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Road-associated edge effects in Amazonia change termite community composition by modifying environmental conditions

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A B S T R A C T

Roads and road-building are among the most important environmental impacts on forests near urban areas, but their effects on ecosystem processes and species distributions remain poorly known. Termites are the primary decomposer organisms in tropical forests and their spatial distribution is strongly affected by vegetation and soil structure. We studied the impacts of road construction on termite community structure in an Amazonian forest fragment near Manaus, Brazil. One leading question was whether the fragment under study was large enough to maintain the termite species pool present in nearby continuous forests. We also asked how soil moisture and canopy openness varied with proximity to roads, and whether these changes were associated with changes in termite species richness and composition in the fragment. While the forest fragment had a termite composition very similar to that of continuous forests, roads caused important changes in soil moisture and canopy openness, especially when close to forest edges. At distances of up to 81 m from roads, changes in soil moisture were significantly related to changes in termite species composition, but there was no correlation between canopy openness and species richness or composition. These results suggest that fragmentation caused by roads impacts termites in a different and less damaging manner than fragmentation caused by other kinds of degradation, and that even fragments bisected by roads can support very diverse communities and even undescribed taxa of termites. We conclude that a buffer zone should be established for conservation purposes in the reserves surrounded by roads.

Introduction

As studies of natural areas in the vicinity of cities grow more common, such areas—which often protect the last remaining fragments of the landscape's original forests—are increasingly recognised as having a significant conservation value. Parks and forests near cities are frequently encircled or bisected by roads, however, and these represent an important threat to conservation (Bennett 1991; Lunney et al. 2002; Ries et al. 2001). Roads can drive changes at large scales by altering environmental conditions and biological communities, and their impacts can reach deep into forest interiors (Forman 2000) far from edges (Forman & Alexander 1998). Such changes can result in some organisms becoming locally extinct by wreaking havoc on community diversity and structure over the short or long term, but the precise impacts of road-associated fragmentation vary among different types of organisms (Harper et al. 2005; Tilman et al. 1994).

While the severe impacts that logging and fire inflict on natural habitats have received considerable attention (Ackerman et al. 2009; Lima et al. 2000), the impacts of roads and road construction on fragmented areas remain poorly understood. This is especially true for small organisms in general and decomposer organisms in particular. For example, environmental changes caused by logging and major habitat alterations have been shown to have massive effects on termite species richness and composition across different landscapes (Ackerman et al. 2009; Davies et al. 2003). Similar assessments of the impacts of road construction on termite assemblages are not available and could potentially have different implications for conservation, since road-building can be comparatively less destructive than forest fires and logging operations and may impact termites less profoundly, especially if large portions of the landscape remain intact.

Research on invertebrates, and particularly the largest and best-studied groups of invertebrates, can help guide conservation measures in natural landscapes (Nichols et al. 2007). For example,

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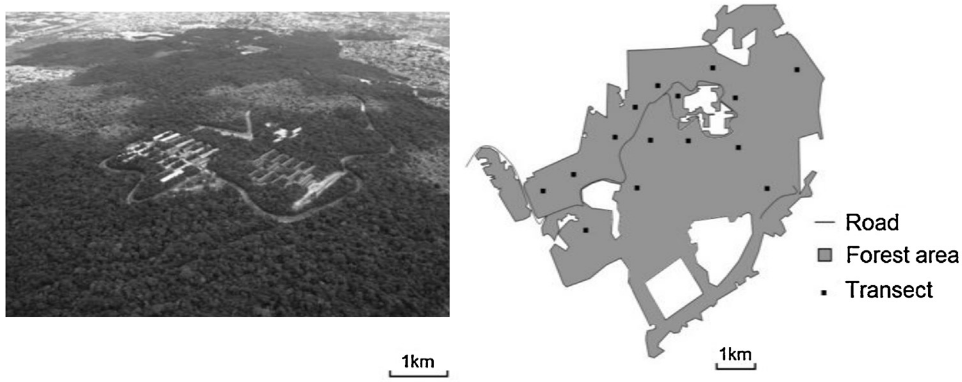

Fig. 1. An aerial view and map of the Amazonas Federal University (UFAM) forest where the study was carried out, in Manaus, Amazonas state, Brazil.

studying impacts on decomposer communities can elucidate long-term impacts on ecosystem processes. Because termites are also important drivers of nutrient cycling, changes in termite community structure will have a delayed effect on vegetation structure. These organisms are arguably the most important insect decomposer group in Amazonia (Luizão & Schubart 1987), processing 40–50% of total litterfall in some areas (Bandeira 1991). Understanding how termite distributions respond to disturbances can thus help predict longer-term effects of fragmentation based on changes in decomposition processes.

In this study, we examined the termite fauna of a forest fragment near the city of Manaus, Brazil. The effects of roads on termite species richness and composition were analysed by documenting turnover of species and feeding guilds at various distances from roads. We also examined how two environmental variables that are believed to affect termites in altered environments (soil moisture and canopy openness; Camargo & Kapos 1995) varied along a gradient of proximity to roads. Our primary questions were: (1) How large must an urban forest fragment be to maintain a termite species composition similar to that of a continuous forest? (2) How far into the forest interior do roads change environmental conditions important to termite communities? and (3) Do changes in soil moisture and canopy openness caused by road construction cause corresponding changes in termite species richness and composition, as has been observed in the case of large-scale deforestation?

Materials and methods

Study site

The study was carried out in a forest fragment near the Amazonas Federal University (Universidade Federal do Amazonas, or UFAM; Fig. 1), in Manaus, Amazonas state, Brazil. The climate at the study site is classified as “Afi” under the Köppen system. Mean annual temperature is 25.6 °C and mean annual rainfall 2458 mm, with a well-defined dry season extending from June to October. Data collected in the study area by Brazil’s National Meteorological Institute (INMET) from 1961 to 1990 indicate maximum and minimum temperatures of 31.5 °C and 23.2 °C, respectively (mean = 26.7 °C), and mean relative humidity of ~83%.

The entire study area measures 800 ha and includes a 592-ha portion managed for conservation. The dominant vegetation is tropical terra firme rainforest not subject to flooding. The landscape is composed of plateaus, sloping areas, and bottomlands. Soils are mostly clayey, but some areas have sandy soils with shrubby vegetation (Nery et al. 2004). The fragment is traversed by several roads, and the ones we studied were 25–30 m wide.

Sampling design and data collection

The termite species composition is not likely to change over small time intervals (e.g. from season to season; Jones & Eggleton 2000), thus the data collection occurred in just one sampling season between May and July 2010. To collect data on termite communities and environmental conditions we established 15 transects measuring 100 m × 2 m (Fig. 1). Transects were oriented parallel to and at variable distances from roads. The distance from the road at which each individual transect was established was determined by selecting at random one of 15 previously determined distances spaced at 7-m intervals up to 105 m (i.e., 7, 14, 21, 28, 35, . . ., 105 m from the road). This design reflects the fact that edge effects have been shown to extend ~120 m into the forest interior in highly fragmented landscapes (Nichols et al. 2007). The approach also allowed us to control for variables associated with edge effects but randomise the effects of other variables that are not associated with edge effects but that could influence species distributions (e.g., historical processes related to road age).

Each transect included five evenly spaced subplots measuring 5 m × 2 m. Termites were collected during a 20-min period in each of these subplots by three people collecting manually and investigating all trunks and other possible habitats. Our method is a modification of Jones and Eggleton’s (2000) transect method which minimises collection effort, maximises the number of captured species, and is well-suited for rapid biodiversity assessments.

Canopy openness data were obtained from ten hemispheric photographs of the forest canopy taken along each transect. Openness was measured in the photographs using version 2.0 of the GLA-Gap Light Analyzer program (Frazer et al. 1999).

We measured soil moisture by collecting soil from each subplot. Soil moisture was quantified using the gravimetric method as described by Bandeira (1989). The difference in the weight of each soil sample before and after drying was divided by the original (wet) weight, yielding the proportion of water in each sample.

Termite specimens were identified with Constantino’s (1999) soldier key and by comparing our specimens with those in the collection of Brazil’s National Institute of Amazonian Research (INPA). Species were assigned to feeding guilds based on morphological and nesting traits previously described (Apolinário 1993; Constantino 1999; Mathews 1977).

Analysis

In each subplot we documented the number and identities of all termite species recorded. Data on abundance were not collected; since termites are considered modular organisms, we opted to use presence–absence data. The expected number of species for each

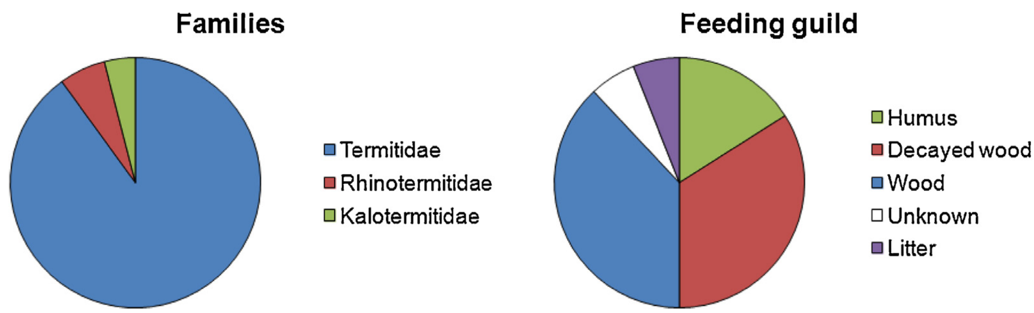

Fig. 2. Proportion of termite species at the study site belonging to different families and feeding guilds.

area was calculated using the Chao *I* non-parametric richness estimator (Chao et al. 2009).

Environmental variables were first submitted to a Pearson's correlation test to ensure independence, and a Kolmorov–Smirnoff test to ensure normality. We carried out regressions between distance from roads and the other variables in order to examine how forest edges along roads affect fragmentation processes.

Relationships between species richness and composition on one hand and environmental variables on the other were determined using presence–absence matrices. Species composition was quantified via Principal Coordinates Analysis (PCoA) using a Jaccard dissimilarity matrix. We carried out multiple regression tests of environmental variables and the first axis of the PCoA, and between environmental variables and species richness. This procedure allowed us to assess the effect of road proximity on changes in species number and composition.

To determine the effect of road proximity on the other variables (threshold) we used piecewise regression (Toms & Lesperance 2003).

Alpha significance levels were fixed at 0.05. This alpha was not adjusted with the Bonferroni correction for multiple tests (Rice 1989), which we felt was overly conservative. Instead, we chose to report all significant and non-significant relationships, as suggested by Moran (2003).

We assessed Moran's *I* index versus geographic distance in order to assure spatial independence in the distribution of the dependent and independent variables included in the analyses. No variable showed a significant relationship with linear distance.

All analyses were carried out in the R software program (R Development Core Team 2010) using the Vegan (Oksanen et al. 2008) and SiZer (Sonderegger et al. 2009) modules.

Results

Overall termite richness and composition

We recorded 55 termite species distributed in three families: Termitidae (50 species and 91% of the total); Rhinotermitidae (three species, 5%); and, Kalotermitidae (two species, 4%; Fig. 2). In total, 275 termite colonies were recorded. Of these, 241 belonged to the family Termitidae (87%), 32 to Rhinotermitidade (10%), and two to Kalotermitidae (3%). Termite subfamilies included Nasutitermitinae, Termitinae, Apicotermitinae, Coptotermitinae, Heterotermitinae, and Rhinotermitinae. The most diverse of these was Nasutitermitinae, with 26 species. The most frequent species were *Cylindrotermes parvignathus* Emerson, which was recorded in every transect, and *Heterotermes tenuis* (Hagen) and *Nasutitermes banksi* Emerson, which were each recorded ten times. The Chao *I* richness estimator showed that approximately 76 species exist at our study site; these would likely be recorded by more intensive sampling.

The most diverse termite feeding guilds comprised termites that feed on wood (19 species and 38% of the total) and termites that feed on intermediate material like humus and decaying wood (17 and 34%). Termites that feed on humus were represented by eight species (16%) and those that feed on leaf litter by three (6%; Fig. 2). We were unable to classify *Cornicapritermes* sp.1, *Genuotermes spinifer* Emerson, and *Inquilinitermes* sp.1 into feeding guilds, since their feeding and nesting habits are poorly known.

Relationships between road proximity, species richness, and species composition

Road proximity was significantly correlated with canopy openness. Hemispheric photographs of plots that were farther from roads and deeper in the forest interior showed a larger number of dark pixels and thus a more closed canopy (df = 10; $F = 14.59$; $p < 0.001$; $R^2 = -0.59$; Fig. 3a). Soil moisture also showed a weak significant relationship with road distance (df = 12; $F = 4.031$; $p = 0.02$; $R^2 = 0.38$; Fig. 3b). Sites farther from roads and deeper in the forest had wetter soils, but this relationship was only significant up to 81 m. Beyond that distance, roads no longer had any effect on soil moisture. Moreover, the soil moisture was not significantly correlated to canopy openness (df = 10; $F = 1.241$; $p = 0.29$; $R^2 = 0.11$).

Roads did not affect species richness by altering soil moisture nor by promoting greater canopy openness. Soil moisture was significantly correlated with termite species composition (df = 12; $F = 8.02$; $p = 0.01$; $R^2 = 0.40$), indicating species turnover along a gradient of soil moisture (Fig. 4). Besides the weak correlation of this factor with the termite species composition, soil moisture was a stronger determinant than canopy openness, which did not show a direct relationship with the other community parameters.

Fig. 5 shows where species were recorded relative to road proximity. In the figure, species are ranked by the distance from the road at which they were most commonly recorded. No feeding guild showed greater abundance or richness at a given distance from roads ($p > 0.4$ for all relationships).

Discussion

Termite species richness documented in this study was greater than that reported in most earlier publications from the central Amazon, which include studies of both continuous and urban-influenced forests, and which have typically reported fewer than 50 species (Bandeira 1979; Mill 1982). However, most studies used sampling methods different from ours, which complicates comparisons. We know of no previous large-scale studies of termites in urban-influenced forests, and ours is the first to show the significant potential of these areas as refuges for continuous forest termite species. Indeed, even the species abundance distribution observed was similar to that documented in continuous forests where most species are rare and the communities have a strongly log series

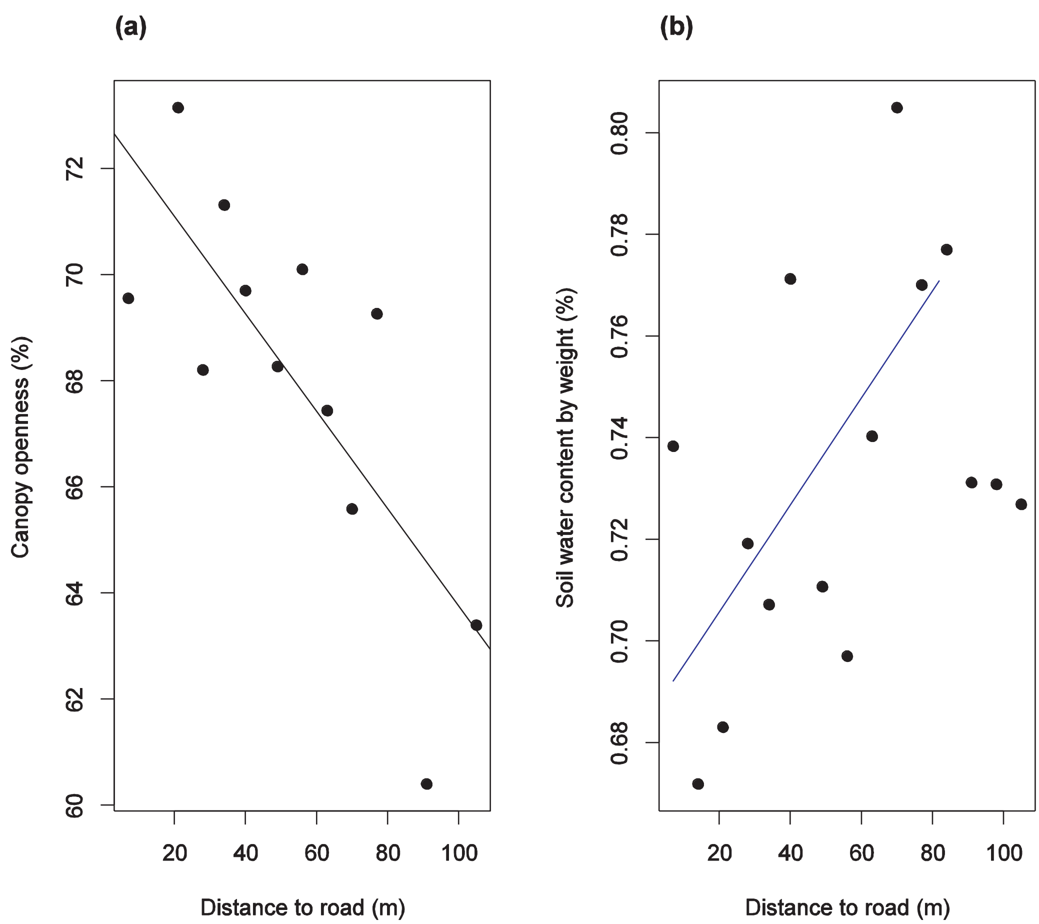

Fig. 3. Piecewise regressions show variation in soil moisture and canopy openness as a function of proximity to roads.

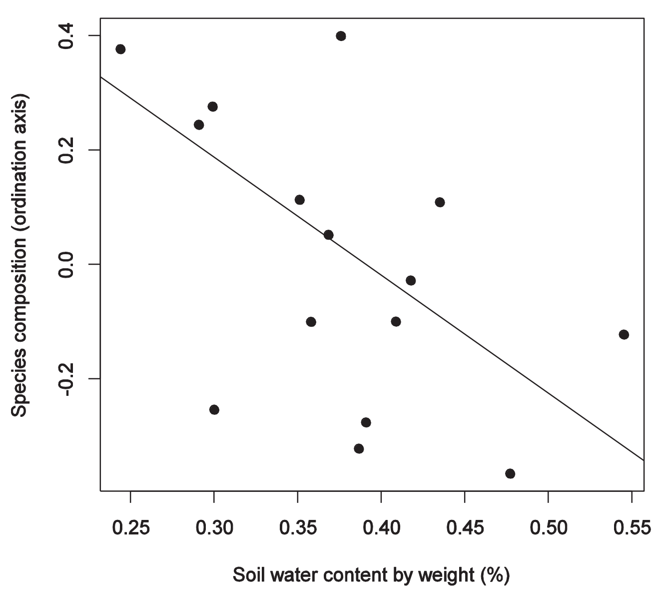

Fig. 4. Regression shows changes in termite species composition associated with changes in soil moisture.

distribution (Ackerman et al. 2007; Apolinário 1993; Apolinário & Martius 2004).

According to Bandeira (1989), termites in the family Kalotermitidae typically predominate in fragmented environments or they can be more easily found in the canopy (Roisin et al. 2006) because those are more open habitats. At our study site some species of Kalotermitidae had previously been recorded and/or are currently being described (L. Pierrot, personal communication), and these are infrequent in continuous forests. However, the fact that those species were mostly recorded at sites close to forest edges corroborates our observation that other families dominate the community in the interior of the fragment. Most of the termite species we recorded feed on wood and belong to the Termitidae, the dominant family in most South American forests (Bignell & Eggleton 2000).

Forest fragmentation leads to a long-term decrease in soil moisture and a long-term increase in canopy openness (Murcia 1995) and increases species' extinction risk (Fahrig 2002). Degradation caused by road construction caused these same impacts on the forest interior, and we were able to quantify the extent of road influence by measuring these impacts in continuous fashion along a gradient of road proximity. While road construction caused decreased soil moisture up to a distance of 81 m, it influenced canopy openness up to the farthest distance we sampled (105 m). Additional studies are needed to determine if changes extend past this distance, which seems likely, and to precisely evaluate the effect of the distance to the roads on soil moisture. Larger roads or fragmentation of a different type may have a larger impact on these parameters, but large-scale perturbations are beyond the scope of this study.

Soil moisture influenced species composition at sites closest to forest edges. Highly disturbed vegetation types unlike those found in continuous forest are not capable of maintaining termite species composition and richness (Ackerman et al. 2009; Barros et al. 2002; Bignell & Eggleton 2000; De Souza & Brown 1994). At our study site, however, where the landscape remains similar to that in natural

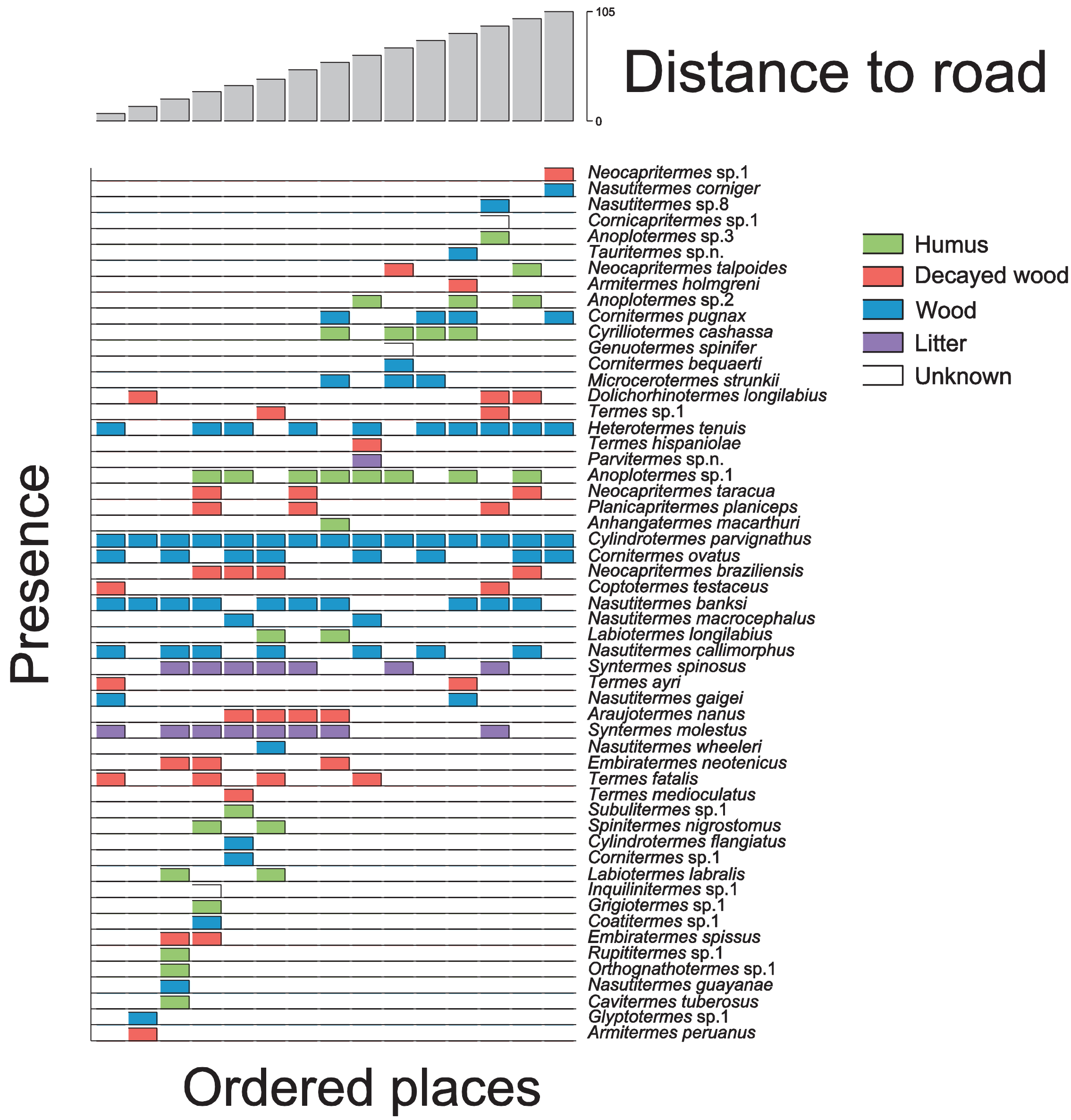

Fig. 5. Observed presence and absence of termite species and feeding guilds along a gradient of distance from roads, showing species turnover from the forest edge to the forest interior. Species are ranked by their mean distance from roads, with species found only in the forest interior at the top and species found only along the forest edge at the bottom.

environments, species numbers did not vary greatly with changes in soil moisture; instead, it was the identities of individual species that changed. This lack of relation between the distance to the border and species richness could indicate other non-measured factors to be more important (e.g. predators). Other studies have shown that ant species richness does not vary with increasing distance from edges or increasing isolation of the forest patch (Carvalho & Vasconcelos 1999; Sobrinho & Schoereder 2007). While it has been reported that soil termites are especially sensitive to changes in soil moisture (Abensperg-Traun & Boer 1990) and canopy openness (Ackerman et al. 2009; Bandeira & Vasconcellos 2002; Eggleton et al. 1997; Martius et al. 2004), we were unable to detect a relationship between that particular guild and road construction. This suggests that the type of fragmentation caused by road building does not have as strong an impact on termites as forest fires or other types of degradation even though small roads can also deeply change the surrounding environment (Bohac et al. 2004; Koivula 2003). In agreement with our results, Melis et al. (2010) found that the distance to small roads changed the beetle species composition but had little effect on the species richness; whereas large roads influenced both.

In general, species that tend to be common in urban areas were not so common in our study area, where they showed a distribution more similar to that in continuous forest, even considering that our sampling method can under represent rare species. For example, *Nasutitermes corniger* (Motschulsky) was infrequent. Likewise, species that are exclusive to forests with few impacts, such as *Subulitermes* spp. and *Neocapritermes talpoides* Krishna & Araujo, were found not far from forest edges in our study (Fig. 5). Edge effects in continuous forests are different from those in thoroughly fragmented forests. Both show alterations in species composition, but continuous forests are capable of maintaining species richness along forest edges.

Roads per se cause impacts close to edges, especially to plant species that are accustomed to forest interiors and that cannot tolerate high temperatures. Laurance and Vasconcelos (2009) emphasised that edge effects on fragmented forests are diverse and include abiotic changes to species abundances and ecological processes. They also noted that the distance to which edge effects penetrate fragments varies widely.

We have shown that termites, which are among the leading drivers of decomposition in tropical forests, are also strongly influenced by factors associated with habitat degradation caused by roads, but environmental changes at our study site affected termites differently than in more fragmented areas. Since the soil fauna plays a significant role in plant growth (Jouquet et al. 2006) and nutrient cycling processes (Luizão & Schubart 1987), these relatively large blocks of urban forests are capable of maintaining relatively intact termite communities. Based on our data, we propose establishing a buffer zone 81 m wide along roads to conserve the biota of protected environments.

Our study shows that the interior of a forest fragment near a large Amazonian city is capable of preserving distributions of feeding guilds, families, and subfamilies that are very similar to those found in continuous forests. Such fragments can also preserve species that are considered rare or infrequent in nature, as long as they include a significant expanse of vegetation far from their edges. Nevertheless, it is important to note that changes in community parameters can lead to deleterious processes over longer time scales, which makes developing large-scale monitoring programs crucial. Likewise, it is clear that the effective conservation of forest fragments in the Brazilian Amazon will require additional research and management and that future studies are required to elucidate the effect of the microclimate changes on the termite communities and ecosystem processes as well to show the effect of the interaction of soil moisture and other variables on termite species composition. An undescribed species was recently discovered in the fragment we studied and is currently being described. We conclude by emphasising that the total number of species and the number of rare species in the fragment we studied was high even compared to some continuous forests. Unless such fragments are protected, increasing anthropogenic pressures will likely lead to the extinction of undescribed species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jnc.2013.02.003.

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