

Changes in Ground-dwelling Ant Functional Diversity are Correlated with Water-Table Level in an Amazonian *Terra Firme* Forest

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ABSTRACT

Areas with shallow water tables comprise a significant portion of tropical forests and have distinct forest structure and plant-assemblage composition. It is not clear, however, how the water table regime shapes the distributions of other organisms. Here, we evaluated the influence of water-table level on ant-assemblage richness, abundance, and composition in a terra firme forest, in Central Amazonia. We sampled ants in ten 250 m-long transects, regularly distributed over 5 km² by extracting ants from 100 1-m² litter samples, 100 pitfall traps, and 100 sardine baits. During 1 year, the water-table level in each transect was monitored every 15 d with a 6-m deep dipwell. Overall the abundance of individuals and occurrence of species were lower in areas where the water table was closer to the surface (< 1 m depth) for longer periods (~ 5.5 mo). The number of ant species, however, was higher in transects where the water table was close to the surface more frequently. Changes in number of species were mainly a result of an increase in generalist species associated with a decrease in the number of specialist predators and small hypogeic generalist foragers. Although disturbance by the water table may increase local alpha diversity, only one third of generalist species seems to prefer areas with shallow water table.

Abstract in Portuguese is available in the online version of this article.

Key words: disturbance; flooding; functional group; guild; hydrology; tropical forest; riparian zone; species distribution.

THE SPATIAL AND TEMPORAL DISTRIBUTION OF SOIL WATER IS AN IMPORTANT DESCRIPTOR IN MANY TERRESTRIAL ECOSYSTEMS (Jansson *et al.* 2007). In tropical forests, seasonal changes in rainfall and spatial differences in topography and soil properties create gradients of soil moisture, and determine forest structure and plant species distributions (Rodríguez-Iturbe 2000). Sandy and frequently waterlogged soils in valleys generally harbor different plant species than sites on plateaus with clay soils and relatively deeper water tables (Costa *et al.* 2005, Kinupp & Magnusson 2005, Drucker *et al.* 2008, Zuquim *et al.* 2008, Schietti *et al.* in press). Although some environmental variables are correlated along the soil–water gradient, several herbs, and palm species are confined to the bottomlands, suggesting incapacity to withstand the water stress in the upland clayey soils (Costa *et al.* 2005, 2008). Like plants, ants are relatively sessile organisms and may experience stress caused by local changes in soil–water availability. Once established, ant nests tend to relocate locally (McGlynn *et al.* 2004), with relatively longer distances traveled only by inseminated winged females during the reproductive phase

(Perfecto & Vandermeer 2002). Thus, areas with a shallow water table may limit the distributions of ground- and litter-dwelling ant species by drowning established nests or preventing the foundation of new colonies.

Changes in ant-assemblage structure related to spatial distribution of soil water are evident in areas subjected to seasonal flooding. In those areas, non-arboreal ants avoid drowning by evacuating nests to higher sites or vegetation (Adis & Junk 2002). During high-water periods, the colonies need to survive on stored energy sources or subsist on suboptimum energetic resources until floodwaters recede (Adis 1983, Adis & Junk 2002). Such disturbance limits the establishment of species that are not adapted to inundation, changing ant-assemblage composition (Majer & Delabie 1994, Ballinger *et al.* 2007, Mertl *et al.* 2009). Specialist and predatory species appear to have low tolerance to flooding, probably as a response to the reduction in prey availability (Adis *et al.* 1984, Adis & Junk 2002), while generalist and omnivorous species may be favored (Milford 1999, Ballinger *et al.* 2007). Although the major changes in ant assemblage composition and richness are related to degree of flooding, disturbance caused by low flood frequency and low flood intervals can also impact ant assemblage structure (Mertl

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et al. 2009). Therefore, it seems reasonable that disturbance caused by vertical changes in the water table may also be operating even in sites not subject to flooding. In contrast to flooding, the effect of water table fluctuation may be more subtle, limiting the soil volume available for ant colonies, which in turn may limit the spatial distribution of ant species (Seal & Tschinkel 2010).

Studies that have investigated the effect of water-table fluctuations on ant community structure are restricted to the subtropics (Tschinkel 1988, Seal & Tschinkel 2010, Tschinkel *et al.* 2012). Although areas with a potentially shallow water table comprise a large part of tropical forests (Sombroek 2000, Renno *et al.* 2008), the role of water-table level in structuring tropical litter- and ground-dwelling ants is virtually unknown. Here, we evaluate the influence of water-table level on epigeic-ant richness, abundance, and species composition in a tropical forest that is not subject to periodic flooding. To examine ecological correlates of ant-distribution patterns, we also used a functional group approach, based on diet, nesting habits, external morphology, and phylogeny (Delabie *et al.* 2000, Silvestre *et al.* 2003, Silva & Brandão 2010), which provides a useful framework to describe and analyze ant-assemblage structure. Based on previous studies, we predicted that species occurrence and richness would be lower in areas with a relatively shallow water table. We also predicted that changes in community composition would be mediated mainly by decrease in occurrence and number of hypogeic and specialist species in areas where the water table is closer to the surface.

METHODS

STUDY SITE AND SAMPLING DESIGN.—The study was conducted in the Manaquiri module, a Brazilian Biodiversity Research Program (PPBio) site established by the State of Amazonas PRONEX program located between the Purus and Madeira Rivers, Brazil (03°41' S, 60°34' W). The terrain is flat to gently undulating (elevation 37–45 m asl based on Shuttle Radar Topography Mission – SRTM images) and characterized by seasonally water-logged soils with small intermittent streams. The site is covered by relatively undisturbed dense forest, but small areas around houses show evidence of human disturbance, such as selective logging and extraction of non-timber forest products (Fig. S1). The area receives an average of 2225 mm of rain annually, which is distributed seasonally (based on interpolated rainfall-gauge data from 1970 to 2011 available from CPTEC web site <http://ban-codados.cptec.inpe.br/downloadBDM>). The rainy season occurs between November and April and a drier period between May and October.

As the terrain is predominantly flat and the soils are silty loam and poorly drained, some areas located near intermittent streams may be flooded. Those flooded areas are not equivalent to *varzea* and *igapó* forests, however, which receive a predictable and regular flood pulse from overflow of large rivers. Flooded areas in the Manaquiri module are more unpredictable and normally related to heavy rains, especially during the rainy season.

Those floods create temporary small water bodies (1–3 m diam), submerging the soil and litter for relatively short periods (10–12 h) after rain, but the litter and the soil remained saturated with water for longer periods. Depending on the rainfall regime, some non-flooded areas may remain with a shallow water table for several weeks.

We sampled ten 250 m-long transects that were regularly distributed over 5 km². Sampling was carried out along the center lines of RAPELD plots (Costa & Magnusson 2010), which follow terrain contours, located at 1 km intervals along two 5 km-long trails (Fig. S1). As plot center lines follow the topographic contours, variation in water-table depth within transects was minimized.

ANT SAMPLING.—Ten sampling stations were established at 25-m intervals along each transect, avoiding small depressions which may be filled with water after heavy rains during the rainy season. No visual clues of flooding, such as watermarks on trees or mud covering litter, were detected around the sampling stations. Each sampling station consisted of a pitfall trap, a 1 m² litter sample (Winkler sacks) and a bait sample. At each sampling station, 1 m² of litter was sifted through a 1 cm² mesh, placed in Winkler sacks and hung in a field camp at ambient temperature (about 28 ± 8°C) for 48 h to extract the ants. A 9.5 cm internal-diameter pitfall trap, partially filled with 96 percent alcohol and a drop of detergent, was established adjacent (~2 m) to each litter-sampling point and left for 48 h. After removing the pitfall traps, approximately 5 g of canned sardine was placed on white paper (10 cm by 7 cm) on the litter surface. After 60 min, all ants on the paper were collected and preserved in 96 percent alcohol. The baiting and litter-sampling procedures were undertaken between 0800 and 1700 h. The site was sampled in October 2009 during the dry season, to avoid temporary reduction in foraging activity during times of high precipitation.

The ants from the Winkler sacks, pitfall traps and bait samples were identified to morphospecies or species whenever possible. Voucher specimens were deposited in the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus, Brazil). The raw data and metadata describing collection protocols can be downloaded from PPBio web site <http://ppbio.inpa.gov.br/sitios/br319/infra>.

Species were placed into functional groups based on the classifications for Neotropical ants (Delabie *et al.* 2000, Silvestre *et al.* 2003, Silva & Brandão 2010) and on our observations of their foraging behavior, food choice, and nesting sites. This functional group scheme is based on microhabitat distribution, natural history information, eye size, body size and shape, and phylogeny; grouping species with potentially similar life styles. We followed the nomenclature proposed by Silva and Brandão (2010): (1) large-sized epigeic generalist predators; (2) medium-sized epigeic generalist predators; (3) dacetini predators (specialist predators with kinetic mandible and cryptic behavior); (4) hypogeic predators; (5) small-sized hypogeic generalist foragers; (6) generalists; and (7) litter-nesting fungus growers. We grouped the Medium-sized hypogeic generalist predators,

hypogeic generalist predators with vestigial eyes and specialist predators living in soil superficial layers into a single hypogeic predators functional group, because these three groups represent species from the same trophic position and have relatively large overlap in morphological space (Silva & Brandão 2010). Arboreal species that occasionally forage in soil/litter, army ants and subterranean mealy bug specialists were not included in analyses. These species are not adequately sampled with the sampling methods used and may increase the noise in analyses. A list of species membership for each functional group can be found in Table S1.

MEASURING WATER TABLE VARIATION.—A 6 m-deep dipwell was installed in each transect, approximately 5.5 m below and 0.5 m above ground level. The dip well consisted of a 5 cm diam plastic pipe with holes drilled in the lower portion (30 cm) to permit water flow. The holes were covered with a thin polyester mesh to avoid obstruction by mud, and the dip wells were capped to prevent entry of rainwater and litter. A lateral orifice equilibrated the air pressure in the pipe. Between January 2010 and January 2011, the water-table level was manually monitored every 15 d using a measuring tape.

We used the number of 15-day periods in which the water table was < 1 m from the surface as a measure of disturbance caused by water-table level on ant assemblages. When the water table is less than 1 m depth, vertical water percolation decreases favoring the superficial soil saturation by water capillarity, or capillary fringe (Fan & Miguez-Macho 2010). The capillary fringe is the zone above the water level where the air-entry pressure is less than that required to penetrate the water table (Berkowitz *et al.* 2004). The thickness of the capillary fringe depends on the soil properties, but can reach up to 1.5 m above the water-table level in silty loam soils (Dingman 2002). Therefore, silty loam soils with the water table less than 1 m deep may have 90–95 percent of water saturation in the first 25 cm depth, which represents potential disturbance and relatively less vertical soil available for ant colonies.

DATA ANALYSIS.—The number of 15-day periods in which the water table was ≤ 1 m from the surface was used as a predictor variable for changes in ant abundance, frequency, richness, and composition. To avoid abundance bias toward large colonies, we used the number of occurrences of each species per transect, rather than number of individuals in assemblage analysis. Thus, the occurrence range for each species varied from zero to a maximum of 10 per transect. Given the distance between sampling stations (25 m), the number of species occurrences per transect may be interpreted as a surrogate for number of ant nests. The total ant occurrence and total number of ant species per transect were regressed against the frequency of water table depth ≤ 1 m from the surface. To describe and interpret the major pattern in detail, the occurrence and number of ant species in each functional group was also individually regressed against the frequency of water table depth ≤ 1 m. Residual analyses were used to check the error distribution and the suitability of the regression models.

We used non-metric multidimensional scaling (NMDS), to evaluate the relationship between the water-table gradient and overall ant-assemblage composition. NMDS analysis was performed with frequency standardizations per plot and the Bray-Curtis index as the dissimilarity measurement. The adjusted r^2 of the original ant dissimilarity matrix regressed against the dissimilarity in the two-dimensional NMDS was used to evaluate the adequacy of the ordination (McCune & Grace 2002). We fitted the water-table gradient (frequency of water table depth ≤ 1 m) to the NMDS ordination using the `envfit`-function of the R package `vegan`. The significance of the correlation of point projections (ant species composition in each plot) onto the predictor vector (frequency of water table depth ≤ 1 m) was estimated with 999 permutations. This analysis estimates the correlation between overall species composition and the environmental gradient.

For the most common species (> 20 individuals and sampled in ≥ 5 plots), raw abundances from pitfall and Winkler samples were summed per transect and individually regressed against water-table gradient. We used a Poisson distribution controlled for overdispersion, to meet regression-analysis assumptions. To identify species with abundance peaks in the middle of the gradient, we also investigated the correlation between ant abundance and water-table gradient with quadratic models. The analyses were undertaken with R software (R Core Team 2011) using the `vegan` package (Oksanen *et al.* 2011).

RESULTS

We collected 177 ant species/morphospecies representing 42 genera in nine subfamilies. Strictly arboreal, subterranean mealy bug dependent species and army ants comprised 25 species distributed in ten genera (*Acropyga*, *Azteca*, *Cephalotes*, *Camponotus*, *Crematogaster*, *Dolichoderus*, *Eciton*, *Labidus*, *Platythyrea* and *Pseudomyrmex*), and were not included in analyses. The most species-rich genus of ground-dwelling ants was *Pheidole* with 36 species, followed by *Solenopsis* and *Strumigenys* with 11 species each. At least one of these three genera was collected in 20 percent of baits, 32 percent of pitfall traps and 29 percent of Winkler samples, and was recorded in all sampling stations (300). *Solenopsis* sp.1 and *Strumigenys* cf. *denticulata* were the most abundant species, sampled in 35 and 25 percent of sampling stations, respectively. Thirty-one percent of species, however, were recorded in only one sampling station.

Water-table level showed marked variation between seasons, following the rainfall regime of the field site. Two transects had water in the dipwell throughout the year (Fig. S2). Although during the dry season, the water-table level in the remaining eight transects was below our dipwells. The number of 15-day periods when the water table was ≤ 1 m ranged from zero to 11 (approx. 5.5 mo) among transects (Fig. S2). Only riparian areas, which were not sampled, showed flooding events after rains.

The overall ant occurrence, measured by the number of stations occupied by each species per transect (Fig. 1A), was lower

in areas with a shallow water table ≤ 1 m ($r^2 = 0.44$, $P = 0.038$). Contrary to our prediction, however, the total number of ant species (Fig. 1B) increased in areas where the water table was close to the surface for longer periods ($r^2 = 0.47$, $P = 0.029$). The overall ant assemblage composition was also related to the water-table gradient. The major pattern of ant-assemblage composition captured by the NMDS analysis showed a strong correlation with the frequency of water-table depth ≤ 1 m ($r^2 = 77.62$, $P = 0.008$). The final configuration of the NMDS

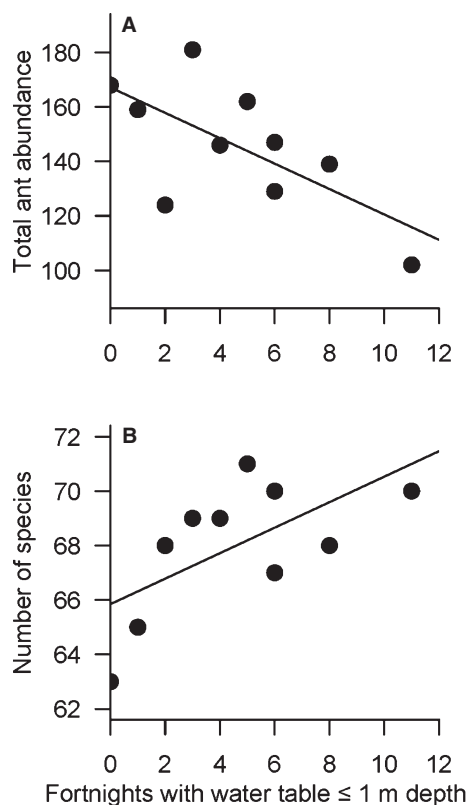


FIGURE 1. Relationships between the number of fortnights with water-table depth ≤ 1 m and (A) ant abundance, measured as the sum of the number of stations occupied by each species per transect, and (B) number of ant species.

with two axes (stress 0.13) explained ~ 73 percent of the variance in ant-species composition.

All functional groups, except generalist species, decreased in number of occurrences with increase in frequency of water-table depth ≤ 1 m (Table 1), but this pattern was more evident for the large-sized epigeic predators (Fig. 2A) and the small-sized hypogeic generalist foragers (Fig. 2B). The number of species per functional group did not show a similar trend. The overall increase in species richness was mainly caused by an increase of nearly 40 percent in generalist species in areas where the peaks of shallow water table were more frequent (Fig. 2C). Conversely, specialized species, represented by small-sized hypogeic species (Fig. 2D) and Dacetini predator species (Fig. 2E) decreased as the number of periods with the water table ≤ 1 m depth increased. The number of species of large-sized epigeic generalist predators, medium-sized epigeic generalist predators, hypogeic generalist predators, and litter-nesting fungus growers were not correlated with the gradient of water-table level (Table 1).

Of the 152 species of litter and ground-dwelling ants used in analyses, 51 species that were represented by more than 20 individuals and occurred in five or more transects were used in species-abundance analysis. Approximately 55 percent (28 species) had abundances correlated with the water-table gradient (Table S2). *Hypoponera* sp. 9 was the only species that showed a significantly higher abundance at the extremes of the gradient, and was treated here as a species not related to the water table. Seven species (~ 14 percent) were positively correlated, increasing their abundances in transects with a shallow water table (Fig. 3). All species of this group were generalist species, nesting in soil/litter and/or lower vegetation, such as *Crematogaster limata*, *C. brasiliensis*, *C. nigropilosa* and *Wasmannia auropunctata*. Four species (~ 7 percent) showed abundance peaks in the middle of water-table gradient (Fig. 3). Except for *Strumigenys tridifera*, which nests in litter, all species in this group are typically ground nesters. The remaining 17 species (~ 33 percent) were less abundant in transects with a shallow water table for longer periods (Fig. 3). This group includes the three most abundant species in our samples (*Solenopsis* sp.1, *P. exigua* and *P. meinerti*), and species with clearly different nesting and foraging habits, such as the large predator *Pachycondyla crassinoda*, some hypogeic *Hypoponera* species, specialist

TABLE 1. Results of regression models relating the number of fortnights with water table depth ≤ 1 m and abundance and richness (number of ant species per sampling unit) per functional group. Occurrence was estimated as the total number of sampling stations occupied by each species per transect.

Functional groups	Occurrence			Richness		
	r^2	Slope	P	r^2	Slope	P
Dacetini predators	0.33	-0.69	0.080	0.62	-0.25	0.007
Generalists	0.01	0.36	0.781	0.60	1.06	0.009
Hypogeic generalist predators	0.02	-0.20	0.676	0.13	-0.09	0.297
Large-sized epigeic generalist predators	0.76	-0.99	0.001	0.01	0.06	0.758
Litter-nesting fungus growers	0.18	-0.51	0.221	0.01	0.06	0.788
Medium-sized epigeic generalist predators	0.12	-0.25	0.328	0.02	-0.08	0.672
Small-sized hypogeic generalist foragers	0.43	-0.72	0.040	0.45	-0.22	0.035

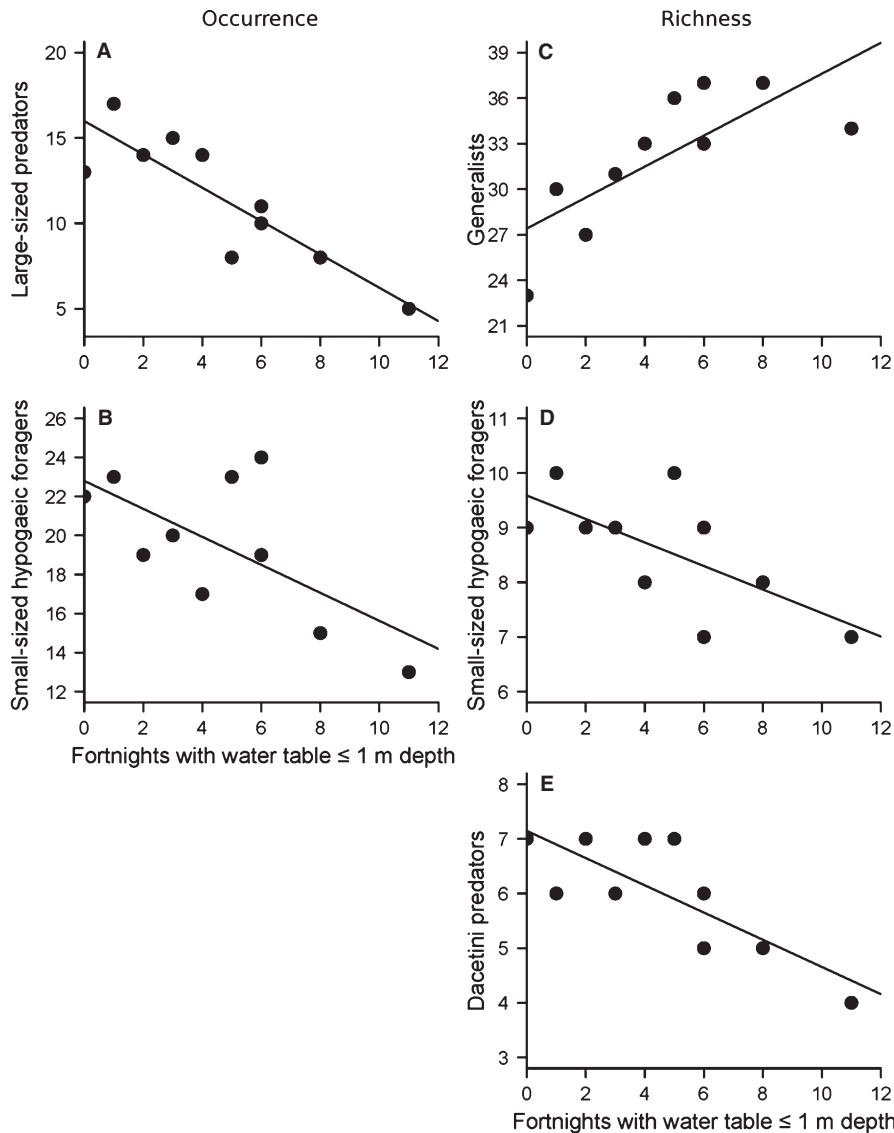


FIGURE 2. Relationships between number of fortnights with water-table depth ≤ 1 m and (A) frequency of large-sized epigeic predators; (B) frequency of small-sized hypogaecic generalist foragers; (C) number of generalists species; (D) number of hypogaecic generalist predators species and (E) number of Dacetini predator species.

predators with kinetic mandibles (*Strumigenys* sp.2 and *S.* sp.4) and several generalists species.

DISCUSSION

Water-table level was strongly correlated with changes in abundance, richness and assemblage composition of ground-dwelling ants at our site in Central Amazonia. As hypothesized, the overall ant occurrence was lower in areas with a shallow water table (≤ 1 m depth). Contrary to our prediction, however, the number of ant species increased in areas with water table less than 1 m from the surface. Changes in species richness were mainly due to an increase in generalist species associated with a decrease in the number of specialist predators and the

small-sized hypogaecic generalist foragers. The different responses among ant functional groups suggest that the effects of water table in this forest are more subtle than in tropical seasonally flooded environments.

A shallow water table means less soil volume available for ant colonies (Tschinkel 1988, Seal & Tschinkel 2010), but also means relatively higher soil moisture and therefore less desiccation risk. Soil/litter moisture can favor some species and also modify the activity of ant species even in tropical ecosystems. Overall, ant activity and species richness tend to be higher in more humid seasons and habitats (Kaspari & Weiser 2000). Therefore, the moisture gradient may explain why we found more species in areas with relatively superficial water table. This process is hard to reconcile with the decrease in overall ant

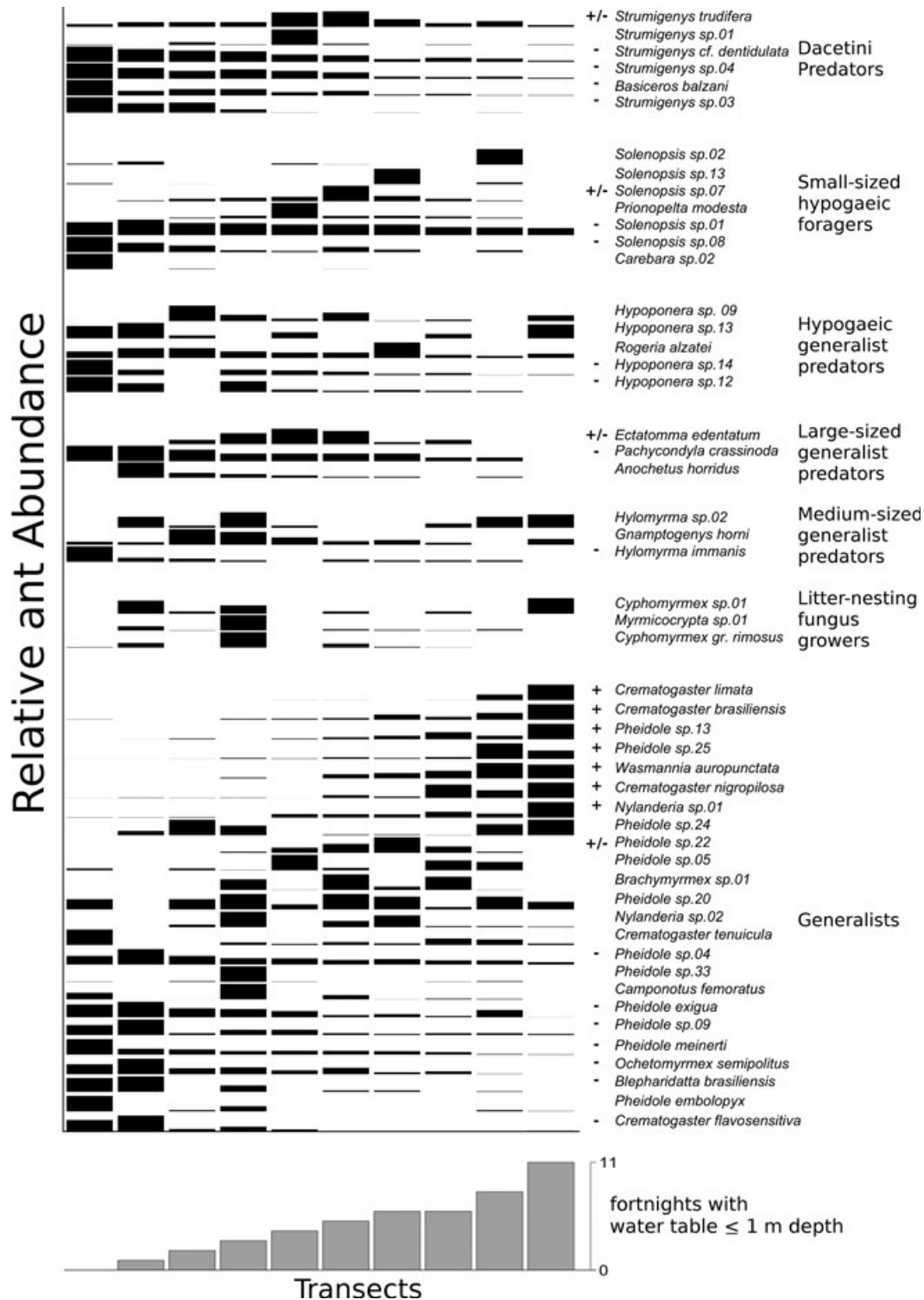


FIGURE 3. Relationship between ant abundance along the gradient of fortnights with water table \leq 1 m from surface. The abundance was scaled to proportions for each species to facilitate visualization; raw abundances are available in the supplementary information (Table S1). The vertical order of species within functional groups was based on the mean value per individual of the species along the gradient. Species more abundant in the drier part of the gradient are placed near the bottom of the graph and species more abundant in transects with shallow water table for longer periods are positioned near the top. The symbols -, +, and \pm indicate species with negative, positive or quadratic relationship with the water-table gradient. Statistical model results on which these relationships are based are presented in the Supporting Information (Table S2).

abundance in these areas, however, suggesting that another mechanism may be operating.

More generalist species associated with less specialized species in humid plots, suggests that the water table is a source of disturbance for ant species rather than a simple moisture gradient. Little information about ant-nest architecture is available for tropical forests, but the drop in ant activity and diversity below 25 cm, has been associated with higher water-table level in an Amazonian Ecuadorian forest (Ryder Wilkie *et al.* 2007). A shallow water table may increase the capillary fringe layer, favoring lateral water percolation and flooding, especially near small streams. Although the scale and level of disturbance caused by water-table fluctuations are more subtle than in areas subjected to a regular flood pulse. Periodic flooding in *varzea* and *igapó* forests may shape ant communities regionally, reducing diversity in large and continuous areas close to river margins (Adis & Junk 2002). Superficial water-table fluctuation may disrupt ant assemblages locally, leaving small patches of relatively well-drained soil available. Therefore, disturbance mediated by changes in water-table level in *terra firme* ant assemblages, may be similar to low flooding intensity areas in floodplains (Mertl *et al.* 2009), favoring generalist species and limiting colony establishment and growth of specialist and hypogeic species.

The Dacetini predator guild is a relatively well-studied set of cryptic specialist species that live and forage in the leaf litter and rotten wood (Bolton 1999). Although, little information about small-sized hypogeic generalist foragers is available, their morphology (small ants with very small or vestigial eyes), suggest that these species live and forage in the soil (Brown 2000). Both groups' show specialized foraging and nesting habitats, which are expected to be more sensitive to disturbance caused by soil water (Majer & Delabie 1994, Mertl *et al.* 2009). Species-abundance analysis showed that most of these species are more abundant in dryer areas of the study site, or occur in the middle of the water-table gradient. This pattern is scaling up for functional groups, especially for small-sized hypogeic generalist foragers, suggesting that recurrent disturbance events caused by increase in water-table level may force nest relocation to avoid drowning and/or limit the establishment of colonies of these species.

Except for *Hylomyrma imannis*, *Hypoponera* sp. 12 and *H.* sp.14, which were less abundant in transects with shallow water table, the rest of the litter-fungus growers, medium-sized epigeic species and hypogeic generalist predators showed no clear pattern of abundance distribution. No relationship was detected between occurrence of individual species or species richness and the water-table gradient, indicating that species in these functional groups may be tolerant to disturbance mediated by changes in water table level. As the life styles of medium-sized epigeic generalist predator species have some overlap with generalist species (Silva & Brandão 2010), it is possible that nesting and foraging habits also allow them to recolonize or persist during the rainy season in areas with shallow water table. The lack of evidence of a decrease in occurrence, abundance and richness of litter fungus growers in more disturbed transects, however, was surprising. The fungus-gardening ant species feed the developing brood and,

to a lesser extent, adult workers on symbiotic fungus (Bass & Cherrett 1995). The symbiotic fungus has narrow humidity and temperature requirements and, consequently, adequate conditions for fungus growth in the soil layer are limited (Roces & Kleineidam 2000, Bollazzi *et al.* 2008, Seal & Tschinkel 2010). Our results suggest that, unlike fungus-growing species that nest in the soil, litter fungus growers have broader microhabitat tolerances. Some litter fungus growers species can also take advantage of litter trapped by tree trunks and palms aboveground and use them as complementary nesting sites during the rainy season. Moreover, as litter receives unpredictable inputs of vegetable and animal detritus and its organic material is constantly subject to decomposition (Facelli & Pickett 1991), a broader microhabitat tolerance for symbiotic-fungus growth may be an evolutionary adaptation to higher disturbance and more variable environment.

The functional-classification approach simplifies assemblage composition to a few groups, facilitating assemblage-structure comparisons among areas that have few or no species in common (Andersen 1997). Generalization, however, comes with a price. The set of species grouped as generalists showed contrasting responses to the water-table gradient. In contrast to other functional groups which had more consistent results, 33 percent of the generalist species analyzed were less abundant in transects with shallow water table and 33 percent showed the opposite pattern. These results suggest that there is a greater compartmentalized structure in relation to the water-table gradient among this set of species than for the other functional groups. Similar results were found in an Ecuadorian tropical forest, where ~ 28 percent of 39 *Pheidole* species, which normally are grouped as generalist species, were more abundant in floodplains and 38 percent was intolerant to flooding (Mertl *et al.* 2010). The disturbance created by a relatively shallow water table may have favored the occurrence of other generalists species, such as *C. limata*, *C. brasiliensis*, *C. nigropilosa*, *Nylanderia* sp.1 and *Wasmannia auropunctata* besides two *Pheidole* species. These generalists' species are omnivores with varied nesting habitats and, except for *C. nigropilosa* and *Nylanderia* sp.1, show aggressive behavior against co-occurring species at artificial resources (Delabie *et al.* 2000, Baccaro *et al.* 2012). Aggressive behavior and competitive traits favor nest relocation and/or colony maintenance under stress, facilitating establishment in disturbed areas (King & Tschinkel 2008, Vonshak *et al.* 2009, Krushelnycky & Gillespie 2010). As our sampling was undertaken during the dry season, generalists species may have time to colonize areas with shallow water table during the last rainy season. However, to what extent the increase in abundance of some generalist species is a result of colonization/competition abilities or disturbance resistance requires further study.

Taken as a whole, disturbance mediated by the water table appears to increase species richness, but with proportionally fewer specialists and hypogeic species than generalist species. The functional classification approach seems to be useful for sets of species with relatively narrow ecological niches. For generalist species, however, this classification needs to be complemented with more information about natural history to improve our understanding of the process behind these compositional changes. Given that

areas with shallow water table, in most cases riparian zones, are among the most threatened ecosystems in tropical forests (Tockner & Stanford 2002), understanding the relationship between ant diversity and the local water table has important implications for conservation. Moreover, as ants are frequently recognized as a keystone group, human modification of the water-table dynamics may lead to changes in ant-assemblage diversity that could affect many other elements in the ecosystem.

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SUPPORTING INFORMATION

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

TABLE S1. *Abundance of individuals and % of occurrence in 100 sampling stations in a terra firme forest, Central Amazonia, Brazil.*

FIGURE S1. Map of the study region based on Shuttle Radar Topography Mission.

FIGURE S2. Water-table level monitored fortnightly between January 2010 and January 2011 in 10 transects.

LITERATURE CITED

- ADIS, J. 1983. Eco-entomological observations from the Amazon III: How do leafcutting ants of inundation forests survive flooding? *Acta Amazonica* 12: 839–840.
- ADIS, J., AND W. J. JUNK. 2002. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: A review. *Freshw. Biol.* 47: 711–731.
- ADIS, J., Y. D. LUBIN, AND G. G. MONTGOMER. 1984. Arthropods from the canopy of inundated and terra firme forests near Manaus, Brazil, with critical considerations on the pyrethrum-fogging technique. *Stud. Neotrop. Fauna Environ.* 19: 223–236.
- ANDERSEN, A. N. 1997. Functional groups and patterns of organization in North American ant communities: A comparison with Australia. *J. Biogeogr.* 24: 433–460.
- BACCARO, F. B., J. L. P. DE SOUZA, E. FRANKLIN, V. L. LANDEIRO, AND W. E. MAGNUSON. 2012. Limited effects of dominant ants on assemblage species richness in three Amazon forests. *Ecol. Entomol.* 37: 1–12.
- BALLINGER, A., P. S. LAKE, AND R. MAC NALLY. 2007. Do terrestrial invertebrates experience floodplains as landscape mosaics? Immediate and longer-term effects of flooding on ant assemblages in a floodplain forest. *Oecologia* 152: 227–238.
- BASS, M., AND J. M. CHERRETT. 1995. Fungal hyphae as a source of nutrients for the leaf-cutting ant *Atta sexdens*. *Physiol. Entomol.* 20: 1–6.
- BERKOWITZ, B., S. E. SILLIMAN, AND A. M. DUNN. 2004. Impact of the capillary fringe on local flow, chemical migration, and microbiology. *Vadose Zone J.* 3: 534–548.
- BOLLAZZI, M., J. KRONENBITTER, AND F. ROCES. 2008. Soil temperature, digging behaviour, and the adaptive value of nest depth in South American species of *Acromyrmex* leaf-cutting ants. *Oecologia* 158: 165–175.
- BOLTON, B. 1999. Ant genera of the tribe Dacetoniini (Hymenoptera Formicidae). *J. Nat. Hist.* 33: 1639–1689.
- BROWN, W. L. J. 2000. Diversity of ants. *In* D. Agosti, J. D. Majer, L. Alonso, and T. R. Schultz (Eds.). *Ants standard methods for measuring and monitoring biodiversity*, pp. 45–79. Smithsonian Institution Press, Washington, DC.
- COSTA, F. R. C., J.-L. GUILLAUMET, A. P. LIMA, AND O. S. PEREIRA. 2008. Gradients within gradients: The mesoscale distribution patterns of palms in a central amazonian forest. *J. Veg. Sci.* 20: 1–10.
- COSTA, F. R. C., AND W. E. MAGNUSON. 2010. The need for large-scale, integrated studies of biodiversity - the experience of the program for biodiversity research in Brazilian Amazonia. *Natureza & Conservação* 8: 3–12.
- COSTA, F. R. C., W. E. MAGNUSON, AND R. C. LUIZÃO. 2005. Mesoscale distribution patterns of Amazonian understory herbs in relation to topography, soil and watersheds. *J. Ecol.* 93: 863–878.
- DELABIE, J. H. C., D. AGOSTI, AND I. C. NASCIMENTO. 2000. Litter ant communities of the Brazilian Atlantic rain forest region. *In* D. Agosti, J. D. Majer, L. Alonso, and T. R. Schultz (Eds.). *Sampling ground-dwelling ants: Case studies from the world's rain forests*, pp. 1–17. Perth, Australia: Curtin University School of Environmental Biology Bulletin 18.
- DINGMAN, S. L. 2002. *Physical hydrology*. Waveland Press Inc., Long Grove, IL, 656 p.
- DRUCKER, D. P., F. R. C. COSTA, AND W. E. MAGNUSON. 2008. How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. *J. Trop. Ecol.* 24: 65–74.
- FACELLI, J. M., AND S. T. A. PICKETT. 1991. Plant litter: Its dynamics and effects on plant community structure. *Bot. Rev.* 57: 1–32.
- FAN, Y., AND G. MIGUEZ-MACHO. 2010. Potential groundwater contribution to Amazon evapotranspiration. *Hydrol. Earth Syst. Sci.* 14: 2039–2056.
- JANSSON, R., H. LAUDON, E. JOHANSSON, AND C. AUGSPURGER. 2007. The importance of groundwater discharge for plant species number in Riparian Zones. *Ecology* 88: 131–139.
- KASPARI, M., AND M. D. WEISER. 2000. Ant activity along moisture gradients in a Neotropical forest. *Biotropica* 32: 703–711.
- KING, J. R., AND W. R. TSCHINKEL. 2008. Experimental evidence that human impacts drive fire ant invasions and ecological change. *Proc. Natl Acad. Sci. USA* 105: 20339–20343.
- KINUPP, V. F., AND W. E. MAGNUSON. 2005. Spatial patterns in the understory shrub genus *Psychotria* in Central Amazonia: Effects of distance and topography. *J. Trop. Ecol.* 21: 363–374.
- KRUSHELNYCKY, P. D., AND R. G. GILLESPIE. 2010. Correlates of vulnerability among arthropod species threatened by invasive ants. *Biodivers. Conserv.* 19: 1971–1988.
- MAJER, J. D., AND J. H. C. DELABIE. 1994. Comparison of the ant communities of annually inundated and terra firme forests at Trombetas in the Brazilian Amazonia. *Insectes Soc.* 41: 343–359.
- MCCUNE, B., AND J. GRACE. 2002. *Analysis of ecological communities*, MjM Software Design, Corvallis, OR.
- MCGLYNN, T. P., R. A. CARR, J. H. CARSON, AND J. BUMA. 2004. Frequent nest relocation in the ant *Aphaenogaster araneoides*: Resources, competition, and natural enemies. *Oikos* 106: 611–621.
- MERTL, A. L., M. D. SORENSON, AND J. F. A. TRANIELLO. 2010. Community-level interactions and functional ecology of major workers in the

- hyperdiverse ground-foraging Pheidole (Hymenoptera, Formicidae) of Amazonian Ecuador. *Insectes Soc.* 57: 441–452.
- MERTL, A. L., K. T. R. WILKIE, AND J. F. A. TRANIELLO. 2009. Impact of flooding on the species richness, density and composition of Amazonian litter-nesting ants. *Biotropica* 41: 633–641.
- MILFORD, E. R. 1999. Ant communities in flooded and unflooded riparian forest of the middle rio grande. *Southwest. Nat.* 44: 278–286.
- OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. H. H. STEVENS, AND W. HELENE. 2011. Vegan: Community Ecology Package. R package version 1.17-12. Available at: <http://CRAN.R-project.org/package=vegan> (accessed 15 July 2011).
- PERFECTO, I., AND J. VANDERMEER. 2002. Quality of agroecological matrix in a tropical montane landscape: Ants in coffee plantations in Southern Mexico. *Conserv. Biol.* 16: 174–182.
- R Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org/> (accessed 15 July 2011).
- RENNO, C., A. NOBRE, L. CUARTAS, J. SOARES, M. HODNETT, J. TOMASELLA, AND M. WATERLOO. 2008. HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia. *Remote Sens. Environ.* 112: 3469–3481.
- ROCES, F., AND C. KLEINEIDAM. 2000. Humidity preference for fungus culturing by workers of the leaf-cutting ant *Atta sexdens rubropilosa*. *Insectes Soc.* 47: 348–350.
- RODRIGUEZ-ITURBE, I. 2000. Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamics. *Water Resour. Res.* 36: 3–9.
- RYDER WILKIE, K. T., A. L. MERTL, AND J. F. A. TRANIELLO. 2007. Biodiversity below ground: Probing the subterranean ant fauna of Amazonia. *Naturwissenschaften* 94: 725–731.
- SCHIETTI, J., T. EMILIO, C. D. RENNÓ, D. P. DRUCKER, F. R. C. COSTA, A. NOGUEIRA, F. B. BACCARO, F. FIGUEIREDO, C. V. CASTILHO, V. KINUPP, J.-L. GUILLAUMET, A. R. M. GARCIA, A. P. LIMA, AND W. E. MAGNUSON. in press. Vertical distance from drainage drives floristic composition changes in an Amazonian terra-firme rainforest. *Plant. Ecol. Divers.* doi:10.1080/17550874.2013.783642.
- SEAL, J. N., AND W. R. TSCHINKEL. 2010. Distribution of the fungus-gardening ant (*Trachymyrmex septentrionalis*) during and after a record drought. *Insect Conserv. Divers.* 3: 134–142.
- SILVA, R. R., AND C. R. F. BRANDÃO. 2010. Morphological patterns and community organization in leaf-litter ant assemblages. *Ecol. Monogr.* 80: 107–124.
- SILVESTRE, R., C. R. F. BRANDÃO, AND R. R. SILVA. 2003. Grupos funcionales de hormigas: El caso de los gremios del Cerrado. In F. Fernández (Ed.) *Introducción a las hormigas de la región Neotropical*, pp. 113–148. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.
- SOMBROEK, W. 2000. Amazon landforms and soils in relation to biological diversity. *Acta Amazonica* 30: 81–100.
- TOCKNER, K., AND J. A. STANFORD. 2002. Riverine flood plains: Present state and future trends. *Environ. Conserv.* 29: 308–330.
- TSCHINKEL, W. R. 1988. Distribution of the fire ants *Solenopsis invicta* and *S. geminata* (Hymenoptera Formicidae) in Northern Florida in relation to habitat and disturbance.pdf. *Ann. Entomol. Soc. Am.* 81: 76–81.
- TSCHINKEL, W. R., T. MURDOCK, J. R. KING, AND C. KWAPICH. 2012. Ant distribution in relation to ground water in north Florida pine flatwoods. *J. Insect Sci.* 12: 1–20.
- VONSHAK, M., T. DAYAN, A. IONESCU-HIRSH, A. FREIDBERG, AND A. HEFETZ. 2009. The little fire ant *Wasmannia auropunctata*: A new invasive species in the Middle East and its impact on the local arthropod fauna. *Biol. Invasions* 12: 1825–1837.
- ZUQUIM, G., F. R. C. COSTA, J. PRADO, AND R. BRAGA-NETO. 2008. Distribution of pteridophyte communities along environmental gradients in Central Amazonia, Brazil. *Biodivers. Conserv.* 18: 151–166.