary.com].

three fragments. The exception was El Hático where species richness was positively correlated with little fire ant presence (Appendix S2: Fig. A3).

Prediction 4

We detected 61 species from 33 genera from the pitfall traps and additional baiting in three fragments (AL, EH and CO) (Appendix S2: Table A2). Fifteen species were sufficiently common (>10% of displayed baits) to calculate dominance and discovery indices (Table 4). Two species (Crematogaster curvispinosa, Mayr, 1862; and W. auropunctata) obtained the highest discovery scores, and, five species (Solenopsis azteca, Forel, 1893; P. synarmata, Monomorium floricola, Jerdon, 1851; Pheidole radoszkowskii, Mayr, 1884; and Solenopsis geminata, Fabricius, 1804) obtained the highest dominance scores (Table 4). Wasmannia auropunctata was the only species that overall had a high capacity for dominating resources by both means of discovery (76.4% of the baits) and monopolization (88.2%). In addition, this species had the highest residual discovery index (5.3); the little fire ant was the most efficient at discovering resources in this environment independent of its incidence estimated from pitfall traps (Table 4). Other species efficient at discovering resources relative to their incidence in the environment included Crematogaster sotobosque (Longino, 2003) and C. curvispinosa. In contrast, species including P. radoszkowskii, P. ca. sabella, and S. azteca discovered fewer baits than expected.

Across the three sites, there was a negative relationship between the rank of dominance and rank of discovery for the 15 most common ant species at baits (Spearman correlation rho = -0.75, P = 0.001), suggesting a trade-off between dominance and discovery abilities for this subset of the community (Fig. 6A). However, while still negative, this relationship was no longer significant when controlling for the prevalence of each species in the environment (i.e. residual of discovery) (rho = -0.48, P = 0.07) (Fig. 6B). Two species that appear to 'break' this trade-off are *W. auropunctata* and *C. sotobosque*, both of which are better at discovering resources than predicted based on their prevalence in the environment (Fig. 6B; note the dispersion of points representing those species). These two species drove the differences between colony and worker-level comparisons. By removing these from the analysis using the residuals, the trade-off between dominance and discovery is reestablished (rho = -0.71, P = 0.006). This pattern using data from all three fragments was not seen at the level of individual fragments (Appendix S2: Fig. A4).

Discussion

We found evidence supporting the general hypothesis that anthropogenic disturbance can influence ant community structure through changes in competitive interactions. Sites with lower levels of disturbance were more likely to show evidence of structured assemblages (consistent with competitive dynamics) and more disturbed fragments were more likely to exhibit patterns consistent with random species co-occurrences. Additionally, fragments with lower disturbance had more co-occurrence at baits while sites with higher levels of disturbance were more likely to have baits monopolized by W. auropunctata. Finally, using additional bait and pitfall trap data at three sites, we found evidence of a dominance-discovery trade-off among the 15 most common ants, and that W. auropunctata may be able to break the trade-off by means of scouting, finding and monopolising resources with high numerical dominance. As a whole, the results suggest that habitat disturbance can modify competitive interactions between species.



Fig 5. Regressions models to evaluate the number of ant species and the proportion of baits used by ants in relation to the proportion of baits that *W. auropunctata* exploited in each fragment of tropical dry forest. In (A), the relationship between the proportion of capture of *W. auropunctata* and the richness of species for each fragment (linear regression: y = 33.375-24.336x), and (B), the relationship between the proportion of the little fire ant with the proportion of other ant species on baits across sites (logistic regression). Grey bands represent the 95% CI. The abbreviation for the names of forests are displayed in the legend of Fig. 1. [Colour figure can be viewed at wileyonlinelibrary.com].

We assessed the role of interspecific competition on the structure of ant assemblages in fragments of tropical dry forest and compared the scores of co-occurrence based on changes in levels of perturbation (*Prediction 1*). Higher levels of disturbance led to a change of co-occurrence patterns in ant assemblages, with a shift from structured communities (mainly segregation) towards randomness in more disturbed habitats. Remarkably, forests that displayed a segregated pattern of co-occurrence, independently from the score of disturbance, harboured a high number of species foraging on baits (>25 species) and in general low dominance of *W. auropunctata*. Dominant ants can disassemble community structure (Sanders *et al.*, 2003; Sanders *et al.*, 2007), and disturbed environments may be particularly prone to community disassembly (Philpott *et al.*, 2010). Our results suggest that random co-occurrence patterns may emerge in disturbed environments as a consequence of competitive exclusion in species-poor

Table 4.	Competitive ability	indices for the most	common species at ba	its from the	e discovery-0	dominance exp	periment associa	ated wit	h Prediction	4.
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Species (abbreviation)	% dominated baits	% discovered baits	Residual discovering		
Wasmannia auropunctata (W.a)	88.2 (6)	76.4 (2)	5.31 (1)		
Crematogaster sotobosque (C.s)	85.7 (7)	57.1 (6)	2.72 (2)		
Crematogaster curvispinosa (C.c)	0 (15)	100 (1)	2.49 (3)		
Pheidole rugiceps (P.ru)	66.7 (11)	66.7 (3)	1.69 (4)		
Camponotus novogranadensis (Ca.n)	33.3 (13)	66.7 (3)	1.23 (5)		
Linepithema iniquum (L.i)	80 (9)	40 (7)	0.21 (6)		
Pheidole susannae (P.su)	33.3 (13)	66.7 (3)	-0.05 (7)		
Monomorium floricola (M.f)	100 (1)	0 (14)	-0.26 (8)		
Solenopsis pollux (S.p)	66.7 (11)	33.3 (8)	-0.31 (9)		
Pheidole synarmata (P.sy)	100 (1)	20 (12)	-0.79 (10)		
Solenopsis geminata (S.g)	100 (1)	33.3 (8)	-0.80(11)		
Nylanderia steinheili (N.s)	77.8 (10)	33.3 (8)	-1.36 (12)		
Pheidole radoszkowskii (P.ra)	100 (1)	0 (14)	-2.31 (13)		
Pheidole ca. sabella (P.sa)	85.7 (7)	28.6 (11)	-3.64 (14)		
Solenopsis azteca (S.a)	100 (1)	10 (13)	-4.13 (15)		

Percentage of dominated baits refers to baits monopolized by a species after 2 h. The discovering measure represents the percentage of baits discovered by a species during the first 5 min of exposure, and the residual discovering is a measure of expected baits discovery by each species given its abundance in the environment. The highest values for each index are given in bold. (Rank of each species within the index).

communities containing dominant taxa. However, despite evidence that competition is important for structuring ant communities at local scales (Fellers, 1987; Savolainen & Vepsäläinen, 1988; Albrecht & Gotelli, 2001; Parr & Gibb, 2010), ants in one fragment (El Medio) displayed an aggregated pattern of species co-occurrence (Table 3). Therefore, we cannot definitively attribute the non-random pattern of species co-occurrence in fragments with lower levels of disturbance to competition. Other factors, such as habitat filters (Sanders *et al.*, 2007) or micro-scale responses of ants to abiotic conditions are also important in structuring ant assemblages and remain to be tested in this system.

Our results also support that changes in resource partitioning can occur along a gradient of disturbance (Prediction 2). Resource partitioning can be modified by abiotic factors such as habitat structure (Parr & Gibb, 2010; Blight et al., 2014). Previous surveys in these forests found that fragments with low disturbance contain higher nesting resources, represented by the number of small trunks, branches, and hollow fruits and seeds relative to forests with high disturbance (Arcila-Cardona, 2007). These results are consistent with studies documenting that the success and rate of foraging in ants are affected by habitat complexity (Gibb, 2005), with high structural complexity slowing the rate of monopolization (Gibb & Parr, 2010) and facilitating coexistence in ant communities in tropical environments (Sarty et al., 2006). However, co-occurrence patterns alone are insufficient to suggest a prominent role of ecological interactions mediating community structure (Blanchet et al., 2020), a limitation of using presence/absence data whether at baits (i.e. 'momentary' diversity; see Andersen, 1992) or with pitfall trap data. In the three fragments where we sampled with both pitfall traps and baits, comparing occurrence patterns between sample methods suggests that reduced diversity on baits could arise from competitive exclusion (mainly by W. auropuctata), rather than due to reduced species richness within fragments (Appendix S2: Fig. A3). Yet, without directly measuring the

strength of ecological interactions in this system, our results should be interpreted with caution.

Wasmannia auropunctata was dominant both in number of workers and the frequency of occurrence at baits. The little fire ant's foraging is characterized by recruiting a large number of workers to resources (Clark et al., 1982; Tennant, 1994). Subsequently, the little fire ant can act as an agent of disturbance; its numerical dominance is correlated with a decline in species richness and abundance of ants competing for the same resources at baits in this ecosystem (Prediction 3) (Armbrecht & Ulloa-Chacón, 2003; Achury et al., 2012). Numerical dominance is an important determinant of the outcome of interference interactions between ant colonies (Parr & Gibb, 2010). Based on differences among sites in dominance and abundance of W. auropunctata, numerical dominance is a possible causal mechanism that could explain how this species monopolises baits. Some dominant species, such as the little fire ant (Vonshak et al., 2012), the Argentine ant L. humile (Holway, 1999), or Aphaenogaster picea (Wheeler, 1908) (Warren et al., 2020), do not perform well in one-on-one interactions; however, competitive supremacy comes from their high worker densities.

The little fire ant has an unusual reproductive system and social organisation that may promote its success in disturbed areas (Foucaud *et al.*, 2009; Orivel *et al.*, 2009; Chifflet *et al.*, 2018). In French Guiana, for example, anthropogenic sites had higher population densities and a unicolonial social organisation. In these human-modified habitats, clonal populations (Foucaud *et al.*, 2006) are favoured and supercolonies that cover an area of a few hundred to a few thousand meters are formed (Foucaud *et al.*, 2009). Our results seem to be in concordance with those for *W. auropunctata* in its native range, with more disturbed sites harbouring a higher abundance and dominance of this species. However, we do not have information on this ant's reproductive system for the study area, and future studies in this part of its native range remain open to test the hypothesis of human disturbance as a trigger



Fig 6. Trade-off between dominance and discovery abilities for the 15 species with the greatest number of occurrences in baits that were examined for this analysis (Abbreviation for ant species displayed in Table 4). (A) Relationship between dominance rank and discovery ability; and (B) relationship between dominance rank with the expected (residual) discovery ability. Blue circles represent the species 'breaking' the trade-off. The lowest rank for both abilities indicates the species that was most dominant or fastest discoverer. [Colour figure can be viewed at wileyonlinelibrary.com].

for ecological dominance based on shifts in colony structure (Foucaud *et al.*, 2009; Chifflet *et al.*, 2018).

The competitive ability indices revealed a negative correlation between the exploitation and interference abilities of the most common species (*Prediction 4*). However, this trade-off, which may promote the coexistence of dominant species foraging on baits, was broken by two species that appeared to excel in both discovery and monopolization ability: *W. auropunctata* and *C. sotobosque*. Trade-offs between competitive abilities may explain coexistence of many species that depend on similar resources (Fellers, 1987; Kneitel & Chase, 2004). Davidson (1998) defines ecological dominance as the combination of mechanisms related to numerical dominance (by monopolizing the resource) and mechanisms of behavioural dominance (by being proficient at finding resources rapidly), proposing that ants cannot achieve ecological dominance through both mechanisms. However, these species show patterns of dominance at the colony-level (e.g. worker and nest number) similar

to patterns reported for communities with introduced species including *L. humile* (Holway & Case, 2001; Suarez *et al.*, 2008), *Anoplolepis gracilipes* (Smith, 1857) (Sarty *et al.*, 2006; Ward & Beggs, 2007) and *W. auropunctata* (Clark *et al.*, 1982; Le Breton *et al.*, 2005). This study suggests that populations of species that respond favourably to disturbance, such as *W. auropunctata*, can break this trade-off even within their native range.

Competitive hierarchies constructed to explore patterns of coexistence and community structure have been criticised due to inconsistent results (Parr & Gibb, 2012; Stuble et al., 2017), and their inability to explain multiple interactions among species (Lessard et al., 2009; Stuble et al., 2013). In these fragments, communities may become disassembled due to the highly disturbed nature of the landscape (García et al., 2014). For example, the size of most fragments in this system is less than 10 ha (range 3.5-15.3; average 11.2). Habitat area is a reliable predictor of abundance and activity in ants (Vasconcelos et al., 2000; Brühl et al., 2003), with small fragments promoting the population of dominant species (Suarez et al., 1998), and simpler habitats facilitating both food resource discovery and dominance (Parr & Gibb, 2012). However, studies evaluating trade-offs with habitat complexity or disturbance as a mediating factor (see Parr & Gibb, 2012 and references within) are rarely conducted in the Neotropics (e.g., Calcaterra et al., 2008; Camarota et al., 2018). Additional research on discovery-dominance trade-offs, and the factors that influence them, are needed to identify generalisations and limitations for applying this concept widely in ant communities (Stuble et al., 2017).

The importance of competition in structuring ant communities can be difficult to demonstrate as competitive interactions can vary depending on factors such as habitat heterogeneity and abundance of dominant species (Cerdá *et al.*, 2013). Our co-occurrence analyses suggest the effect of competition can be modified by level of disturbance in Neotropical dry forest fragments. These results may have additional applicability to the study of biological invasions; the globally invasive *W. auropunctata* is native to the study area and stands out as the dominant species. However, additional studies throughout its native range are required to understand how its dominance arises and is maintained under different abiotic (e.g. anthropogenic disturbance) and biotic factors (e.g. absence of parasitism by the wasp *Orasema minutissima*; López *et al.*, 2008).

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AUTHOR CONTRIBUTIONS

All authors designed the research; RA carried out the sampling, analysed all data, and drafted the manuscript; AVS contributed to interpretation of results, writing of the manuscript; all authors reviewed and commented on the manuscript.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting Information

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

Appendix S1. Description for obtaining variables associated to the score of disturbance.

Appendix S2: Table A1. Ant species collected in tropical dry forest in the inter-Andean valley of the Cauca river, Colombia.

Appendix S2: Table A2. Ant species detected with pitfall traps and additional baiting in three forest with contrasting level of disturbance.

Appendix S2: Fig. A1. Latitudinal gradient of disturbance across the study area.

Appendix S2: Fig. A2. Analyses of co-occurrence for three fragments using the pitfall trap data.

Appendix S2: Fig. A3. Number of ant species collected with pitfall traps and relationship with the occurrence of *W. auropunctata*.

Appendix S2: Fig. A4. Trade-off between dominance and discovery abilities using data for three fragments.

Appendix S3. Analyses of spatial distributions among the little fire ant and the most abundant species.

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