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SHORT COMMUNICATION

Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest

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Leaf-cutting ants (genera *Atta* and *Acromyrmex)* have been denoted key species of American rain-forest ecosystems (Fowler *et al.* 1989) because of their multifarious effects on the vegetation. Being dominant herbivores, cutting up to 13% of the standing leaf crop in a colony's territory per year, they affect directly and significantly individual plants, plant communities and ecosystems (Wirth *et al.* 2003). The considerable ecological impact of these ants is paralleled by the well-known fact that some species strongly benefit from human-driven habitat alterations and represent prime pests throughout Latin America (Cherrett 1986). Numerous studies have documented populations of leaf-cutting ant to increase with increasing agricultural land use, deforestation and/or disturbance (Fowler *et al.* 1986, Jaffe & Vilela 1989, Jonkman 1979). Specifically, elevated colony densities have been recorded in (1) transformed vegetation such as pastures (Fowler 1983) and plantations (Jaffe 1986, Oliveira *et al.* 1998), (2) early successional forests (Vasconcelos & Cherrett 1995), and recently (3) isolated forest remnants (Terborgh *et al.* 2001).

Surprisingly, despite frequent records in disturbed areas, published observations/assessments of increased *Atta* densities along forest edges are completely lacking. This is unexpected considering that an increasing proportion of the global forested landscape is in close proximity to anthropogenic edges (Harper *et al.* 2005) and edge effects are a driving force behind many of the biological alterations induced by forest fragmentation (Fagan *et al.* 1999, Murcia 1995). In fact, generalist herbivores have been repeatedly observed to be more abundant in edge than interior forests (Barbosa *et al.* 2005, Wirth *et al.*, in press). Here we provide a survey of *Atta* spp. in order to (1) evaluate whether the abundance of colonies changes with distance to the forest edge, (2) estimate the depth of edge influence, and (3) analyse whether *A. sexdens* (L.) and *A. cephalotes* (L.), two co-occurring *Atta* species (cf. Corrêa *et al.* 2005), respond differentially to edges.

The study was carried out in Coimbra, the single largest remnant of the Atlantic forest of north-east Brazil. Located in the state of Alagoas (9°S, 35°52′W), it covers approximately 3500 ha of largely well-conserved lower montane rain forest (Veloso *et al.* 1991), completely surrounded by sugar cane fields along its 40 km of relatively old (at least 60 y) borders (Urbas *et al.* in press). The region has a tropical climate characterized by a 5-mo dry season ($< 110\ \mathrm{mm\ mo^{-1}}$) lasting from September to January (annual precipitation = 2000 mm); the prevailing soils are latosols and podzols (IBGE 1985). The edge zone (0–100 m into the forest) has been shown to be largely dominated by pioneer species (Oliveira *et al.* 2004). We estimated colony densities of leaf-cutting ants (*Atta* spp.) with increasing distance from the forest edge towards the forest interior along 27 haphazardly laid transects. We used pre-existing, narrow (< 1 m) foot trails, which varied considerably in length, ranging from 70 to 3070 m. Trail entrances into the forest were separated on average by 1.67 ± 0.97 km (mean ± SD). The total distance surveyed was 28 km. Thus, with a fixed belt width of 10 m to each side (as used by Jaffe & Vilela 1989, Wirth *et al.* 2003), the transects amounted to a total area of 56 ha sampled, in which all *Atta* colonies were recorded. Since nest

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mounds were not always visible from transects, we used additional evidence to locate colonies, such as foraging trails (active or physical) or fresh refuse material around nest entrances. Ants were identified as described in Corrêa *et al.* (2005) and voucher specimens were deposited in the collection of the Laboratório de Invertebrados Terrestres da UFPE, Recife, Brazil. The location of each colony was determined using a GPS-receiver equipped with an external antenna (eMap, Garmin Ltd., Romsey, UK) set on averaging mode, resulting in an estimated resolution better than 10 m. Both transects and forest border line were recorded using the tracking function of the GPS. Where GPS data were not available the forest border was estimated based on aerial photographs (scale 1:8000 from 2002, courtesy of M. Tabarelli). All spatial data were compiled in a geographic information system (ArcView GIS 3.2, Environmental Systems Research Institute, Redlands, CA, USA). The forest area was divided into 50-m distance zones parallel to the forest border line, extending up to 1000 m into the forest interior. Transects were intersected with these distance zones, resulting in 180 sample areas (0.36 ± 0.27 ha). The number of colonies occurring per sample area was determined and a colony density calculated. When transects had an area in common (crossings of trails) this was included only once in one of the transects. To account for disproportionate sampling of the forest interior due to a smaller number of long transects, we pooled distance zones > 300 m. This resulted in a total of seven distance zones, i.e. 0–50 m, 50–100 m, 100–150 m, 150–200 m, 200–250 m, 250–300 m and > 300 m. To test whether density of leaf-cutting ant colonies was influenced by ant species or distance, we conducted a repeated-measures ANOVA with species as the main factor and distance as a repeated-measure factor. Differences among distance zones were evaluated with Tukey's post hoc test. As the interaction between variables was of particular interest in this study, we used this design despite deviations from the required ANOVA assumptions. According to Fry (1993) and Zar (1996), this approach was legitimate, because the ANOVA is robust enough if the results are highly significant and can be confirmed by a non-parametric equivalent (e. g. Kruskal–Wallis), as was true in our case. All analyses were carried out using STATISTICA v. 6.0 (StatSoft Inc, Tulsa, USA).

Within the surveyed 56 ha we encountered a total number of 80 *Atta* colonies, 43 belonging to *A. cephalotes* and 37 to *A. sexdens*. The colony densities of these co-occurring leaf-cutting ant species changed drastically with distance to the forest edge (effect of distance: $F_{6,180} = 13.9$, $P < 0.00001$; Figure 1). However, although both species similarly increased along the edge (no main effect of species; $P < 0.78$), the magnitude of the edge effect was species-specific, as indicated by a significant interaction term between species and distance ($F_{6,180} = 3.07$, $P < 0.007$). Colony density of *A. cephalotes* was low in the forest interior (0.33 ± 1.11 ha^{-1}, pooling all zones > 50 m into the forest) and sharply increased by a factor of about 8.5 towards the first 50 m (2.79 ± 3.30 ha^{-1}, Figure 1). On the other hand *A. sexdens* was more uniformly distributed. Colony densities in distance zones > 200 m (ranging from 0 ± 0 to 0.19 ± 0.51 ha^{-1}) were significantly different from those in the first two zones (2.14 ± 3.32 and 1.79 ± 4.09 ha^{-1}, Tukey's post hoc as shown in Figure 1b), indicating that for *A. sexdens* the edge effect might reach up to 200 m into the forest. Combining the two species, colonies occurred about five times more frequently in the 50-m edge zone (4.94 ± 3.67 ha^{-1}) than in the forest interior (1.01 ± 2.58 ha^{-1}, pooling all zones > 50 m). Variation of colony densities was generally large within distance zones because of colony-free samples due to (1) small sample areas per transect and distance zone and (2) clumped *Atta* distribution throughout the surveyed forest area (pers. obs.).

This study demonstrated for the first time a profound edge effect on the colony density of *A. cephalotes* and *A. sexdens* – two widespread leaf-cutting ant species in Latin America. Our findings suggest that populations of these species strongly benefit from the presence or creation of forest edges, and thus add to the list of disturbed habitats (e.g. secondary forests, plantations, pastures, roads, forest isolates) facilitating the spread of these dominant herbivores. Within the study area *A. cephalotes* was restricted to forested sites, while *A. sexdens* in addition inhabited open areas, such as dirt roads within sugar cane plantations (pers. obs.). This accords with known habitat preferences of the two species: *A. cephalotes* is a fragmentation-sensitive leaf-cutting ant species (Corrêa *et al.* 2005) commonly found in mature or old-growth forests (Jaffe & Vilela 1989, Rockwood 1973), while *A. sexdens* occurs in a wide range of habitats and is known as one of the species benefiting most from human-induced disturbances (Fowler *et al.* 1989, Vasconcelos 1990). We believe that the more uniform within-forest distribution of *A. sexdens* as compared to a pronounced edge concentration of *A. cephalotes* is a consequence of differences in the degree of foraging specialization. *Atta sexdens* forages opportunistically, simultaneously using trees and a wide variety of (ephemeral) resources for fungus culturing including seedlings, juveniles, flowers and dead leaves from ground litter (Vasconcelos 1990, pers. obs.). In contrast *A. cephalotes* concentrates its foraging on fresh leaves of large forest trees (Vasconcelos 1990) with a clear preference for pioneer species (Farji-Brener 2001), which are more frequent in forest edges and gaps (Laurance *et al.* 1998, Oliveira *et al.* 2004). Thus, *A. cephalotes* may respond more pronounced to the frequency of pioneer species, and therefore the edge, than *A. sexdens*.

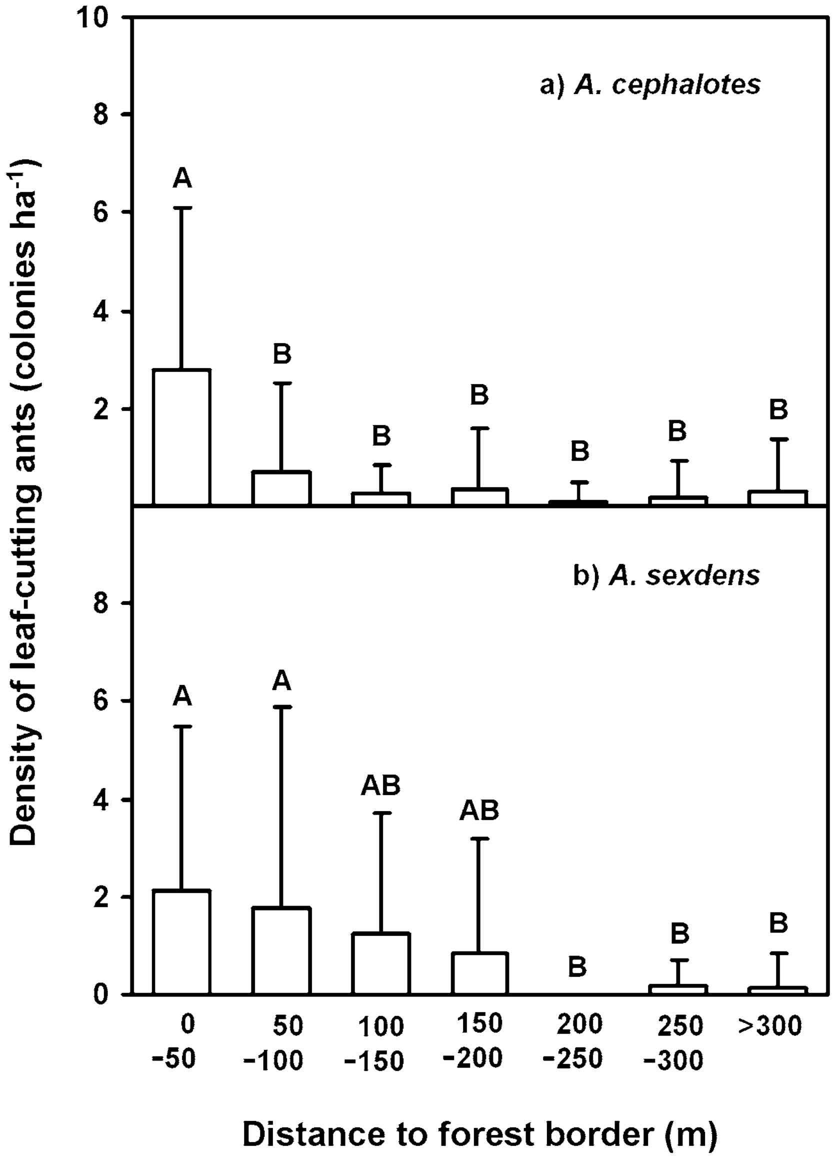

Figure 1. Mean colony density (+ SD) of *Atta cephalotes* (a), and *Atta sexdens* (b) in seven distance zones paralleling the forest border in the Atlantic forest of north-east Brazil. Different letters indicate significant differences (Tukey's post hoc test, $P < 0.05$). Sample sizes for the different distance zones were as follows: 0–50 m = 23, 50–100 m = 24, 100–150 m = 22, 150–200 m = 22, 200–250 m = 19, 250–300 m = 16, and > 300 m = 54.

Colony densities in the undisturbed forest interior of Coimbra more than 300 m from any edge (0.12 ha^{-1} for *A. sexdens* and 0.31 ha^{-1} for *A. cephalotes*) were within the range reported earlier for *Atta* species in mature continuous rain forests (e.g. Cherrett 1968: 0.6 ha^{-1}, Jaffe & Vilela 1989: 0.045 ha^{-1}, Vasconcelos 1988: 0.03 ha^{-1}, Wirth *et al.* 2003: 0.033 ha^{-1}). We thus are confident that the studied forest remnant was large enough to investigate edge effects without interference from other potential factors, such as fragment size or habitat fragmentation per se. The results indicate that drastic population growth of leaf-cutting ants is not only a feature of secondary forests or small forest fragments, but also takes place along the border of large, relatively undisturbed forest tracts. In this context our findings may have relevance for forest management and conservation, e.g. to estimate '*Atta*-free' core areas of forest fragments.

An increased availability of fast-growing, less effectively defended pioneer species (Coley 1983) has been most frequently invoked to explain high abundances of leaf-cutting ants in secondary forests (Farji-Brener 2001, Jaffe & Vilela 1989, Vasconcelos & Cherrett 1995) because the ants show a clear preference for early successional food plants (Farji-Brener 2001, Wirth *et al.* 2003). We suggest that this bottom-up explanation particularly applies to edge-associated leaf-cutting ant species along pioneer-dominated forest edges (Laurance *et al.* 1998, Oliveira *et al.* 2004), although truncated top–down forces and increased availability of nesting sites may also play a role. In fact, as we have demonstrated at the site of this study, *A. cephalotes* colonies harvested considerably more leaf area in edge vs. interior habitats (Urbas *et al.*, in press). As a consequence, edge forests experience a spatial concentration of *Atta* damage caused by both increased colony density and herbivory rate.

In the light of the ever-increasing pervasiveness of edge habitats (Harper *et al.* 2005) and the growing awareness of their significant impact on ecosystem processes (Fagan *et al.* 1999, Laurance *et al.* 2002), edge-driven accumulations of *Atta* colonies may have far-reaching consequences for forest edges in the Neotropics. In synthesis, we suggest that edge creation promotes high *Atta* densities, resulting in drastic changes on forest structure, microclimate, soil disturbance, and any subsequent impact on ecological processes, which may in turn reinforce deleterious edge effects (Fagan *et al.* 1999, Murcia 1995, Wirth *et al*., in press).

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