

Impact of Flooding on the Species Richness, Density and Composition of Amazonian Litter-Nesting Ants

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ABSTRACT

Litter-nesting ants are diverse and abundant in tropical forests, but the factors structuring their communities are poorly known. Here we present results of the first study to examine the impact of natural variation in flooding on a highly diverse (21 genera, 77 species) litter-nesting ant community in a primary Amazonian forest. Fifty-six 3 × 3 m plots experiencing strong variation in flooding and twenty-eight 3 × 3 m terra firme plots were exhaustively searched for litter-nesting ants to determine patterns of density, species richness and species composition. In each plot, flooding, litter depth, twig availability, canopy cover, plant density, percent soil nitrogen, carbon, and phosphorus were measured. Degree of flooding, measured as flood frequency and flood interval, had the strongest impact on ant density in flooded forest. Flooding caused a linear decrease in ant abundance, potentially due to a reduction of suitable nesting sites. However, its influence on species richness varied: low-disturbance habitat had species richness equal to terra firme forest after adjusting for differences in density. The composition of ant genera and species varied among flood categories; some groups known to contain specialist predators were particularly intolerant to flooding. *Hypoponera* STD10 appeared to be well-adapted to highly flooded habitat. Although flooding did not appear to increase species richness or abundance at the habitat scale, low-flooding habitat contained a mixture of species found in the significantly distinct ant communities of terra firme and highly flooded habitat.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: Formicidae; Hymenoptera; *Hypoponera*; intermediate disturbance; litter ants; *Pheidole*; terra firme forest.

ANTS ARE DIVERSE, ABUNDANT AND ECOLOGICALLY IMPORTANT in tropical ecosystems (Fittkau & Klinge 1973, Adis *et al.* 1984, Wilson 1987, Folgarait 1998, Brühl *et al.* 2000), yet the factors that structure their communities are poorly understood. Tropical ant diversity is high in the leaf litter (Byrne 1994, Kaspari 1996a, Agosti *et al.* 2000), and litter-ant communities have frequently been used to compare ant diversity among sites or habitats (Belshaw & Bolton 1993, Fisher 1999, Ward 2000). Litter-nesting ants are a particularly useful group for community level comparisons because litter can be exhaustively searched, providing accurate data on nest density and species richness regardless of weather. The impact of disturbance on litter-ant communities has only begun to be examined (Vasconcelos 1999, Kaspari *et al.* 2003).

Disturbance can strongly affect community structure (Abugov 1982, Petraitis *et al.* 1989, Huston 1994, Rosenzweig 1995) and reduce diversity (Bobbink *et al.* 1998, Levine 2000), but may also be vital to its maintenance (Petraitis *et al.* 1989, Rosenzweig 1995). The preeminent theoretical explanation of the positive effects of disturbance on diversity is the intermediate disturbance hypothesis (IDH; Hutchinson 1953, Connell 1978), which states that moderate levels of disturbance might increase diversity by facilitating the coexistence of colonizing species and competitively dominant climax species. However, only 16 percent of studies on 116 disturbance gradients support the IDH (Mackey & Currie 2001), demonstrating that disturbance does not have consistent, predictable effects across faunal groups and ecological systems.

Most studies on the effects of disturbance on ant communities have examined anthropogenic factors; examples include logging

(Floren *et al.* 2001), agriculture (Bestelmeyer & Wiens 1996, Vasconcelos 1999, Perfecto *et al.* 2003), pollution (Hoffmann *et al.* 2000), mining (Andersen 1993), burning (Andersen 1991), and forest fragmentation (Carvalho & Vasconcelos 1999, Brühl *et al.* 2003). Likewise, most studies do not support the IDH, particularly those on litter-ant communities (Belshaw & Bolton 1993, Vasconcelos *et al.* 2000, Kalif *et al.* 2001, Watt *et al.* 2002, Armbricht & Perfecto 2003, Brühl *et al.* 2003). The effects of natural disturbance on ants, other than the aftermath of temperate forest fires (York 1994, Ratchford *et al.* 2005, Rodrigo & Retana 2006), have rarely been examined. Tropical litter-nesting ants are exposed to a broad array of environmental disturbances such as treefalls (Feener Jr & Schupp 1998), army ant predation (Franks & Bossert 1984, Kaspari & O'Donnell 2003), and periodic flooding (Majer & Delabie 1994). While litter-ant communities appear resilient to short-term litter disturbance such as manual removal (Kaspari 1996a) or trampling (McGlynn 2006) of the litter over the course of a few months, the long-term impacts of a periodic natural disturbance such as flooding are not well understood.

All studies that have examined the impact of flooding on ant diversity have focused on severe or seasonal flooding. Ant richness decreased after a major flood in Australian red gum forest; the impact was stronger in areas submerged for longer periods of time (Ballinger *et al.* 2007). The seasonal flooding that characterizes *varzea* rainforests has also been found to have a striking impact on leaf-litter communities. Invertebrates, including ants, are generally less species rich in *varzea* forest (Majer & Delabie 1994, Adis & Junk 2002). Litter-nesting ants may be particularly sensitive to flooding; twig-nesting *Pheidole* species, for example, show a stronger nest-evacuation response to the presence of water at their nests than soil-nesting species (Wilson 1986). However, not all floodplain forests experience extended seasonal floods. Low

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elevation riparian habitats in Amazonia experience temporary flooding after heavy rains (Burnham 2002). Intervals between flooding vary with elevation and distance from rivers, creating quantifiable variation in disturbance onto which species and nest density can be mapped.

We investigated the impact of a natural flooding on tropical ant diversity by surveying litter-nesting ants in floodplain and terra firme habitat in Amazonian Ecuador. Our study had two goals: (1) to determine the effect of flooding on the density of litter-nesting ants relative to other environmental variables; and (2) to compare the abundance, richness and species composition of litter-nesting ants between floodplain forest and terra firme forest.

METHODS

STUDY SITE.—Research was conducted at Tiputini Biodiversity Station (TBS), Orellana, Ecuador ($0^{\circ}37'55''$ S, $76^{\circ}08'39''$ W, 230 m asl; annual rainfall *ca* 3000 mm, 650 ha), bordering Yasuní National Park. This predominantly lowland rainforest has a diverse tree community dominated by the palm *Iriartea deltoidea* (Pitman *et al.* 2001). The Tiputini River, a tributary of the Napo River, forms the southern boundary of the station and has a wide floodplain stretching over 70 m into the forest at its maximum (A.L. Mertl, pers. obs.). The station is remote and thus has experienced minimal anthropogenic disturbance. Total ant richness at TBS is estimated at over 500 species (Ryder Wilkie *et al.* 2007). TBS experiences a drier season from October to April and a wetter season from May to September, although no month receives < 100 mm of rainfall (Bonaccorso *et al.* 2007).

Flooded forest at TBS is not equivalent to *varzea* forest. Floodplains at TBS are frequently flooded for short periods, typically when the height of rivers and streams rise after heavy rains (Burnham 2002). These floods create a temporary pool of standing water, completely submerging the litter, which remains after the water recedes, now coated in a thin layer of mud (Fig. S1). Due to topographic variation, not all floodplains flood at the same river height; those that require a higher river level to flood consequently flood less often.

SURVEYING THE LITTER-NESTING ANT FAUNA.—In January 2004 we selected six floodplain sites (Sites 1–6) and three nonflooding terra firme sites (Sites 7–9; Table S1). Within each site, four to twelve 3×3 m plots were established (total = 84 plots, 56 in floodplains, 28 in terra firme). Plots were separated by a minimum of 5 m to ensure independent samples (Byrne 1994, McGlynn 2006). The number of plots per site varied due to natural variation in the size of floodplains (*ca* 200–1000 m²). Plot locations were chosen at random within each site by tossing a pen and moving 5–10 m in the direction indicated, based on the distance necessary to allow for a minimum of 5 m between all plots and between plots and the edges of floodplains. If, due to the position of previous plots, there was no open space within 5–10 m, a new direction was determined. We also adjusted plot positions to avoid trees with dbh > 10 cm to equalize ground surface area (Byrne 1994). Because trees < 10 cm dbh were impossible to avoid, we included plant density in our measures of environmental variation. All litter within the 84 plots (total = 756 m²) was exhaustively searched for ant nests (a nest containing adults and larvae). Nests found in twigs, between leaves, or

inside nuts and seedpods were considered litter nests. Founding queens with larvae were also considered nests, although only nine (3% of nests) were found. Queens without larvae (rarely collected) were not counted as colonies because insemination was not determined. Queens and workers without larvae were never found. We examined every piece of litter down to bare soil, searching for 4–10 person-hours in each plot, depending on litter depth.

Ants were preserved in 70 percent ethanol and identified to species or morphospecies. Species determinations were made using type specimens at the Harvard Museum of Comparative Zoology (MCZ) or were sent to experts for confirmation. Vouchers were deposited at the MCZ.

QUANTIFYING FLOODING DISTURBANCE.—We surveyed litter-nesting ants during the drier season at TBS when flooding is less frequent. However, occasional floods can occur unpredictably. We attempted to minimize the potential bias of these floods by distributing the dates of sampling for plots within each site over the 3-mo period. For each site, half of the plots were sampled January 28–February 16, 2004, and remaining plots were sampled March 16–28, 2004. Sample dates were chosen at the start of the field season, without knowing when floods would occur. We recorded incidents of flooding to ensure nonflooding and rarely flooding sites were not preferentially sampled when other floodplain sites were underwater. Only one flood, high enough to cover three sites (Sites 1, 2 and 3) for 3 d, occurred during sampling. Six dry plots were sampled during this flood, the remainder of the 84 plots were sampled when all plots were dry.

We estimated degree of flooding disturbance for each plot in two ways: (1) flood frequency (total number of floods during a 5-yr period); and (2) flood interval (days between the date each plot was sampled and the date of the flood that occurred immediately before sampling). To quantify flooding, we monitored the six flooding sites from January to March 2004 and July to August 2004, recording the height of the Tiputini River at an established reference point during floods. River height was recorded for a minimum of three floods per site, with the exception of one site (Site 6) that flooded only once. All plots in a site flooded at the same river height. We then used a database of river levels recorded daily at TBS from January 2003 to December 2007 (the longest river-height record available) to determine flood frequency for each site, based on the river level at which each site had been observed to flood. We used this same database to estimate flood intervals for our plots (Table S1).

MEASURING ENVIRONMENTAL VARIATION.—Within each plot, 1 m² was selected at random and all twigs (including those with ant colonies) located therein were counted to estimate nest availability. Twigs were measured (length and width) and classified according to degree of decay. Twigs were defined based on size: < 1.5 m in length and < 10 cm in diameter (Byrne 1994); 98.4 percent were < 0.5 m in length. We rated twig decay on a scale of 1 (no decay, audible snap when broken) to 5 (highly decayed, crumble at touch; Byrne 1994). Twig volume was estimated using the formula for a cylinder. Litter depth was determined for each subplot by placing a wire flag at the corner and measuring the highest point at which litter touched the wire (Agosti *et al.* 2000). Plants < 10 cm dbh were counted to determine

plant density. Canopy cover was estimated with a spherical densitometer (Concave Model C, Forest Densitometers, Bartlesville, OK).

Approximately 30 g of soil was collected using a standard container by removing litter and scraping 5 cm deep in the center of each plot. Samples were oven dried at 60°C for two weeks to remove all moisture and tested for percent carbon and nitrogen by combustion in an elemental analyzer (Model NC2500, CE Instruments, Rodano, Italy). Percent phosphorus was measured from dried samples after a sodium bicarbonate extraction and sulfuric acid persulfate digest (Carter 1993) using an autoanalyzer (Quickchem FIA+8000, Lachat Instruments, Loveland, CO). Percent carbon, nitrogen and phosphorus were chosen as nutrient measures because they correlate with invertebrate diversity or abundance (Burghouts *et al.* 1992, Ritchie 2000, McGlynn *et al.* 2007).

DATA ANALYSIS.—Principal components analysis (PCA) and multiple regression were used to determine the effect of environmental variation on litter-nesting ant density (nests/plot) and species density (species/plot). A PCA was performed on the 56 flooded forest plots using seven environment variables (litter depth, twig availability, canopy cover, plant density, percent nitrogen, carbon, and phosphorus), as well as flood frequency and interval (Table S1). C:P ratio (%C/%P) was also included in the PCA, as it is a correlate of invertebrate density (McGlynn *et al.* 2007). Twig volume and decay were not included to reduce redundant twig variables. A separate PCA was performed on the 28 terra firme plots, as these plots could not be differentiated by the two flooding variables (particularly flood interval which is effectively infinite in terra firme). Data was standardized by conversion to Z-scores before PCA of the un-rotated correlation matrix to correct for different scales of measurement (Gotelli & Ellison 2004). Principal components were chosen based on relative percent variance criteria; their effects on nest and species density were determined using multiple regression (least squares method). Flooding and terra firme plots were again considered separately.

To compare flooded forest and terra firme (TF) forest, we used hierarchical clustering to separate the 56 flooded plots based on Z-scores for flood frequency and interval. Plots clustered into two categories: high flood disturbance (HIGH: 36 plots from three sites, 41 ± 7.2 floods/5 yr, 20.5 ± 12.6 d since last flood); and low flood disturbance (LOW: 20 plots from three sites, 11.4 ± 7.4 floods, 197.4 ± 72.4 d; Table S1). This categorization was supported by multiple distance measures (Euclidean, Manhattan, Jaccards, Bray-Curtis, Raup-Crick) with bootstrap values between 51 and 100 (100 replicates). We used one-way ANOVA to compare means of environmental variables among the three groups. Plant density, twig availability, percent carbon, nitrogen, and phosphorus, and twig volume were log transformed before ANOVA to improve normality. Because sample sizes in the three flood categories were not equivalent, we used the Brown-Forsythe test for equal variances to compare categories before ANOVA (Brown & Forsythe 1974, Conover *et al.* 1981). Variance was not significantly different for most variables ($P > 0.05$), except for percent carbon ($P = 0.031$), percent nitrogen ($P = 0.013$) and twig decay ($P < 0.0001$). Therefore, we used a Welch ANOVA (Welch 1951) to compare these

variables among flooding categories. Clustering was performed in PAST version 1.57 (Hammer *et al.* 2001). PCA, regression and ANOVA were performed using JMP version 5.0.1 (SAS Institute Inc., Cary, NC, 1989–2002).

We surveyed only ant nests found in the litter; individual foragers were not collected. Abundance measures in our study thus always refer to number of nests, not number of individual ants. Some species of litter-nesting ants are polydomous (Kaspari 1996b); we did not identify all polydomous colonies in our plots. However, the density of satellite nests has been shown to respond similarly to disturbance as overall nest density (Kaspari 1996a). Therefore, counting satellite nests does not affect our results. Because polydomous nests are not independent species samples, we used the incidence of species in plots when analyzing species richness and species composition.

Nest abundance (nests/m²) was significantly right-skewed (Shapiro-Wilk, $P < 0.0001$) and could not be normalized by transformation. Therefore, the nonparametric Kruskal-Wallis test was used. Because of differences in area surveyed between flood categories, we could not directly compare total species richness among disturbance groups (Magurran 2004). Sample-based rarefaction curves can overcome this problem, although comparisons of species richness among groups can still be biased by significant differences in abundance (Chazdon *et al.* 1999, Gotelli & Colwell 2001). We therefore calculated sample-based rarefaction curves and then rescaled to individual-based rarefaction to adjust for both area surveyed and nest abundance (McCabe & Gotelli 2000, Gotelli & Colwell 2001). ‘Individual’ in our study refers to each nest collected.

Sample-based rarefaction curves and confidence intervals were computed in EstimateS 7.0 (Colwell 2005), using the Mau Tau method (100 runs, no replacement). Curves were rescaled to individual-based curves using the average number of nests per sample for each category (Gotelli & Colwell 2001). We then calculated adjusted species richness values for the TF, LOW, and HIGH groups by truncating curves to the number of nests found in the least dense group (HIGH, 47 nests) and comparing predicted species richness (McCabe & Gotelli 2000).

We used the accumulation of unique species (species found in only one of n plots for each group) with sampling effort to test inventory completion. We estimated total species richness for each group using the nonparametric Jack2 estimator (Burnham & Overton 1979) because accumulation curves did not reach a clear asymptote (Fig. S2). We chose Jack2 as an estimator for data sets in which sample coverage is predicted to be 50–74 percent by most estimators (Brose *et al.* 2003). Jack2 and similar indices typically underestimate true species richness (Longino *et al.* 2002, Melo 2004), thus we consider Jack2 estimates as minimum species richness estimates. Unique species accumulation curves and Jack2 were computed in EstimateS 7.0 (Colwell 2005) using the Mao Tau method (100 runs, no replacement).

We compared similarity in species composition among flood disturbance groups using nonmetric multidimensional scaling (NMDS), Chao’s Adjusted Jaccard Index (CAJI; Chao *et al.* 2005) and Analysis of Similarity (ANOSIM). Indicator species for each

disturbance group were also determined using Similarity Percentage (SIMPER). CAJI was calculated in the SPADE program (version 3.1) using incidence data (Chao & Shen 2003). Standard error was calculated with 200 bootstraps. NMDS was computed in PAST (version 1.57), using the Raup-Crick Index on incidence data, while ANOSIM and SIMPER were carried out on Bray-Curtis Similarity Index values of incidence data also using PAST (Hammer *et al.* 2001). Raup-Crick and Bray-Curtis were chosen as a widely used and well-tested indices (Clarke & Warwick 2001, Hammer *et al.* 2001, Magurran 2004). Plots in which no species were found were not included in analyses of species composition.

To account for multiple statistical comparisons, we applied Benjamini and Hochberg's (1995) method of controlling the false discovery rate. We applied this criterion to the 24 *P* values used for hypothesis testing (in multiple regression, ANOVA and ANOSIM), and all *P* values > 0.0188 were considered insignificant based on the highest *P* value to satisfy the constraint, $P_{(9)} = 0.0001 \leq (9/24) \times 0.05 = 0.0188$.

RESULTS

IMPACT OF FLOODING AND ENVIRONMENTAL VARIATION.—Three principal components explained 71 percent of ecological variation in flooding plots (Table S2). PC1 was primarily percent N and C (33% of total variation), PC2 was flooding (frequency and interval, 22%), while availability of nest sites (twigs and litter depth) made up PC3 (16%). A linear multiple regression model provided a significant fit for both nest density ($F_{3,52} = 10.3$, $P < 0.0001$, adjusted $R^2 = 0.35$) and species density ($F_{3,52} = 10.4$, $P < 0.0001$, adjusted $R^2 = 0.35$). A linear model provided a good fit to the data based on residual plots showing no correlation between residuals and fitted values (for residual plots see Fig. S3), and normally distributed residuals (Shapiro-Wilk, $P = 0.164$ for nests, $P = 0.848$ for species). PC2 was a significant predictor of both nest density ($t = -5.34$, $P < 0.0001$) and species density ($t = -5.71$, $P < 0.0001$), whereas PC1 and PC3 were not significant predictors of

either (PC1, nests: $t = 0.50$, $P = 0.619$, species: $t = 0.95$, $P = 0.349$; PC3, nests: $t = 1.94$, $P = 0.058$, species: $t = 0.173$, $P = 0.195$).

In terra firme plots, three principal components explained 74 percent of the variation (Table S2). PC1 was again percent N and C (41%), PC2 twig availability and plant density (20%) and PC3 percent P and C:P ratio (15%). A linear multiple regression showed no significant fit for either nest density ($F_{3,24} = 0.115$, $P = 0.950$, adjusted $R^2 = -0.11$) or species density ($F_{3,24} = 0.100$, $P = 0.959$, adjusted $R^2 = -0.12$). Lack of fit was not due to nonlinearity, as plots of residuals showed no correlation (Fig. S3) and residuals were normally distributed (Shapiro-Wilk, $P = 0.051$ for nests, $P = 0.092$ for species). Attempts to fit data to nonlinear models did not produce significant results, suggesting that the variables we measured were not good predictors of species density or nest density in terra firme.

There were no significant differences among flooding categories in twig availability, canopy cover, plant density, litter depth, percent phosphorus, twig volume, percent nitrogen, or percent carbon (Table 1). Only twig decay varied significantly among groups (Table 1). Twigs in TF had the least decay (Tukey's HSD, $P < 0.001$) and twigs in HIGH had the most (Tukey's HSD, $P < 0.0001$).

ABUNDANCE AND SPECIES RICHNESS.—Ant nest abundance varied significantly among flooding groups (Kruskal-Wallis, $\chi^2 = 42.8$, $df = 2$, $P < 0.0001$). The highest density was in TF, with a mean of nearly one nest per meter, and density progressively decreased to approximately one nest every seven meters in HIGH (Table 2).

PCA/regression analysis revealed that species density linearly decreased with flooding. Species richness, however, showed a different pattern. Overall, 77 ant species in 21 genera were collected from a total of 347 nests (Supporting Table S3). TF contained the majority of species, followed by LOW and HIGH (Table 2). Rarefied sample-based curves rescaled to individual-based curves showed that the TF and LOW groups accumulated new species at a nearly equivalent rate per nest (Fig. 1A). The curve for the HIGH groups was short due to low nest density, but its slope suggests a lower rate of species accumulation than in TF or LOW sites.

TABLE 1. Environmental variation among flood sites. Values represent the mean (\pm SD) of $N \times 3 \text{ m}$ plots, except for twig volume and decay level (mean \pm SD of N twigs). Values in brackets represent the minimum/maximum values for each group. ANOVA was used to compare the three group means for each variable.

Flooding Group (<i>N</i> plots, <i>N</i> twigs)	Twig density (per m ²)	Litter depth (cm)	Percent canopy cover	No. plants < 10 cm dbh (per m ²)	Percent C	Percent N	Percent P	Twig volume (cm ³)	Twig decay
Terra firme (28, 1541)	54 (22) [13/115]	2.5 (1) [0.9/5.5]	56 (7.3) [36/71]	12.8 (6.7) [3/27]	5.6 (2.6) [1.7/12]	0.47 (0.1) [0.2/0.8]	0.002 (0.0007) [0.003/0.0006]	74 (1406) [0.1/42,194]	3.8 (0.8) [1/5]
Low disturbance (20, 1049)	52 (24) [24/124]	1.9 (1) [0.5/4.3]	54 (14) [22/81]	9.9 (5.1) [4/24]	5.9 (2) [3.7/11.5]	0.53 (0.1) [0.4/0.9]	0.002 (0.0007) [0.004/0.001]	26 (163) [0.1/2983]	3.6 (1) [1/5]
High disturbance (36, 1919)	52 (27) [17/158]	2 (1) [0.4/5]	55 (10) [35/76]	14 (7.6) [2/31]	5.7 (3.3) [2/13]	0.5 (0.2) [0.1/0.9]	0.002 (0.001) [0.005/0.0007]	48.2 (844) [0.1/32,094]	3.4 (0.9) [1/5]
Total (84, 4509)	53 (24)	2.1 (1)	56 (10)	12.6 (6.9)	5.7 (2.8)	0.5 (0.2)	0.002 (0.001)	52 (993)	3.6 (0.9)
<i>F</i>	0.12	3.44	0.66	1.66	0.87	2.01	1.41	1.81	63.7
<i>P</i>	0.888	0.037	0.519	0.196	0.426	0.144	0.251	0.163	< 0.001*

*Significance at $P < 0.0188$.

TABLE 2. Abundance and species richness among sites. Values for abundance represent the mean \pm SD and (minimum/maximum) of $N \times 3 \text{ m}$ plots. Adjusted species richness is the predicted richness after adjusting TF and LOW to the lower density level of HIGH based on species/individual rarefaction curves (Fig. 1) and is shown \pm 95% CI. Minimum estimated species richness calculated using Jack 2.

Site (<i>N</i>)	Abundance (density in nests/m ²)	Observed number of species/genera	Adjusted species richness	Minimum estimated species richness	Most abundant genus
Terra firme	0.84 \pm 0.44				
TF (28)	(0.1/2)	56/18	23 \pm 6.2	114	<i>Pheidole</i>
Low disturbance	0.49 \pm 0.31				
LOW (20)	(0/1)	33/13	22 \pm 6.6	68	<i>Pheidole</i>
High disturbance	0.15 \pm 0.2				
HIGH (36)	(0/0.67)	14/10	14 \pm 6.6	26	<i>Hypoponera</i>
Total (84)	0.46 \pm 0.44	21	— 140		<i>Pheidole</i>

Truncating the curves to the reduced nest abundance of the HIGH group predicted nearly equal adjusted species richness for the TF and LOW groups, and lower richness for the HIGH group (Table 2; Fig. 1B).

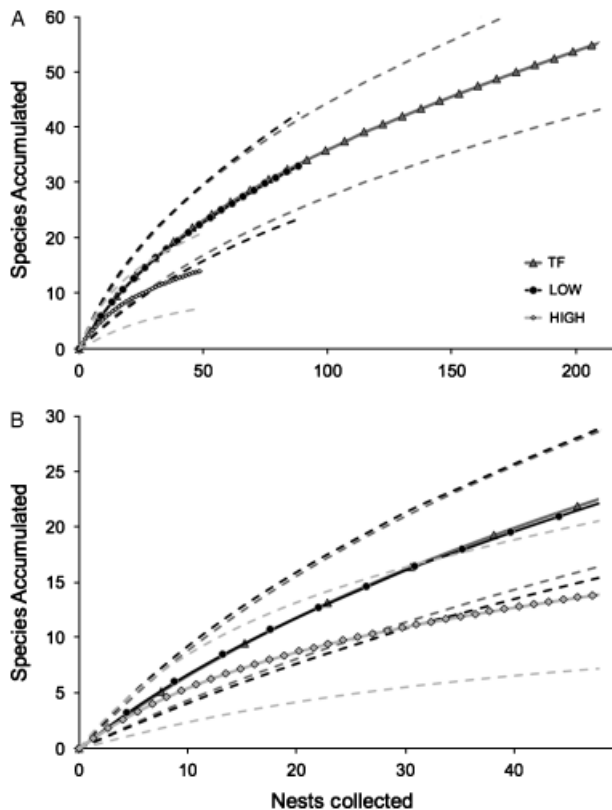


FIGURE 1. Rarefied species/individual curve comparisons of flood-disturbance groups. (A) Curves for the terra firme (TF), low flooding (LOW), and high flooding (HIGH) sites. Differences in area surveyed and density lead to large differences in the number of nests collected between groups. (B) The same curves truncated to the number of nests collected in the HIGH group (47). All curves are sample-based curves re-scaled to individuals (Gotelli & Colwell 2001). Dashed lines show the 95% CI for each curve.

The degree of completion of species inventories varied among groups. Although we found the fewest species and nests in HIGH, its inventory nevertheless appeared to approach completion (Fig. S2). TF and LOW groups, however, showed high rates of species accumulation after sampling 28 and 20 plots, respectively (Fig. S2). Minimum estimated species richness was highest in TF and progressively decreased with increased flooding (Table 2). The minimum number of litter-nesting ant species at TBS was estimated at 140.

SPECIES COMPOSITION.—Plots from the three flooding groups separated graphically in NMDS. HIGH plots clumped together, whereas TF plots were distributed along both NMDS axes and did not overlap with HIGH plots. LOW plots overlapped with both HIGH and TF plots (Fig. S4). Species similarity was significantly different among groups (ANOSIM, $R = 0.235$, $P < 0.0001$). Although TF and LOW sites showed the highest estimated similarity (CAJI: 0.76 ± 0.16), their ant communities remained significantly different in pairwise ANOSIM comparisons ($R = 0.23$, $P < 0.0001$). Additionally, TF communities were significantly different from HIGH ($R = 0.36$, $P < 0.0001$) with low estimated similarity (0.11 ± 0.07). LOW and HIGH plots showed somewhat higher estimated similarity (0.37 ± 0.15), and were not significantly different ($R = 0.05$, $P = 0.054$).

The relative representation of ant genera and species varied. *Pheidole* was the most prevalent ant genus in TF and LOW sites, comprising 40 percent of nests (32% of species) and 35 percent of nests (45% of species), respectively. *Pheidole* was the most diverse genus in HIGH sites, but was surpassed in abundance by *Hypoponera* (Table S3; Fig. 2). Some diverse litter-nesting ant genera (*Pheidole*, *Solenopsis*) decreased in proportional representation in nests as flooding increased, while nests of other genera (*Paratrechina*, *Wasmannia*) became more prevalent (Fig. 2). *Wasmannia auropunctata*, while invasive elsewhere, is native to the Neotropics (McGlynn 1999). Several groups known to contain specialized predators were well represented only in terra firme. *Gnamptogenys* appeared to have very low flood tolerance: 27 nests of five species were found in TF, but only one nest occurred in LOW and none in HIGH. *Gnamptogenys horni*, collected at TBS, specializes on ants (Hölldobler & Wilson 1990). *Strumigenys*, a specialist predator of

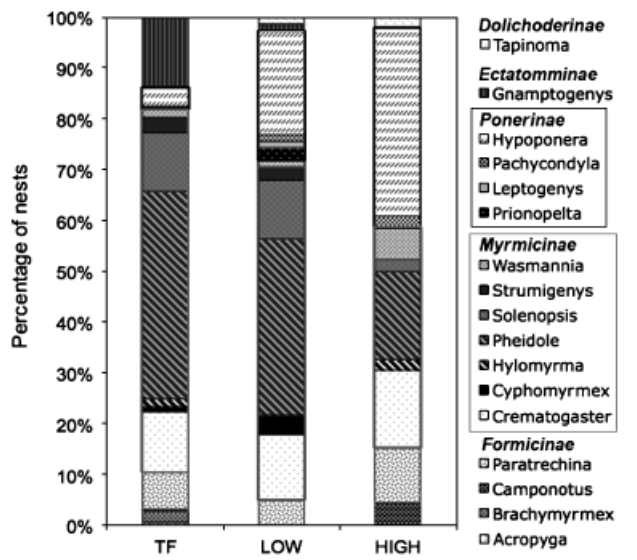


FIGURE 2. Distribution of 17 ant genera in five subfamilies across sites: terra firme (TF), low disturbance (LOW), and high disturbance (HIGH). Ponerine and Myrmicine subfamilies are highlighted for clarity. Four genera (*Pseudomyrmex*, *Octostruma*, *Odontomachus*, *Megalomyrmex*) are not shown due to representation by a single nest in TF.

collembolans, followed a similar pattern (nine nests in TF, one in LOW). *Prionopelta amabilis*, which feeds on dipturans and centipedes, was found only in TF and LOW sites. Predatory genera such as *Odontomachus* and *Leptogenys*, although rare, were also found only in TF.

Hypoponera was restricted to TF and LOW sites, with the important exception of *H. STD10* (Table S3; Fig. 2). Predominant in LOW and HIGH, *H. STD10* appears to be adapted to flood disturbance. It increased proportionally in abundance with increased flooding, with only one nest (< 0.01% of nests) in TF, 13 nests (17%) in LOW and 13 nests (28%) in HIGH. *H. STD10* had a large proportional contribution to species dissimilarity between TF and floodplain, as well as between LOW and HIGH (Table 3). Other possible flood-adapted species included *Cyphomyrmex* sp. 2

TABLE 3. Percent contribution of species with a high (> 5%) contribution to the average dissimilarity of species communities between flooding categories, based on SIMPER analysis.

Species	TF vs. LOW	TF vs. HIGH	LOW vs. HIGH	TF vs. Floodplain (LOW and HIGH)
<i>Pheidole amazonica</i>	6.68	6.83		6.77
<i>Hypoponera STD10</i>	6.36	5.78	12.8	6.05
<i>Pheidole pholeops</i>	6.18	7.37		6.83
<i>Pheidole allarmata</i>	5.42	6.67		6.10
<i>Solenopsis</i> sp. 1		5.54		5.05
<i>Crematogaster</i> sp. 1			8.33	
<i>Solenopsis</i> sp. 7			6.35	

(three nests in LOW), *Pheidole* ALM022 (four nests in HIGH), *Pheidole biconstricta* (four nests in LOW), and *Solenopsis* sp. 9 (three nests in LOW).

The most abundant species was *Pheidole amazonica* (32 nests), followed by *H. STD10* (27), *Crematogaster* sp. 1 (17), *Pheidole allarmata* (16) and *Pheidole pholeops* (16). *Pheidole amazonica* is polydomous; its 32 nests represent total nest site usage but not colony number. These species all had high proportional contributions to the species dissimilarity between flood categories; the abundance of *P. amazonica*, *P. pholeops*, and *P. allarmata* nests distinguished TF from floodplain, while *C. sp. 1* abundance distinguished HIGH from LOW (Table 3).

DISCUSSION

Flooding impacted the density, richness and community composition of litter-nesting ants at our sites in Amazonian Ecuador. Only degree of flooding (frequency and interval) had a significant impact on nest density and species density in flooded forest. Flooding did not appear to remove twigs or litter; there were no significant differences in twig number, twig volume or litter depth among flooding categories. Twig decay, however, was significantly reduced in TF relative to LOW and HIGH sites, suggesting that flooding may instead impact nest site availability by damaging nest materials, reducing their suitability for ant colonization by increasing decay and/or microbial growth. Twig availability, litter depth, plant density, canopy cover and soil nutrients did not correlate with nest or species density in TF, suggesting factors such as predation, prey density or plant diversity (Armbrecht *et al.* 2004) may regulate litter-nesting ant abundance in nonflooding sites.

The impact of flooding on species richness was more difficult to discern than its impact on density. We found a total of 77 species in 21 genera, the majority nesting in hard litter substrates (twigs, nuts and seedpods) rather than between leaves (Table S3). We estimated a minimum of 140 litter-nesting species at TBS, based on more sampling from floodplain than terra firme forest. However, terra firme had the highest observed species richness (Table 2), and because the area of terra firme at TBS is substantially greater than floodplain forest (Burnham 2002), the actual number of species is undoubtedly higher. Hand-collecting at TBS to date has yielded a total of 110 litter-nesting ant species in 27 genera (A. Mertl, unpubl. data). Both observed species richness and minimum estimated species richness decreased with increased flooding (Table 2), but after controlling for abundance, species accumulation and adjusted species richness were nearly equal in TF and LOW (Table 2; Fig. 1). This suggests that while absolute species richness is reduced in flooding forest due to reduced abundance, low-flooding sites may be proportionally as diverse as nonflooding sites. Low levels of flooding could enable coexistence between terra firme and floodplain species, as suggested by the IDH. Our results do not unequivocally support this theory, as we found lower total species richness in flooded sites. Many studies on anthropogenic disturbance on litter-ant richness have also found lower richness in disturbed sites, or no difference among disturbance categories (Belshaw & Bolton 1993, Vasconcelos *et al.* 2000, Kalif *et al.* 2001, Watt *et al.* 2002,

Armbrecht & Perfecto 2003). Nevertheless, the mechanism of disturbance promoting coexistence could still explain the high species accumulation and adjusted species richness in LOW sites, even if it does not lead to higher total richness in intermediate habitats.

Species composition data support the idea of species coexistence in low flood disturbance. HIGH plots clumped along NMDS axes and did not overlap with TF sites. LOW plots, however, overlapped with both HIGH and TF plots (Fig. S4). TF and LOW plots were not clumped, which may reflect that sampling in these two habitat types was incomplete (Fig. S2). CAJI and ANOSIM values show conflicting results: LOW habitat was estimated to be more similar to TF than to HIGH. In contrast, LOW and TF contained significantly different communities, whereas LOW and HIGH did not. Although this conflicting result may again be due to incomplete sampling in the LOW and TF habitats, analyses suggest that the LOW community is a mix of species from TF and HIGH.

A species of particular note in our survey was *H. STD10*, which increased from < 0.01 percent of nests in TF to 28 percent of nests in HIGH and thus appeared to be a flooded-forest specialist. *Hypoponera* STD 10 contributed a high proportion of species dissimilarity between TF and flooding forest, as well as between LOW and HIGH sites (Table 3). The decreased abundance of prominent twig-nesting *Pheidole* (particularly *P. amazonica*, and *P. allarmata*) also appeared to be due to flooding (Table 3). It is unclear if *H. STD10* and other ants found primarily in flooding forest are restricted in distribution due to flooding or to disturbance in general. In a preliminary study of the recovery of ant species richness in plots in which litter nests were manually removed, *H. STD10* increased in proportional abundance 1 mo after removal in floodplain, but not terra firme, sites (A. Mertl, K. Ryder Wilkie & J. Traniello, unpubl. data). *Hypoponera* STD10 could be behaviorally and/or physiologically adapted to flooding, as are some invertebrates in mangrove forest (Nielsen 1997) and Amazonian *varzea* (Adis 1997). Competition in the higher density terra firme ant community may also relegate *H. STD10* to flooding sites as its realized niche, whether or not it is specifically adapted to these areas. Unfortunately, life-history data is lacking for this species and most tropical litter-nesting ants, limiting our understanding of ecologically relevant traits underlying differences in species composition. Genera known to contain specialist predators (*Gnamptogenys*, *Strumigenys*, and *Prionopelta*) appeared to have low tolerance to flooding. This could be due to a reduction in invertebrate prey in flooded sites (Adis & Junk 2002), similar to the reduced abundance of ant genera specializing on ants and termites along an elevation gradient of decreasing invertebrate prey (Brühl *et al.* 1999).

The density of litter-nesting ants at our study site (0.84 ± 0.44 nests/m² in terra firme) was low compared with previous studies on Neotropical litter-nesting ants, which report densities of 5–7.48 nests/m² in terra firme (Byrne 1994, Kaspari *et al.* 2000, McGlynn 2006). We do not believe this difference can be attributed to search effort: we exhaustively examined each piece of litter in all plots and could not have overlooked ≈ 80 percent of nests. More likely, our densities reflect ecological differences between habitats. Mean terra firme litter depth and twig availability were lower in our study (2.5 cm [3.2 cm for Kaspari *et al.* 2000],

54 twigs/m² [115.2 twigs/m² for Byrne 1994]), although the magnitude of these differences may not be sufficient to explain differences in density. Differences in the degree of competition or predation pressure between sites could also be determinants of litter-nesting ant density.

Army ant predation can strongly affect litter-ant diversity and nest abundance (Franks & Bossert 1984, Kaspari 1996a, Kaspari & O'Donnell 2003). Army ants were present in both terra firme and floodplain forest sites, and at least nine species conduct litter raids at TBS (O'Donnell *et al.* 2007). Differences in predation pressure from army ants could therefore influence differences in terra firme litter-ant density among Neotropical sites. The effects of flooding on army ants have not been studied, however, flooding may inhibit their nesting and foraging. For example, Majer and Delabie (1994) found no army ants in a Brazilian *varzea* forest, compared with three species in nearby terra firme, including *Eciton vagans* and *Labidus coecus*, which are both present at TBS (O'Donnell *et al.* 2007). It is therefore unlikely that lower species richness and density in floodplain forest could be due to increased predation in floodplain forest rather than a direct result of flooding disturbance.

In summary, the density, richness and community composition of litter-nesting ants in Amazonian Ecuador was impacted by flooding. Degree of flooding had a negative effect on ant density, potentially due to decreased quality of twig-nesting sites in flooded areas. Species richness also decreased with flooding, although low levels of flooding may nevertheless play a role in the maintenance of tropical ant diversity by allowing coexistence between the distinct litter-nesting ant communities of terra firme and highly flooded forest. Although lower in overall density and richness, flooded forest may serve as a refuge from competition for otherwise rare species, such as *H. STD10*, and contain ant communities that are compositionally different from terra firme. Therefore, at the landscape level, an area containing both floodplain and terra firme forest may have higher species richness of litter-nesting ants and a greater likelihood of maintaining richness over time than a terra firme forest per se.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Flooding forest at Tiputini Biodiversity Station.

FIGURE S2. Unique species rarefaction curves for the three flood-disturbance groups.

FIGURE S3. Plots of predicted values vs. residuals for four multiple regression analyses.

FIGURE S4. Nonmetric multidimensional scaling analysis separating plots from three flood disturbance levels based on species composition.

TABLE S1. *Flood occurrence and sample plot distribution.*

TABLE S2. *Eigenvectors from PCA analysis.*

TABLE S3. *Twig- and litter-nesting ant species at Tiputini Biodiversity Station.*

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