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Research Article

Ant (Hymenoptera: Formicidae) species diversity in secondary forest and three agricultural land uses of the Colombian Pacific Coast

Diversidad de especies de hormigas (Hymenoptera: Formicidae) en bosque secundario y tres usos agrícolas de tierra en la costa pacífica colombiana

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Abstract. The study area pertains to the Chocó Biogeography, one of the most biodiverse areas in the world, where around 40,000 ha of rainforest has been cleared for oil palm plantations. We surveyed the ant species' richness and diversity in four differently disturbed areas in Tumaco, Colombia, using pitfall traps and Winkler sacks. Study sites were two oil palm plantations of three- and seven- years' existence, a peach palm plantation *Bactris gasipaes* of 20 years, and an area of secondary forest of 10 years. A total of 93 ant species or morphospecies, comprising 31 genera in 8 subfamilies were identified. The subfamily Myrmicinae had the highest number of species (57), followed by Ponerinae (10) and Formicinae (9). The hybrid palm oil plantations harbored 46 species (7 years) and 50 species (3 years), respectively, while the peach palm plantation was composed of 53 species, and the secondary forest had 62 species. *Ectatomma ruidum* was the most dominant species in the oil palm plots (≥ 80% of specimen), but significantly less in the peach palm and secondary forest. The most species-rich genera were *Pheidole* spp. (23) and *Solenopsis* spp. (13). No differences were observed in the ant species' diversity between the secondary forest and peach palm, contrasting with the significant differences between the secondary forest and the two oil palm areas. A comparison with studies in natural areas suggests that the oil palm monocultures have dramatically reduced the species' richness and that ten years of recovery does not bring back anything close to the original diversity.

Key words: Ant communities; *Bactris gasipaes*; hybrid oil palm; secondary forest.

Resumen. El área de estudio pertenece al Chocó Biogeográfico, una de las áreas con mayor biodiversidad del mundo, donde se han talado alrededor de 40.000 ha de selva tropical para el establecimiento de palma aceitera. Se realizó un estudio de la riqueza y diversidad de las especies de hormigas en cuatro áreas perturbadas en Tumaco, Colombia, utilizando trampas de caída y sacos de Winkler. Los sitios de estudio fueron dos plantaciones de palma aceitera híbrida de tres y siete años, una plantación de palma de chontaduro *Bactris gasipaes* de 20 años y un área de bosque secundario de 10 diez años. Se identificaron 93 especies de hormigas o morfoespecies, distribuidas en 31 géneros y 8 subfamilias. La subfamilia Myrmicinae tuvo el mayor número de especies (57),

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seguida de Ponerinae (10) y Formicinae (9). Las plantaciones de palma aceitera híbrida albergaron 46 especies (7 años) y 50 especies (3 años), respectivamente, mientras que la plantación de palma *B. gasipaes* presentó 53 especies y el bosque secundario 62 especies. *Ectatomma ruidum* fue la especie dominante en las parcelas de palma aceitera (≥ 80% del espécimen), pero significativamente menos abundante en la plantación de palma de chontaduro y el bosque secundario. Los géneros más numerosos en especies fueron *Pheidole* spp. (23) y *Solenopsis* spp. (13) . No se observaron diferencias en la diversidad de especies de hormigas entre el bosque secundario y la palma de chontaduro, en contraste, se encontraron diferencias significativas entre el bosque secundario y las dos áreas de palma aceitera. Una comparación con estudios en áreas no perturbadas sugiere que los monocultivos de palma aceitera han reducido drásticamente la riqueza de especies y que diez años de recuperación vegetal no han establecido una diversidad similar a la original.

Palabras clave: Bosque secundario; *Bractis gasipaes*; comunidad de hormigas; palma de aceite híbrida.

Introduction

The Pacific lowlands around Tumaco in southwestern Colombia were the epicenter of the Colombian palm oil industry with approximately 40,000 ha planted in a cleared rainforest (Corredor *et al.* 2008; Fedepalma 2008). From 2006, a large-scale outbreak of bud rot led to area-wide eradication or abandonment of the plantations (Corredor *et al.* 2008). The development of hybrid palm oils based on the American palm oil, *Elaeis oleifera* Kunth (Arecaceae), conferred tolerance on the hybrids and allowed for a recovery of the industry (Fedepalma 2015). By 2018, more than 15,000 ha had been replanted; however, many of the formerly cultivated areas remained untended and gave rise to young secondary forest growth.

The Tumaco area is part of the biogeographic Chocó region, recognized as one of the world's 25 biodiversity hotspots by Myers *et al.* (2000). This region is endowed with some of the most diverse and unique rainforests in the world. However, the intensification and expansion of agriculture is the greatest global threat to biodiversity (Fitzherbert *et al.* 2008) and associated ecosystem services (Cardinale *et al.* 2012). This threat is a particular problem of the palm oil industry, owing to the massive increase in cultivation in recent years and its center of production being within the most biodiverse regions and habitats of the planet like Southern Nigeria, South-East Asia, and Tropical South America (Sodhi *et al.* 2010; Turner *et al.* 2008).

The conversion of rainforest to oil palm plantations has been shown to harm overall biodiversity (Fitzherbert *et al.* 2008), including the species' richness and diversity of specific insect taxa such as beetles (Chung *et al.* 2000a, 2000b; Davis & Philips 2005), moths (Chey 2006) and ants (Pfeiffer *et al.* 2008). Changes in assemblages, particularly the loss of functionally important species, can significantly impact ecosystem functioning (Hooper *et al.* 2005; Bihn *et al.* 2010; van der Plas 2019; Hood 2020). However, not all studies have shown a definitive negative impact of habitat conversion on biodiversity. Liow *et al.* (2001) found in Malaysia and Singapore, higher species richness of bees in oil palm plantations than in areas of primary forest. Mayfield (2005) in Costa Rica did not find a significant difference in the number of insect species visiting oil palm inflorescences close to and far away from forest fragments. Other studies have found a higher abundance of species in oil palm plantations (Davis & Philips 2005; Hassall *et al.* 2006), although these are probably species previously characteristic of open habitats or agricultural areas (Chey 2006; Davies & Philips 2005).

Ants constitute significant proportions of the soil biomass (Basset *et al.* 2015) and biodiversity in tropical ecosystems (Griffiths *et al.* 2018). The ant diversity in different tropical crops has been studied in different world regions. Ant communities are very sensitive to habitat changes, and human disturbance usually results in a significant alteration of ant species composition (Philpott *et al.* 2009; Achury *et al.* 2012; Bihn *et al.* 2010; González *et al.* 2018; Rabello *et al.* 2021). Overall, oil palm plantations reduced ant species' richness compared with primary and secondary forests, and the composition of species assemblages changed significantly after a forest's conversion to oil palm plantations (Room 1975; Taylor 1977; Fitzherbert *et al.* 2008; Brühl & Eltz 2010; Fayle *et al.* 2010; Savilaakso *et al.* 2014).

In this study, we evaluated the abundance, richness, and diversity of ant communities that inhabit and forage the lower strata (soil, litter and understory) in four differently disturbed areas in the lowlands of the Colombian Pacific coast. In addition, we analyze how the community of ants changes in four different land uses.

Material and Methods

Study sites. The study was conducted at El Mira Research Center (1°32'58" N - 78°41'21" W) of the Colombian Corporation for Agricultural Research (AGROSAVIA), located 38 km southeast of the town of Tumaco, Nariño state. The center is located at an altitude of 16 masl; the average annual precipitation and temperature are 3,067 mm and 25.5 °C, respectively. The rainy season occurs in January, where the precipitation reaches its peak, with an average of 468 mm. The rainfall decreases in the months of August to November (IDEAM 2020). The center comprises 564 ha dedicated to research in oil palms (*Elaeis* spp.), peach palms *Bactris gasipaes* Kunth (Arecaceae), *Theobroma cacao* L. (Malvaceae), and non-timber forestry products.

The sampling sites comprised four areas: three contiguous and one at about a distance of 1 km (Fig. 1). Of the neighbouring areas, one was a secondary forest ten years of age and 14 ha in extension, mainly populated by *Cecropia* sp. (Urticaceae); adjacent was a juvenile (3 years at the onset of the collections) hybrid (OxG) oil palm plantation of 14 ha, followed by a peach palm (*B. gasipaes*) germplasm collection of 9.9 ha, planted in 1997. The fourth area of 3 ha at about 1 km away was planted with OxG hybrids seven years of age when the experiment started. The peach and oil palm plantations were regularly weeded and fertilized, and the younger oil palm field had been treated with Engeo 247SC (Thiometoxam and Lambda-cyhalothrin) two months before trap establishment. No maintenance activities were carried out in the secondary forest.

Ant sampling. At all study sites, a transect of 100 m length was established with ten pitfall traps set at 10 m intervals. The traps consisted of small (150 ml) transparent plastic cups, two of which were stacked and interred to leave the upper rim of the top cup level with the soil surface. Both cups remained in place between the trapping events, the top cup covered with a lid. A roof made of three bamboo skewers (300 mm long) and a 250 mm diameter Styrofoam plate was placed over the trap to avoid flooding during heavy rain. For the fortnightly trapping events, the top cup was replaced by a cup filled with 50 ml of 70% EtOH to act as a preservative and one drop of dish-washing liquid to eliminate the surface tension. Traps were in the field for 24 hours, samples were collected via removal of the collection cup and replacing it with the one with a cover. Throughout one year, 22 collections were made with two collections per month except for August 2016 and February 2017, which had only one collection.

To complement the pitfall collections, leaf litter samples were obtained by collecting the surface material within a 0.5 m^2 wood frame once a month on three stations alongside the pitfall transects of all four fields. The litter of each sample was sifted using a Winkler sack (Biologika®, Bogotá) with a 1 cm^2 grid size to exclude larger debris. The remaining material was transferred for extraction to a Winkler sack for four days, and the emerging specimens were collected in a sampling container with 70% alcohol. Six monthly collections were made from July-December 2016.

All samples were sorted, counted, and kept in labeled Eppendorf tubes (4 ml) in 70% alcohol for later identification in the laboratory. Ant specimens were identified as morphospecies or species according to their external morphology (Serna & Vergara 2001; Fernández 2003; Fernández & Arias-Penna 2008). Doubtful specimens were sent for confirmation by a myrmecologist. The whole collection is preserved in the National Taxonomic Collection "Luis María Murillo" of AGROSAVIA, located at Tibaitatá Research Center, Cundinamarca, Colombia.

The collections were carried out within "Permiso Marco de Recolección de Especímenes de Especies Silvestres de la Diversidad Biológica con Fines de Investigación Científica No Comercial Resolución 1466 del 3 Dic 2014", recognized by Autoridad Nacional de Licencias Ambientales (ANLA, [National Authority of Environmental Licenses]).

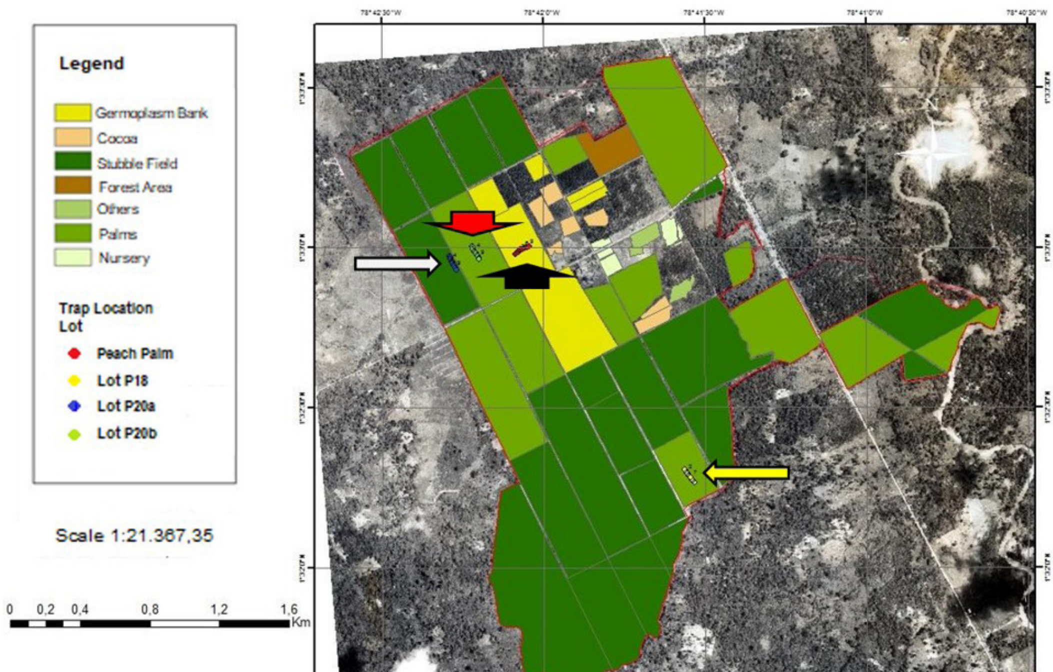

Figure 1. Map of El Mira Research Center of the Corporación Colombiana de Investigación Agropecuaria, Tumaco, Nariño, Pacific Coast of Colombia, with the location (arrows) of the pitfall trap transects. Yellow hybrid oil palm 7 years old; red hybrid oil palm 3 years old; black peach palm; white secondary forest. / Mapa del Centro de Investigación El Mira de la Corporación Colombiana de Investigación Agropecuaria, Tumaco, Nariño, costa pacífica de Colombia con la ubicación (flechas) de las trampas pitfall en los transectos. Amarillo palma de aceite híbrido 7 años; rojo palma de aceite híbrido 3 años; negro palma de chontaduro; blanco bosque secundario.

Data analysis. We conducted statistical analyses to examine trends in abundance, richness, and diversity. Ant frequency (number of ants of a given species per total number of traps) and species richness (number of ant species) were tabulated for each studied area. Species accumulation curves were computed using the combined data from pitfall traps and Winkler sieve by means of the Jack1 function in the EstimateS program (Colwell 2009) (supplementary material). The order ^qD diversity or equivalent numbers (effective number of species) was calculated using the Hill series (Jost 2006, 2007). The order 0 diversity (^0D) represents the richness of the species, while the diversity of order 1 (^1D) is known as the diversity of Shannon in its exponential form and represents the diversity of common or typical species of the community (fairness). According to Jost (2006), it is the most useful measure with which to compare changes in diversity. Additionally, we used the sample coverage estimator ($\hat{C}n$) proposed by Chao and Jost (2012) to evaluate the completeness of the inventory. The statistical significance of differences between the four study sites was tested using the non-parametric tests: Kruskal-Wallis and Mann-Whitney pairwise; the non-normality was corroborated by the Shapiro-Wilk test (W).

A Bray-Curtis analysis of dissimilarity of the four areas of trapping was conducted and resulted in the joint clustering of both oil palm areas while the peach palm and the secondary forest were separate. All analyses were performed with the packages iNEXT and Vegan, R software (V. 3.1.3, R Development Core Team 2018).

Results

In total, we collected 23,952 ant individuals comprised of 93 species and morphospecies, distributed among 7 subfamilies and 31 genera. The subfamily Myrmicinae had the highest number of species (57), followed by Ponerinae (10) and Formicinae (9). The genus *Pheidole* Westwood had the highest species richness (23), followed by *Solenopsis* Westwood (13), *Strumigenys* Smith (7), *Hypoponera* Santschi and *Gnamptogenys* Roger (4, each), *Camponotus* Mayr, *Cyphomyrmex* Mayr, *Nylanderia* Emery, and *Pseudomyrmex* Lund (3 each), *Azteca* Forel, *Brachymyrmex* Mayr, *Eciton* Latreille, *Ectatomma* Smith, *Labidus* Jurine, *Octostruma* Forel, *Pachycondyla* Smith and *Pyramica* Roger (2 each), and *Acromyrmex* Mayr, *Atta* Fabricius, *Crematogaster* Lund, *Leptogenys* Roger, *Linepithema* Mayr, *Monomorium* Mayr, *Neoponera* Emery, *Odontomachus* Latreille, *Platythyrea* Roger, *Sericomyrmex* Mayr, *Tapinoma* Foerster, *Trachymyrmex* Forel, *Paratrechina* Motschoulsky and *Wasmannia* Forel (1 each) (Tab. 1).

Table 1. Abundance and diversity of ant species (Formicidae) collected in four areas of different land use. El Mira Research Center, Tumaco, Nariño, Pacific Coast of Colombia. / Abundancia y diversidad de especies de hormigas (Formicidae) recolectadas en cuatro áreas con diferente uso de tierra. Centro de Investigación El Mira, Tumaco, Nariño, costa pacífica de Colombia.

Subfamilies and species	Secondary forest	Peach palm 20 years	Hybrid oil palm 7 years	Hybrid oil palm 3 years	Sampling technique
Dolichoderinae					
Azteca sp. 1	2	-	-	-	P
Azteca sp. 2	1	-	-	-	P
Linepithema sp.	-	-	-	1	P
Tapinoma melanocephalum (Fabricius, 1793)	5	-	2	1	P, W
Dorylinae					
Eciton vagans (Olivier, 1792)	-	-	-	2	P
Eciton sp.	1	-	-	-	W

Labidus coecus (Latreille, 1802)	20	57	4	4	P, W
Labidus praedator (Smith, 1858)	624	511	100	124	P
Ectatomminae					
Ectatomma ruidum (Roger, 1860)	**2875**	**2615**	**7117**	**4210**	P, W
Ectatomma sp. 1	-	1	-	-	P
Gnamptogenys sp. 1	1	36	1	-	P, W
Gnamptogenys sp. 2	1	-	3	-	P
Gnamptogenys sp. 3	1	-	-	2	P
Gnamptogenys sp. 4	1	1	-	-	P
Formicinae					
Brachymyrmex patagonicus Mayr, 1868	698	170	99	396	P, W
Brachymyrmex australis Forel, 1901	4	2	2	1	P, W
Camponotus atriceps (Smith, 1858)	-	1	-	-	W
Camponotus ca. *claviscapus* Forel, 1899	6	-	-	1	P
Camponotus sp.	-	-	1	-	P
Nylanderia cf. *steinheili* (Forel, 1893)	164	74	29	9	P, W
Nylanderia sp. 1	4	28	2	2	P, W
Nylanderia sp. 2	9	3	8	2	P, W
Paratrechina longicornis (Latreille, 1802)	-	-	-	1	P
Myrmicinae					
Acromyrmex octospinosus (Reich, 1793)	-	12	-	10	P, W
Atta cephalotes (Linnaeus, 1758)	133	2	-	20	P
Crematogaster crinosa Mayr, 1862	2	15	-	-	P
Cyphomyrmex hamulatus Weber, 1938	10	38	42	39	P, W
Cyphomyrmex salvini pos. Forel, 1899	-	12	2	-	P, W
Cyphomyrmex sp. 1	-	1	-	-	W
Monomorium floricola (Jerdon, 1851)	-	-	1	-	P

Octostruma balzani (Emery, 1894)	52	45	9	1	P, W
Octostruma sp. 1	19	-	-	2	P, W
Pheidole sp. 1	-	-	9	-	P
Pheidole sp. 2	-	1	-	-	P
Pheidole sp. 3	19	56	3	7	P, W
Pheidole sp. 4	-	2	-	-	W
Pheidole sp. 5	1	1	-	6	P, W
Pheidole sp. 6	4	9	-	4	P, W
Pheidole sp. 7	1	-	-	1	W
Pheidole sp. 8	50	3	2	6	P, W
Pheidole sp. 9	4	-	-	3	P, W
Pheidole sp. 10	2	-	-	-	P
Pheidole sp. 11	5	31	13	13	P, W
Pheidole sp. 12	15	96	17	21	P, W
Pheidole sp. 13	-	-	1	-	P
Pheidole sp. 14	1	-	1	-	P
Pheidole sp. 15	-	-	1	26	P
Pheidole sp. 16	22	3	-	12	P, W
Pheidole sp. 17	1	-	-	-	P
Pheidole sp. 18	1	-	-	-	P
Pheidole sp. 19	8	6	1	-	P, W
Pheidole sp. 20	-	3	-	-	W
Pheidole sp. 21	9	103	10	15	W
Pheidole sp. 22	-	-	-	1	W
Pheidole sp. 23	-	1	-	-	W
Pyramica sp. 1	1	-	1	-	P,W
Pyramica sp. 2	-	2	-	-	W
Sericomyrmex mayri Forel, 1912	4	-	-	-	P
Solenopsis sp. 1	8	31	4	10	P, W
Solenopsis sp. 2	47	14	54	44	P, W
Solenopsis sp. 3	431	342	246	94	P, W
Solenopsis sp. 4	-	87	4	-	P, W
Solenopsis sp. 5	65	13	3	2	P, W
Solenopsis sp. 6	3	2	18	-	P, W
Solenopsis sp. 7	29	21	2	26	W
Solenopsis sp. 8	-	17	-	1	W
Solenopsis sp. 9	3	36	1	57	P, W
Solenopsis sp. 10	113	-	-	-	W
Solenopsis sp. 11	3	-	-	-	W
Solenopsis sp. 12	1	-	-	-	P

Solenopsis sp. 13	-	1	-	-	P
Strumigenys cf. *precava* Brown, 1954	51	17	9	29	P, W
Strumigenys sp. 3	4	18	8	9	W
Strumigenys sp. 4	64	4	2	9	W
Strumigenys sp. 5	2	-	-	-	W
Strumigenys sp. 6	-	-	-	1	W
Strumigenys sp. 7	-	1	-	-	W
Strumigenys sp. 8	2	-	-	-	W
Trachymyrmex sp. 1	1	1	-	-	P
Wasmannia auropunctata (Roger, 1863)	158	84	337	18	P, W
Ponerinae					
Hypoponera sp. 1	6	14	1	9	P, W
Hypoponera sp. 2	-	-	2	1	P, W
Hypoponera sp. 3	-	-	1	-	P
Hypoponera sp. 4	1	-	-	-	P
Leptogenys sp.	1	-	-	2	P
Neoponera verenae Forel, 1922	29	3	1	-	P
Odontomachus bauri Emery, 1892	9	9	-	8	P, W
Pachycondyla harpax (Fabricius, 1804)	15	12	4	5	P
Pachycondyla sp.	-	-	-	1	P
Platythyrea sp.	-	-	-	1	P
Pseudomyrmex sp. 1	-	-	3	-	P
Pseudomyrmex sp. 2	-	-	1	-	P
Pseudomyrmex sp. 3	5	-	-	-	P
Total species	**62**	**53**	**46**	**50**	
Total abundance	**5832**	**4668**	**8182**	**5270**	**23952**

Richness by sampling area. The largest number of species was found in the secondary forest (62 sp.), followed by the peach palm germplasm bank (53 sp.), and the hybrid oil palm plantations of seven (46 sp.) and three years (50 sp.). Additionally, the same behavior is presented by frequency values and exclusive species, showing that the forest tends to have more diversity than the areas cultivated (Tab. 2).

No differences were observed in ^{0}D diversity between the secondary forest and peach palm, contrasting with the significant differences between the secondary forest and the two oil palm areas (Fig. 2).

The Kruskal-Wallis test indicated significant differences in ant species diversity between the sites ($\chi^2_{21} = 7.895$; $P < 0.0330$). Pairwise comparison revealed differences between the secondary forest and the two oil palm areas but not the peach palm plantation (Tab. 3).

Table 2. Frequency values (F), exclusive species (E), observed species richness (${}^0D$), Shannon diversity (${}^1D$) and coverage index ($\hat{C}n$) of ants collected in four areas under different land use. El Mira Research Center, Tumaco, Nariño, Pacific Coast of Colombia. / Valores de frecuencia (F), especies exclusivas (E), riqueza de especies observada (${}^0D$), diversidad de Shannon (${}^1D$) e índice de cobertura ($\hat{C}n$) de las hormigas colectadas en cuatro áreas con diferente uso de tierra. Centro de Investigación El Mira, Tumaco, Nariño, costa pacífica de Colombia.

	Secondary forest	**Peach palm 20 years**	**Oil palm 7 years old**	**Oil palm 3 years old**
F	239	214	142	174
${}^0D$	62	53	46	50
${}^1D$	46.53	38.86	32.14	34.81
$\hat{C}n$	0.71	0.74	0.60	0.63
SE	81.81	83.75	86.22	81.67

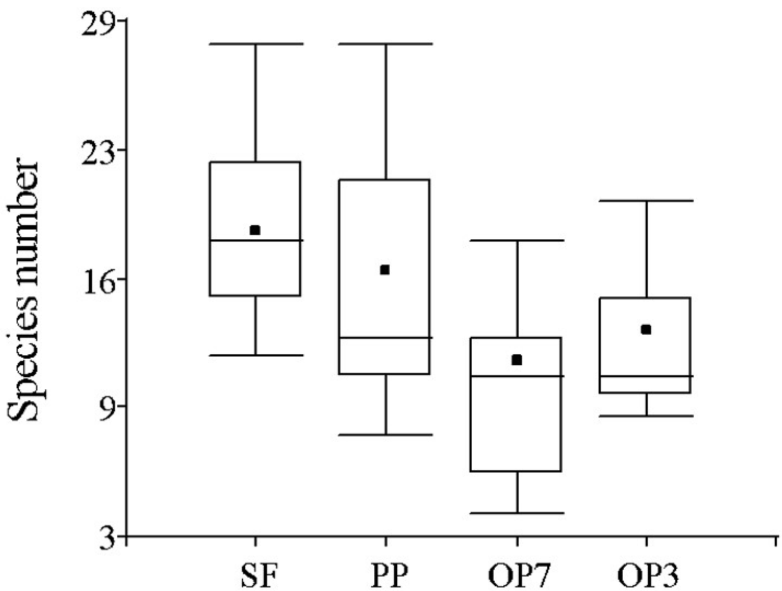

Figure 2. Variation in ${}^0D$ diversity (species number) of Formicidae between four areas of different land use: El Mira Research Center, Tumaco, Pacific Coast of Colombia. SF: secondary forest, PP: Peach palm, OP7: Oil palm 7 years old, OP3: Oil palm 3 years old. / Variación en la diversidad ${}^0D$ (número de especies) de Formicidae entre cuatro áreas con diferente uso de tierra. Centro de Investigación El Mira de la Corporación Colombiana de Investigación Agropecuaria, Tumaco, Nariño, costa pacífica de Colombia.

Table 3. *P* values for pair-wise comparison of the ant diversity (${}^1D$ index) between four areas of different land use (Mann-Whitney test). / Valores de *P* para la comparación pareada de la diversidad de hormigas (índice 1D) entre cuatro áreas con diferente uso de tierra (Prueba Mann-Whitney).

	Secondary forest	Peach palm 20 years	Oil palm 7 years old	Oil palm 3 years old
Secondary forest		0.281	0.004*	0.050*
Peach palm 20 years			0.098	0.447
Oil palm 7 years				0.299

* marked values are significant.

Ectatomma ruidum (Roger, 1860) was by far the most common ant species, with 16,095 individuals collected in the pitfalls, and was the one most consistent with presence in 826 out of 880 pitfall trap collections. Even though its presence across the for ascertaining four areas of collection was similar, significant differences between the areas were recorded the dominance in the respective collection: in both oil palm plantations, *E. ruidum* comprised over 80% of all specimens collected; this value was much lower in the peach palm plantation (55.3%) and the lowest in the secondary forest (4.1%) (Tab. 4). The second most numerous species was *Brachymyrmex patagonicus* Myer, 1868 with 1,363 specimens overall, slightly more frequent and numerous in the secondary forest, than in the other areas (Tab. 4). *Labidus praedator* (Smith, 1858) (1,359) was more numerous and frequent in the forest and peach palm plantation, followed by *Solenopsis* sp. 3 (1,113), also predominantly in the forest and the peach palm plantation (Tab. 4). The next most abundant species were *Wasmannia auropunctata* (Roger, 1863), *Nylanderia* cf. *steinheili* (Forel, 1893) and *Solenopsis* sp. 2, all three falling below 500 specimens captured.

Fourteen species were unique to the secondary forest, but except for *Atta cephalotes* (Linnaeus, 1758) and *Solenopsis* sp. 10, most were singletons. Ten species were unique to the peach palm plot, again mostly singletons, and of the 16 species unique to the two oil palm plots, only *Pheidole* sp. 4 was captured repeatedly (Fig. 3). Three species were shared between forest and peach palm, ten between forest and oil palm, and four between peach palm and oil palm (Fig. 3). *Solenopsis* sp. 4, was shared between all palm plots, and *Pheidole* sp. 8, shared between forest and oil palms, was the only species with a considerable number of individuals. Thirty-six species within a total of 23,519 specimens collected were shared among the four areas and constituted 97.3% of all collected specimens (Fig. 3).

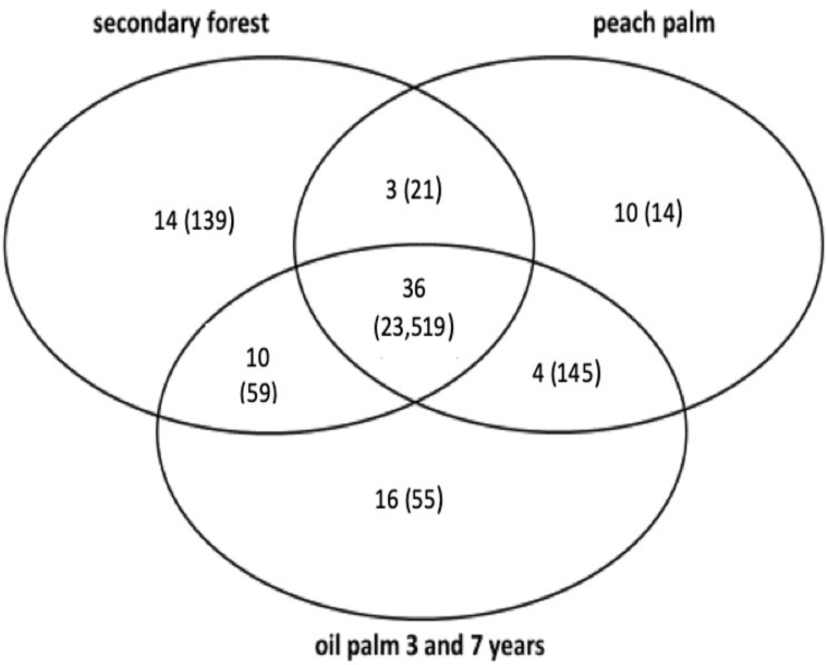

Figure 3. Number of shared ant species and total number of specimens caught (pitfall and Winkler sack) between four areas of different land use. Two oil palm plots of three and seven years of age were pooled. El Mira Research Center, Tumaco, Pacific Coast of Colombia. / Número de especies de hormigas compartidas y número total de individuos capturados (Pitfall y sacos Winkler) entre cuatro áreas con diferente uso de tierra. Las dos parcelas de palma de aceite de tres y siete años fueron agrupadas. Centro de Investigación El Mira, Tumaco, Nariño, costa pacífica de Colombia.

Table 4. Predominant species of Formicidae in pitfall trap and Winkler samples from four areas of the Pacific lowlands under different land use. / Especies predominantes de Formicidae en muestras de trampas pit fall y sacos Winkler de cuatro áreas de tierra bajas del Pacífico bajo diferente uso de tierra.

	Secondary forest	Peach palm 20 years	Oil palm 7 years old	Oil palm 3 years old
Ectatomma ruidum Roger				
Presence*	92.5	85.0	94.7	93.4
Participation**	49.1	55.3	87.3	80.6
Brachymyrmex patagonicus Mayr				
Presence	23.9	11.5	15.0	22.6
Participation	12.7	3.7	1.2	7.8
Labidus praedator (Smith)				
Presence	11.1	5.8	0.9	1.8
Participation	10.7	11.3	0.7	1.9
Solenopsis sp. 3				
Presence	17.3	14.6	8.0	8.0
Participation	7.8	7.5	3.1	1.8
Wasmannia auropunctata (Roger)				
Presence	10.2	8.4	4.4	3.1
Participation	1.1	1.7	4.2	0.3
Nylanderia cf. *steinheili* (Forel)				
Presence	3.1	2.7	2.2	1.3
Participation	3.0	1.6	0.4	0.2
Solenopsis sp. 2				
Presence	11.9	2.7	11.9	10.2
Participation	0.9	0.3	0.6	0.8

* percentage occurrence in individual sampling events; ** proportion of all specimens captured.

Discussion

The ant communities in the secondary forest and the peach palm plot were different from the communities present in the oil palm plantations; also, they could even potentially have species that were not detected in the sampling. These marked differences might be due to the fact that ant communities are highly influenced by habitat type (Costa-Milanez *et al*. 2014), vegetation structure (Luke *et al*. 2014; Sanabria *et al*. 2014), or long-term effects of the establishment phase of the oil palm monocultures (Turner & Foster 2009; Fayle *et al*. 2010; Wang & Foster 2015; Philip *et al*. 2018; Hood 2020). Andersen (2000) considered low temperature, lack of nest sites, poor food supply, and high structural complexity of foraging surfaces to be the main stressors limiting ant populations. In this study, it is possible that the secondary forest and peach palm plantation may offer conditions that favor greater ant abundance, in which nest sites and food supply are available. However, more highly disturbed habitats, such as oil palm plantations, could support fewer species due to differences in tree density and diversity (Klimes *et al*. 2012), the conversion to a hotter and drier microclimate (Turner & Foster 2006), and the removal of understory vegetation (Fayle *et al*. 2010; Wang & Foster 2015; Hood *et al*. 2020). We found that ant communities in the oil palm plantations of three and seven years showed high similarities among plots, which may be due to the homogeneous understory vegetation in oil palm plantations in the site and the similar management practices.

Overall, we found that the functional group composition of ant communities showed variable associations with habitat type and land management. Species in the genera *Pheidole*, *Ectatomma*, *Nylanderia*, *Brachymyrmex* and *Solenopsis* were present in all four land-use types. They can be characterized as generalists and are probably species that originate from the primary forest and tolerated the transformation to plantations (Perfecto & Vandermeer 2006).

The Myrmicinae subfamily with the genus *Pheidole* was the most diverse (23 morphospecies) in the areas sampled, followed by *Solenopsis* (13). Even though the former is of cosmopolitan occurrence, its highest diversity is found in the Neotropics, where it is dominant and megadiverse (Wilson 2003). *Pheidole* is predominant in all terrestrial ecosystems in terms of species diversity, geographical distribution, and abundance, due to its wide tolerance of environmental conditions (Corrêa *et al.* 2006). In the case of *Solenopsis*, some species are valuable predators of insects that develop on the soil surface or underground (Zenner 1994) even though the genus is not renown as predacious but rather as a generalist (Risch & Carroll 1982).

The second-best represented subfamily was Ponerinae, which generally includes hunting ants, although some species resort to food of plant origin. They form small colonies of less than 300 workers but can be extremely populous because of their high nest density (Peeters 1997). The most common species was *Ectatomma ruidum*, a dominant neotropical ground-dwelling ant species of great interest due to its predatory functional importance in relation to biological systems altered by humans (agroecosystems) (Fontalvo-Rodríguez & Domínguez-Haydar 2009) and for its potential as a biological control agent (Lachaud 1990). The dominance of *E. ruidum* in this study was evident, which accounted for 70% of all ant specimens captured. The fact that this species was absent in only 54 out of 880 capture events confirms its ubiquity and the stability of its populations over time.

Ectatomma ruidum is generally considered a species that prospers in man-altered environments (Arias-Penna 2007). Indeed, in this study, the population of *E. ruidum* responded in an increasing way in the 3- and 7-year-old oil palm plantations. The population response of *E. ruidum* reflects the high degree of adaptability of this species, which makes it easier to tolerate stress conditions and extend the range of its population.

Furthermore, the ants adapt their thermal tolerance to local conditions (Villalta *et al*. 2020). It is well established that *E. ruidum* is a thermophilous species on the local scale (Schatz & Lachaud 2008; Santamaría *et al*. 2009), which could explain the high densities of this species found in oil palm plantations that consist of open and sunny areas.

Coral *et al.* (2004) associated two hunting ants, *Pachycondyla harpax* (Fabricius, 1804) and *P. obscuricornis* (Emery, 1890), to a low level of damage by *Sagalassa valida* (Walker, 1735) (Lepidoptera: Brachodidae) in some oil palm plantations of the Pacific region. However, in our collections that covered four different environments and a considerably longer sampling time, only 29 specimens of this genus were collected.

Furthermore, army-ants *Labidus praedator* and *Labidus coecus* (Latreille, 1802) of Dorylinae subfamily were found in all sampling areas. Ants belonging to the genus *Labidus* are one of the main insect predators (Monteiro *et al.* 2008; Powell & Baker 2008). The high diversity of predatory ants of the subfamilies Ponerinae and Dorylinae in the research center indicates a wide availability of prey resources, implying a high ecological complexity in their agroecosystems.

Brachymyrmex patagonicus is native to Paraguay and Argentina but widely spread over the South American Neotropics (Quiran *et al.* 2004). It forms colonies in cavities underground and in vegetation, and its main sustenance is honeydew and nectar, often from extrafloral nectaries (MacGown *et al.* 2007). A significant reason for the success of *B. patagonicus* in terms of abundance may be due to its ability to thrive in a variety of habitats, especially disturbed sites (MacGown *et al.* 2007). Other contributing factors could be its ability to coexist with dominant ant species, such as *E. ruidum*. This is similar to other species of *Brachymyrmex*, which usually occur with many other ant species that are larger, faster, more hard-bodied, and armed with stingers and more powerful mandibles (MacGown *et al.* 2007).

Nylanderia cf. *steinheili* is an abundant and widespread neotropical species adapted to a wide range of ecological conditions. It is commonly found in Winkler leaf litter collections (Ward 2000) – as was the case in our study – and is a generalist scavenger both on the ground and in the forest canopy.

Few studies have been conducted in the Pacific lowland rainforest to measure ant diversity and thus obtain a proxy for overall biodiversity. Valdés-Rodríguez *et al.* (2014) listed 107 soil and ground-dwelling ant species on Gorgona Island with less disturbed forests than in this study, part of the same Chocó biome, from our own data and through a compilation of the results of three earlier surveys, where 52% of the species were obtained by manual collection. The composition of their collection in terms of subfamilies was similar to our results (Myrmicinae > Ponerinae > Formicinae). However, none of the species they listed as numerous and frequent occurred in our collections. The most represented genera in their collection, *Pachycondyla* and *Camponotus,* only occurred with 31 and 8 individuals in our study, a clear indication that the ten years of forest regrowth could not re-establish anything near the original diversity. This is even more evident when our results are compared with a study on the Calima River watershed at a slightly higher altitude (Aldana de la Torre & Chacón de Ulloa 1999) where the total number of species recorded was 227 against our 96, and the secondary forest still harboured 47 exclusive species, more than three times the value/number in our study. This is somewhat different from observations of other arthropods where higher numbers of specimens were registered for Coleoptera, Diptera, Hemiptera and Orthoptera in the secondary forest for the same area (Löhr & Narváez 2021). We attribute these differences to the wholesale deforestation of a huge area for oil palm plantations and the greater difficulties for ants to re-establish themselves in comparison to winged arthropods.

Conclusions

The transformation of primary forests to monocultures is invariably accompanied by drastic changes in biodiversity, and consequently, severe changes in ant communities. Even though we cannot present data on the original diversity, studies in similar areas indicate the changes must have been dramatic. A reason for concern is that even more than ten years of forest regrowth were insufficient to establish significant differences in ant diversity between the secondary forest and the more intervened oil palm plantations.

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Literature Cited

Achury, R., Chacón, P. and Arcila, A. (2012) Effects of the heterogeneity of the landscape and the abundance of *Wasmannia auropunctata* on ground ant assemblages in a Colombian tropical dry forest. *Psyche, 2012*: 1-12. https://doi.org/10.1155/2012/960475

Aldana de la Torre, R. and Chacón de Ulloa, P. (1999) Megadiversidad de hormigas (Hymenoptera: Formicidae) en la cuenca media del río Calima. *Revista Colombiana de Entomología, 25*: 37-47.

Andersen, A. (2000) A global ecology of rainforest ants: functional groups in relation to environmental stress and disturbance. Ants: standard methods for measuring and monitoring biodiversity (ed, Agosti, D., Majer, J., Alonso, L., Schultz, T.), pp 25-34. Smithsonian Institution Press, Washington, United States.

Arias-Penna, T.M. (2007) Capítulo 3: Subfamilia Ectatomminae. Sistemática, Biogeografía y Conservación de las hormigas cazadoras de Colombia. (ed, Jiménez, E., Fernández, F., Arias, T., Lozano, F.), pp 53-108. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá D.C, Colombia.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A., Schmidl, J. and Winchester, N.N. (2015) Arthropod distribution in a tropical rainforest: tackling a four dimensional puzzle. *PLoS ONE, 10*(12): e0144110.

Bihn, J.H., Gebauer, G. and Brandl, R. (2010) Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology, 91*: 782-792.

Brühl, C. and Eltz, T. (2010) Fuelling the biodiversity crisis: species loss of ground-dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo). *Biodiversity and Conservation, 19*: 519-529.

Cardinale, B., Duffy, J., Gonzalez, A., Hooper, D., Perrings, C. and Venail, P. (2012) Biodiversity loss and its impact on humanity. *Nature, 486*: 59-67.

Chao, C. and Jost, L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology, 9*: 2533-2547.

Chey, V. (2006) Impacts of forest conversion on biodiversity as indicated by moths. *Malayan Nature Journal, 57*: 383-418.

Chung, A.Y., Eggleton, P., Speight, M.R., Hammond, P.M. and Chey, V.K. (2000a) The diversity of beetle assemblages in different habitat types in Sabah, Malaysia. *Bulletin of Entomological Research, 90*: 475-496.

Chung, A.Y., Hammond, P.M., Eggleton, P., Speight, M.R. and Chey, V.K. (2000b) A general survey of the Staphylinidae (Insecta: Coleoptera) assemblage in Sabah, Malaysia. *Malayan Nature Journal, 54*: 355-368.

Colwell, R.K. (2009) EstimateS: Statistical estimation of species richness and shared species from samples. Versión 8.2. http://purl.oclc.org/estimates

Coral, J., Calvache, H., Salamanca, J.C., Aldana, R.C. and Chávez, C. (2004) Reconocimiento de insectos depredadores del barrenador de raíces *Sagalassa valida* Walker en la palma de aceite. *Palmas, 25*: 232-239.

Corrêa, M., Fernandes, W. and Leal, R. (2006) Diversidade de formigas epigéicas (Hymenoptera: Formicidae) em capões do Pantanal Sul Matogrossense: relações entre riqueza de espécies e complexidade estrutural da área. *Neotropical Entomology, 35*: 724-730.

Corredor, A., Martínez, G. and Silva, A. (2008) Problemática de la pudrición del cogollo en Tumaco e instrumentos para su manejo y la renovación del cultivo. *Palmas, 29*: 11-16.

Costa-Milanez, C., Lourenço, G., Castro, P., Majer, J. and Ribeiro, S. (2014) Are ant assemblages of Brazilian veredas characterized by location or habitat type? *Brazilian Journal of Biology, 74*: 89-99.

Davis, A. and Philips, T. (2005) Effect of deforestation on a southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa Conservation area. *Environmental Entomology, 34*: 1081-1088.

Fayle, T., Turner, E., Snaddon, J., Chey, V., Chung, A., Eggleton, P. and Foster, W. (2010) Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic and Applied Ecology, 11*: 337-345.

Federación Nacional de Cultivadores de Palma de Aceite (Fedepalma) (2008) The oil palm agroindustry in Colombia and the world. Statistical yearbook. Bogotá, Colombia.

Federación Nacional de Cultivadores de Palma de Aceite (Fedepalma) (2015) The oil palm agroindustry in Colombia and the world. Statistical yearbook. Bogotá, Colombia.

Fernández, F. (2003) Introducción a las hormigas de la región Neotropical. Instituto Humboldt, Bogotá, Colombia. 398 pp.

Fernández, F. and Arias-Penna, T. (2008) Las hormigas cazadoras de la región neotropical. Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia (ed. Jiménez, E.; Fernández, F.; Arias, T.M.; Lozano- Zambrano, F. H), pp. 3-39. Instituto de Investigación de Recursos Biológicos Alexander Von Humboldt, Colombia.

Fitzherbert, E., Struebig, M., Morel, A., Danielsen, F., Brühl, C., Donald, P. and Phalan, B. (2008) How will oil palm expansion affect biodiversity?. *Trends and Ecology & Evolution, 23*: 538-545.

Fontalvo-Rodríguez, L. and Domínguez-Haydar, Y. (2009) *Ectatomma ruidum* (Roger) como indicadora de diversidad de hormigas cazadoras (Hymenoptera: Formicidae) y relación con estructura vegetal en parches de bosque seco del Caribe colombiano, *Intropica, 4*: 29-39.

González, E., Buffa, L., Defagó, M., Molina, S., Salvo, S. and Valladares, G. (2018) Something is lost and something is gained: loss and replacement of species and functional groups in ant communities at fragmented forest. *Landscape Ecology, 33*: 2089-2102.

Griffiths, H.M., Ashton, L.A., Walker, A.E., Hasan, F., Evans, T.A., Eggleton, P. and Parr, C.L. (2018) Ants are the major agents of resource removal from tropical rainforests. *Journal of Animal Ecology, 87*: 293-300.

Jost, L. (2006) Entropy and diversity. *Oikos, 113*: 363-375.

Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology, 88*: 2427-2439.

Hassall, M., Jones, D., Taiti, S., Latipi, Z., Sutton, S. and Mohammed, M. (2006) Biodiversity and abundance of terrestrial isopods along a gradient of disturbance in Sabah, East Malaysia. *European Journal of Soil Biology, 42*: 197-207.

Hood, A. (2020) The effect of habitat management on biodiversity and ecosystem functions in oil palm plantations in Sumatra, Indonesia. Doctoral thesis. University of Cambridge.

Hood, A.S., Advento, A.D., Stone, J., Fayle, T.M., Fairnie, A., Waters, H., Foster, W., Snaddon, J., Ps, S., Caliman, J.P., Naim, M. and Turner, E. (2020) Removing understory vegetation in oil palm agroforestry reduces ground-foraging ant abundance but not species richness. *Basic and Applied Ecology, 48*: 26-36.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. and Wardle, D. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs, 75*: 3-35.

Instituto de Hidrología, Meteorología y Estudios Ambientales - IDEAM (2020) Comunicado especial No. 43. Actualización a seguimiento de las precipitaciones del año 2020. Colombia. 7 pp.

Klimes, P., Idigel, C., Rimandai, M., Fayle, T., Janda, M., Weiblen, G. and Novotny, V. (2012) Why are there more arboreal ant species in primary than in secondary tropical forests?. *Journal of Animal Ecology, 81*: 1103-1112.

Lachaud, J. (1990) Foraging activity and diet in some neotropical ponerine ants. I. *Ectatomma ruidum* Roger (Hymenoptera, Formicidae). *Folia Entomologica Mexicana, 78*: 241-256.

Liow, L., Sodhi, N. and Elmqvist, T. (2001) Bee diversity along a disturbance gradient in tropical lowland forests of South-East Asia. *Journal of Applied Ecology, 38*: 180-192.

Löhr, B. and Narváez, A. (2021) Land use and terrestrial arthropods at the Colombian Pacific coast. *Revista Colombiana de Entomología, 47*(1): e7640.

Luke, S.H., Fayle, T.M., Eggleton, P., Turner, E.C. and Davies, R.G. (2014) Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodiversity and Conservation, 23*: 2817-2832.

MacGown, J., Hill, J. and Deyrup, M. (2007) *Brachymyrmex patagonicus* (Hymenoptera: Formicidae), an emerging pest species in the Southeastern United States. *Florida Entomologist, 90*: 457-464.

Mayfield, M. (2005) The importance of nearby forest to known and potential pollinators of oil palm (*Elaeis guineensis* Jacq.; Arecaceae) in southern Costa Rica. *Economic Botany, 59*: 190-196.

Monteiro, A.F., Sujii, E.R. and Morais, H.C. (2008) Chemically based interactions and nutritional ecology of *Labidus praedator* (Formicidae: Ecitoninae) in an agroecosystem adjacent to a gallery forest. *Revista Brasileira de Zoologia, 25*: 674-681.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature, 403*: 853-858.

Peeters, C. (1997) Morphologically 'primitive' ants: Comparative review of social characters, and the importance of queen–worker dimorphism. The Evolution of Social Behaviour in Insects and Arachnids. (ed. Choe, J. and Crespi, B.), pp. 372-391. Cambridge: Cambridge University Press, United Kingdom.

Perfecto, I. and Vandermeer, J. (2006) The effect of an ant-hemipteran mutualism on the coffee berry borer *Hypothenemus hampei* in southern Mexico. *Agriculture Ecosystems & Environmental, 17*: 218-221.

Pfeiffer, M., Ho, C. and Chong, T. (2008) Exploring arboreal ant community compostion and co-occurrence patterns in plantations of oil palm *Elaeis guineensis* in Borneo and Peninsula Malaysia. *Ecography, 31*: 21-32.

Philip, A.J., Fayle, T.M. and Yusah, K.M. (2018) Selectively logging old growth rain forest twice changes canopy ant species composition, while conversion to oil palm changes composition and reduces species richness and diversity. *Journal of Tropical Biology and Conservation, 15*: 139-154.

Philpott, S.M., Perfecto, I., Armbrecht, I. and Parr, C. (2009) Effects of disturbance and habitat transformation on ant diversity and function. Ant Ecology. (ed. Lach, L., Parr, C. and Abbott, K.L.), pp. 137-156. Oxford University Press, United Kingdom.

Powell, S. and Baker, B. (2008) Os grandes predadores dos neotrópicos: comportamento, dieta e impacto das formigas de correição (Ecitoninae). Insetos sociais: da biologia à aplicação. (ed. Vilela, E., Santos, I., Shoereder, J.H., Serrão, J.E., Campos, L.A.O. and Neto, J.L.), pp. 1837. Universidade Federal de Viçosa, Brasil.

Quiran, E.M., Martínez, J.J. and Bachmann, A.O. (2004) The Neotropical genus *Brachymyrmex* Mayr 1868 (Hymenoptera: Formicidae) in Argentina. Redescription of the type species, *B. patagonicus* Mayr 1868; *B. bruchi* Forel, 1912 and *B. oculatus* Santschi, 1919. *Acta Zoologica Mexicana (n.s.), 20*: 273-285.

Rabello, A., Parr, C., Queiroz, A., Braga, D., Santiago, G. and Ribas, C. (2021) Taxonomic and functional approaches reveal different responses of ant assemblages to land-use changes. *Basic and Applied Ecology, 54*: 39-49. https://doi.org/10.1016/j.baae.2021.04.001.

Risch, S.J. and Carroll, R. (1982) Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical agroecosystem. *Ecology, 63:* 1979-1983.

R Development core team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.

Room, P. (1975) Diversity and organization of the ground foraging ant faunas of forest, grassland and tree crops in Papua New Guinea. *Australian Journal of Zoology, 23*: 71-89.

Sanabria, C., Lavelle, P. and Fonte, S.J. (2014) Ants as indicators of soil-based ecosystem services in agroecosystems of the Colombian Llanos. *Applied Soil Ecology, 84*: 24-30.

Santamaría, C., Armbrecht, I. and Lachaud, J. (2009) Nest distribution and food preferences of *Ectatomma ruidum* (Hymenop- tera: Formicidae) in shaded and open cattle pastures of Colombia. *Sociobiology, 53*: 517-541.

Savilaakso, S., García, C., Garcia-Ulloa, J., Ghazoul, J., Groom, M., Guariguata, M.R., Laumonier, Y., Nasi, R., Petrokofsky, G., Snaddon, J. and Zrust, M. (2014) Systematic review of effects on biodiversity from oil palm production. *Environmental Evidence, 3*: 4.

Schatz, B. and Lachaud, J. (2008) Effect of high nest density on spatial relationships in two dominant ectatommine ants (Hymenoptera: Formicidae). *Sociobiology, 51*: 623-643.

Serna, F. and Vergara, E. (2001) Claves para la identificación de subfamilias y géneros de hormigas de Antioquia y Chocó, Colombia. *Revista de I.C.N.E, 7*: 1.

Sodhi, N.S., Posa, M.R.C., Lee, T.M., Bickford, D., Koh L.P. and Brook, B.W. (2010) The state and conservation of Southeast Asian biodiversity. *Biodiversity and Conservation, 19*: 317-328.

Taylor, B. (1977) The ant mosaic on cocoa and other tree crops in Western Nigeria. *Ecological Entomology, 2*: 245-255.

Turner, E.C., Snaddon, J.L., Fayle, T.M. and Foster, W.A. (2008) Oil palm research in context: identifying the need for biodiversity assessment. *PLoS ONE, 3*: e1572.

Turner, E.C. and Foster, W.A. (2006) Assessing the influence of bird's nest ferns (*Asplenium* spp.) on the local microclimate across a range of habitat disturbances in Sabah, Malaysia. *Selbyana, 27*: 195-200.

Turner, E.C. and Foster, W.A. (2009) The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. *Journal of Tropical Ecology, 25*: 23-30.

Valdés-Rodríguez, S., Chacón de Ulloa, P. and Armbrecht, I. (2014) Especies de hormigas del suelo en el Parque Nacional Natural Gorgona, Pacífico Colombiano. *Revista de Biologia Tropical, 62*: 265-276.

van der Plas, F. (2019) Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews, 94*: 1220-1245.

Villalta, I., Oms, C.S., Angulo, E., Molinas, C., Devers, S., Cerdá, X. and Boulay, R. (2020) Does social thermal regulation constrain individual thermal tolerance in an ant species? *Journal of Animal Ecology, 89*: 2063-2076.

Wang, W.Y. and Foster, W.A. (2015) The effects of forest conversion to oil palm on ground-foraging ant communities depend on beta diversity and sampling grain. *Ecology and Evolution, 5*: 3159-3170.

Ward, P.S. (2000) Broad-scale patterns of diversity in leaf-litter ant communities. Ants: Standard Methods for Measuring and Monitoring Biodiversity. (ed. Agosti, D., Majer, J.D., Alonso, L.A. and Schultz, T.R), pp. 99-121. Smithsonian Institution Press, Washington, D.C.

Wilson, E.O. (2003) *Pheidole* in the New World: A dominant, hyperdiverse ant genus. Harvard University Press. Cambridge, United States. 297 pp.

Zenner, I. (1994) Hormigas depredadoras en el ecosistema de palma de aceite. *Palmas, 15*: 33-39.