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Multiple Environmental Controls on Cockroach Assemblage Structure in a Tropical Rain Forest

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ABSTRACT

Arthropod abundance and diversity are remarkable in tropical forests, but are also spatially patchy. This has been attributed either to resources, predators, abiotic conditions or disturbances, but whether such factors may simultaneously shape arthropod assemblage structure is little known. We used cockroaches to test for multiple environmental controls on assemblage structure in 25 km^2 of Amazonian forest. We performed nocturnal, direct searches for cockroaches in 30 plots (250 m × 2 m) during two seasons, and gathered data on biotic and abiotic factors from previous studies. Cockroach abundance increased with dry litter mass, a measure of resource amount, while species richness increased with litter phosphorus content, a measure of resource availability. Cockroach abundance and species richness decreased with ant relative abundance. Cockroach species composition changed along the gradient of: (1) soil clay content, which correlates with a broad differentiation between flood-prone and non-flooded forest; (2) soil relative moisture, consistent with known interspecific variation in desiccation tolerance; and (3) according to the abundance of ants, a potential predator. Turnover in species composition was correlated with abiotic conditions—sorting species according to physiological requirements and to disturbance-related life history traits—and to ants' selective pressure. Cockroach abundance, diversity, and composition seem to be controlled by distinct sets of environmental factors, but predators which were represented by ants, emerged as a common factor underlying cockroach distribution. Such patterns of community structure may have been previously overlooked by undue focus on single or a few factors, and may be common to tropical forest arthropods.

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

Key words: bottom-up limitation; competition; distribution; environmental filter; top-down limitation.

ARTHROPODS ARE DOMINANT ORGANISMS IN TERRESTRIAL ECOSYSTEMS. This is particularly evident in tropical forests, where they can encompass more than half of the total animal biomass (Fittkau & Klinge 1973) and reach over 18,000 species/ha (Basset *et al.* 2012). However, this remarkable component of biodiversity is not homogeneously distributed in space. Attempts to explain variation among arthropod communities in tropical forests have focused on several factors individually. Some studies have found arthropod (or a subset of arthropods) abundance and diversity to be limited by resources such as habitat space and nutrient availability (Kaspari 1996, McGlynn *et al.* 2007, 2009, Kaspari & Yanoviak 2009, Sayer *et al.* 2010), both possibly promoted by floristic diversity (Basset *et al.* 2012), while others have provided evidence for limitation by predators (Dial & Roughgarden 1995, Kalka *et al.* 2008). In parallel, abiotic factors such as substrate moisture (Levings & Windsor 1984) and natural disturbances (*e.g.*, floods; Mertl *et al.* 2009) have also been found to play a role in the arthropod assemblage structure. Thus, multiple factors may simultaneously shape arthropod distribution in tropical forests, but their relative contributions are not well resolved. For instance, while there is evidence that food availability and predation pressure can jointly shape abundance (Richards & Coley 2007, Bennett 2010) and that different mechanisms can underlie different components of assemblages (*e.g.*, Sayer *et al.* 2010), the prevalence or generality of such patterns is not clear.

Cockroaches (Blattaria, except termites) comprise a diverse clade of detritivore-herbivore insects that account for a meaningful share of the arthropod biomass in some natural environments (Collins 1980, Basset 2001, Ellwood & Foster 2004) and can have large impacts on nutrient cycling and energy fluxes (*e.g.*, Irmler & Furch 1979). In some ecosystems, termites—a lineage of eusocial cockroaches which are major detritivores in the tropics—may even be replaced by other blattarians as the main agents of organic matter turnover (Bell *et al.* 2007), and some cockroaches are also important pollinators (Nagamitsu & Inoue 1997, Momose *et al.* 1998). However, cockroaches have been

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largely studied from the perspective of pests of human dwellings or as model organisms in physiology and behavior (Bell *et al.* 2007). Consequently, quantitative data on their ecology under natural conditions is limited (Grandcolas & Pellens 2012). Cockroach abundance and diversity is highest in the tropics (Bell *et al.* 2007), but little is known about the factors structuring tropical cockroach assemblages (*e.g.*, Schal & Bell 1986, Boyer & Rivault 2006).

Cockroaches occur from the horizontal compartments of the soil to the vertical strata and canopy of standing trees (Sinclair *et al.* 2001, Bell *et al.* 2007). Tropical rain forest landscapes in turn feature significant variation in topographic, soil, and vegetation properties (Castilho *et al.* 2006), which may create habitat heterogeneity affecting cockroach abundance, species richness, and composition. For instance, in a hand sorting survey of litter macrofauna undertaken in 72 × 250 m long plots in an Amazonian rain forest, it was found that cockroaches were found in 68 percent of the plots, and that their density ranged from 0 to 0.6 adult individuals m^{-2} (Morais J. W. & Franklin E., unpubl. data), suggesting considerable patchiness in their distribution.

As cryptic animals with a detritivore-herbivore diet, cockroaches can use plant substrates—either live or dead tissues—as both refuge and food. Accordingly, there is evidence that both cockroach species richness and abundance are related to litter depth (Abenserg-Traun *et al.* 1996). Moreover, recent studies suggest that tropical rain forest arthropods can be limited by specific elements, particularly phosphorus, which plays a key role in anabolism and whose availability is generally low and patchy in tropical landscapes (McGlynn *et al.* 2007, Kaspari & Yanoviak 2008, 2009). At the same time, predation may also contribute to distribution patterns, as cockroaches are prey of numerous animals, especially ants (Schal *et al.* 1984, Grandcolas & Pellens 2012), and there is evidence that the latter may limit cockroach densities (Otis *et al.* 1986).

Beyond resources and predators, many tropical forest landscapes feature a dense drainage system where clayish plateaus and sandy bottomlands alternate, with the latter being prone to waterlogging during the rainiest months (*e.g.*, Hodnett *et al.* 1997). Species whose life histories are not adapted to the seasonal disturbance may be excluded from seasonally inundated forests (Adis & Junk 2002). Furthermore, cuticular permeability varies almost fourfold among cockroach species (Appel *et al.* 1983), so that the natural moisture gradients of tropical forests (*e.g.*, Kaspari & Weiser 2000) are likely to influence their distribution (Boyer & Rivault 2006). These potential effects are not mutually exclusive, rather, their different combinations represent alternative hypotheses that may account for variation in cockroach assemblage structure across tropical landscapes.

In this study, we investigate multiple environmental controls on the cockroach assemblage structure across an old growth, tropical rain forest landscape (25 km^2) in Amazonia. Specifically, we expected cockroach species richness and abundance to increase with putative resources (*i.e.*, tree biomass, tree species richness, dry litter mass, and litter phosphorus content) and soil moisture, and to decrease with predation pressure (*i.e.*, relative abundance of ants, a generalist predator) and on clay-poor, flood-prone soils. We further hypothesized that cockroach species composition would change along both biotic (resources and predators) and abiotic gradients (soil relative moisture and clay content), assuming that species differ both in their performances in biotic interactions (*e.g.*, competition and predation) and in their physiological and life cycle requirements. To our knowledge, this is the first assessment of factors underlying cockroach distribution across a tropical rain forest landscape in the Amazon.

METHODS

Study site.—The Reserva Ducke has topographic and edaphic variation typical of many areas in the Amazon Basin and has a total area of 10,000 hectares situated northwest of Manaus, at km 26 on the AM-010 highway (2°57′S, 59°56′W). Disturbance is minimal in the reserve because anthropic-disturbed areas are small and located at the edges of the forest, around the headquarters and access roads. It is a moderately rugged terrain (elevation 30–180 m asl). Soils are acidic and very low in nutrients such as P, Ca, and K. They are classified as Xanthic Hapludox (‘*Latossolo Amarelo*’ in the Brazilian system) on plateaus, Typic Epiaquods (‘*Espodossolo Cárbico*’ in the Brazilian system) on slopes, and Typic Endoaquods (‘*Espodossolo Ferrocárbico*’ in the Brazilian system) associated with small streams in valleys (Chauvel *et al.* 1987, Bravard & Righi 1989).

The vegetation is ombrophilous dense forest with a closed canopy, and the undergrowth is characterized by abundant stemless palms, such as *Astrocaryum* spp. and *Attalea* spp. (Chauvel *et al.* 1987, Guillaumet 1987). There are approximately 1200 species of trees (Costa *et al.* 2009) with a canopy height of 30–37 m, some reaching 40–45 m. The mean annual temperature and rainfall in 2010–2011 were 25°C and 2763 mm, respectively, with a short, drier season between July and September (Coordination of Environmental Dynamics, INPA).

Sampling design.—The study site contains a grid of six regularly spaced north–south and six east–west trails. Each trail is 5 km long, forming a 5 km × 5 km grid. The east–west trails have five 250 m plots that follow terrain contours to minimize the variation in soil features and their correlates within plots, thus maximizing between-plot variation (RAPELD method, Magnusson *et al.* 2005). The grid allows access to 30 uniformly distributed sample plots, located 1 km apart along the trails (Table S1). The width of the plot is not fixed, but varies according to the biological group being sampled (Costa & Magnusson 2010). For cockroach sampling, each plot consists of a transect 250 m long × 2 m wide.

Cockroach sampling.—To increase the likelihood of sampling species occurring on a given plot, we sampled cockroaches during two periods of 6 d in 30 plots at Reserva Ducke. The first period was between November and December 2010 (beginning of the rainy season), and the second in May 2011 (end of the rainy season). The best method to sample cockroaches is through direct sampling during the first hours of the night (Grandcolas & Pellens 2012). Accordingly, two experienced collectors carried out an active survey with 1 h of effort in each plot beginning at 1830 h. The same collectors sampled each plot in both periods, keeping a distance of 30 m between each other along the central axis of the plot, and inspecting 1 m to both sides. Disturbance in the environment was minimized to increase sampling efficiency. Total effort in both periods was 60 h. We manually collected adult cockroaches present on the litter, fallen trunks, branches, and shrubby vegetation, and placed them in a plastic container (mouth diameter 7.5 cm, 10 cm in depth) with the addition of a killing agent and preservative (50 mL of ethanol 75%). We sampled cockroaches present on the leaves by placing the plastic container below the leaf and, with the help of the lid placed on the top of the leaf, the animal was pushed to the interior of the container. On other surfaces, we used forceps to catch the animals.

We identified adult cockroaches to species or sorted to morphospecies under the supervision of specialists from the National Museum of Rio de Janeiro (MNRJ), in Rio de Janeiro City, Brazil. We also consulted the reference collection of the museum, and deposited biological material in the Entomological Collection of INPA, Manaus, Brazil, and MNRJ. The raw data are available at the website of the Brazilian Program for Biodiversity Research (PPBio; Table S1).

ENVIRONMENTAL DATA.—Environmental data included soil clay content, soil relative moisture, litter dry mass, litter phosphorus content, tree biomass and tree species richness (dbh >10 cm trees), and ants. We obtained data for the independent variables measured at the same 30 plots where we sampled the cockroaches, as well as full descriptions of sampling methods from previous surveys made available by the website of the PPBio. We conducted soil textural analyses and nutrient analyses according to the recommendations of EMBRAPA (1997).

To determine soil clay content (Table S1) and relative moisture, we sampled and combined six soil subsamples to a depth of 5 cm and at least 50 m distant from each other for each plot and analyzed them at the Soil Laboratory of the Agronomy Department at INPA. Soil relative moisture consisted of the difference between the wet weight and dry weight of the soil sample, divided by the dry weight and multiplied by 100 (T. Pimentel, unpubl. data).

We obtained litter dry mass (Table S1) from each plot by collecting all the fine litter (leaves, fruits, and woody items with diameter <2 cm) in five quadrats (0.4 m × 0.6 m) distant at least 50 m from each other. Litter was dried at 65°C for 5 d and then weighed to determine dry mass (mean value: 121.5 g; range: 59.2–231.5 g). Further, we grinded leaves and subjected them to nitric-perchloric digestion, each sample being subsequently diluted in 50 mL distilled water. We determined litter phosphorus content (g/Kg) by colorimetry under a spectrophotometer, in the presence of ammonium molybdate and ascorbic acid (mean value: 0.23651 g/kg; range: 0.19008–0.30245 g/kg). Diameter at breast height (dbh) >10 cm trees species composition was obtained from Castilho *et al.* (2006) (personal contact for metadata). The mean of each plot was used in analyses for all soil and litter variables.

We obtained tree biomass, including palm trees (mean value: 330.16 Mg/ha; range: 254.7–400 Mg/ha) from Castilho *et al.* (2006). We sampled trees with dbh ≥30 cm in 1 hectare (250 m × 40 m), and trees at dbh of 10–30 cm and 1–10 cm in 0.5 ha (250 m × 20 m) and 0.1 ha (250 m × 4 m), respectively. We counted and measured trees, and estimated total biomass using published allometric equations (see Castilho *et al.* 2006). Plant species richness (mean value: 155.63 per plot; range: 118–192 per plot) is available on the PPBio website (Table S1).

We sampled ants between June and August 2012 in the same 30 plots at Reserva Ducke (Oliveira 2013). Although we sampled ant and cockroach data in different years, ant colonies are relatively long-lived and their assemblages generally stable at time scales of a few years (Andersen 2008). Thus, we considered that both datasets could still be reasonably compared. In each plot, we placed one pitfall trap (95 mm diameter; 8 cm depth; 500 mL volume) every 25 m along the central axis of the plot, for a total of 10 traps. We buried pitfall traps so as to place their top at ground level, then partially filled them with a killing and preservative solution (100 mL of 70% ethanol and a drop of odorless detergent), covered them to exclude rain and leaves, and left them on the ground for 48 h. For each plot, we counted the number of traps (0–10) in which each ant species occurred, a reasonable measure of ant species relative abundance (King 2010). Species counts were summed by plot to estimate overall ant relative abundance per plot. A full reference collection of this material was deposited in INPA's Entomological Collection.

DATA ANALYSIS.—We used Chao's abundance-based estimator of species richness (Colwell *et al.* 2012) to infer the total number of cockroach species (including unobserved ones) for each plot. Sampling plots were ordinated as a function of cockroach species composition using Principal Coordinate Analysis (PCoA) applied to Sørensen's pairwise dissimilarities among plots (Legendre & Legendre 2012). The first and the second PCoA axes preserved 23 and 18.5 percent of the variance of the original dissimilarities, with <5 percent of this variance preserved from the third axis onwards, and were used to represent the main gradients in cockroach species turnover across the landscape.

Each possible combination of predictors was treated as an alternative hypothesis on the factors underlying (1) cockroach abundance (total count of individuals per plot); (2) estimated species richness; and (3) species composition (scores of first and second PCoA axes). The seven environmental variables potentially influencing the three cockroach-dependent variables were combined into alternative regression models, with a maximum of three predictors (one for each 10 observations) to preserve a reasonable number of degrees of freedom per model (Gotelli & Ellison 2004). We first included tree biomass with the other five environmental variables, and then we substituted it for tree richness with the same variables, to see if plant diversity would underlie the diversity of cockroaches. For each dependent variable, the most supported set of predictors was inferred using Akaike's information criterion corrected for sample size (AICc), with the model with the lowest AICc being favored (Burnham & Anderson 2002). We also computed the Akaike weight *w* (*i.e.*, the probability of a model being the most supported one under a given model set) as a measure of the relative support for each model. The analyses were undertaken with R software (R Development Core Team. 2013).

RESULTS

A total of 1004 individuals were sorted to 41 species and/or morphospecies in three families (Table S2). Of these, 11 species were nominally identified and 30 remained as morphospecies. The number of species observed per plot varied between 5 and 15, while estimated species richness varied from 5 to 70. The number of individuals sampled per plot varied between 13 and 65. Ectobiidae showed the highest number of species (31) representing 78 percent of the number of species collected, followed by Blaberidae and Corydiidae with nine and only one species, respectively. The most abundant family was Ecotobiidae with 853 individuals, followed by Blaberidade and Corydiidae, with 150 and six individuals, respectively. *Xestoblatta vera* and *Neoblattella poecilops* were the most abundant, representing 29 and 19.6 percent of all sampled individuals, respectively. Nine and five species had only one and two individuals collected, respectively. The Chao abundance-based estimator indicated a total of almost 50 species, suggesting that the sampling captured most of the species collectable with this technique.

The variation in cockroach abundance across the rain forest landscape was best explained by a model including dry litter mass and ant relative abundance (Table 1; Table S3). Partial regressions indicated that cockroaches achieved higher abundance with increasing dry litter mass, but lower abundance with increasing ant relative abundance (Figs. 1A and C). Likewise, the most supported model accounting for variation in cockroach species richness included litter phosphorus content and ant relative abundance (Table 1). Cockroach species richness increased with the amount of phosphorus in the litter, but decreased with increasing ant relative abundance (Figs. 1B and D).

Cockroach species composition, as summarized by the first PCoA axis, showed a pattern of turnover across plots (Table 1; Fig. 2A). Changes in species composition were mainly associated with soil clay content and relative moisture (Figs. 2B and C). The second PCoA axis also showed a pattern of turnover across plots (Table 2; Table S4; Fig. 3A). Changes in species composition

TABLE 1. *Evaluation of competing models on the response of cockroach abundance, species richness and species composition to environmental features (soil clay content, soil moisture, litter dry mass, litter phosphorus content, tree biomass and ant relative abundance) in an Amazonian rain forest. Models are ranked in increasing order by their respective values of the Akaike Information Criterion corrected for sample size (AICc). Parameter estimates are given for the five best models for each response variable; for the remaining models, see Table S1 in Supporting Information*

Response variable	Intercept	Soil clay content (%)	Ant relative abundance	Litter phosphorus content (g/kg)	Dry litter mass (g)	Soil moisture (%)	Tree biomass (Mg/ha)	R^2	AICc	ΔAICc	*w*
Cockroach abundance	28.465		−0.239		0.16			0.337	238.664	0	0.209
	0.954				0.173	0.276		0.318	239.524	0.86	0.136
	17.237		−0.169		0.165	0.155		0.358	240.59	1.926	0.08
	12.907				0.169			0.218	240.946	2.281	0.067
	41.519		−0.223	−54.2	0.15			0.349	240.986	2.322	0.065
Cockroach richness	−9.685		−0.238	175				0.23	240.178	0	0.174
	−21.912		−0.235	194.2	0.062			0.26	241.865	1.688	0.075
	−15.989			141				0.105	241.998	1.821	0.07
	−0.38	−0.06	−0.256	151.9				0.256	242.024	1.846	0.069
	2.386		−0.291	160.3		−0.13		0.245	242.469	2.292	0.055
Cockroach composition (First PCoA axis)	0.067	0.007				−0.009		0.676	−22.871	0	0.43
	0.235	0.007	−0.002			−0.01		0.69	−21.28	1.591	0.194
	0	0.007			0.001	−0.009		0.682	−20.568	2.303	0.136
	0.23	0.007		−0.63		−0.009		0.681	−20.421	2.45	0.126
	−0.042	0.007				−0.009	0	0.677	−20.134	2.737	0.109
Cockroach composition (Second PCoA axis)	−0.372	0.002	0.005					0.223	−2.787	0	0.157
	0.13	0.003				−0.007		0.2	−1.924	0.863	0.102
	−0.223		0.004					0.104	−1.19	1.597	0.071
	−0.167	0.003	0.003			−0.004		0.254	−1.106	1.681	0.068
	−0.266	0.002	0.004		−0			0.243	−0.645	2.142	0.054

R^2 = explained variance; ΔAICc = difference between each model's AICc and the minimum AICc found; w = Akaike weight.

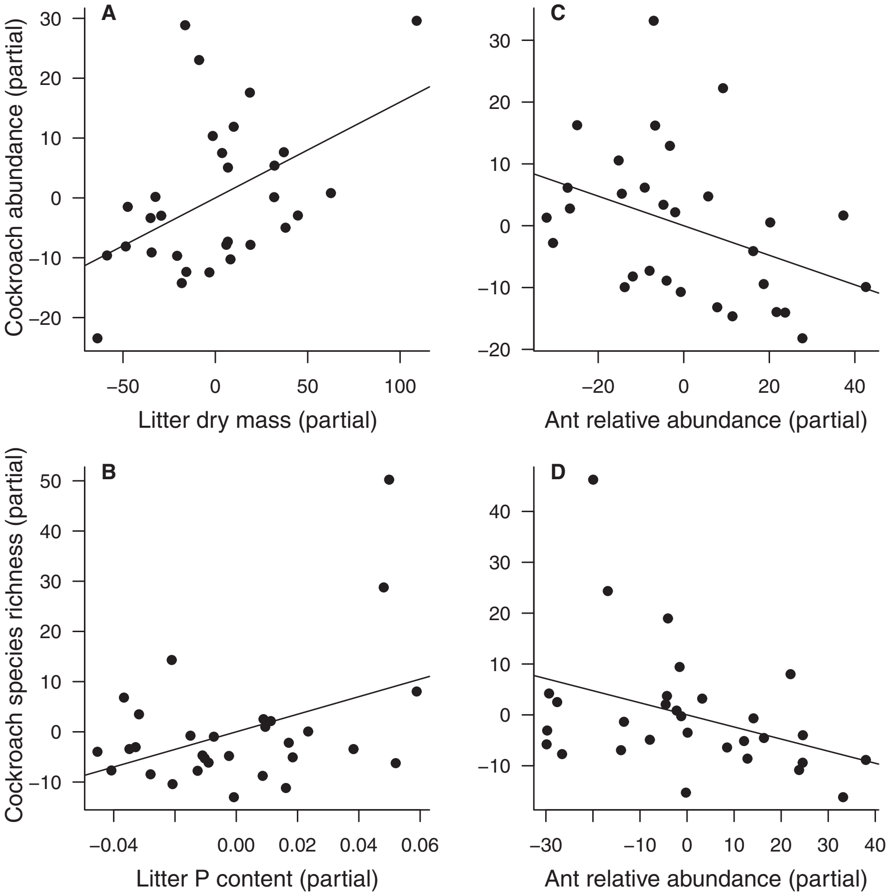

FIGURE 1. Partial regressions of most supported effects on cockroach abundance and species richness, as inferred with Akaike's Information Criterion corrected for sample size. Cockroach abundance increased with dry litter mass (A) and decreased with ant relative abundance (C), while cockroach species richness increased with litter phosphorus content (B) and decreased with ant relative abundance (D).

were again associated with soil clay content (Fig. 3A), but ant relative abundance appeared as another factor influencing cockroach species composition (Fig. 3B). Some species such as *Neoblattella poecilops*, *Xestoblatta vera*, *Amazonina* sp. 1, and *Cariblatta vera* occurred across the whole gradient. In all cases, some species were associated with the extremes of the gradients (Figs. 2A and 3A).

DISCUSSION

This study revealed multiple and complex environmental controls on cockroach assemblage structure. Cockroach abundance reflected primarily biotic factors, *i.e.*, dry mass of litter, a resource, and the relative abundance of ants, a potential predator. Similarly, cockroach species richness increased with a resource, litter phosphorus content, and decreased with ant relative abundance. Cockroach species composition was also a function of abiotic factors, in particular soil features (*i.e.*, clay content and relative moisture), and of a biotic factor, the ants, acting as a potential predator. Thus, although different components of the cockroach community seem to be controlled by distinct sets of environmental factors, predators—as represented by ants—emerge as a common factor underlying cockroach distribution. Biotic interactions and several abiotic factors have also been implied in the coexistence among cockroach species in insular sugar-cane fields in the Réunion Island, located in the Indian Ocean (Boyer & Rivault 2006). Our results also indicate that multiple factors shape cockroach assemblage across tropical landscapes.

The increase in cockroach abundance with dry litter mass is consistent with the hypothesis that cockroach numbers are limited by resource availability, and contrasts with a negative association between cockroach abundance and woody litter amount reported elsewhere (Abenserg-Traun *et al.* 1996). Litter could provide both food (*i.e.*, decaying organic matter) and refuge for cockroaches, as the litter layer provides a stable, favorable microclimate (Sayer 2006). Similarly, the increase in cockroach species richness with litter phosphorus content suggests that cockroach diversity is limited by this element. The mechanism could either involve direct phosphorus limitation, or an indirect effect through microbial biomass, which serves as food to detritivores and is known to be limited by phosphorus (Kaspari & Yanoviak 2008, 2009).

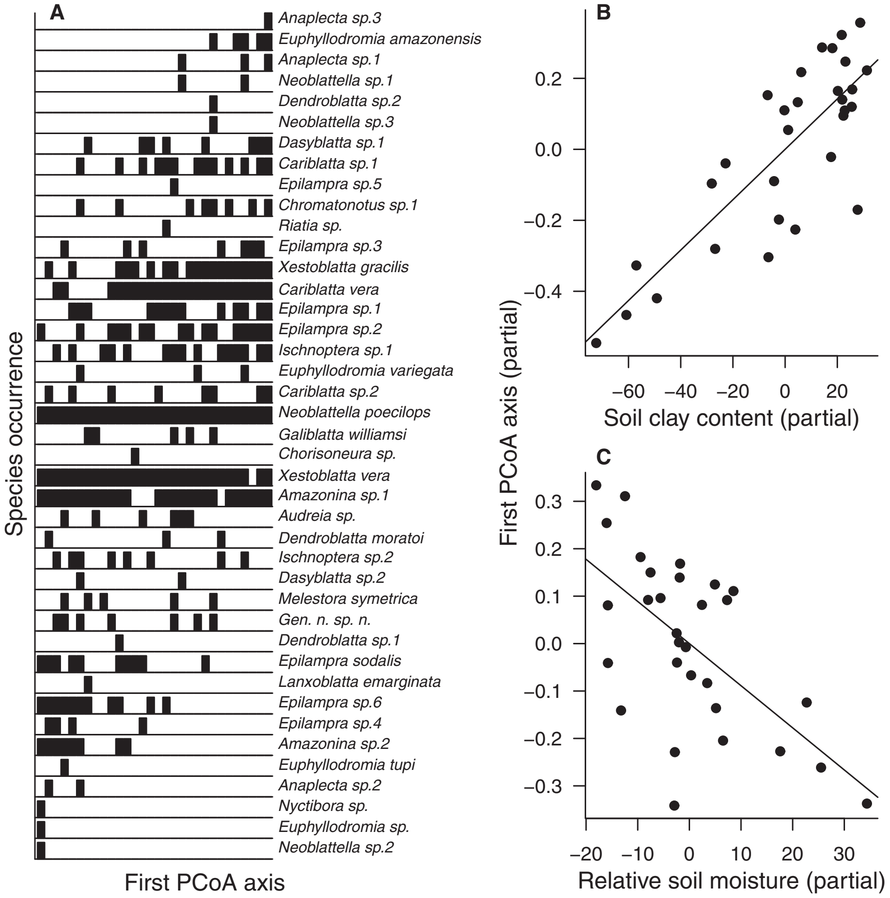

FIGURE 2. Partial regressions of most supported effects on cockroach species composition, as inferred with Akaike's Information Criterion corrected for sample size. Plots were ordinated according to species composition as summarized by the first Principal Coordinate (first PCoA axis) based on Sørensen's dissimilarities, with scores increasing from left to right (A). Cockroach species composition changed with soil clay content (B) and soil relative moisture (C).

Regardless, in plots with low phosphorus content, competition is likely to be more intense, and species more efficient in exploiting this resource may have an advantage over (and potentially exclude) others. Jacquemin *et al.* (2012) showed that experimental fertilization with phosphorus enhanced litter decomposition and reduced litter amount, decreasing the abundance of ants. They also detected the opposite or no effect on the rest of the invertebrates, including cockroaches. Thus, the increasing of the mesofauna density (*i.e.*, springtails and mites) represented a higher prey availability for predators. One may suppose that if phosphorus increases decomposition rate and a lower amount of litter reduces the abundance of ants, then the positive effect of phosphorus on the cockroach species richness could be indirect and reflecting the exclusion of predators (ants). However, we included ants together with phosphorus in the models and the effects of both were detected, meaning that both effects are independent. Probably the effect of phosphorus has nothing to do with ants, but with nutrient availability. Thus, phosphorus availability may promote the coexistence of cockroach species in the studied rain forest. High phosphorus environments have been found to promote the abundance of litter detritivores in tropical forests elsewhere (McGlynn *et al.* 2007, 2009*,* Kaspari & Yanoviak 2009), but we found no such pattern with respect to cockroach abundance.

The decline of both cockroach abundance and species richness with ant relative abundance could be either due to direct predation by ants or active avoidance of ant-rich sites by cockroaches, perhaps by means of chemical recognition. Cockroaches inhabiting the ground litter exhibit reaction to ants, especially army ants, which attack all species, except those showing thanatosis (Grandcolas & Deleporte 1994*,* Grandcolas & Pellens 2012). Thus, some species may be more prone to predation than others. Overall, our results suggest that cockroach abundance and species richness are simultaneously under 'bottom-up' (*i.e.*, resources) and 'top-down' control (*i.e.*, predators) across the studied landscape. This contradicts previous suggestions that the detritivore fauna would be mainly limited by resource availability (*e.g.*, Chen & Wise 1999*,* Ponsard *et al.* 2000*,* Dyer & Letourneau 2003*,* McGlynn *et al.* 2007*,* Kaspari & Yanoviak 2009). Rather, our results are more consistent with a scenario in which resources set carrying capacity, while predators harvest populations to a level below that (McIntosh *et al.* 2005, Boyer & Rivault 2006, Richards & Coley 2007).

TABLE 2. *Evaluation of competing models on the response of cockroach abundance, species richness, and species composition to environmental features (soil clay content, soil moisture, litter dry mass, litter phosphorus content, tree richness, and ant relative abundance) in an Amazonian rain forest. Models are ranked in increasing order by their respective values of the Akaike Information Criterion corrected for sample size (AICc). Parameter estimates are given for the five best models for each response variable; for the remaining models, see Table S1 in Supporting Information.*

Response variable	Intercept	Soil clay content (%)	Soil moisture (%)	Dry litter mass (g)	Litter phosphorus content (g/kg)	Tree richness	Ant relative abundance	R^2	AICc	ΔAICc	*w*
Cockroach abundance	28.465			0.16			−0.239	0.337	238.664	0	0.206
	0.954		0.276	0.173				0.318	239.524	0.86	0.134
	17.237		0.155	0.165			−0.169	0.358	240.59	1.926	0.078
	12.907			0.169				0.218	240.946	2.281	0.066
	41.519			0.15	−54.209		−0.223	0.349	240.986	2.322	0.064
Cockroach richness	−9.685				175.039		−0.238	0.23	240.178	0	0.173
	−21.912			0.062	194.164		−0.235	0.26	241.865	1.688	0.074
	−15.989				140.964			0.105	241.998	1.821	0.07
	−0.38	−0.063			151.877		−0.256	0.256	242.024	1.846	0.069
	2.386		−0.13		160.348		−0.291	0.245	242.469	2.292	0.055
Cockroach composition (First PCoA axis)	0.067	0.007	−0.009					0.676	−22.871	0	0.419
	0.235	0.007	−0.01				−0.002	0.69	−21.28	1.591	0.189
	0	0.007	−0.009	0.001				0.682	−20.568	2.303	0.132
	−0.124	0.006	−0.008			0.001		0.682	−20.528	2.342	0.13
	0.23	0.007	−0.009		−0.626			0.681	−20.421	2.45	0.123
Cockroach composition (Second PCoA axis)	−0.372	0.002					0.005	0.223	−2.787	0	0.146
	0.13	0.003	−0.007					0.2	−1.924	0.863	0.095
	−0.223						0.004	0.104	−1.19	1.597	0.066
	−0.167	0.003	−0.004				0.003	0.254	−1.106	1.681	0.063
	−0.266	0.002		−0			0.004	0.243	−0.645	2.142	0.05

R^2, explained variance; ΔAICc, difference between each model's AICc and the minimum AICc found; *w*, Akaike weight.

We found that cockroach species turnover was driven by two soil features, namely relative soil moisture and soil clay content. The influence of soil moisture on species composition is consistent with the fourfold variation in cuticular permeability among cockroach species (Appel *et al.* 1983), although this variable was not measured in our study. Nonetheless, this wide variation should filter cockroach species according to desiccation tolerance. On the other hand, we also detected the relation between cockroach species composition with clay percentage and ants. The relation with clay percentage suggests a broad differentiation between assemblages subject to a more dynamic or disturbed environment (the valleys, which are more prone to seasonal inundation and where the mineral fraction of soil is almost pure sand) and assemblages inhabiting a more stable environment (plateaus, with more clay-rich soil). Although soil texture could directly influence cockroach species with fossorial habits (Bell *et al.* 2007), none of the species we collected are known to be fossorial. Thus, we hypothesize that the species turnover observed along the soil clay gradient resulted from species being filtered according to their life histories, with species inhabiting clay-poor, seasonally waterlogged plots more likely to display traits relevant to enduring seasonal disturbance (*e.g.*, seasonal phenology, vertical migration ability, or submersion tolerance). Interestingly, soil clay percentage has also been shown to affect the distribution of most other taxa investigated in the Amazon Basin, including palms (Costa *et al.* 2009), ants (Oliveira *et al.* 2009), and edaphic oribatid mites (Moraes *et al.* 2011). The results also showed that the ants can collectively exert pressure on cockroaches along the studied landscape. Predator presence has varying effects on the prey, and can influence prey population dynamics, reflecting both direct effects of predation and indirect effects of predator avoidance and other changes in prey behavior (Richards & Coley 2007, Creel & Christianson 2008). We suggest that local cockroach populations are primarily limited by litter amount and potential predators, with successfully established species, then being assembled according to their competitive abilities regarding phosphorus availability and their predation susceptibilities. Interestingly, this pattern mirrors that reported by Sayer *et al.* (2010), who found that overall arthropod abundance increased with forest floor mass, while arthropod diversity increased with soil phosphorus.

Our hypothesis that tree biomass and/or tree richness would influence the cockroach distribution (*e.g.*, by providing food or habitat) was not supported. This contrasts with the finding that cockroach occurrence was more likely as the percent cover of the

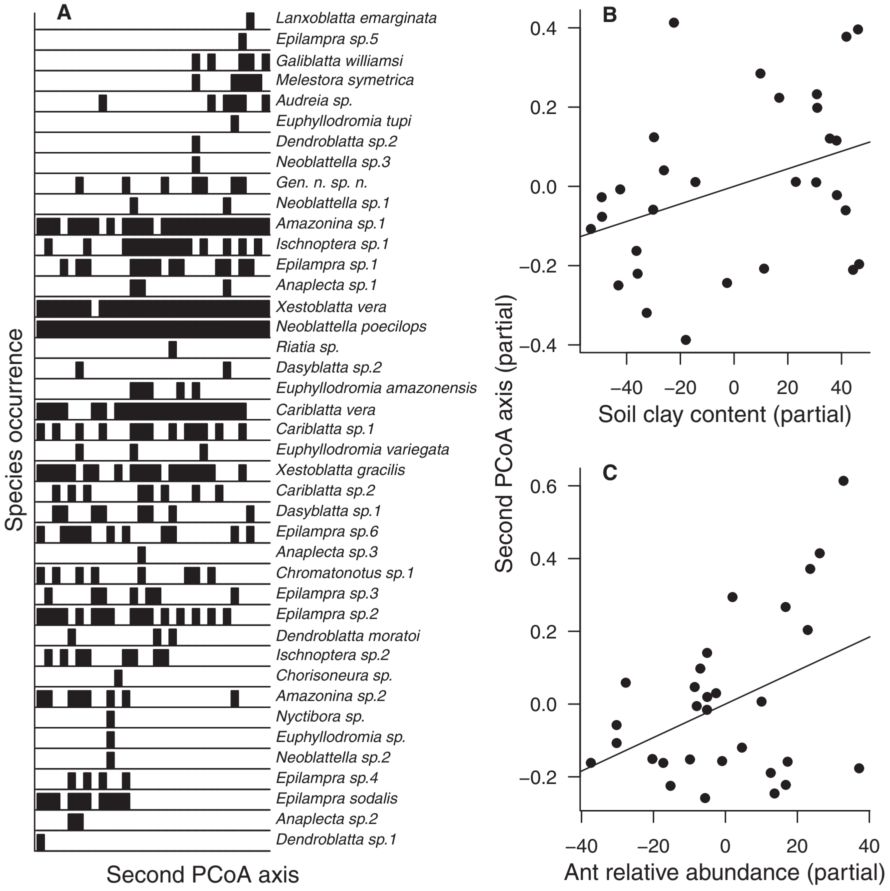

FIGURE 3. Partial regressions of most supported effects on cockroach species composition, as inferred with Akaike's Information Criterion corrected for sample size. Plots were ordinated according to species composition as summarized by the second Principal Coordinate (second PCoA axis) based on Sørensen's dissimilarities, with scores increasing from left to right (A). Cockroach species composition changed with soil clay content (B) and ant relative abundance (C).

most common tree species increased in alpine vegetation (Sinclair *et al.* 2001). However, cockroaches may inhabit a certain substrate during the day and forage at night in another (Grandcolas & Pellens 2012), possibly in response to predation risk (Schal *et al.* 1984). This might explain why any effect of tree biomass or richness, if it exists, could not be detected.

This study revealed a complex picture of how cockroach assemblages are structured across a tropical rain forest landscape in the Amazon. Earlier studies shed light on factors shaping cockroach assemblages at smaller spatial extents in primary tropical rain forest (*e.g.,* Schal & Bell 1986). Here, we provided evidence that biotic interactions—in particular, competition for resources and predation—set how many individuals and species can coexist locally. Abiotic filters appear to sort species according to desiccation tolerance and, possibly, to life history traits that promote persistence under seasonal disturbance. We also found evidence that collectively ants can have selective pressure on cockroaches. These ideas could be tested experimentally by measuring relevant traits in representative species whose distribution patterns are known. More generally, we suggest that future studies take into account multiple, alternative mechanisms that may affect tropical arthropod assemblages to gain explanatory and predictive power.

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SUPPORTING INFORMATION

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

TABLE S1. *Data deposited in the digital repository of the Brazilian Biodiversity Research Program.*

TABLE S2. *Diversity, abundance, and frequency of cockroaches recorded in 30 plots in the tropical forest in Reserva Ducke.*

TABLE S3. *Evaluation of competing models on the response of cockroach abundance, species richness, and species composition to environmental features in an Amazonian rain forest.*

TABLE S4. *Evaluation of competing models on the response of cockroach abundance, species richness, and species composition to environmental features in an Amazonian rain forest.*

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