



Termite (Insecta: Isoptera) Species Composition in a Primary Rain Forest and Agroforests in Central Amazonia

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ABSTRACT

Termites play important roles in organic matter decomposition, nutrient cycling, and soil structure in tropical rain forests. When forests are replaced by agriculture, termite species richness, abundance, and function often decline. We compared the termite assemblage of a primary forest site with that of a low plant diversity, palm-based agroforest (five plant species) and a high plant diversity, home-garden agroforest (10 plant species) using a rapid biodiversity assessment protocol. In comparing the primary forest termite species composition to previously published studies, we found soil feeders and the Apicotermittinae to be more dominant than previously reported in Amazonia. Thirty percent of the species belonged to the Apicotermittinae, and an unusually high percentage (57%) of species were soil feeders. Unexpectedly, the palm-based agroforest, despite its lower plant diversity, was closer to primary forest in termite species composition, rate of species accumulation, and proportions of species in taxonomic and functional classes than was the home-garden agroforest. This suggests that particular plant attributes may better determine the termite assemblage than plant diversity alone in these agroecosystems. Unlike other agroecosystems reported in the literature, Apicotermittinae and soil feeders were proportionally more abundant in these agroforests than in primary forest. The ability of agroforests to support populations of soil feeders has a potentially positive effect on soil fertility in these agroecosystems; inasmuch as feeding guild is a proxy for function, these closed-canopy agroforests may be able to sustain the same termite-mediated functions as primary forest.

Key words: agroforestry; Amazon; biodiversity; Brazil; rapid biodiversity assessment protocol; soil ecology; soil fauna; tropical forest.

TERMITES ARE AN INTEGRAL PART OF TROPICAL RAIN FOREST ECOSYSTEMS. Though not easily observed, they are often the dominant arthropod detritivore (Jones & Eggleton 2000). A diverse range of termite species processes a variety of plant organic matter at all stages of decomposition, from leaf litter, to rotten wood, to soil humus. Tropical rain forest is often associated with low-fertility soils (Jordan 1985), and termites' cycling of organic matter contributes to the efficient return of nutrients to the vegetation.

In extensive areas of Amazonia, forest ecosystems have been replaced with agroecosystems. Pastures, crops, and fallows occupy over 500,000 km² of the forest's original extent (INPE 2004). Information on how conversion of forest to agricultural usage impacts termite fauna is scarce (Okwakol 2000), but investigations in Africa and Asia, and a handful of studies from Amazonia have contributed to what we know. Loss of termite diversity has been shown in Africa by Collins (1980), Eggleton *et al.* (1996, 2002), and Okwakol (2000), and in Asia by Abe and Watanabe (1983), Watanabe *et al.* (1984), and Abe and Matsumoto (1979). At an African site, Okwakol (2000) found that 60 percent of termite species were eliminated upon forest clearance, and that only two species survived cultivation. At a site in northeastern Brazil, termites were 11 times less abundant in a banana plantation than in a disturbed primary forest (Bandeira & Vasconcellos 2002). While there are few data

from Amazonia, Bandeira (1983) found termite species richness to be reduced by half upon primary forest conversion to pasture.

Some types of termites appear to be more susceptible to land clearance than others. Soil-feeding termites seem to be especially vulnerable to clearing and cultivation, decreasing in species richness and abundance over other types of termites such as wood feeders (De Souza & Brown 1994; Eggleton *et al.* 1997, 2002, Bandeira & Vasconcellos 2002; Bandeira *et al.* 2003). This decline is unfortunate, as soil feeders help create and maintain soil conditions favorable to plant growth. Soil feeders are linked to an increase in soil exchangeable cations (Anderson & Swift 1983), to release of nitrogen and phosphorus, to organic matter humification and stabilization, and to the improvement of soil drainage and aeration (Lavelle *et al.* 1997). Dibog *et al.* (1999) found soil-feeding termite abundance to be positively correlated with agricultural yield.

While little is known about the recovery potential of macrofauna after clearance (Mathieu *et al.* 2005), soil fauna communities are believed to be best conserved when the derived system is similar in structure to the primary vegetation—such as tree-based systems in forest areas (Decaëns *et al.* 1994, 2002; Fragozo *et al.* 1997; Barros *et al.* 1999). There is a call for more investigation into the interactions of these agroecosystems with soil fauna (Beare *et al.* 1997, Lavelle *et al.* 2001, Barros *et al.* 2002), and especially for using comparable sampling protocols among agroecosystems (Vohland & Schroth 1999, Lavelle *et al.* 2003).

In the Amazon Basin, agroforestry systems are a promising agricultural alternative (Fernandes & Matos 1995), maintaining a

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structural diversity that imitates the native forest better than do conventional pasture, crops, and monoculture plantations. This study examines to what extent two agroforestry management regimes support a termite assemblage with a species composition, diversity, and function (by feeding guild) that resemble those of primary forest at a site in Central Amazonia. In particular we were interested in how hospitable these agroforestry systems would be to soil-feeding termites, which are considered important to soil fertility.

We compared the termite assemblage of a primary forest with that of two agroforestry systems: a low plant diversity, palm-based agroforest and a high plant diversity, home-garden agroforest. We expected the species richness and abundance of termites to be lower in the agroforests than in the primary forest, and for the soil feeders to be especially affected, though not to the extent found in the literature for other agroecosystems. We expected the home-garden agroforest to be intermediate to the primary forest and the palm-based agroforest in these measures, due to its intermediate diversity of plant species.

Another goal of the study was to add to the basic knowledge of Neotropical termite fauna. The termite fauna of Amazonia is little known compared to that of the rain forests of the Old World Tropics (Martius 1994). Only a handful of surveys of termite species in Amazonia have been published to date (Snyder 1926; Mill 1982; Bandeira 1983, 1989; Bandeira & Torres 1985; Constantino 1992; Apolinário 1993; De Souza & Brown 1994). Of these, studies that compare primary forest with agricultural systems (those of Bandeira and co-investigators) are even scarcer, and geographically restricted to Eastern Amazonia.

METHODS

STUDY SITE.—The study site was located at 02°31'04" S, 60°01'48" W, 60 m asl at the Empresa Brasileira de Pesquisa Agropecuária (Embrapa) research station at 54 km of the highway BR-174 north of Manaus, Amazonas, Brazil. Soils on the plateau where this study was conducted are classified as dystrophic, isohyperthermic, clayey, kaolinitic Xanthic Hapludox (Demattê & Demattê 1993). The climate is tropical humid. Mean annual precipitation is 2400–2500 mm, with an average maximum in February–March of *ca* 320 mm and an average minimum in August–September of *ca* 80 mm (Marques *et al.* 1981, de Paiva 1996). Mean annual air temperature is 26°C, and atmospheric humidity is *ca* 84 percent (Vose *et al.* 1992).

Three land uses were chosen for this study: a primary forest, a home-garden agroforest, and a palm-based agroforest (Table 1). The home-garden and palm-based agroforests had been established on pastureland abandoned 10 yr prior to this study, and had accumulated 34 and 42 Mg aboveground C/ha, respectively (McCaffery 2003). Each plot measured 50 × 60 m. The agroforests were replicated on three blocks according to their land-use history: blocks one, two, and three had been in pasture for 4, 5, and 8 yr previously, and in fallow for 3, 4, and 5 yr prior to the establishment of the agroforests. These sites occurred on the plateau of the study

TABLE 1. Species composition and spacing of the agroforests at the study site in Central Amazonia (after McCaffery 2003). The abundance and spacing of *Gliricidia sepium* and *Theobroma grandiflorum* were the same in the two agroforests.

Agroforest	Plant species	Abundance (plants/ha)	Spacing (m)
Home-garden	<i>Gliricidia sepium</i> Jacq.	375	2 × 2
	<i>Theobroma grandiflorum</i> Willd. Ex Spreng	83	6 × 6
	<i>Bertholletia excelsa</i> Berg.	79	10 × 10
	<i>Eugenia stipitata</i> McVaugh	79	6 × 6
	<i>Genipa americana</i> Linn.	144	6 × 6
	<i>Inga edulis</i> Mart.	120	2 × 6
	<i>Malpighia glabra</i> Linn.	194	2 × 6
	<i>Musa paradisiaca</i> L.	300	2 × 6
	<i>Swietenia macrophylla</i> King	40	6 × 8
	<i>Tectona grandis</i> Linn.	90	6 × 8
Palm-based	<i>Gliricidia sepium</i>	375	2 × 2
	<i>Theobroma grandiflorum</i>	83	6 × 6
	<i>Colubrina glandulosa</i> Perkins	125	6 × 12
	<i>Bactris gasipaes</i> H. B. K.	650	2 × 6
	<i>Euterpe oleracea</i> Mart.	596	2 × 6

site, and were surrounded by primary forest on the surrounding slopes. The primary forest site sampled was 3500 m away, selected as the nearest accessible primary forest on the study site that also occurred on the plateau. Three plots were chosen in the primary forest, at the same distance apart as the plots in the agroforests. The primary forest site was part of continuous, closed-canopy, dense, evergreen nonflooding forest (Veloso *et al.* 1991), which occupies about 90 percent of the Amazon Basin (Schubart 1983). In this region, canopy height is 20–30 m, with an open understory dominated by stemless palms (De Souza & Brown 1994).

SAMPLING.—We assessed termite species composition using the protocol recommended by Bignell and Eggleton (2000). This protocol has been shown to provide unbiased samples of the total termite species assemblage other than drywood termites (Jones & Eggleton 2000), and it standardizes effort across sampling sites. The method employs a 100-m belt transect with 20 contiguous 2 × 5 m sections sampled sequentially. Our transect length was limited to 50 m, the width of the agroforest plots. We established a transect through the middle of each plot, amounting to three transects in each land cover, nine in total. A team of two collectors sampled as many species as possible in 30 min in each 2 × 5 m section. We collected in soil, litter, dead wood, mounds, nests, soil to 5 cm depth, and runways to 2 m height in the vegetation. The presence of a species in each section was considered an encounter and used as a surrogate for relative abundance. Observations on feeding substrates and nesting locations were recorded simultaneously.

Termites were preserved in vials of 80 percent ethanol and labeled with section number for later identification to species or

morphospecies by the second author. The collection was deposited in the Entomological Museum of the National Institute for Amazonian Research (INPA), Brazil.

Genera were assigned to feeding guilds based on known feeding habits (Apolinário 1993, De Souza & Brown 1994, Constantino 1999, Hanne 2001, Roisin & Leponce 2004) and the first and second authors' observations in the field. These groups were: (1) soil feeders: species that feed on mineral soil and humus; (2) litter feeders: species that feed on leaf and small woody litter; (3) soil/wood interface feeders: species that feed on very decayed wood that has become soil-like; (4) wood feeders: species that feed on dead wood; and (5) pest species: species that feed on living plant tissue (Constantino 2002).

STATISTICAL ANALYSIS.—We used reciprocal averaging (Hill 1973, Gauch 1982) to ordinate the species and samples of the data set, using FORTRAN code (H. G. Gauch, Jr., pers. obs.). Reciprocal averaging is also called correspondence analysis, weighting species abundance by location. Species that were encountered rarely in the survey (three times or less) were not included in this analysis, as the quantity of observations was not sufficient to place them along an ecological gradient. The similarity in the species composition of the three land uses was evaluated using Bray–Curtis cluster analysis (Biodiversity Professional, Version 2, The Natural History Museum and the Scottish Association for Marine Science).

To determine if species had preferences among the land uses studied, we tried a novel application of the additive main effects and multiplicative interactions (AMMI) model, to evaluate the species-by-environment interaction. This model uses principal component analysis to partition the multiplicative structure within the interaction, where interaction is the residual from the ANOVA (Gauch 1992). It is most often used for genotype-by-environment field trials for crops. The AMMI model was run in the software MATMODEL (Microcomputer Power, Ithaca, NY).

Chi-square tests of independence were used to test for differences in both functional and taxonomic composition of the termite species between the three land uses. Both species richness and relative abundance (number of species encounters) were tested. The chi-square test was also used to compare the proportions of unique species among the land uses.

RESULTS

A graph of the average species richness over the three transects in each land use is displayed in Figure 1. The rate of new species discovery was higher in primary forest than in the agroforests (Fig. 1), though not significantly higher at this sample size. The palm-based agroforest was intermediate to the primary forest and the home-garden agroforest in its rate of species accumulation (Fig. 1). The rate of accumulation appeared to be approaching zero in the home-garden agroforest after 100 m² of sampling, but continued to be positive in the primary forest and palm-based agroforest (Fig. 1).

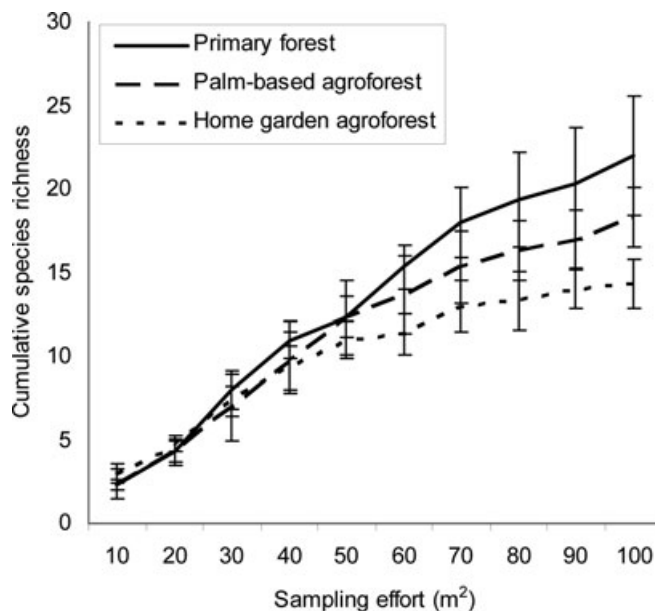


FIGURE 1. Cumulative species richness over sampling effort for each land use, Central Amazonia, Brazil. Each series of values is in the real sampling order. Each point is a mean of three transects. Bars are SEs of the mean. Each 10-m² of sampling effort is equivalent to one person-hour of sampling.

The termites collected belonged to two families (Rhinotermitidae and Termitidae), three Termitidae subfamilies (Apicotermitinae, Nasutitermitinae, and Termitinae), 32 genera, and 67 species (Table S1). Of these, 47, 31, and 23 species were collected in the primary forest, palm-based agroforest, and home-garden agroforest, respectively (Table S1). In the primary forest, 32 species were collected that were unique to that environment, while only six and four unique species were collected in the palm-based and home-garden agroforests, respectively. There was no block effect (land-use history) on termite species richness in the agroforests ($P = 0.6$).

Very rare species (encountered only once) made up a significantly higher percentage ($P < 0.01$) of the primary forest samples than of the agroforest samples (40%, 13%, and 13% of species, respectively). The most commonly encountered species was *Heterotermes tenuis* (Hagen), found in a third of all sections.

SIMILARITY.—The cluster analysis of termite species composition showed a low similarity between the primary forest and agroforest species composition (21%; Fig. 2). The greatest similarities occurred among transects of the agroforests (48–64%), while the transects of the primary forest were not similar to each other (Fig. 2).

ORDINATION.—In reciprocal averaging, similar species are brought together and dissimilar species far apart; likewise for similar and dissimilar samples. The scores of the first axis in this ordination technique maximize the correlation of the samples and species (Gauch 1982). Arranging the samples in a rank order of their first-axis ordination scores will have their largest values concentrated along the

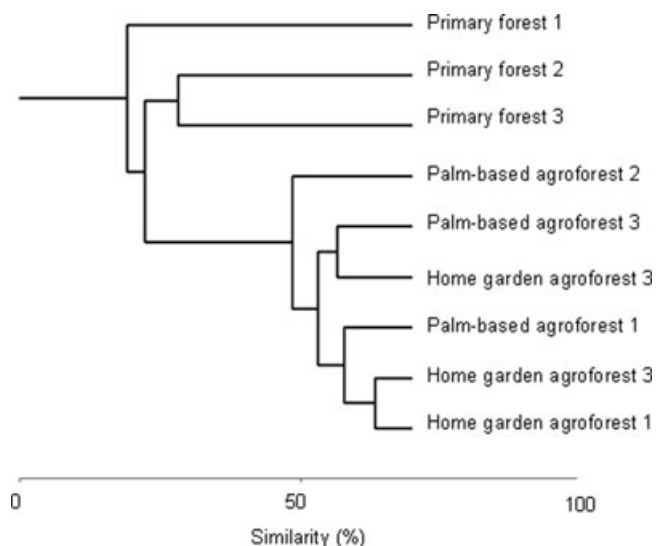


FIGURE 2. Cluster analysis (Bray-Curtis similarity index) of termite species assemblages in primary forest and agroforests, Central Amazonia, Brazil.

matrix diagonal (Gauch 1982). This ordination demonstrated a gradient in species composition from primary forest to home-garden agroforests, with the palm-based agroforests intermediate to the two.

LAND USE/SPECIES INTERACTION.—The AMMI model demonstrated a strong interaction between species and land use (Table 2). Early interaction principal component axes (IPCA) selectively recover signal, whereas late IPCAs selectively recover noise (Gauch 1992, Gauch 2006). The signal in the species-by-environment interaction had an estimated sum of squares of 20.2, which nearly equaled that of the first two IPCAs (13.7 + 8.9 = 22.6). Therefore, IPCA1 and IPCA2 captured mostly signal, whereas higher components captured mostly noise and hence were discarded and

TABLE 2. Analysis of variance associated with the additive main effects and multiplicative interaction (AMMI) model. Species refers to termite species and environment to primary forest, palm-based agroforests, and home-garden agroforests. The species-by-environment interaction is estimated to contain sums of squares (SS) of 20.2 for signal and 22.0 for noise.

Source	df	SS	MS	F	P
Total	6029	293.2	0.05		
Treatment	602	66.5	0.11		
Species	66	23.9	0.36		
Environment	8	0.4	0.05		
Species × Environment	528	42.2	0.07		
IPCA 1	73	13.7	0.19	4.7	< 0.001
IPCA 2	71	8.9	0.13	3.3	< 0.001
Residual	384	19.6	0.05		
Error	5427	226.7	0.04		

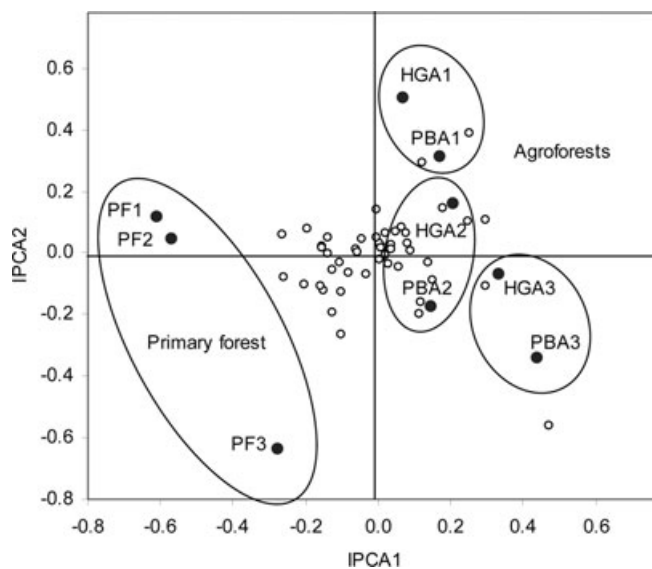


FIGURE 3. AMMI bi-plot of termite species and land uses, Central Amazonia, Brazil. Species are open circles, land uses are solid circles. HGA = Home-garden agroforests, PBA = palm-based agroforests, PF = primary forest. The number following the land use is the transect number. Any two sites or species are highly correlated if they are at nearly the same angle from the center of the plot, negatively correlated if opposing, and nearly uncorrelated if the angle between them is close to 90 degrees. The first and second IPCAs account for 32 and 21 percent of the interaction, that is, the differential response of species to environments. The higher components beyond IPCA2 capture mostly noise and are not ecologically interpretable.

ignored (Table 2). The first IPCA ($P < 0.001$) corresponded to an opposition between the primary forest and the agroforests in terms of termite species preference (Fig. 3). The second IPCA ($P < 0.001$) discriminated among the land-use history blocks of the agroforestry systems and between one transect and the other two in the primary forest (Fig. 3).

TAXONOMIC COMPOSITION.—The proportion of termite species in the four taxonomic groups did not differ significantly between the primary forest and agroforests (Fig. 4A). However, the proportion of species encounters did ($\chi^2 = 39.2; P = 0.000$). There were more encounters of the Apicotermiteinae subfamily in the agroforests than in the primary forest, and correspondingly lower proportions of Nasutitermitinae and Termitinae encounters (Fig. 4B).

FUNCTIONAL COMPOSITION.—Likewise, the proportion of species across feeding guilds did not differ significantly among the different land uses (Fig. 5A), but the proportion of species encounters did ($\chi^2 = 30.3; P = 0.000$). The proportion of soil/wood interface feeders was reduced in the agroforests, and soil feeders were actually more prevalent (Fig. 5B). None of the species encountered in the study are known to be pest termites of the plant species in the agroecosystems studied, according to Constantino (2002), except

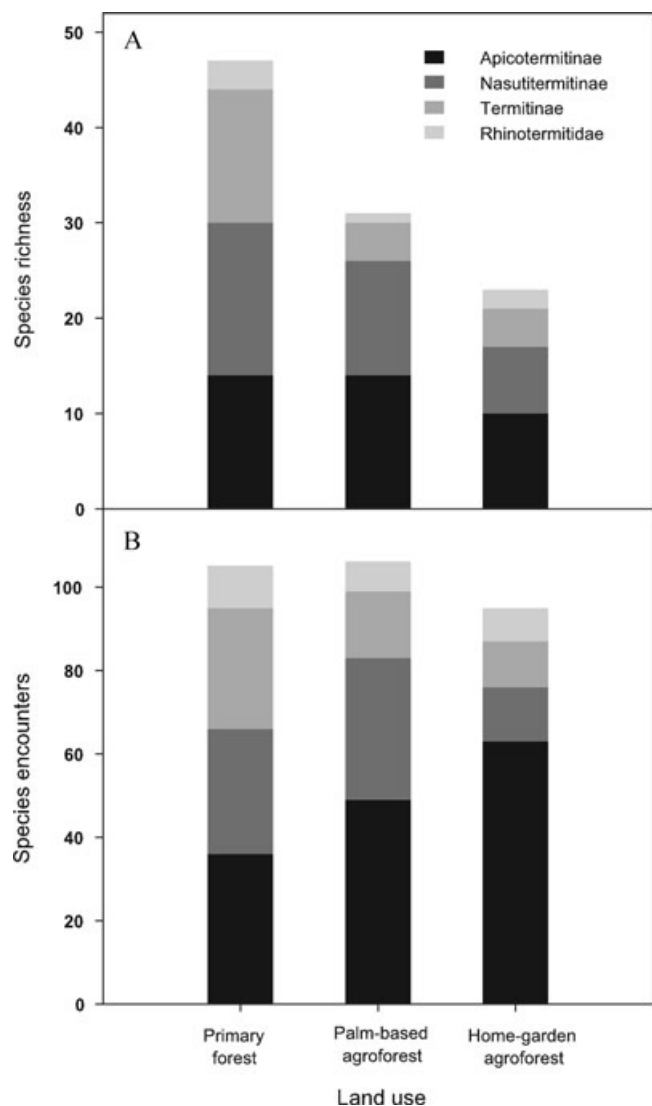


FIGURE 4. Taxonomic composition of termite (A) species richness and (B) abundance (number of encounters) in primary forest and agroforests, Central Amazonia, Brazil. Values are pooled over all three transects in each land use.

for *Rhinotermes marginalis* (Linnaeus), considered to be a minor agricultural pest in Amazonia (Constantino 2002).

DISCUSSION

Of the studies in nonflooding primary forests of Amazonia, Bandeira (1979), Mill (1982), Bandeira and Torres (1985), Bandeira and Macambira (1988), Bandeira (1979), and Apolinário (1993) each sampled plots amounting to 1 ha and observed 30–90 species. The total species richness found in the primary forest in this study fell within this range, at 52. The termite assemblage sampled in this study differed from previous studies in the region, however (Snyder 1926, Mill 1982, Bandeira & Torres 1985, Bandeira 1989,

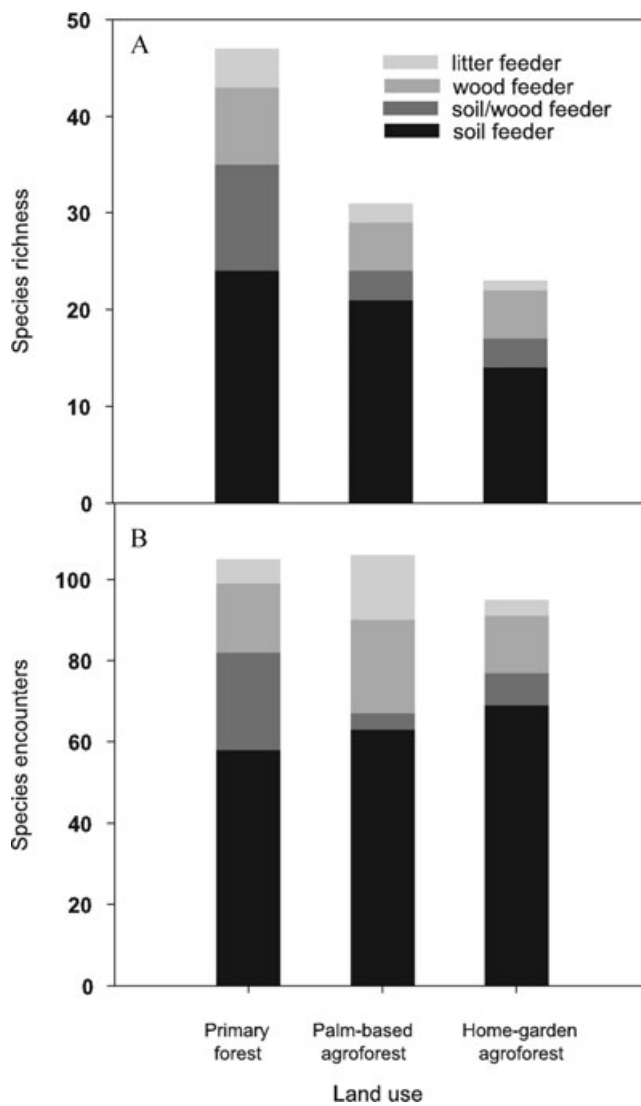


FIGURE 5. Functional composition of termite (A) species richness and (B) abundance (number of encounters) in primary forest and agroforests, Central Amazonia, Brazil. Values are pooled over all three transects in each land use.

Constantino 1992, Apolinário 1993, De Souza & Brown 1994). In terms of taxonomic composition, we found the Nasutitermittinae subfamily and the *Nasutitermes* genus to be less dominant than in these previous studies. Martius’s review (1994) of this literature found that the Nasutitermittinae family usually accounts for about 50 percent of the species, and the *Nasutitermes* genus for 25 percent. We found 35 percent and 14 percent, respectively.

In terms of feeding guild, we found the majority of species to be soil feeders (57%), while wood feeders have been characterized to be the most dominant guild among the South American termite fauna (Bignell & Eggleton 2000). For example, Bandeira (1989) found wood feeders to dominate soil feeders, at 54 and 22 percent of species, respectively. Apolinário (1993) similarly reported proportions of 45 and 19 percent.

Several factors may contribute to the difference in results between this study and others: (1) real differences in proportions between this site and those in the other studies (there is only site-level replication in this experiment); (2) imprecision in the classification of feeding habits (e.g., species of *Araujotermes*, *Atlantitermes*, and *Paraconvexitermes* may be soil/wood interface feeders rather than purely soil feeders [R. Constantino, pers. obs.]); or (3) the sampling methods may differ in their emphasis on particular substrates. The rapid biodiversity assessment protocol (Jones & Eggleton 2000) we used thoroughly samples surface soil, and Eggleton *et al.* (2002) found an extremely high species richness of soil-feeding termites in using this method as well.

As expected, the difference in species composition was greatest between primary forest and agroforests, and termite species turnover was greater between primary forest transects than between agroforest transects. Individual termite species indicated strong preferences for particular land uses, contrasting the primary forest transects with those of the agroforests; some discrimination by termite species based on the land-use history of the agroforests was also evident. Although we had expected the termite species composition of the home-garden agroforest to be the most similar of the two agroforests to the primary forest, we found that the termite species composition of the palm-based agroforest more closely resembled the primary forest site.

Unlike the agroecosystems investigated by De Souza and Brown (1994), Eggleton *et al.* (1997, 2002), Bandeira and Vasconcellos (2002), and Bandeira *et al.* (2003), these agroecosystems maintained the same proportion of species among taxonomic classes and feeding guilds as primary forest. In terms of the distribution of termite *relative abundance* among taxonomic classes and feeding guilds, however, the agroforests did distinguish themselves from primary forest. We were surprised to find that both agroforests hosted a higher abundance of soil feeders than did the primary forest. The capacity of the agroforests to create favorable conditions for soil feeders is likely a positive feedback on the fertility of these agroecosystems. These results offer promising evidence of the potential for tree-based agriculture in the Amazon to support the function of soil termite fauna, even on previously degraded pastureland.

The palm-based agroforest more closely imitated the makeup of the primary forest site in terms of the proportion of abundance of termites in different feeding classes, with a higher proportion of soil feeders. Davies *et al.* (2003) found that the termite assemblage in a primary forest in Guiana, and that of soil feeders in particular, was influenced by palm density. Barros *et al.* (2003), in their study in western Brazilian Amazonia, found termite density under peach palm (*Bactris gasipaes*) to be significantly higher in general than soil under the nonpalm species cupuassu (*Theobroma grandiflorum*). These results suggest that particular plant functional attributes (Gillison *et al.* 2003) could be more important drivers of termite species richness than plant species richness alone.

The authors above attributed the higher termite density to greater litter inputs around palms, but root turnover and root quality could also be contributing factors. Palm species in agroforests had significantly higher root densities than the other principal agro-

forestry species measured by Gallardo-Ordinola (2005). Açai palm (*Euterpe oleracea*) and peach palm (*B. gasipaes*) had 6 and 7 Mg/ha of roots, respectively. Turnover of fine roots in palm species was also significantly higher than that of other principal agroforestry species, at 3 Mg/ha/y. In terms of root quality as well, peach palm roots had the lowest lignin content of the species measured (Gallardo-Ordinola 2005). Palm litter, in the rainy season, had significantly lower polyphenol content than the home-garden agroforest litter (da Silva 2005). Peach palm also contributed visible amounts of root exudates to the soil (I. Ackerman, pers. obs.). Canopy cover has been shown to be an important factor in determining termite abundance (Dibog *et al.* 1999), and the canopy cover of this palm-based agroforest was greater than that of the home-garden agroforest, as measured by leaf area index (Welch 2006). The results of this study and those cited suggest that canopy cover and the presence of palm species in particular may encourage the abundance of soil-feeding termites.

In summary, this study yielded the following observations that are notable or worthy of further investigation. (1) The abundance of soil-feeding termites in the agroecosystems in this study is promising for the capacity of agroforests to support soil fertility restoration on degraded pasturelands. (2) All ecosystems in this study hosted an unusually high proportion of soil feeders compared to other study results in Amazonia. Would a similarly intensive soil sampling reveal this in other regions as well, or is this study site unusual, and if so, why? (3) Inasmuch as feeding guild serves as a proxy for function, closed-canopy agroforests may be able to sustain the same termite functions as primary forest. For more sophisticated analysis of the relationships between termite community composition and agroecosystem function, additional dimensions of insect function beyond feeding guild could be explored: nitrogen fixation ability, body width, digestion type, nest construction type, and building material. To support this, more taxonomic work in the Apicotermitinae, and species-level biological research to support it, will be needed. (4) Termite diversity was not explained by plant diversity alone among these sites. Plant attributes should be considered as factors in future studies, and attributes of palms in particular could be investigated as potential drivers of termite abundance and diversity.

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SUPPORTING INFORMATION

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

TABLE S1. *Number of termite species encounters (number of species in parentheses) in primary forest, palm agroforest, and home-garden agroforests in Central Amazonia, Brazil*

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LITERATURE CITED

- ABE, T., AND T. MATSUMOTO. 1979. Studies on the distribution and ecological role of termites in a lowland rain forest of West Malaysia (3) Distribution and abundance of termites in West Pasoh Forest Reserve. *Jap. J. Ecol.* 29: 337–351.
- ABE, T., AND H. WATANABE. 1983. Soil macrofauna in a subtropical rain forest and its adjacent cassava plantation in Okinawa—with special reference to the activity of termites. *Physiol. Ecol. Japan* 20: 101–114.
- ANDERSON, J. M., AND M. J. SWIFT. 1983. Decomposition in tropical forests. *In* S. L. Sutton, *et al.* (Eds.). *Tropical Rain Forest: Ecology and Management*. pp. 287–389, Blackwell Scientific Publications, Oxford, UK.
- APOLINÁRIO, F. B. 1993. Composição faunística e hábitos de nidificação de térmitas (Insecta: Isoptera) em floresta de terra firme da Amazônia Central, MSc Dissertation, INPA/FUA, Manaus, Brazil.
- BANDEIRA, A. G. 1979. Notas sobre a fauna de cupins (Insecta: Isoptera) do Parque Nacional da Amazônia (Tapajós), Brasil. *Bol. Mus. Paraense Emílio Goeldi: Zool.* 96: 1–12.
- BANDEIRA, A. G. 1983. Estrutura ecológica de comunidades de cupins (Insecta, Isoptera) na Zona Bragantina, estado do Pará. PhD Dissertation, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.
- BANDEIRA, A. G. 1989. Análise da termitofauna (Insecta: Isoptera) de uma floresta primária e de uma pastagem na Amazônia Oriental, Brazil. *Bol. Mus. Paraense Emílio Goeldi: Zool.* 5: 225–241.
- BANDEIRA, A. G., AND M. F. P. TORRES. 1985. Abundância e distribuição de invertebrados do solo em ecossistemas da Amazônia Oriental O papel ecológico dos cupins. *Bol. Mus. Paraense Emílio Goeldi: Zool.* 2: 13–38.
- BANDEIRA, A. G., AND M. L. J. MACAMBIRA. 1988. Térmitas de Carajás, estado do Pará, Brasil: Composição faunística, distribuição, e hábito alimentar. *Bol. Mus. Paraense Emílio Goeldi: Zool.* 4: 175–190.
- BANDEIRA, A. G., AND A. VASCONCELLOS. 2002. A quantitative survey of termites in a gradient of disturbed highland forest in northeastern Brazil (Isoptera). *Sociobiology* 39: 429–439.
- BANDEIRA, A. G., A. VASCONCELLOS, M. P. SILVA, AND R. CONSTANTINO. 2003. Effects of habitat disturbance on the termite fauna in a highland humid forest in the caatinga domain, Brazil. *Sociobiology* 42: 1–11.
- BARROS, E., A. NEVES, E. C. M. FERNANDES, E. WANDELLI, AND P. LAVELLE. 1999. Soil macrofauna community of Amazonian agroforestry systems. *International Symposium Multi-Strata Agroforestry Systems with Perennial Crops*. Pp. 166–170. CATIE, Turrialba, Costa Rica.
- BARROS, E., B. PASHANASI, R. CONSTANTINO, AND P. LAVELLE. 2002. Effects of land-use system on the soil macrofauna in western Brazilian Amazonia. *Biol. Fertil. Soils* 35: 338–347.
- BARROS, E., A. NEVES, E. BLANCHART, E. C. M. FERNANDES, E. WANDELLI, AND P. LAVELLE. 2003. Development of the soil macrofauna community under silvopastoral and agrosilvicultural systems in Amazonia. *Pedobiologia (Jena)* 47: 273–280.
- BEARE, M. H., M. V. REDDY, G. TIAN, AND S. C. SRIVASTAVA. 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: The role of decomposer biota. *Appl. Soil Ecol.* 6: 87–108.
- BIGNELL, D. E., AND P. EGGLETON. 2000. Termites in ecosystems. *In* T. Abe, *et al.* (Eds.). *Termites: Evolution, sociality, symbioses, ecology*. pp. 363–388. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- COLLINS, N. M. 1980. The effect of logging on termite (Isoptera) diversity and decomposition processes in lowland dipterocarp forests. *In* J. I. Furtado, (Ed.). *Tropical ecology and development*. pp. 113–121. International Society of Tropical Ecology, Kuala Lumpur, Malaysia.
- CONSTANTINO, R. 1992. Abundance and diversity of termites (Insecta, Isoptera) in 2 sites of primary rain-forest in Brazilian Amazonia. *Biotropica* 24: 420–430.
- CONSTANTINO, R. 1999. Chave ilustrada para identificação dos gêneros de cupins (Insecta: Isoptera) que ocorrem no Brasil. *Mus. de Zool. da Universidade de São Paulo* 40: 387–448.
- CONSTANTINO, R. 2002. The pest termites of South America: Taxonomy, distribution and status. *J. Appl. Entomol.* 126: 355–365.
- DA SILVA, G. C. 2005. Estudos Ecológicos no Solo de Sistemas Agroflorestais da Amazônia Central. PhD Dissertation, INPA, Manaus, Brazil.
- DAVIES, R. G., L. M. HERNÁNDEZ, P. EGGLETON, R. K. DIDHAM, L. L. FAGAN, AND N. M. WINCHESTER. 2003. Environmental and spatial influences upon species composition of a termite assemblage across Neotropical forest islands. *J. Trop. Ecol.* 19: 509–524.
- DE PAIVA, E. M. C. D. 1996. Regime de precipitação na Amazônia e sua relação com o desmatamento e temperatura da superfície do mar. PhD Dissertation, Universidade Federal do Rio Grande do Sul, Brazil.
- DE SOUZA, O. F. E., AND V. K. BROWN. 1994. Effects of habitat fragmentation on Amazonian termite communities. *J. Trop. Ecol.* 10: 197.
- DECAËNS, T., P. LAVELLE, J. J. JIMENEZ, G. ESCOBAR, AND G. RIPPSTEIN. 1994. Impact of land management on soil macrofauna in the Oriental Llanos of Colombia. *Eur. J. Soil Biol.* 30: 157–168.
- DECAËNS, T., N. ASAKAWA, J. H. GALVIS, R. J. THOMAS, AND E. AMÉZQUITA. 2002. Surface activity of soil ecosystem engineers and soil structure in contrasted land use systems of Colombia. *Eur. J. Soil Biol.* 38: 267–271.
- DEMATTÊ, J. L. I. AND J. A. M. DEMATTÊ. 1993. Comparações entre as propriedades químicas de solos das regiões da floresta Amazônica e do Cerrado do Brasil Central. *Scientia Agricola, Piracicaba* 50: 272–286.
- DIBOG, L., P. EGGLETON, L. NORRGROVE, D. E. BIGNELL, AND S. HAUSER. 1999. Impacts of canopy cover on soil termite assemblages in an agrosilvicultural system in southern Cameroon. *Bull. Entomol. Res.* 89: 125–132.
- EGGLETON, P., D. E. BIGNELL, W. A. SANDS, N. A. MAWDSLEY, J. H. LAWTON, T. G. WOOD, AND N. C. BIGNELL. 1996. The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philos. Trans. R. Soc. Lond. B* 351: 51–68.
- EGGLETON, P., R. HOMATHEVI, D. JEEVA, D. JONES, R. G. DAVIS, AND M. MARYATI. 1997. The species richness and composition of termites (Isoptera) in primary and regenerating lowland dipterocarp forest in Sabah, East Malaysia. *Ecotropica* 3: 119–128.
- EGGLETON, P., R. G. DAVIES, S. CONNETABLE, D. E. BIGNELL, AND C. ROULAND. 2002. The termites of the Mayombe Forest Reserve, Congo (Brazzaville): Transect sampling reveals an extremely high diversity of ground-nesting soil feeders. *J. Nat. Hist.* 36: 1239–1246.
- FERNANDES, E. C. M., AND J. C. DE S. MATOS. 1995. Agroforestry strategies for alleviating soil chemical constraints to food and fiber production in the Brazilian Amazon. *In* P. R. Seidl, *et al.* (Eds.). *Chemistry of the Amazon: Biodiversity, natural products, and environmental issues*, pp 34–50. American Chemical Society, Washington, DC.
- FRAGOSO, C., G. G. BROWN, J. C. PATRÓN, E. BLANCHART, P. LAVELLE, B. PASHANASI, B. SENAPATI, AND T. KUMAR. 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of earthworms. *Appl. Soil Ecol.* 6: 17–35.
- GALLARDO-ORDINOLA, J. L. E. 2005. Biomassa e dinâmica de raízes em sistemas agroflorestais implantados em áreas de pastagens abandonadas da

- Amazônia Central. PhD Dissertation. INPA/Universidade Federal do Amazonas, Manaus, Brazil.
- GAUCH, H. G. JR. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, New York, New York.
- GAUCH, H. G. JR. 1992. *Statistical analysis of regional yield trials: AMMI analysis of factorial designs*. Elsevier, The Netherlands. 278 pp.
- GAUCH, H. G. JR. 2006. Winning the accuracy game. *American Scientist* (March-April): 133–141.
- GILLISON, A. N., D. T. JONES, F.-X. SUSILO, AND D. E. BIGNELL. 2003. Vegetation indicates a diversity of soil macroinvertebrates: A case study with termites along a land-use intensification gradient in lowland Sumatra. *Org. Divers. Evol.* 3: 111–126.
- HANNE, C. 2001. *Die Rolle der Termiten im Kohlenstoffkreislauf eines amazonischen Festlandregenwaldes*. PhD Dissertation, Johann Wolfgang Goethe University, Frankfurt, Germany.
- HILL, M. O. 1973. Reciprocal averaging: An eigenvector method of ordination. *J. Ecol.* 61: 237–249.
- INPE. 2004. [Online]. Available by Instituto Nacional de Pesquisas Espaciais (INPE). <http://www.obt.inpe.br/prodes/>
- JONES, D. T., AND P. EGGLETON. 2000. Sampling termite assemblages in tropical forests: Testing a rapid biodiversity assessment protocol. *J. Appl. Ecol.* 37: 191–203.
- JORDAN, C. F. 1985. *Nutrient cycling in tropical forest ecosystems: Principles and their application in management and conservation*. John Wiley & Sons, Ltd., Chichester, UK.
- LAVELLE, P., D. BIGNELL, M. LEPAGE, V. WOLTERS, P. ROGER, P. INESON, O. W. HEAL, AND S. DHILLION. 1997. Soil function in a changing world: The role of invertebrate ecosystem engineers. *Eur. J. Soil Biol* 33: 159–193.
- LAVELLE, P., E. BARROS, E. BLANCHART, G. BROWN, T. DESJARDINS, L. MARIANI, AND J. P. ROSSI. 2001. SOM management in the tropics: Why feeding the soil macrofauna? *Nutr. Cycl. Agroecosys.* 61: 53–61.
- LAVELLE, P., B. K. SENAPATI, AND E. BARROS. 2003. Soil macrofauna in agroforestry systems. In G. SCHROTH AND F. SINCLAIR (Eds.). *Trees, crops and soil fertility: Concepts and research methods*. pp. 303–323. CABI Publishing, Wallingford, UK.
- MARQUES, A. de O., M. DE N. G. RIBEIRO, H. M. DOS SANTOS, AND J. M. DOS SANTOS. 1981. Estudos climatológicos da Reserva Florestal Ducke—Manaus-Am. IV. Precipitação. *Acta Amazon.* 11: 759–768.
- MARTIUS, C. 1994. Diversity and ecology of termites in Amazonian forests. *Pedobiologia* 38: 407–428.
- MATHIEU, J., J.-P. ROSSI, P. MORA, P. LAVELLE, P. F. DA S. MARTINS, C. ROULAND, AND M. GRIMALDI. 2005. Recovery of soil macrofauna communities after forest clearance in Eastern Amazonia, Brazil. *Conserv. Biol.* 19: 1598–1605.
- MCCAFFERY, K. A. 2003. *Carbon and nutrients in land management strategies for the Brazilian Amazon*. PhD Dissertation, Cornell University, Ithaca, New York.
- MILL, A. E. 1982. Populações de térmitas (Insecta: Isoptera) em quatro habitats no baixo rio Negro. *Acta Amazon.* 12: 53–60.
- OKWAKOL, M. J. N. 2000. Changes in termite (Isoptera) communities due to the clearance and cultivation of tropical forest in Uganda. *Afr. J. Ecol.* 38: 1–7.
- ROISIN, Y., AND M. LEPONCE. 2004. Characterizing termite assemblages in fragmented forests: A test case in the Argentinean Chaco. *Austral Ecol.* 2004: 637–646.
- SCHUBART, H. O. R. 1983. *Ecologia e utilização das florestas*. In E. Salati, *et al.* (Eds.). *Amazonia: Desenvolvimento, Integração, Ecologia*. pp. 101–143. CNPq Editora Brasiliense, São Paulo, Brazil.
- SNYDER, T. E. 1926. Termites collected on the Mulford biological exploration of the Amazon Basin, 1921–1922. *Proc. U.S. Nat. Hist. Mus.*, Washington 68: 1–76.
- VELOSO, H. P., A. L. RANGEL FILHO, AND J. C. A. LIMA. 1991. *Classificação da vegetação brasileira, adaptada a um sistema universal*. IBGE, Rio de Janeiro, Brazil.
- VOHLAND, K., AND G. SCHROTH. 1999. Distribution patterns of the litter macrofauna in agroforestry and monoculture plantations in central Amazonia as affected by plant species and management. *Appl. Soil Ecol.* 13: 57–68.
- VOSE, R. S., R. L. SCHMOYER, P. M. STEURER, T. C. PETERSON, R. HEIM, T. R. KARL, AND J. K. EISCHEID. 1992. *The global historical climatology network: Long-term monthly Temperature, Precipitation, Sea Level Pressure, and Station Pressure Data ORNL/CDIAC-53, NDP-041*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- WATANABE, H., H. TAKEDA, AND S. RUAYSOONGNERN. 1984. Termites of Northern Thailand with special reference to changes in species composition due to shifting cultivation. *Mem. Coll. Agric. Kyoto Univ.* 125: 45–57.
- WELCH, S. A. 2006. *Light and water resource capture on abandoned pastureland in the Brazilian Amazon*. PhD Dissertation, Cornell University, Ithaca, New York.