

Do morphological traits of ground-dwelling ants respond to land use changes in a neotropical landscape?

Catalina Sanabria^{a,b,*}, Sébastien Barot^{a,2}, Steven J. Fonte^{c,3}, Florence Dubs^{a,4}

^a IRD, CNRS, INRA, UPEC Institute of Ecology and Environmental Sciences - Paris, iEES -Paris, Sorbonne Université, 75005 Paris, France

^b Terrestrial Ecology, Department of Ecology and Ecosystem Management, Technical University of Munich, 85354 Freising, Germany

^c Department of Soil and Crop Sciences, Colorado State University, Fort Collins, CO 80523, USA

ARTICLE INFO

Handling Editor: Yvan Capowiez

Keywords:

Land uses
Ant species
Soil management
Soil properties
RLQ analysis

ABSTRACT

Analyzing the impacts of agricultural activities on biodiversity requires a full knowledge of the ecology of the studied species. Using a trait-based approach may improve our ability to understand land use impacts on less well-studied species in order to establish general trends that will facilitate the prediction of these impacts. In this study, we applied a trait-based approach to understand the impact of land use change on ant communities in the Colombian Llanos region. Five common land uses were considered (annual crops, rubber plantations, oil palm plantations, improved pastures and semi-natural savannas) to test whether some morphological traits respond to soil properties and land uses. An RLQ analysis shows a significant common structure between species distribution, environmental factors, and morphological ant traits. This indicates that morphological traits could be used to predict the response of ant communities in different land uses since they respond to environmental characteristics as vegetation complexity, composition and management. Based on the selected morphological ant traits, three groups of land uses were differentiated: grazing-based systems, agroforestry plantations and annual crops. Agroforestry plantations, especially rubber plantations tend to host larger and specialized ant species, while grazing-based systems (i.e. improved pastures) mainly host small and generalist ants, and annual crops host more pigmented ants. These findings suggest that certain morphological traits can reflect the ability of ant species to settle down and survive in a given land use system. Our study shows that improving knowledge about trait-environment associations could be a useful way to better understand how ecological filtering shape neotropical ant communities and how they respond to landscape transformation and land use changes.

1. Introduction

Agriculture often involves large-scale shifts in nutrient flux and plant productivity and is a major driver of biodiversity change and habitat (Marta et al., 2021). The growing need for food production and energy resources continues to increase the pressure to expand agricultural lands, such that “agricultural frontiers” are now reaching the last unprotected natural areas in many regions of the world (Hubert et al., 2010; Decaëns et al., 2018). In the Eastern Plains (Llanos) of Colombia, diverse agricultural activities have exerted growing pressure on natural ecosystems during the last 50 years (Romero-Ruiz et al., 2012). The

widespread conversion of natural ecosystems to intensive agriculture results in habitat loss and fragmentation, which subsequently impacts the integrity and function of biological communities, from weeds, large mammals and birds to small soil-dwelling animals (Altieri and Nicholls, 2003; Fischer et al., 2006). In tropical countries, predicting how land uses and land use changes affect these communities remains challenging, but new approaches based on species traits may be used to describe them and their dynamics in order to tackle these issues.

Many methods to predict the impacts of agricultural activities on biodiversity have been developed (Carvalho et al., 2020; Schmidt and Diehl, 2008). The most obvious is to describe taxonomic diversity and

* Corresponding author at: Terrestrial Ecology, Department of Ecology and Ecosystem Management, Technical University of Munich, 85354 Freising, Germany.
E-mail address: catasanabria@gmail.com (C. Sanabria).

¹ ORCID: 0000-0003-1795-4006.

² ORCID: 0000-0002-5910-538X.

³ ORCID: 0000-0002-3727-2304.

⁴ ORCID: 0000-0002-6657-9911.

use it to predict the impact of land uses on species. However, this restricts predictions to species that have been identified and thoroughly studied (Moretti et al., 2013; Vandewalle et al., 2010). Instead, the trait-based approach uses different types of traits (i.e. morphological, eco-physiological and life history characteristics) (Wong et al., 2019). This approach could be used to better understand the impact of land use change and agriculture on biological communities (Carvalho et al., 2020; de Bello et al., 2010) and to explain general patterns that could allow for improved prediction and mitigation of these impacts (Pey et al., 2014; Linksvayer and Janssen, 2009; Webb et al., 2010). In this sense, species traits can be used to predict species distribution and community composition (Gibb et al., 2013; Sarty et al., 2006) and can help to clarify what different bioindicator groups are actually indicating (Carvalho et al., 2020). Traits are comparatively easy to describe but it is necessary to define and standardize the methodologies to assess them (Pey et al., 2014; Ribera et al., 2001; Vandewalle et al., 2010; Wong et al., 2019).

Ant communities provide a good model to examine relationships between environmental characteristics, communities (Gotelli and Ellison, 2002) and traits (Campbell and Crist, 2016). They constitute a diverse and abundant group in most terrestrial communities of ground-dwelling organisms (Hölldobler and Wilson, 1990). They are also involved in a range of important ecological functions, such as the modification of the physical-chemical environment (Cammeraat et al., 2002). Ants can also affect plant communities and a range of other soil organisms (Folgarait, 1998; del Toro et al., 2013). They nest in different substrates (soil, ground, litter, etc.) and have very diverse diets (scavengers, predaceous, granivorous, herbivorous, etc.) (Hölldobler and Wilson, 1990; Retana et al., 2015).

Land use clearly influences the distribution of neotropical ant species in agricultural landscapes of Colombian Llanos (Sanabria et al., 2016). Different land uses have distinct vegetation types and influence ants through a variety of factors: microclimatic effects, resource availability, the abundance of predators and the intensity and frequency of disturbances (Gotelli and Ellison, 2002; Schilman et al., 2007). Soil properties also represent a key component of the ant environment and can have marked impacts on abundance and distribution those insects (de Bruyn and Conacher, 1990; Sanabria et al., 2016). It has been demonstrated that microclimatic conditions, such as soil moisture or temperature, may also affect ant distributions at various spatio-temporal scales (Jacquemin et al., 2012). For example, niche partitioning between ant species can be based on temperature preferences for their brood (Mezger and Pfeiffer, 2011; Mezger and Pfeiffer, 2011), while soil moisture can influence foraging activity, food abundance, suitability of nest sites, and predation by other ants (Levings, 1983).

Several studies have pointed out that ant species have specific morphological traits that are correlated with environmental characteristics in which they live, which can be explained by the ecology or behavior of the species (Kaspari, 1993; Schilman et al., 2007; Wong et al., 2019). For example, leg length has been shown to be negatively correlated with vegetation cover and could allow species to forage for food in the upper part of the litter to discover food resources more quickly (Wiescher et al., 2012). Weber's length has been found to be associated with habitat complexity, and scape length and ocular index to associate with mobility (Gibb et al., 2013; Yates et al., 2014). Some studies have demonstrated strong relationships between ant morphological traits (i.e. pilosity, presence of spines, leg length) and habitat complexity and disturbance (Bihn et al., 2010; Chown and Gaston, 2010; Ribera et al., 2001; Silva and Brandão, 2010; Yates et al., 2014). However, the relationship between a set of traits and a set of environmental characteristics has been rarely tested for neotropical ants. Ultimately, because ants should be adapted to the habitat where they preferentially occur, ants found in different land uses and types of soil should exhibit particular morphological characteristics (Costa-Milanez et al., 2017; Salas-Lopez et al., 2018; Linksvayer and Janssen, 2009). In this study, we expect that field management expressed as soil characteristics and

landscape scale-simplification expressed as land use, are both filtering some morphological traits in soil ants. Thus, morphological traits as pigmentation, small size, etc., are linked with a higher adaptability to extreme conditions, perturbation and should be more frequent in less complex land uses.

2. Materials and methods

2.1. Study area

Fieldwork was carried out in three municipalities: Puerto López (PL), Puerto Gaitán (PG) and Carimagua (CAR), in the eastern plains of Colombia (between 3°55'21"N–71°01'43"W and 4°38'07"N–72°53'55"W), between June and August 2011. The Llanos region extends to the northeast from the Meta department to the Venezuelan border and is bounded to the northwest by the Andean Eastern Cordillera. At roughly 200 m in elevation, the region has a humid tropical climate, with an average annual temperature of 26 °C, rainfall totaling 2500 mm per year and a marked dry season between December and March (Decaëns et al., 2001; Sanabria et al., 2014).

2.2. Sampling scheme

Five representative land uses were sampled in the region: 1. annual crops (including rice, maize and soybeans (AC), 2. improved pastures (*Brachiaria* spp. (IP) 3. oil palm plantations (*Elaeis guineensis* (OP), 4. rubber plantations (*Hevea brasiliensis* (R), and 5. semi-natural savannas (S) (See Appendix A, [supplementary material](#)). Although it was not possible to get precise information on the age and history of the cultivated plots, some general information could be collected on land uses. The original savanna has been disturbed for a long time with a clear management intensity gradient from Carimagua, where best-preserved savannas with rather dense tree cover are found, to Puerto Lopez where nearly all of the trees have been eliminated and grazing pressure is high. Improved pastures are rather heterogeneous, since the oldest ones may have been established 10–15 yrs. before sampling and in many cases are degraded with relatively high densities of weeds and compacted soils. Annual crops were implemented relatively recently since cropping is usually maintained for only 2–4 yrs. before perennial tree crops or improved pastures were installed. Rubber and oil palm plantations had been installed 3–10 yrs. prior to sampling in all cases. These systems are typically installed in fields following annual crops, while some rubber plantation plots, mainly in Carimagua were directly converted from savannas (Lavelle et al., 2014).

For each one of the five land uses, fifteen replicates were taken (75 fields were sampled in total). In each sampled field, one transect of three sampling points was implemented, leading to a total of 225 sampling points. At each sampling point, a modified Tropical Soil Biology and Fertility-TSBF protocol (Anderson and Ingram, 1994) was used to collect soil macrofauna. Each sampling point consisted in the excavation of a central monolith (25 × 25 cm × 20 cm deep) and two adjacent monoliths (25 cm × 25 cm × 10 cm deep) located 10 m to the North and South of each central monolith leading to a total of 675 fauna samples (225 sampling points × 3 monoliths). All the macrofauna from the litter and soil of each monolith was hand-sorted. Standing plant biomass was cut 2–3 cm above the soil surface, and removed prior to sampling (Sanabria et al., 2014; Sanabria et al., 2016).

2.3. Ant identification

At each sampling point, ants were collected along with other groups of soil macrofauna (only ant data was use here). In the laboratory, ants were separate from other macrofauna taxa and were preserve in 96 % Ethanol. Identification of ants to the genus level was made following keys by Bolton (1994), Palacio and Fernández (2003), Lozano-Zambrano et al., 2008 (keys therein). When possible, species were identified using a variety of sources including AntWeb (2016; and references

therein), Longino's ants of Costa Rica (2004), and Pheidole working group (Longino, 2013). Additionally, some species were compared with voucher specimens at Museo de Entomología de la Universidad del Valle (MEUV). A reference collection of material from this study was deposited in the MEUV.

In total, 92 ant species belonging to 35 genera and 9 subfamilies were identified, 70.3 % to the species level and the remaining 29.7 % to the morphospecies level (28). However, only soil-dwelling ant species were taken into account in analyses: a total of 43 ant species belonging to 22 genera (see Appendix B, [supplementary material](#) for the complete list of species).

2.4. Soil characteristics

A total of eleven soil physical properties were used (Lavelle et al., 2014): volumetric (VM) and gravimetric moisture (GM) content, microporosity (<0.03 µm; MIC), mesoporosity (0.03–3 µm; MES) and macroporosity (>3 µm; MAC), available water storage capacity (AWC), bulk density (BD), resistance to vertical penetration (POR), sand (Sa), and silt (Si) contents. Sixteen soil chemical properties were measured including total soil C and N content, cation exchange capacity (CEC), Al saturation (AIS), macro and micronutrient content (Ca, K, Mg, P Bray II (PBr), Al, B, Fe, Mn, Cu and Zn) (Table 1). All soil chemical measurements were conducted on soil excavated from the 0–20 cm layer, after sorting out macrofauna, while soil physical measurements were conducted using soil collected within metal rings removed from the vertical walls of the central monolith.

2.5. Trait description

Seven morphometric traits were described in the ants, including six measurements, an index, and a cuticle-associated trait (see Table 2 for full description of traits). The morphological measurements were taken using an ocular micrometer attached to a microscopy stereoscope (Nikon SMZ 500). Each of those traits was measured on five randomly selected workers of each species (Silva and Brandão, 2010; Yates et al., 2014; Gibb et al., 2015; Wong et al., 2019, among other authors) In the cases of morphological dimorphism (*i.e.* *Pheidole*) or polymorphism only minor workers were measured. Pigmentation (P) was coded with 0 for

Table 1

Physical-chemical soil parameters (see Lavelle et al. 2014 for more details) evaluated from soils collected in the Llanos Region of Colombia in 2011.

	Variables	Names	Units
Chemical	pH	Hydrogen potential	–
	N	Nitrogen Total	g kg ⁻¹
	C	Carbon Total	g kg ⁻¹
	PBr	Available Phosphorus Total	mg kg ⁻¹
	K	Potassium Total	mg kg ⁻¹
	Ca	Calcium Total	mg kg ⁻¹
	Mg	Magnesium Total	mg kg ⁻¹
	Al	Aluminum Total	mg kg ⁻¹
	CEC	Cation Exchange Capacity	cmol kg ⁻¹
	SAI	Aluminum Saturation	%
	S	Sulfur Total	mg kg ⁻¹
	B	Boron Total	mg kg ⁻¹
	Fe	Iron Total	mg kg ⁻¹
	Mn	Manganese Total	mg kg ⁻¹
	Cu	Copper Total	mg kg ⁻¹
	Zn	Zinc Total	mg kg ⁻¹
Physical	SM	Soil Moisture	g 100 g ⁻¹
	VM	Volumetric Moisture	cm 100 cm ⁻¹
	BD	Bulk density	g cm ⁻³
	AWC	Available Water Capacity	%
	MAC	Macropores (>3µm)	%
	MES	Mesopores (0.03–3 µm)	%
	MIC	Micropores (<0.03 µm)	%
	Sa	Sand,	%
	Si	Silt	%

Table 2

Morphological traits, abbreviations given and measures taken for soil-dwelling ant communities collected in the Llanos Region of Colombia in 2011. All lengths were measured in five minor workers and in those polymorphic species; we attempt to select randomly small, medium, and large workers.

Trait name	Code.	Measure	Trait functional significance
Weber's length	WL	Viewing mesosoma in lateral profile, distance from approximate inflection point, where downward sloping pronotum curves into anteriorly projecting neck, to posteroventral propodeal lobes	Indicative of worker body size (Weber, 1938), correlates with metabolic function and habitat complexity.
Head width	HW ^a	Maximum width of head in face view, including eyes if they project beyond the sides of the head	Size of gaps through which worker can pass (Sarty et al. 2006); mandibular musculature.
Scape length	SL ^a	Length of scape shaft from apex to basal flange, not including basal condyle and neck	Mechanical and chemoreception. Sensory abilities, longer scapes facilitate following of pheromone trails (Weiser and Kaspari, 2006).
Eye length	EL ^a	Measured along maximum diameter	Eye size indicates feeding behavior, predatory ants have smaller eyes, and activity times (Weiser and Kaspari, 2006).
Head length	HL ^b	Perpendicular distance from line tangent to rearmost points of vertex margin to line tangent to anterior most projections of clypeus, in full face view	May be indicative of diet; longer length may indicate herbivory (Gibb and Cunningham 2011, Silva and Brandão, 2010).
Cephalic index	CI	100*HW/HL	Frequently used as index of overall size and to construct ant community morphospace (Weiser and Kaspari, 2006)
Pigmentation	P	Presence or absence of pigmentation in workers	More pigmented species, have higher ability to withstand sunlight (Yates et al. 2014).

^a : As many size related characteristics are correlated, in the statistical analysis these features were considered as residuals based on the regression with Weber's length.

^b : Because HL is used in the cephalic index computations, we don't included it in the statistical analysis.

absence of pigmentation (white or very light yellow) and 1 for pigmented species (black, red, brown, etc.). All these morphological traits have been used previously for ants and the literature provides insight on the ecological significance of most of them and their links with the occupation of a heterogeneous agricultural landscape (Table 2).

2.6. Data analysis

Abundance data was converted into species occurrence tables (number of monoliths per field in which the species occurred). This is a common procedure for ants, due to the social nature of these insects allowing a single sample to contain an extremely high abundance of a rare species (Hölldobler and Wilson, 1990; Longino et al., 2010). This procedure provides consistent information on species presence and relative abundance inside the community. However, only species that occurred in more than five samples were included in the analysis. The morphological trait values of HW, HL, SL and EL were log-transformed to reduce the effect of extreme values and regressed against log_e(WL). Other authors when analyzing morphological traits in order to reduce

correction between body measures and body size widely use this procedure. We used the residuals of these regressions as traits, since they are independent of body size (Gibb et al., 2015; Martello et al., 2018). HL was used in the Cephalic index computation, so we did not include it in the final statistical analysis.

To describe the relationships between traits and environmental variables we performed a RLQ analyzing the link between table R (environmental variables) and table Q (species traits) through the table L (abundance-based species distribution). The RLQ analysis (see Dolédec et al., 1996) consisted of analyzing the joint structure of these three tables in order to decompose the eigenvalue of the cross-matrix and provides the common ordination axes onto which traits and environmental variables are projected. We used three data tables for the RLQ: the environmental characteristic table (R for physical and chemical parameters and land use types), the species table (L for species occurrence) and the morphological trait table (Q). First, each table was separately analyzed by specific multivariate analysis, which allowed the determination of the proportion of the total variance of each table represented in the RLQ. The species table (table L) was analyzed by correspondence analysis. Principal component analysis (PCA) was applied to quantitative morphometric traits + Pigmentation (table Q). A Hill-Smith ordination was applied to environmental site characteristics (table R), as this table included continuous (soil) variables together with land use. The significance of the relationship between the environmental attributes and morphological traits (Q) was tested using random permutations (Montecarlo permutation: $N = 9999$ times). Here values of sites and traits were permuted (i.e., permutes entire rows of tables R and Q; Dray and Legendre, 2008; Ter Braak et al., 2012). Finally, a Ward's hierarchical classification based on Euclidian distance between species along the first two RLQ axes allowed defining response groups of ant species. Each of them was further described by its trait distribution. The difference between species response groups was calculated using type II sums of squares for unbalanced in a linear model. Effects were compared using multiple comparisons of means (Tukey's Honestly Significant Difference).

All analyses were conducted using the ADE-4 (Thioulouse et al., 1997) and the car (Fox and Weisberg, 2011) packages in the R environment software, version 3.1.1 (R Core Team, 2017).

3. Results

3.1. Joint analysis of traits, environmental variables and ant community

The RLQ is significant ($P = 0.023$). The first two axes of the RLQ analysis extracts 83.89 % of the total variance (67.74 % and 16.15 % respectively). The proportion of variance attributed to each RLQ axis and the proportion of variance that they represent from the multivariate analyses done on environment characteristics of sites (Hill-Smith ordination), quantitative morphological traits (principal component analysis) and species distribution (correspondence analysis) are shown in Table 3.

The first axis of the RLQ accounts for 70 % of the eigenvalue of the first axis of the Hill-Smith ordination performed on environmental characteristics and represents 73 % of the variability of the PCA ordination performed on the morphological traits table. This is evidence of a good representation of the environmental characteristics and the set of morphological traits on the first RLQ axis. When considering the two first axes of the RLQ, the representation of environmental characteristics and morphological traits is still very good, as they account for 66% of the eigenvalue of the first two axes of the Hill-Smith ordination on environmental characteristics and for 86% of the variability of the first two axes of PCA ordination done on the morphological traits. However, the strength of the relationship between environmental characteristics and morphological traits is relatively low (correlation between the two new sets of factorial scores projected onto the RLQ axes = 0.26 on the first RLQ axis and 0.19 on the second RLQ axis). The first RLQ axis represents

Table 3

Statistical results from RLQ Analysis. Total inertia: 0.982. *Inertia %*: percentage of total variance accounted for by each RLQ axis. *Covariance*: covariance between the two new sets of factorial scores projected onto the first two RLQ axes (square root of eigenvalue). *Correlation*: correlation between the two new sets of factorial scores projected onto the first two RLQ axes.

Eigenvalues decomposition	Eigenvalues	Inertia %	Covariance
RLQ axis 1	0.62	67.74	0.79
RLQ axis 2	0.14	16.15	0.38
Inertia & coinertia R	Inertia	max	ratio
Axis 1	6.34	9.05	0.70
Axes 1 and 2	8.85	13.33	0.66
Inertia & coinertia Q	Inertia	max	Ratio
Axis 1	1.44	1.96	0.73
Axes 1 and 2	3.07	3.57	0.86
Correlation L	Correlation	max	Ratio
Axis 1	0.26	0.81	0.32
Axes 1 and 2	0.19	0.78	0.24

a major co-structure between the three tables R, L and Q. Fig. 1 shows the projection of axes for each separate analysis (i.e. the Hill-Smith performed on environmental characteristics, R1 and R2, and the PCA performed on morphological traits, Q1, Q2 and Q3, on the first two RLQ ordination axes).

The results of the RLQ analysis are best summarized by representing the scores of the environment, species and trait variables on the RLQ axes (Fig. 2). The first axis of the RLQ (RLQ1; Fig. 2a) is positively associated with rubber (LU.R), oil palm plantations (LU.OP), Available Water Capacity (AWC), Mesoporosity (MES), pH and Sand (Sa). This axis is negatively associated with improved pasture (LU.IP), savanna (LU.S), microporosity (MIC), cation exchange capacity (CEC), copper total (Cu) and sulfur total (S). Considering the traits, the first axis of the RLQ1 is positively associated with Weber's length (WL) and negatively associated with eye length (EL) (Fig. 2c). The RLQ1 axis opposes species with larger body size from those with larger eyes. Meanwhile, annual crop was the factor that determines the second axis of the RLQ (positive side of the RLQ2). This axis is positively associated with aluminum total (Al), magnesium total (Mg), manganese total (Mn) and macroporosity (MAC). In addition, it is possible to observe that improved pastures (LU.IP) and savannas (LU.S), which are the land uses with high microporosity and high CEC are placed in opposite position to annual crops (LU.AC) which correspond to the land use with the high Mn, Mg and Al contents. This axis was also positively associated with more pigmented ants (P) and negatively associated with ants having larger antennae and heads (CI and HW) (Fig. 2). The RLQ2 axis represents a gradient of species distribution according to their pigmentation.

The distribution of land uses along the factorial plane of the RLQ (Appendix C in supplementary material) showed that rubber (R) and oil palm (OP) plantations were on the positive side, while annual crops (AC), improved pastures (IP) and savannas (S) were on the negative side of that axis. RLQ1 separated on the positive side agroforestry plantation (i.e. land uses with trees such as rubber and oil palm plantations) that have soils capable of storing water, from grazing-based systems (improved pastures) and annual crops located on the negative side that have more fertile soils (based on presence of most macro and micro nutrients).

3.2. Classification of species based on environmental variables and species traits

Four species groups were defined based on the mean position of the species on the first two RLQ axes. Each group was represented on the RLQ factorial plan (Fig. 2b) and described through the distribution of morphological traits (Fig. 3) and it is important to notice that the description of the response groups is based on general tendencies, but particular species of a group might not follow the general pattern (see Appendix B, for further information of the species).

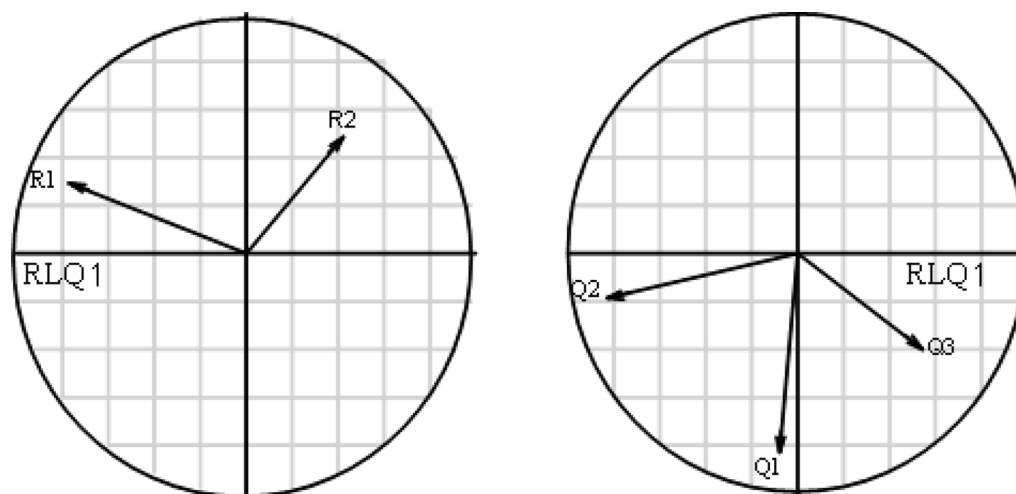


Fig. 1. Projection of the axes of the Hill-Smith ordinations done on R and the principal correspondence analysis done on Q, respectively on the first two RLQ joint ordination axes (RLQ1 and RLQ2). a) the two axes (R1 and R2 respectively) of the Hill-Smith on the environmental data and b) the first three axes (Qe1, Qe2 and Qe3, respectively) of the principal correspondence analysis on the morphological traits of ants collected in the Llanos Region of Colombia in 2011.

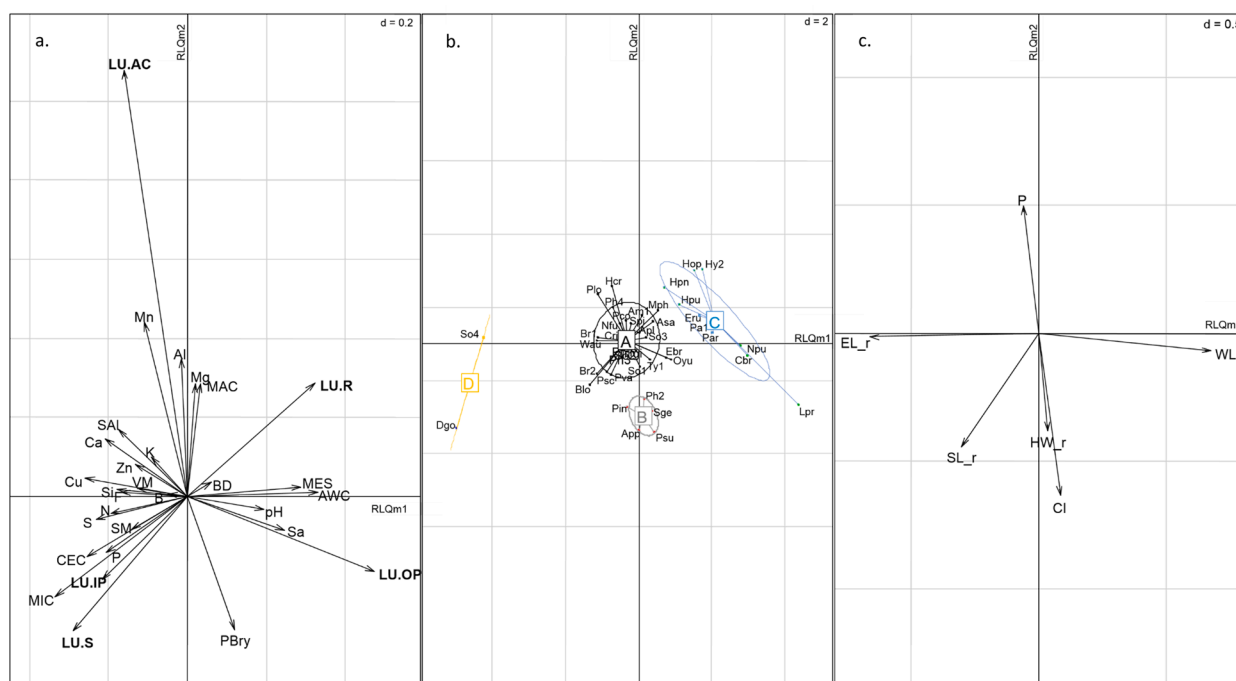


Fig. 2. Multiple representations of the RLQ ordination on the first two axes: a) environmental variables, b) mean position of species and species response groups, c) morphological traits (see Tables 1 and 2 for full names of variables and Appendix B for species names). Projected inertia: 67.74%, 16.15% for axes 1 to 2 respectively. The d value refers to the grill size.

Species response group A – This group is formed by 25 species (included *Acanthostichus sanchezorum*, *Brachymyrmex longicornis*, *Cyphomyrmex rimosus*, *Paratrechina longicornis*, *Pheidole vallifica*, *Nylanderia fulva*, *Solenopsis picea*, etc.), which represents 60.47% of the soil-dwelling ant species collected. It is not easy to indicate the characteristics that the species in this group have in common due to its position near the origin of the RLQ factorial plan. This group was however mainly comprised of small and medium size species (Fig. 3).

Species response group B – With 5 species (*Acropyga palaga*, *Solenopsis geminata*, *Pheidole* sp. 2, *Pheidole subarmata* and *Pheidole inversa*), this group is characterized by more proportionate heads (+/- as long as wide) and were mainly less pigmented species (Fig. 3).

Species response group C - This group comprises 10 species

(*Hypoponera opacior*, *Hypoponera punctatissima*, *Hypoponera creola*, *Hypoponera* sp. 2, *Pachycondyla* sp.1, *Ectatomma ruidum*, *Labidus praedator*, *Neivamyrmex punctaticeps*, *Centromyrmex brachycola*, *Rasopone arhuaca*). This group is mainly characterized by large and more pigmented species with narrow and smaller eyes (Fig. 3).

Species response group D - This group contains only two species (*Dorymyrmex goeldii* and *Solenopsis* sp. 4) that are small species with big eyes (Fig. 3).

The barycenter of species response group D is on the negative side of the first RLQ axis, while species response group C is on the positive side of this axis. In addition, species response group B is on the negative side of the second RLQ axis and the species response group A is close to the axis origin (Fig. 2b). In land uses dominated by grasses and with higher

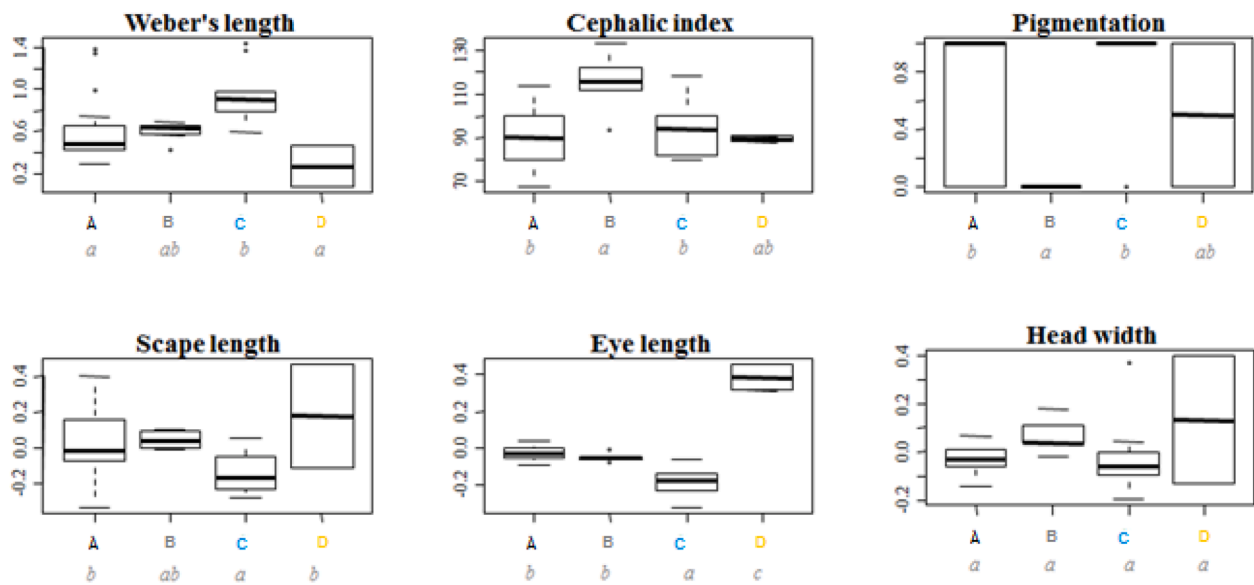


Fig. 3. Morphological traits distribution in response groups. Uppercase letters (A, B, C and D) correspond to the four species response groups. Lowercase letters (a, b) indicates the statistical differences among species response groups. (see Table 2 and Appendix B, for further information about traits and species).

chemical fertility (negative side of RLQ1), species response group D is dominated by more generalist species. Meanwhile, on the positive side of RLQ1 species response group C is associated to rubber plantations and is mainly composed by species categorized as hunter ants (*Hypoconer punctaticeps*, *Centromyrmex brachycola*, *Rasopone arhuaca*, *Hypoconer opacior*, etc.) and army ants (*Neivamyrmex punctaticeps* and *Labidus praedator*). In general, these species tend to be specialists with a carnivorous diet. Additionally, species group B contained species belonging to genera such as *Pheidole* and *Solenopsis* that commonly nest in disturbed soils and that were located between oil palm plantations and savannas on the RLQ. In summary, these results suggest that RLQ1 represented a gradient of species specialization according to the presence/absence of tree cover and soil properties (i.e. chemical fertility, water availability, pH, mesoporosity and soil litter).

4. Discussion

The RLQ analysis shows a strong gradient structuring both the environmental characteristics and the morphological species traits distribution. This gradient located along the X-axis is opposed on one side to agroforestry plantations (i.e. rubber and oil palm plantations. On the other side to pasture-based systems (i.e. sites with a significant grass component such as savanna and improved pastures), and it is possible to distinguish that all these systems are located away from annual crops (along the second RLQ axis). This study in the Llanos Orientales of Colombia supports that the morphological traits of ants are correlated both to land uses (Salas-Lopez et al., 2018; Martello et al., 2018; Wong et al., 2019) and to soil properties (Schmidt and Diehl, 2008; Wong et al., 2019).

4.1. The response of traits to land uses

Our results indicate that soil-dwelling ants with a more pigmented cuticle could be more frequently found in annual crops, although this land use is not clearly associated with a specific ant response group. This could be explained by the fact that annual crops have soils that are more exposed to sunlight and are the most disturbed of the study area (e.g. tillage and high fertilizer inputs; Sanabria et al., 2016). Such intensive agricultural practices lead to extremely disturbed conditions where few species can survive.

In agroforestry plantations, such as rubber plantations, ant

communities tend to include some larger species (group C) that can use both the epigeic and hypogaeic strata (Sanabria-Blandon and Chacon de Ulloa, 2011) and have a more specialized diet. It is known that rubber plantations host fewer species than natural systems such as forests (Fayle et al., 2010; Fitzherbert et al., 2008; Martello et al., 2018) and in some cases also fewer than oil palm plantations (Sanabria et al., 2014). However, these systems also host hunter and army ants which are considered as specialists (mainly predators) with particular requirements for microclimatic conditions (Kaspary and O'Donnell, 2003; Sanabria-Blandon and Chacon de Ulloa, 2011). The presence of such species is likely explained by the presence of a permanent tree cover with a complex vertical structure and a thick litter layer which are known to these species (Chadab and Rettenmeyer, 1975; Sanabria-Blandon and Chacon de Ulloa, 2011). At the same time, these agroforestry plantations, mainly oil palm plantations are monocultures that likely host abundant populations of pests (Andow, 1983; Ali et al., 2012), which could constitute a large food supply for these predator ants. In contrast, grazing-based systems, such as savanna and improved pastures, were related to ant response groups B and D. In general, the species of these groups are smaller, with variable coloration, larger heads, larger eyes and larger antennae. All these traits are all related to the ability to navigate and sense the environment, and they are found in more mobile ants that are common in open and disturbed habitats (Yates et al., 2014; AntWeb, 2018, Sanabria Pers. Obs.) which are demanding from a practical point of view, possibly because these land uses are more complex and heterogeneous (Yates et al., 2018) than annual crops.

Based on our results, we can conclude that, when the response of ant community to land use is studied, a trait-based approach leads to a similar conclusion as a taxonomical approach, i.e. in neotropics, the community ants is constantly associated with the vegetation type (Philpott and Armbrrecht 2006; Sanabria and Ulloa-Chacon, 2011; Sanabria et al., 2016).

Two general mechanisms may explain our results. First, ants are biological control agents and the presence of a tree cover provides different microhabitats allowing the presence of a diverse arthropod community, mainly pests that may be an important food source for these ant species (Schmitz et al., 2000; Perfecto and Vandermeer, 2002; Philpott and Armbrrecht, 2006). Second, due to the recent land use intensification history of the Llanos and the high level of disturbance (Lavelle et al., 2016), rubber tree and oil palm plantations can share many species with natural ecosystems such as disturbed forests and

savannas (Sanabria et al., 2014). Thus, these agroforestry plantations could serve as refuges for some ant species and help the dispersal of these species between remaining fragments of natural ecosystems (Vandermeer and Carvajal, 2001; Martello et al., 2018).

4.2. Response of traits to soil properties

Our results corroborated that morphological traits give information on some aspects of the relationship between ants and their environment, as it has been reported by other authors (Schilman et al., 2007; Menke and Holway, 2006; Wiescher et al., 2012; Sanabria et al., 2016). We found that less compacted soils tend to host ants with smaller body sizes, which can be considered as a characteristic allowing opportunistic ants to easily colonize environments (Kaspary and O'Donnell, 2003; Linksvayer and Janssen, 2009). In highly disturbed sites, opportunistic and generalist ants are often dominant, presumably because these species can easily take advantage of changes in the availability of various resource types (Hoffmann and Andersen, 2003; Kaspary et al., 2003). This is congruent with previous studies that reports clear relationship between traits and macrohabitats, where traits significantly differed between habitat types (Yates et al., 2014; Hevia et al., 2017).

It is known that ants depend on soils characteristics for their engineering activities (Lavelle and Spain, 2001). For example, soil texture determines the ease with which ants can tunnel in the soil and construct chambers (Boulton et al., 2005). In this study, we found that such relations could lead to associations between soil features and morphological ant traits: larger ants are present in soils with a higher water storage capacity, higher mesoporosity and a higher sand content. These characteristics allow ants to move more easily within the soil and establish their colonies. Moreover, high microporosity and high CEC values found in our grazing-based systems (improved pastures and savanna) are mainly associated with species with larger antennae and bigger eyes. Gibb and Parr (2013) have reported that these traits are known to be associated with species that are mobile, adapted to disturbed conditions and have a good capacity to settle down in new environments. In our opinion, there is no clear mechanistic relation between these traits and these soil features. The interpretation of these results would be, therefore, that these traits are associated with land use, which of course is correlated with soil characteristics due to management (but see the first section of the discussion) (Sanabria et al., 2016; Martello et al., 2018).

Finally, we consider that in the future it would be useful to include ecological traits such as nesting site, polymorphism, colony size, dispersal ability, competitive ability or trophic position. All of them have previously shown to be relevant predictors of species sensitivity to fragmentation and land use (Silvestre et al., 2003; Henle et al., 2004; Schweiger et al., 2005; Didham et al., 2007; Retana et al., 2015). Furthermore, it would be interesting to include other morphological traits that can be linked to micro-habitat specialization: jaw size, leg size, pilosity, cuticle sculpturing, etc., (Arnan et al., 2013; Wiescher et al., 2015). Those traits have been reported to be related to key environmental characteristics such as cover complexity (i.e. forest), ground cover, surface temperature and plant species richness (Satry et al., 2006; Schofield et al., 2016). Third, it might be important to include other environmental features that had better describe ant habitat (i.e. percentage of bare ground, canopy cover, the depth and mass of leaf litter, soil and litter temperatures). These characteristics may be better linked to the ecology of ants and, therefore, could be more strongly associated with ant traits (Silvestre et al., 2003).

5. Conclusion

Agroforestry plantations are structurally less complex than natural forests, with homogeneous tree age, lower canopy, sparse undergrowth, and more frequent and stronger human disturbance, and they will never replace the role of natural systems. Nevertheless, due to its undeniable

presence in tropical landscapes, conservation efforts should focus on ways to enhance biodiversity in those plantations (Fitzherbert et al., 2008). It has indeed been shown that on neotropical agroforestry plantations management can be adapted to support a proportion of forest species. This can be accomplished maintaining high performance of the sites, high diversity, density and height of trees (Moguel and Toledo, 1999), improve the connectivity between fragments (Vandermeer and Carvajal, 2001), and may maintain metapopulation dynamics and long-term survival of forest species (Vandermeer and Carvajal, 2001; Perfecto and Vandermeer, 2002; Philpot and Armbrrecht, 2006).

Few studies have examined factors shaping the structure of ant assemblages at the landscape scale in the Colombian Llanos. As for many neotropical landscapes, the study of ant assemblages in this region can be problematic since many of the species that we encountered were new records and/or their ecology remains poorly understood. Nevertheless, some ant morphological traits can be used to analyze how ant species respond to land uses and land use change with distinct plant communities, vegetation cover and management intensity. Based on our data, we have been able to partially explain co-variation between ant morphological traits with land use and some soil characteristics. However, here we have only used morphological traits that are indirectly linked to the life-history strategies and ecological adaptations of ant species. In the future, using ecological traits could allow making important steps but this requires the documentation of ecological traits for ant species that have so far been poorly studied.

Overall, a trait-based approach helps to better understand ant ecology and better define the morphological traits that should be measured, as well as the different functional dimensions needed to describe the environments or niches of ant species (Arnan et al., 2014; Silva and Brandao 2014; Salas-Lopez et al. 2018). Our findings nevertheless suggest that the morphological traits we used in this study could reflect the ability of some ant species to establish and survive in a given environment. These morphological traits can be used to make predictions about ant species distribution, the impacts of management and may also be used as a complementary tool for the conservation and management of ant communities in complex agricultural landscapes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was funded in part by the Colombian Ministry of Agriculture. CS was funded by a doctoral scholarship (PDBCEX Conv. 568) from Ministerio de Ciencia, Tecnología e Innovación - COLCIENCIAS in Colombia. We are grateful to the farmers who allowed us to conduct research on their land and we appreciate the support from a number of researchers and technicians at CORPOICA – La Libertad who provided information and logistical support in field. We also thank the former Soils-LAC team of CIAT including Maria del Pilar Hurtado, Paula Chaparro, Sandra Loaiza, Cesar Botero, Carolina Quintero, Arvey Alvarez, and Edgar Rodriguez who helped with field and laboratory work. Thanks to Joshua Gibson and Rafael Achury for comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2022.115841>.

References

- Ali, A., Ahmad, F., Biondi, A., Wanf, Y., Desneux, N., 2012. Potential for using *Datura alba* leaf extracts against two major stored grain pests, the khapra beetle *Trogoderma*

- granarium and the rice weevil *Sitophilus oryzae*. J. Pest. Sci. 85 (3), 59–366. <https://doi.org/10.1007/s10340-012-0426-1>.
- Altieri, M.A., Nicholls, C.I., 2003. Soil fertility management and insect pests: Harmonizing soil and plant health in agroecosystems. Soil Till. Res. 72, 203–211. [https://doi.org/10.1016/S0167-1987\(03\)00089-8](https://doi.org/10.1016/S0167-1987(03)00089-8).
- Anderson, J.M., Ingram, J.S.I., 1994. Tropical Soil Biology and Fertility: A Handbook of methods. - CAB International. Soil Sci. 157 (4), 265.
- Andow, D., 1983. The extent of monoculture and its effects on insect pest populations with particular reference to wheat and cotton. Agric. Ecosyst. Environ. 11, 25–35. [https://doi.org/10.1016/0167-8809\(83\)90003-8](https://doi.org/10.1016/0167-8809(83)90003-8).
- AntWeb, 2016. www.antweb.org. (Accessed December 2016).
- Arnan, X., Cerdà, X., Anselm, R., Retana, J., 2013. Response of ant functional composition to fire. Ecogr. 36, 1182–1192. <https://doi.org/10.1111/j.1600-0587.2013.00155.x>.
- Bihn, J.H., Gebauer, R., Brandl, R., 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. Ecol. 91 (3), 782–792. <https://doi.org/10.1890/08-1276.1>.
- Bolton, B., 1994. Identification Guide to the Ant Genera of the World. Harvard University Press.
- Boulton, A., Davies, K.F., Ward, P.S., 2005. Species Richness, Abundance, and Composition of ground-dwelling ants in Northern California Grasslands: Role of Plants, Soil, and Grazing. Env. Ent. 34 (1), 96–104. <https://doi.org/10.1603/0046-225X.34.1.96>.
- Cammeraat, L.H., Willot, S.J., Compton, S.G., Incoll, L.D., 2002. The effects of ants' nest on the physical, chemical and hydrological properties of a rangeland soil in semi-arid Spain. Geoderma 105, 1–20. [https://doi.org/10.1016/S0016-7061\(01\)00085-4](https://doi.org/10.1016/S0016-7061(01)00085-4).
- Campbell, K.U., Crist, T.O., 2016. Species traits and environmental characteristics together regulate ant-associated biodiversity. Ecol. Evol. 6 (17), 6397–6408. <https://doi.org/10.1002/ece3.2276>.
- Carvalho, R.L., Andersen, A.N., Anjos, D.V., Pacheco, R., Chagas, L., Vasconcelos, H.L., 2020. Understanding what bioindicators are actually indicating: Linking disturbance responses to ecological traits of dung beetles and ants. Ecol. Ind. 108, 105764. <https://doi.org/10.1016/j.ecolind.2019.105764>.
- Chadab, R., Rettenmeyer, C.W., 1975. Mass recruitment by army ants. Science 188 (4193), 1124–1125.
- Chown, S.L., Gaston, K.J., 2010. Body size variation in insects: A macroecological perspective. Biol. Rev. 85, 139–169. <https://doi.org/10.1111/j.1469-185X.2009.00097.x>.
- Costa-Milanez, C.B., Majer, J.D., Amorim Castro, P.T., Ribeiro, S.P., 2017. Influence of soil granulometry on average body size in soil ant assemblages: implications for bioindication. Pecon. 15, 102–108. <https://doi.org/10.1016/j.pecon.2017.03.007>.
- De Bello, F., Lavorel, S., Diaz, S., Harrington, R., Cornelisse, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., da Silva, P.M., Potts, S.G., Sandin, L., Sousa, J.P., Stoekey, J., Wadell, D.A., Harrison, P.A., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. Biodivers. Conserv. 19, 2873–2893. <https://doi.org/10.1007/s10531-010-9850-9>.
- De Bruyn, L.L.A., Conacher, A.J., 1990. The role of termites and ants in soil modification - a review. Soil Res. 28, 55–93. <https://doi.org/10.1071/SR9900055>.
- Decaens, T., Lavelle, P., Jimenez, J.J., Escobar, G., Rippstein, G., Schneidmadl, J., Sanz, J.I., Hoyos, P., Thomas, R.J., 2001. Impacto del uso de la tierra en la macrofauna del suelo de los Llanos Orientales de Colombia. In: Jimenez, J., Jimenez, J., Thomas, R., Thomas, R. (Eds.), El Arado Natural: Las Comunidades de Macroinvertebrados del Suelo en las Sabanas Neotropicales de Colombia. Pub. CIAT, Cali, Colombia, pp. 21–45.
- Decaens, T., Martins, M.B., Feijoo, A., Oszwald, J., Dolédec, S., Mathieu, J., Arnaud de Sartre, X., Bonilla, D., Brown, G.G., Cuellar Criollo, Y.A., Dubs, F., Furtado, I.S., Gond, V., Gordillo, E., Le Clech, S., Marichal, R., Mitja, D., de Souza, I.M., Praxedes, C., Rougerie, R., Ruiz, D.H., Otero, J.T., Sanabria, C., Velasquez, A., Zarate, L.E.M., Lavelle, P., 2018. Biodiversity loss along a gradient of deforestation in Amazonian agricultural landscapes. Biol. Conserv. 32, 1380–1391. <https://doi.org/10.1111/cobi.13206>.
- Del Toro, I., Towle, K., Morrison, D.N., Pelini, S.L., 2013. Community structure, Ecological and Behavioral Traits of Ants (Hymenoptera: Formicidae) in Massachusetts Open and Forested Habitats. Northeast Nat. 20, 1–12. <https://doi.org/10.1656/045.020.0108>.
- Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T., Ewers, R.M., 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol. Evol. 22, 489–496. <https://doi.org/10.1016/j.tree.2007.07.001>.
- Dolédec, S., Chessel, D., ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three - table ordination method. Environ. Ecol. Stat. 3, 143–166. <https://doi.org/10.1007/BF02427859>.
- Dray, S., Legendre, P., 2008. Testing the Species Traits - Environment relationships: The Fourth-Corner problem revisited. Ecology 89, 3400–3412. <https://doi.org/10.1890/08-0349.1>.
- Dayle, T.M., Turner, E.C., Snaddon, J.L., Chey, V.K., Chung, A.Y.C., Eggleton, P., Foster, W., 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf - litter. Appl Ecol. 11, 337–345. <https://doi.org/10.1016/j.baee.2009.12.009>.
- Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: Ten guiding principles for commodity production landscapes. Front. Ecol. Environ. 4, 80–86. [https://doi.org/10.1890/1549295\(2006\)004\[0080:BEFART\]2.0.CO;2](https://doi.org/10.1890/1549295(2006)004[0080:BEFART]2.0.CO;2).
- Fitzherbert, E., Struebig, M., Morel, A., Danielsen, F., Bruhl, C., Donald, P., Phalan, B., 2008. How will oil palm expansion affect biodiversity? Trends Ecol. Evol. 23 (10), 538–545.
- Folgarait, P.J., 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers. Conserv. 7 (9), 1221–1244. <https://doi.org/10.1023/A:1008891901953>.
- Fox, J., Weisberg, S., 2011. An R companion to applied regression, Second Ed. Sage, Thousand Oaks, CA.
- Gibb, H., Parr, C.L., Fenton, B., 2013. Does Structural Complexity Determine the Morphology of Assemblages? An Experimental Test on Three Continents. PLoS ONE 8 (5), e64005.
- Gibb, H., Stoklosa, J., Warton, D.I., Brown, A.M., Andrew, N.R., Cunningham, S.A., 2015. Does morphology predict trophic position and habitat use of ant species and assemblages? Oecologia 177 (2), 519–531. <https://doi.org/10.1007/s00442-014-3101-9>.
- Gotelli, N.J., Ellison, A.M., 2002. Assembly rules for New England ant assemblages. OikSAA. 3, 591–599. <https://doi.org/10.1034/j.1600-0706.2002.11734.x>.
- Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., de Bello, F., Gonzales, J.A., 2017. Trait-based approaches to analyze links between the drivers if change and ecosystem services: Synthesizing existing evidence and future challenges. Ecol. Evol. 7 (3), 831–844. <https://doi.org/10.1002/ece3.2692>.
- Hölldobler, B., Wilson, E.O., 1990. The Ants. Harvard University Press/Springer.
- Hubert, B., Rosegrant, M., van Boekel, M.A.J.S., Ortiz, R.A., 2010. The future of food: scenarios for 2050. Crop Sci. 50, S33–S50. <https://doi.org/10.2135/cropsci2009.09.0530>.
- Jacquemin, J., Drouet, T., Delsinne, T., Roisin, Y., Laponce, M., 2012. Soil properties only weakly affect subterranean ant distribution at small spatial scales. App Soil Ecol 62, 163–169. <https://doi.org/10.1016/j.apsoil.2012.08.008>.
- Kaspary, M., 1993. Body size and microclimate use in Neotropical granivorous ant. Oecologia 96, 500–507. <https://doi.org/10.1007/BF00320507>.
- Kaspary, M., O'Donnell, J., 2003. High rates of army ant raids in the Neotropics and implications for ant colony and community structure. Evol. Ecol. Res. 5, 933–939.
- Kaspary, M., Yuan, M., Alonso, L., 2003. Spatial grain and the causes of regional diversity gradients in ants. Am. Nat. 161, 459–477. <https://doi.org/10.1086/367906>.
- Lavelle, P., Spain, A.V. (Eds.), 2001. Soil Ecology. Springer Netherlands, Dordrecht.
- Lavelle, P., Rodríguez, N., Arguello, O., Bernal, J., Botero, C., Chaparro, P., Gómez, Y., Gutiérrez, A., Hurtado, M.P., Loaiza, S., Pullido, S.X., Rodríguez, A., Velasquez, E., Velásquez, E., Fonte, S.J., 2014. Soil ecosystem services and land use in the rapidly changing Orinoco River Basin of Colombia. Agric. Ecosyst. Environ. 185, 106–117. <https://doi.org/10.1016/j.agee.2013.12.020>.
- Lavelle, P., Dolédec, S., de Sartre, X.A., Decaens, T., Gond, V., Grimaldi, M., Oszwald, J., Hubert, B., Ramirez, B., Veiga, I., de Souza, S., de Assis, W.S., Michelotti, F., Martins, M., Feijoo, A., Bommel, P., Castañeda, E., Chacon, P., Desjardins, T., Dubs, F., Gordillo, E., Guevara, E., Fonte, S., del Pilar Hurtado, M., Lena, P., Lima, T., Marichal, R., Mitja, D., Miranda, I., Otero, T., Praxedes, C., Pocard, R., de Robert, P., Rodríguez, G., Sanabria, C., Tselouki, S., Velasquez, A., Velasquez, E., Velasquez, J., 2016. Unsustainable landscapes of deforested Amazonia: An analysis of the relationships among landscapes and the social, economic and environmental profiles of farms at different ages following deforestation. Glob Environ Change. 40, 137–155.
- Levings, S.C., 1983. Seasonal, annual, and among - site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. Ecol. Monog. 53, 435–455. <https://doi.org/10.2307/1942644>.
- Linksvayer, T.A., Janssen, M.A., 2009. Traits underlying the capacity of ant colonies to adapt to disturbance and stress regimes. Syst. Res. ans. Behav. Sci. 26, 315–329. <https://doi.org/10.1002/sres.928>.
- Longino, J. 2013. Pheidole Working Group. <http://academic.evergreen.edu/projects/ants/pheidole>. (Accessed May 2013).
- Lozano - Zambrano, F., Fernández, F., Jiménez, E. and Arias, T., 2008. Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia. - Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.
- Marta, S., Brunetti, M., Manenti, R., Provenza, A., Ficitola, G.F., 2021. Climate and land-use changes drive biodiversity turnover in arthropod assemblages over 150 years. Nat. Ecol. Evol. 5 (9), 1291–1300.
- Martello, F., de Bello, F., Morini, M., Silva, R., de Souza-Campana, Ribeiro, M.C., Carmona, C.P., 2018. Homogenization and impoverishment of taxonomic and functional diversity of ants in Eucalyptus plantation. Sci. Rep. 8, 3266. <https://doi.org/10.1038/s41598-02823-1>.
- Menke, S.B., Holway, D.A., 2006. Abiotic factors control invasion by Argentine ants at the community scale. J. Anim. Ecol. 75, 368–376. <https://doi.org/10.1111/j.1365-2656.2006.01056.x>.
- Mezger, D., Pfeiffer, M., 2011. Partitioning the impact of abiotic factors and spatial patterns on species richness and community structure of ground ant assemblages in four Bornean rainforests. Ecography 34, 39–48. <https://doi.org/10.1111/j.1600-0587.2010.06538.x>.
- Moretti, M., de Bello, F., Ibanez, S., Fontana, S., Pezzatti, G.B., Dziock, F., Rixen, C., Lavorel, S., Pakeman, R., 2013. Linking traits between plants and invertebrate herbivores to track functional effects of land - use changes. J. Veg. Sci. 24 (5), 949–962.
- Palacio, E.E., Fernández, F., 2003. Clave para las subfamilias y géneros. In: Fernandez, F. (Eds.), Introducción a las hormigas de la región Neotropical. First ed. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt., pp. 233 - 260.
- Perfecto, I., Vandermeer, J., 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. Biol. Conserv. 16 (1), 174–182. <https://doi.org/10.1046/j.1523-1739.2002.99536.x>.
- Pey, B., Nahmani, J., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., Decaens, T., Deharveng, L., Dubs, F., Joimel, S., Briard, C., Grumiaux, F., Laporte, M.-A., Pasquet, A., Pelosi, C., Pernin, C., Ponge, J.-F., Salmon, S., Santorufu, L., Hedde, M.,

2014. Current use of and future needs for soil invertebrate functional traits in community ecology. *Appl. Ecol.* 15 (3), 194–206.
- Philpott, S.M., Armbricht, L., 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecol. Entomol.* 31, 369–377. <https://doi.org/10.1111/j.1365-2311.2006.00793.x>.
- R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Retana, J., Arnan, X., Cerdá, X., 2015. A multidimensional functional trait analysis of resource exploitation in European ants A multidimensional functional trait analysis of resource exploitation in European ants. *Ecology* 96, 2781–2793. <https://doi.org/10.1890/14-2326.1>.
- Ribera, I., Doledec, S., Downie, I.S., Foster, G., 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology* 82, 1112–1129. [https://doi.org/10.1890/0012-9658\(2001\)082\[1112:EOLDAS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1112:EOLDAS]2.0.CO;2).
- Romero-Ruiz, M.H., Flantua, S.G.A., Tansey, K., Berrio, J.C., 2012. Landscape transformations in savannas of northern South America: Land use/cover changes since 1987 in the Llanos Orientales of Colombia. *Appl. Geogr.* 32, 766–776. <https://doi.org/10.1016/j.apgeog.2011.08.010>.
- Salas-Lopez, A., Violle, C., Mallia, L., Orivel, J., Didham, R., 2018. Land-use change effects on the taxonomic and morphological trait composition of ant communities in French Guiana. *Insect Conserv. Divers.* 11 (2), 162–173.
- Sanabria, C., Dubs, F., Lavelle, P., Fonte, S.J., Barot, S., 2016. Influence of regions, land uses and soil properties on termite and ant communities in agricultural landscapes of the Colombian Llanos. *Eur. J. Soil Biol.* 74, 81–92. <https://doi.org/10.1016/j.ejsobi.2016.03.008>.
- Sanabria, C., Lavelle, P., Fonte, S.J., 2014. Ants as indicators of soil - based ecosystem services in agroecosystems of the Colombian Llanos. *Appl. Soil Ecol.* 84, 24–30. <https://doi.org/10.1016/j.apsoil.2014.07.001>.
- Sanabria-Blandón, M.C., Chacón de Ulloa, P., 2011. Hormigas cazadoras en sistemas productivos del piedemonte amazónico colombiano: diversidad y especies indicadoras. *Acta Amazon.* 41 (4), 503–512. <https://doi.org/10.1590/S0044-59672011000400008>.
- Sarty, M., Abbott, K.L., Lester, P.J., 2006. Habitat complexity facilitates coexistence in a tropical ant community. *Oecologia* 149, 465–473. <https://doi.org/10.1007/s00442-006-0453-9>.
- Schilman, P.E., Lighton, J.R.B., Holway, D.A., 2007. Water balance in the Argentine ant (*Linepithema humile*) compared with five common native ant species from southern California. *Physiol. Entomol.* 37, 1–7. <https://doi.org/10.1111/j.1365-3032.2006.00533.x>.
- Schmidt, F., Diehl, E., 2008. What is the effect of soil use on ant communities? *Neotrop. Entomol.* 37, 381–388. <https://doi.org/10.1111/j.1365-3032.2006.00533.x>.
- Schmitz, O.J., Hamback, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.* 155, 141–153. <https://doi.org/10.1038/s41467-021-25086-5>.
- Schofield, S., Bishop, T.R., Parr, C.L., 2016. Morphological characteristics of ant assemblages (Hymenoptera: Formicidae) differ among contrasting biomes. *Myrmecol. News.* 23, 129–137. <https://doi.org/10.25849/myrmecol.news.023:129>.
- Schweiger, O., Maelfait, J.P., Van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M., Bugter, R., 2005. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *J. Appl. Ecol.* 42 (6), 1129–1139.
- Silva, R.R., Brandão, C.R., 2010. Morphological patterns and community organization in leaf-litter ant assemblages. *Ecol. Monog.* 80 (1), 107–124. <https://doi.org/10.1890/08-1298.1>.
- Silvestre, R., Brandão, C.R.F., Silva, R.R., 2003. Gremios funcionales de hormigas: el caso de los gremios del Cerrado. In: Fernández, F. (Ed.), *Introducción a las hormigas de la región Neotropical*, Fundación Humboldt. Bogotá, Colombia, pp. 113–148.
- Ter Braak, C.J., Cormont, A., Dray, S., 2012. Improved testing of species traits - environment relationships in the fourth-corner problem. *Ecology* 93, 1525–1526. <https://doi.org/10.1890/12-0126.1>.
- Thioulouse, J., Chessel, D., Doledec, S., Olivier, J.M., 1997. ADE - 4 a Multivariate Analysis and Graphical Display Software. *Stat. Comput.* 7, 75–83. <https://doi.org/10.1023/A:1018513530268>.
- Vandermeer, J., Carvajal, R., 2001. Metapopulation Dynamics and the Quality of the Matrix. *Am. Nat.* 158 (3), 211–220. <https://doi.org/10.1086/321318>.
- Vandewalle, M., de Bello, F., Berg, M.P., Bolger, T., Dolédec, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P.A., Lavorel, S., da Silva, P.M., Moretti, M., Niemelä, J., Santos, P., Sattler, T., Sousa, J.P., Sykes, M.T., Vanbergen, A.J., Woodcock, B.A., 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodivers. Conserv.* 19 (10), 2921–2947.
- Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., Poff, N.L., 2010. A structured and dynamic framework to advance trait - based theory and prediction in ecology. *Ecol. Lett.* 13, 267–283. <https://doi.org/10.1111/j.1461-0248.2010.01444.x>.
- Wiescher, P.T., Pearce Duvet, J.M.C., Feener, D.H., 2012. Assembling an ant community: Species functional traits reflect environmental filtering. *Oecologia* 169 (4), 1063–1074. <https://doi.org/10.1007/s00442-012-2262-7>.
- Weiser, M.D., Kaspari, M., 2006. Ecological morphospace of new world ants. *Ecol. Entomol.* 31, 131–142. <https://doi.org/10.1111/j.0307-6946.2006.00759.x>.
- Wong, M.K.L., Guénard, B., Lewis, T.O., 2019. Trait-based ecology of terrestrial arthropods. *Biol. Rev.* 94, 999–1022. <https://doi.org/10.1111/br.12488>.
- Yates, M.L., Andrew, N.R., Binns, M., Gibb, H., 2014. Morphological traits: predictable responses to macrohabitats across a 300 km scale. *PeerJ* 2, 1–20. <https://doi.org/10.7717/peerj.271>.