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Diversity of ground-dwelling ants (Hymenoptera: Formicidae) in primary and secondary forests in Amazonian Ecuador

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Abstract

An inventory of the ground-dwelling ant faunas of primary and secondary forests at the Tiputini Biodiversity Station in Amazonian Ecuador revealed a total of 101 ant species in 32 genera. Eighty species were collected from the primary forest, while 65 species were collected from the secondary forest. Species overlap between the two sites was low (42.6%) and the composition was significantly different ($p < 0.0001$). Actual species richness was estimated to be 126 species for primary forest and 110 for secondary forest. The most species-rich genus in both habitats was *Pheidole* (21 species), which was also the most widespread genus, occurring in 38 of 40 collection sites. In the primary forest, in addition to *Pheidole* (18 species), the most species-rich genera were *Crematogaster* (8 species) and *Pachycondyla* (7 species), whereas *Pheidole* (17 species), *Camponotus* (5 species), and *Pachycondyla* (5 species) were the most species-rich genera in the secondary forest. These results are consistent with past studies showing that the number of ant species in secondary forest increases with time from disturbance and may approach that of primary forest within several decades, but that species composition may take significantly longer to resemble that of the original ant assemblage. The prevalence of different ant functional groups in the two habitats is discussed and the results compared to similar studies in Australia and North America.

Key words: Formicidae, biodiversity, distribution, species richness, conservation, ALL protocol, primary forest, secondary forest, functional groups, tropical rainforest.

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Introduction

The exceptional abundance and diversity of ants reaches its peak in the New World tropics (FITTKAU & KLINGE 1973, MACKAY & VINSON 1989, HÖLLDOBLER & WILSON 1990, BOLTON 1995, 2003, FERNANDEZ & SENDOYA 2004). The Amazon rainforest, in particular, is home to the greatest diversity of ants in the world (MITTERMEIER & MITTERMEIER 1997, MITTERMEIER & al. 1998, MYERS & al. 2000, FERNANDEZ & SENDOYA 2004). As primary tropical rainforests continue to diminish, it becomes increasingly important to understand the processes by which diversity is established and maintained in secondary forest. This is especially true in Ecuador, which suffers the highest deforestation rates in South America (MOSANDL & al. 2008). Because of their importance in community structure, their rapid response to environmental changes (MAJER 1983, ROTH & al. 1994), the extensive body of knowledge on their biology (HÖLLDOBLER & WILSON 1990), as well as the relative ease with which they can be collected and identified (AGOSTI & al. 2000), ants have often been used as indicators of biodiversity, disturbance, and health of secondary forests (BROWN 1991, OLSON 1991, BURBIDGE & al. 1992, MAJER 1992, ROTH & al. 1994, VASCONCELOS 1999, HOFFMANN & ANDERSEN 2003, ANDERSEN & MAJER 2004, DELABIE & al. 2006, MAJER & al. 2007, SILVA & al. 2007).

Lowland primary tropical rainforests generally have higher ant species richness than secondary (re-growth) forest, although richness increases with time since disturbance (OLSON 1991, FLOREN & al. 2001, DUNN 2004a, 2004b, FLOREN & LINSENMAIR 2005, MATHIEU & al. 2005, SILVA & al. 2007). Full recovery of species richness is estimated at 25 - 40 years (CABRERA & al. 1998, DUNN 2004a, 2004b), although recovery of original species assemblages may require more than 100 years (BIHN & al. 2006). Few studies on the recovery of ant faunas have been conducted in South America (CABRERA & al. 1998, BUSTOS & ULLOA-CHACON 1997, VASCONCELOS & al. 2000, KALIF & al. 2001, HITES & al. 2005, SILVA & al. 2007), and there appears to be little known about ant species richness in primary or secondary lowland rainforest in western Amazonia, a biodiversity hotspot (MITTERMEIER & MITTERMEIER 1997, MITTERMEIER & al. 1998, MYERS & al. 2000).

Here we present the results of a survey of ant diversity in lowland rainforest in western Amazonia. We estimated the diversity of epigaeic ants in a primary and secondary forest at the Tiputini Biodiversity Station (TBS) in Amazonian Ecuador. First, we surveyed the species richness of ants at TBS using the ALL protocol (AGOSTI & al. 2000) to enable comparisons with related faunal studies. Second, we compared ground-dwelling ant species diversity and overlap between primary and secondary forest. Based on past studies (CABRERA & al. 1998, DUNN 2004a, 2004b, BIHN & al. 2006) and the age of our secondary forest (14 years),

we expected there to be a significant difference in species diversity between sites, and that species overlap would be low. Lastly, we were interested in the effect of disturbance on ant functional groups, which provide a useful framework to understand ant community dynamics, especially in relation to disturbance (HOFFMANN & ANDERSEN 2003). Although several studies have examined the response of ant functional groups to disturbance in Australia, North America, and South Africa (ANDERSEN 1997, HOFFMANN & ANDERSEN 2003, MAJER & al. 2004), very little is known about environmental variation in ant functional groups in South America.

Site description and methods

Ants were collected at the Tiputini Biodiversity Station (TBS) in the western Amazonian rainforest between 9 February and 8 March 2002. TBS is located in Orellana Province, Ecuador (0° 37' 55" S and 76° 08' 39" W, altitude 230 m, annual rainfall ≈ 3000 mm) and borders Yasuní National Park. The study site is predominantly primary lowland rainforest but also includes a nearby (~ 300 m) secondary forest patch. The secondary forest was the result of 14 years of re-growth at the former site of a helicopter pad (K. Swing, pers. comm.). Based on the existence of similar helipads in the vicinity (VALENCIA & al. 2004), we estimate the size of the patch to be approximately 0.5 ha. The primary forest has a diverse tree community dominated by the palm *Iriartea deltoidea* (see PITMAN & al. 2001), while the secondary forest is dominated by *Cecropia sciadophylla* (see VALENCIA & al. 2004).

We used a variation of the ALL protocol (AGOSTI & al. 2000), which is commonly used in studies of tropical ant diversity. A 200 m transect was established in the primary forest, and another in the secondary forest. The two transects were divided into 20 collection sites (0.5 m^2), each 10 m apart. Three collection methods were used to sample ant diversity in the two habitats: pitfall traps, litter sampling, and baiting.

Pitfall traps made of plastic containers (diameter = 9 cm, volume = 400 ml) were filled with approximately 130 ml of 96% isopropanol (n = 20 per site). After 48 hours, the contents were collected and stored for future study. Litter sampling was also carried out using the same transect format by quickly removing loose leaf litter from 0.5 × 0.5 m quadrats at each site and placing the samples in a smooth-sided bucket. Litter was then hand-sorted to collect surface ants. Bait (cookie crumbs) was placed in the center of the cleared site and for a period of 30 minutes all ground-dwelling ants attracted to the food were collected (n = 20 per site).

To supplement baiting, new transects of 100 m divided into 10 collection sites 10 m apart were established 50 m from the original 200 m transect in both types of forest. A selection of cracker crumbs, peanut butter, and tuna was set out to bait ants for a total of 90 minutes. One worker of each species of ant present at baits was collected every 30 minutes. These transects were repeated day and night (n = 10 per site).

Specimens were identified to species using available keys (BROWN 1958, KEMPF 1973, BROWN 1976, 1978, KUGLER & BROWN 1982, WATKINS 1985, BRANDÃO 1990, DINIZ 1990, MACKAY 1993, LATTKE 1995, FERNANDEZ 2003, WILSON 2003, FERNANDEZ 2006) or were identified by experts (Stefan Cover - *Solenopsis*; Shawn Dash - *Hypoponera*; Stephanie Johnson - *Azteca*; John Longino - *Crematogaster*, *Wasmannia*; William Mackay - *Camponotus*, *Pachycondyla*; Ted Schultz - *Apterostigma*, *Cyphomyrmex*, *Mycocepurus*, *Sericomyrmex*, *Trachymyrmex*; Jeffery Sosa-Calvo - *Myrmicocrypta*, *Pyramica*, *Strumigenys*; James Trager - *Paratrechina*). Whenever possible, ants were compared to specimens in the collection of the Harvard Museum of Comparative Zoology (MCZ), where vouchers have been deposited.

Species accumulation curves and richness estimators were calculated using the Mao Tau method (100 replicates) in EstimateS 8.0 (COLWELL 2005). All samples (pitfall, litter, and baiting) were used to create the curves (n = 50 for each site). HORTAL & al. (2006) recommend 4 indicators of species richness equally (ICE, Jackknife1, Jackknife2, and Chao2) for the most accurate results with this type of data. BROSE & al. (2003) recommend Jackknife2 as the most reliable of these four indicators when all indicators suggest sampling coverage is 50 - 74% of species, therefore we used Jackknife2 to estimate actual species richness. Nonparametric estimators such as Jackknife2 provide an estimate of the actual richness of which, while not exact, allows us to more accurately compare richness between our primary and secondary sites that may differ in density. Similarity in species composition between the two habitats was compared using the Jaccard Similarity Index and Analysis of Similarity (ANOSIM). Jaccard's index comparisons were obtained from EstimateS using combined litter and pitfall samples (n = 20 per site). Baiting data were excluded from this analysis as baiting was conducted on a separate transect, with only 10 samples. ANOSIM was calculated from Bray-Curtis Similarity Index values using the PAST software package (version 1.82, HAMMER & al. 2001). Bray-Curtis was chosen as a widely used and well-tested index for incidence data (CLARKE & WARWICK 2001, MAGURRAN 2004).

Ant genera were classified into seven functional groups (Cryptic Species, Dominant Dolichoderinae, Generalized Myrmicinae, Opportunists, Specialist Predators, Subordinate Camponotini, and Tropical Climate Specialist) according to ANDERSEN (1995, 2000), BROWN (2000), and TOBIN (1994). In cases of uncertainty or lack of prior categorization, we used information on foraging ecology and behavior to classify genera. For *Solenopsis*, *S. virulens* (SMITH, 1858) was classified as a Tropical Climate Specialist whereas other *Solenopsis* were categorized as Cryptic Species based on their ecology.

Results

A total of 101 ant species in 32 genera were collected from the primary and secondary forests at TBS (Fig. 1). Primary forest samples included 80 species in 25 genera, while the secondary forest samples included 65 species in 29 genera (Tab. 1). The most species-rich genus in both habitats was *Pheidole* (21 species). In the primary forest, the most species-rich genera were *Pheidole*, *Camponotus*, *Pachycondyla*, and *Crematogaster*, in decreasing order. In the secondary forest the most common genera were *Pheidole*, *Pachycondyla*, *Crematogaster*, and *Megalomyrmex*, in decreasing order. Genera collected in primary but not secondary forest included *Anochetus*, *Pyramica*, *Sericomyrmex*, and *Solenopsis*. Genera collected in secondary

Tab. 1: List of species collected at Tiputini. Values indicate the sampling incidence of each species out of 50 samples.

Species	Pri.	Sec.
Anochetus diegensis FOREL, 1912	1	0
Apterostigma auriculatum WHEELER, 1925	1	0
Apterostigma sp. 2	0	1
Apterostigma sp. 4	1	0
Azteca sp. SJ-A	0	1
Azteca sp. SJ-B	0	1
Brachymyrmex cavernicola WHEELER, 1938	1	10
Brachymyrmex sp. KTRW-001	3	0
Camponotus atriceps (SMITH, 1858)	1	3
Camponotus bispinosus MAYR, 1870	1	1
Camponotus cacicus EMERY, 1903	1	2
Camponotus femoratus (FABRICIUS, 1804)	31	7
Camponotus integellus FOREL, 1899	1	1
Camponotus nidulans (SMITH, 1860)	1	0
Carebara urichi (WHEELER, 1922)	0	2
Crematogaster acuta (FABRICIUS, 1804)	1	0
Crematogaster brasiliensis MAYR, 1878	0	2
Crematogaster carinata MAYR, 1862	3	0
Crematogaster erecta MAYR, 1866	1	0
Crematogaster flavomicrops LONGINO, 2003	2	0
Crematogaster levior LONGINO, 2003	3	12
Crematogaster limata SMITH, 1858	4	9
Crematogaster sotobosque LONGINO, 2003	1	2
Crematogaster stollii FOREL, 1885	2	0
Cyphomyrmex cf. *rimosus* (SPINOLA, 1851)	2	0
Cyphomyrmex laevigatus WEBER, 1938	0	2
Dolichoderus imitator EMERY, 1894	0	1
Dolichoderus inpai (HARADA, 1987)	3	0
Dolichoderus rugosus (SMITH, 1851)	1	0
Ectatomma edentatum ROGER, 1863	0	2
Ectatomma lugens EMERY, 1894	1	6
Gigantiops destructor (FABRICIUS, 1804)	0	1
Gnamptogenys horni (SANTSCHI, 1929)	1	0
Gnamptogenys sp. KTRW-001	6	4
Gnamptogenys moelleri (FOREL, 1912)	1	1
Gnamptogenys striatula MAYR, 1884	4	1
Hylomyrma blandiens KEMPF, 1961	3	0
Hylomyrma dolichops KEMPF, 1973	6	0
Hylomyrma immanis KEMPF, 1973	2	1
Hypoponera cf. *creola* (MENOZZI, 1931)	5	2
Hypoponera cf. *distinguenda* (EMERY, 1890)	1	0
Hypoponera perplexa (MANN, 1922)	1	1
Hypoponera sp. STD-11	2	0
Labidus praedator (SMITH, 1858)	2	0
Labidus spininodis (EMERY, 1890)	1	2
Megalomyrmex foreli EMERY, 1890	12	18
Megalomyrmex silvestrii WHEELER, 1909	0	1
Mycocepurus smithii (FOREL, 1893)	1	1
Myrmicocrypta cf. *rudiscapa* EMERY, 1913	0	1
Nomamyrmex esenbeckii (WESTWOOD, 1842)	0	1
Ochetomyrmex neopolitus FERNÁNDEZ, 2003	2	1
Ochetomyrmex semipolitus MAYR, 1878	1	0
Odontomachus haematodus (LINNAEUS, 1758)	2	0
Odontomachus meinerti FOREL, 1905	4	2
Odontomachus panamensis FOREL, 1899	0	1
Pachycondyla apicalis (SMITH, 1857)	1	0
Pachycondyla arhuaca (FOREL, 1901)	1	0
Pachycondyla constricta (MAYR, 1884)	9	3
Pachycondyla crassinoda (LATREILLE, 1802)	17	23
Pachycondyla harpax (FABRICIUS, 1804)	5	6
Pachycondyla laevigata (SMITH, 1858)	1	0
Pachycondyla marginata (ROGER, 1861)	1	0
Pachycondyla obscuricornis EMERY, 1890	0	2
Pachycondyla verenae (FOREL, 1922)	0	1
Paratrechina cf. *steinheili* (FOREL, 1893)	4	5
Paratrechina sp. KTRW-001	3	0
Pheidole sp. ALM-006	3	1

Pheidole sp. ALM-013	1	0
Pheidole sp. ALM-025	4	1
Pheidole amazonica WILSON, 2003	4	1
Pheidole araneoides WILSON, 2003	1	2
Pheidole astur WILSON, 2003	18	7
Pheidole biconstricta MAYR, 1870	12	2
Pheidole cephalica SMITH, 1858	1	1
Pheidole deima WILSON, 2003	4	2
Pheidole fimbriata ROGER, 1863	0	2
Pheidole fracticeps WILSON, 2003	2	0
Pheidole gagates WILSON, 2003	0	1
Pheidole horribilis WILSON, 2003	4	1
Pheidole laidlowi MANN, 1916	0	1
Pheidole midas WILSON, 2003	4	6
Pheidole nitella WILSON, 2003	13	7
Pheidole peruviana WILSON, 2003	8	1
Pheidole sagax WILSON, 2003	4	0
Pheidole triplex WILSON, 2003	2	1
Pheidole tristicula WILSON, 2003	2	0
Pheidole xanthogaster WILSON, 2003	3	10
Pyramica denticulata (MAYR, 1887)	1	0
Sericomyrmex sp. 1	2	0
Sericomyrmex sp. 2	2	0
Solenopsis sp. SC-08	1	0
Solenopsis virulens (SMITH, 1858)	2	0
Stegomyrmex manni SMITH, 1946	0	1
Strumigenys dolichognatha WEBER, 1934	0	2
Strumigenys incuba BOLTON, 2000	1	0
Trachymyrmex cf. *bugnioni* (FOREL, 1912)	2	1
Trachymyrmex cf. *opulentus* (MANN, 1922)	0	1
Trachymyrmex farinosus (EMERY, 1894)	2	4
Trachymyrmex ruthae WEBER, 1937	1	1
Tranopelta subterranea (MANN, 1916)	0	2
Wasmannia auropunctata (ROGER, 1863)	7	9

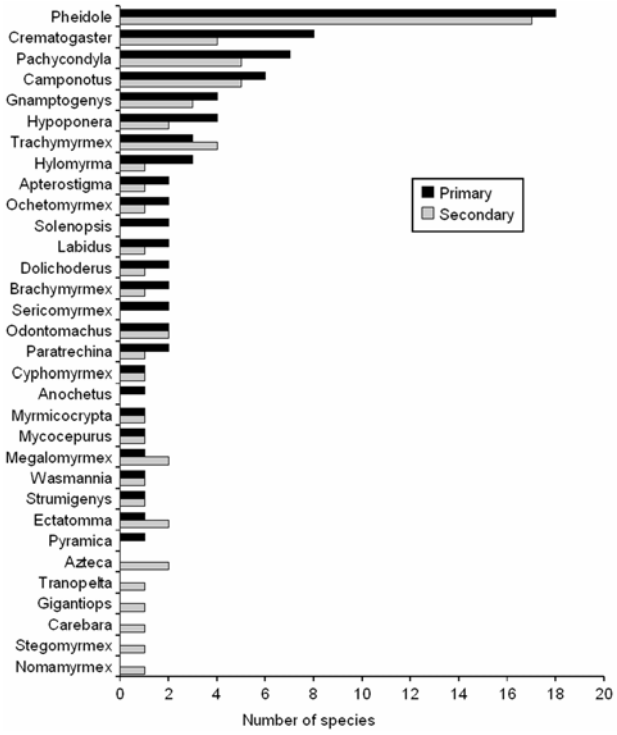

Fig. 1: Species richness (by genus) in primary and secondary forest. Genera are ranked in decreasing order of richness in primary forest.

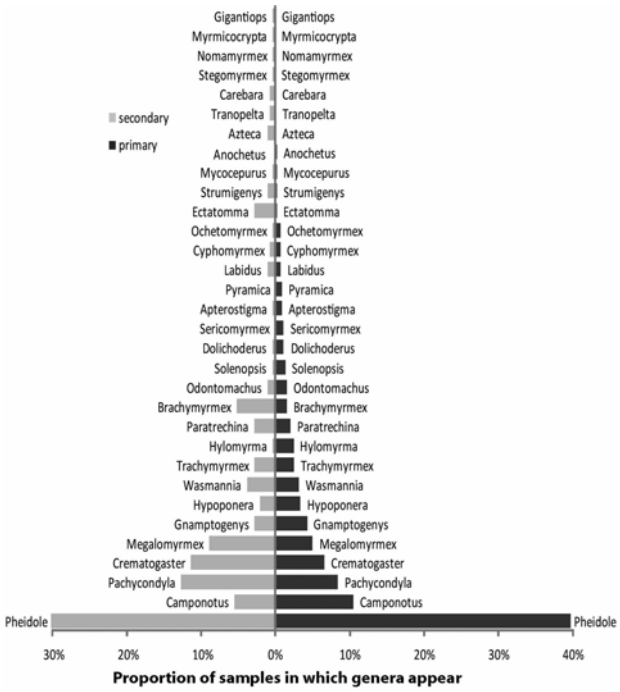

Fig. 2: Comparison of primary and secondary forest habitats using matched ranked abundance plots. Genera are arranged along the y-axis with the most abundant genera in primary forest at the bottom. Abundance measurements are based on presence / absence data of genera in all samples.

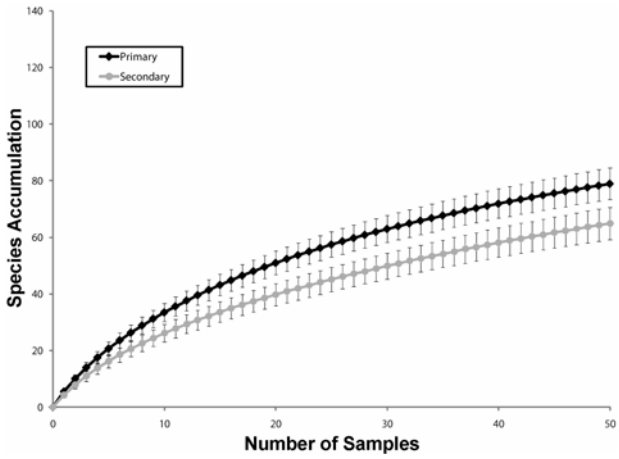

Fig. 3: Species accumulation curves in primary and secondary forest. Standard deviations based on Mao Tau.

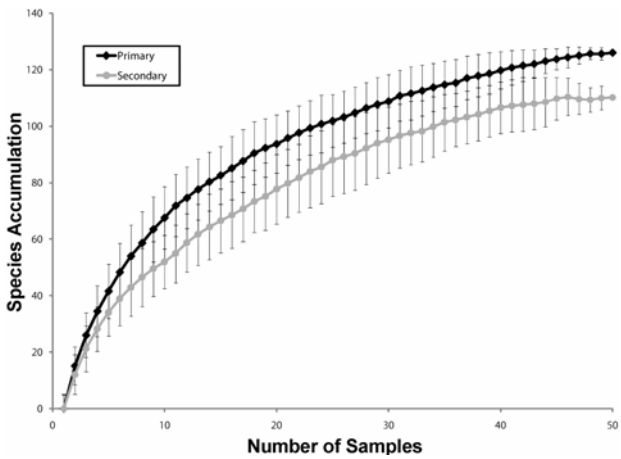

Fig. 4: Estimated species richness (with standard deviations) in primary and secondary forest based on Jackknife 2 index of similarity. Actual species richness is estimated to be 126 (primary) and 110 (secondary).

but not primary forest included *Azteca*, *Carebara*, *Gigantiops*, *Myrmicocrypta*, *Nomamyrmex*, *Stegomyrmex*, and *Tranopelta* (Fig. 1). Genera that appear to be more abundant in one habitat and less abundant in the other include *Ectatomma* and *Brachymyrmex* (in the secondary forest) and *Camponotus* and *Hylomyrma* (in primary forest; Fig. 2).

Species accumulation curves were similar in shape for both habitats (Fig. 3). Neither curve appeared to reach an asymptote, indicating that the survey did not near completion. Actual species richness was estimated to be 126 (primary forest) and 110 (secondary forest) (Fig. 4).

Overlap of species in the two habitats was low: of 101 species, 43 were found in both habitats (42.6%). ANOSIM calculations using the Bray Curtis similarity index show this difference to be significant ($p < 0.0001$, $R = 0.3287$).

Seven of nine functional groups were found in both habitats (Tab. 2). Hot Climate Specialists and Cold Climate Specialists were not collected in either habitat. Three functional groups (Tropical Climate Specialist, Generalized Myrmicinae, Subordinate Camponotini) were less prevalent in secondary forest (Fig. 5, $p < 0.005$). Other differences were not significant.

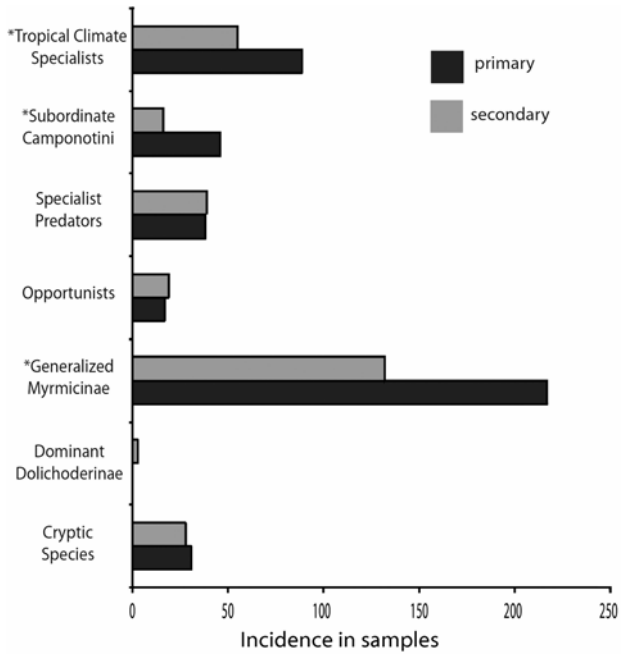

Fig. 5: Incidence of ant functional groups in samples collected in primary and secondary forest: * indicates a significant ($p < 0.005$) difference.

Discussion

Our results support the prediction that ant diversity is greater in undisturbed primary forest than in secondary forest. Eighty species were collected from the primary forest, while 65 species were collected from secondary forest. We also found species overlap between the two sites to be low (42.6%) and the composition to be significantly different, again supporting our prediction. The number of ant species in secondary forest can increase with increasing time from disturbance, approaching levels of the original primary forest within several decades (MAJER 1996, CABRERA & al. 1998, DUNN 2004a, 2004b, SILVA & al. 2007). The composition of those ant assemblages, however, may take significantly longer to recover to pre-disturbance levels (BIHN & al. 2006). Our results are in agreement with past studies.

In a review of 45 studies, HOFFMANN & ANDERSEN (2003) used functional groups as a framework to understand responses to disturbance in Australian ant communities, characterizing ant genera as Increasers or Decreasers based on their response to disturbance. The distribution of functional groups at TBS is similar, with a few notable exceptions. As in Australia, Opportunists and Dominant Dolichoderinae were commonly found to be Increasers at Tiputini, while Cryptic Species, Subordinate Camponotini, and Generalized Myrmicinae were generally Decreasers (Tab. 2). Specialist Predators showed a weak tendency to decrease in numbers in Australia across all habitats surveyed, while at Tiputini they were nearly evenly distributed in primary and secondary forests. Tropical Climate Specialists at Tiputini were shown to be strong Decreasers, but were not analyzed in the Australian study. Although our observations of functional group responses paralleled the results of the Australian study, the changes at Tiputini in the prevalence of

Tab. 2: Distribution of genera in functional groups in primary and secondary forests. LS = litter sampling. Descriptions of ant functional groups can be found in HOFFMANN & ANDERSEN (2003).

Functional Group	Genus	Primary			Total	Secondary			Total
		Bait	LS	Pitfall		Bait	LS	Pitfall	
Cryptic Species	*Brachymyrmex*	1	6	0	7	3	12	0	15
	Carebara	0	0	0	0	0	2	0	2
	Hypoponera	0	15	0	15	0	6	0	6
	Pyramica	0	4	0	4	0	0	0	0
	Solenopsis	1	2	1	4	0	1	0	1
	Stegomyrmex	0	0	0	0	0	1	0	1
	Strumigenys	0	1	0	1	0	3	0	3
Total		2	28	1	**31**	3	25	0	**28**
Domin. Dolichoderinae	*Azteca*	0	0	0	0	0	3	0	3
Total		0	0	0	**0**	0	3	0	**3**
Generalized Myrmicinae	*Crematogaster*	4	14	11	29	9	21	3	33
	Pheidole	27	105	42	174	10	59	19	88
	Wasmannia	4	8	2	14	3	8	0	11
Total		35	127	55	**217**	22	88	22	**132**
Opportunists	*Ectatomma*	0	0	1	1	1	2	5	8
	Odontomachus	1	5	1	7	1	1	1	3
	Paratrechina	1	6	2	9	3	5	0	8
Total		2	11	4	**17**	5	8	6	**19**
Specialist Predators	*Anochetus*	0	1	0	1	0	0	0	0
	Pachycondyla	1	19	17	37	7	15	15	37
	Tranopelta	0	0	0	0	1	1	0	2
Total		1	20	17	**38**	8	16	15	**39**
Subordin. Camponotini	*Camponotus*	12	11	23	46	9	3	4	16
Total		12	11	23	**46**	9	3	4	**16**
Tropical Climate Specialist	*Apterostigma*	0	4	0	4	1	0	0	1
	Cyphomyrmex	0	3	0	3	0	2	0	2
	Dolichoderus	4	1	0	5	1	0	0	1
	Gigantiops	0	0	0	0	1	0	0	1
	Gnamptogenys	2	12	5	19	0	2	6	8
	Hylomyrma	1	5	5	11	0	1	0	1
	Labidus	0	0	3	3	0	0	3	3
	Megalomyrmex	9	6	7	22	11	8	7	26
	Mycocepurus	0	1	0	1	0	1	0	1
	Myrmicocrypta	0	0	0	0	0	1	0	1
	Nomamyrmex	0	0	0	0	0	0	1	1
	Ochetomyrmex	2	1	0	3	0	1	0	1
	Sericomyrmex	0	3	2	5	0	0	0	0
	Solenopsis	2	0	0	2	0	0	0	0
	Trachymyrmex	3	6	2	11	1	7	0	8
Total		23	42	24	**89**	15	23	17	**55**

only three functional groups – decreasing numbers of Generalized Myrmicinae, Subordinate Camponotini, and Tropical Climate Specialists – were statistically significant. *Camponotus*, the sole representative of the Subordinate Camponotini, shows slightly greater richness in primary habitat (6 species to 5) but a much greater abundance differential (11% to 5%; Fig. 2). This is almost entirely due to a single species, *C. femoratus* (FABRICIUS, 1804). As an arboreal

species in need of thicker clumps of epiphytes and larger pieces of dead wood for nesting (SCHONBERG & al. 2004), *C. femoratus* clearly prefers primary forest. However, removing *C. femoratus* from abundance calculations shows *Camponotus* to be five times more abundant in secondary forest (5%) than in primary forest (1%).

At Tiputini, ant species tended to decrease in numbers in response to disturbance. The two exceptions were Opportunists, which by definition thrive in disturbed habitats, and Dominant Dolichoderinae, represented by the single genus *Azteca,* which was only collected in secondary forest. The close association between *Azteca* and *Cecropia* trees (LONGINO 1991a, 1991b), the dominant vegetation type in secondary forest at Tiputini (VALENCIA & al. 2004), explains their prevalence in secondary forest. Interestingly, a similar study (MAJER 1996) in Brazilian rainforest found no *Azteca* in the only secondary plot dominated by *Cecropia*, despite their presence in other secondary plots.

Functional groups in the South American ant fauna do not consistently correlate within those of Australia. For instance, fungus-growing ants (Tribe Attini) have no Australian equivalent, yet appear to play a major role in Amazonian community ecology. In other cases, analogous fauna exist in Australia, but differ in prominence, such as the less prevalent Dominant Dolichoderinae or more dominant Subordinate Camponotini. Nevertheless, the current functional group model, originally based on Australian fauna, has been applied to the ant faunas of North America (ANDERSEN 1997), South Africa (HOFFMANN & ANDERSEN 2003), and rainforest ants globally (ANDERSEN 2000). While an Amazon-specific model of ant functional groups could include separate categories for army ants and fungus-growing ants and might better discern patterns and relationships among species, any functional group system used to make comparisons across geographic regions is likely to compromise detail (ANDERSEN 2000). Functional groups of different regions nevertheless appear to respond to disturbance in similar ways (ANDERSEN 2000). Our study supports these emergent global patterns.

Our study of ground-dwelling ant species richness in primary and secondary forest at TBS represents the first published standardized inventory of ants in lowland rainforest in Ecuadorian western Amazonia. It is nevertheless a preliminary inventory because we did not survey ants in the canopy or below ground. Our previous study, which focused only on subterranean ant diversity at TBS, recorded 47 species (RYDER WILKIE & al. 2007). At adjacent Yasuni National Park, a pilot study of total ant species richness found 109 species (M. Kaspari, pers. comm.). Surveys of the ant fauna of other neotropical habitats include Cuzco-Amazonico, Peru (365 species, TOBIN 1995), Urubamba River Valley, Peru (124 species, ALONSO & al. 2001), Panguana, Peru (520 species, VERHAAGH 1990), Brazilian Amazon (156 species, MAJER & DELABIE 1994; 143 species, VASCONCELOS & al. 2000), Brazilian Atlantic forest (124 species, SILVA & al. 2007), tropical Brazilian forests (206 species, MAJER 1996; 74 species, FOWLER & al. 2000), secondary growth Brazilian tropical forest (124 species, DELABIE & FOWLER 1995), and lowland rainforest in Costa Rica (437 species, LONGINO & al. 2002). These studies vary widely in effort, collection methods, purpose, and identification levels, rendering meaningful comparisons difficult. Our survey of the ants of Tiputini will soon include subterranean and canopy ants (K.T. Ryder Wilkie & al. unpubl.), enabling more detailed comparisons among Amazonian and other tropical ant faunas.

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Zusammenfassung

Eine Bestandsaufnahme der auf der Bodenoberfläche lebenden Ameisenfauna eines Primär- und eines Sekundärwaldes bei der Tiputini Biodiversity Station im Amazonasgebiet Ecuadors ergab insgesamt 101 Arten aus 32 Gattungen. Achtzig Arten wurden im Primärwald gesammelt, 65 Arten im Sekundärwald. Die Überlappung der Arteninventare der beiden Lebensräume war gering (42,6 %) und die Artenzusammensetzungen unterschieden sich signifikant ($p < 0.0001$). Der tatsächliche Artenreichtum wurde für den Primärwald auf 126 Arten, für den Sekundärwald auf 110 Arten geschätzt. Die artenreichste Gattung war in beiden Lebensräumen *Pheidole* (21 Arten) und diese Gattung war auch die in den beiden Lebensräumen insgesamt am weitesten verbreitete, mit Nachweisen an 38 der 40 Sammelstellen. Die artenreichsten Gattungen waren im Primärwald *Pheidole* (18 Arten), *Crematogaster* (8 Arten) und *Pachycondyla* (7 Arten), im Sekundärwald waren dies *Pheidole* (17 Arten), *Camponotus* (5 Arten), und *Pachycondyla* (5 Arten). Diese Befunde passen zu den Ergebnissen anderer Studien, die gezeigt haben, dass die Zahl der Arten in Sekundärwäldern nach Ausbleiben der Störung fortschreitend zunimmt und sich nach einigen Dekaden jener von Primärwäldern annähern kann, dass es aber deutlich länger brauchen dürfte, bis die Artenzusammensetzung wieder jener der ursprünglichen Artengemeinschaft ähnelt. Das Vorherrschen verschiedener funktioneller Gruppen von Ameisen in den beiden Lebensräumen wird diskutiert und die Ergebnisse werden mit ähnlichen Studien aus Australien und Nordamerika verglichen.

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