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SHORT COMMUNICATION

Leaf-cutting ants proliferate in the Amazon: an expected response to forest edge?

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Habitat fragmentation is gradually altering tropical forests all around the globe (Wright 2005), as human populations convert large blocks of pristine forest habitats into permanently fragmented or human-modified landscapes (Tabarelli *et al.* 2004). Fragmentation processes apparently create opportunities for small sets of species, which proliferate across modified landscapes, while others are driven to extinction or remain as minimal populations (Tabarelli *et al.* 2010). This 'winners vs. losers paradigm' (*sensu* McKinney & Lockwood 1999) probably describes one of the most conspicuous rearrangements of tropical biotas in response to human disturbances (in addition to biomass collapse), with unanticipated consequences for ecosystem functioning and long-term biodiversity persistence (Lôbo *et al.* 2011). Despite such appeal, the ecological identity of proliferating organisms and the mechanisms underlying their high abundance levels remains poorly appreciated.

The creation of forest edges due to habitat fragmentation exposes forest habitats to a plethora of environmental shifts recognized as edge effects, with some penetrating over 500 m into the remaining forest (Laurance *et al.* 2002). Therefore, edge-affected habitats drastically differ from core/interior forest, as edges are much more illuminated, exposed to microclimatic extremes and biotic stresses (Laurance *et al.* 2002). While many forest species avoid edge-affected habitats, others seem to proliferate due to relaxed levels of predation and/or increased resource availability (Tabarelli *et al.* 2010, Wirth *et al.* 2008). The latter case may be well exemplified by the leaf-cutting ants (LCAs) – generalist herbivores, which have been viewed as ecosystem engineers by providing resource heterogeneity and microsite diversity across pristine/old-growth neotropical forests, where they frequently occur in very low densities (Jaffe & Vilela 1989, Wirth *et al.* 2003). Yet, recent evidence from the Atlantic forest suggests that some LCA species are in fact experiencing proliferation across human-modified landscapes (Meyer *et al.* 2009, Wirth *et al.* 2007), thereby imposing far-reaching damage on the vegetation of edge-affected habitats (Corrêa *et al.* 2010, Meyer *et al.* 2011, Urbas *et al.* 2007). Objectively, a five-fold increment in the abundance of LCAs (*Atta cephalotes* and *A. sexdens*) was documented along forest edges as compared with old-growth interior of the Atlantic forest (Meyer *et al.* 2009, Wirth *et al.* 2007). Furthermore, this increase in colony density exerted an unprecedented herbivory pressure (36% of the available foliage compared with only 6% in the forest interior) along with substantial nest-driven alterations of forest structure and microclimate (Meyer *et al.* 2011, Urbas *et al.* 2007). Although human-related shifts in the abundance of LCAs have been previously documented, particularly in secondary forests (Farji-Brener 2001, Vasconcelos & Cherrett 1995), the generality of this edge-related accumulation of *Atta* colonies has never been examined, despite the resulting cascade of severe impacts

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on the biological dynamic of human-modified landscapes (Corrêa *et al.* 2010, Meyer *et al.* 2011).

Here we examined the abundance of LCAs across a fragmented landscape in the Amazon region in order to evaluate whether edge-related proliferation of LCAs (an edge effect) is a cross-forest pattern rather than an Atlantic forest phenomenon. We expected to find an increased abundance of LCA colonies (genus *Atta*) across 12 km of forest edges that were created *c.* 40 y ago along the principal (unpaved) road crossing the Biological Dynamics of Forest Fragments Project (the BDFFP landscape hereafter), 80 km north of Manaus, Brazil (2°30′S, 60°W). Road width was approximately 30 m with forest bordering both sides. We also expected lower levels of LCA abundance (relative to Atlantic forest) as the BDFFP landscape is still largely covered by unbroken old-growth forests with an almost intact fauna (Laurance *et al.* 2002, Stouffer & Borges 2001).

To estimate colony density and distribution across forest habitats 45 individual transects were walked one-sided perpendicular to the northern forest edge along the main road. Transect length was on average 2.36 (±0.71) km and a total of 130 km of transect was walked during a single survey period (March–April 2010). Transect entrances were set 200 m apart and, wherever possible, narrow understorey foot trails were used (Figure 1). Given a fixed belt width of 10 m to each side (as used by Jaffe & Vilela 1989, Wirth *et al.* 2003, 2007), the transects amounted to a total area of 260 ha sampled, in which all LCA colonies of the genus *Atta* were recorded and assigned to species level. Colonies and forest habitats were mapped using a GPS-receiver (GPSmap 60CSx, Garmin Ltd., Olathe, KS, USA) set on averaging mode, resulting in an estimated resolution better than 5 m. Spatial data were compiled in a geographic information system (ArcView GIS 3.2, Environmental Systems Research Institute, Redlands, CA, USA). The forest habitat was divided into 50-m distance zones parallel to the forest border line. Transects were intersected with these distance zones, resulting in 842 sample areas (0.49 ± 0.29 ha), in which the density of adult colonies (as determined by the occurrence of a soldier caste) was estimated. Density scores were analysed using a Poisson GLM with colony density as the response variable and distance to the edge (50-m intervals) as a categorical explanatory variable as well as proximity to existing understorey foot trails as a binary explanatory covariate (i.e. a colony is either ≤10 m from a foot trail or ≥200 m away). For a measure of goodness of fit we used the pseudo-R^2, which adopts the difference of null deviance and residual deviance divided by the null deviance. Following Zuur *et al.* (2009), we did not correct for underdispersion because model overfitting was not an issue (no outliers, few explanatory variables). Statistical analyses were conducted using the R software Package (R Development Core Team, http://www.R-project.org). Similar approaches have been adopted elsewhere (Zuur *et al.* 2009).

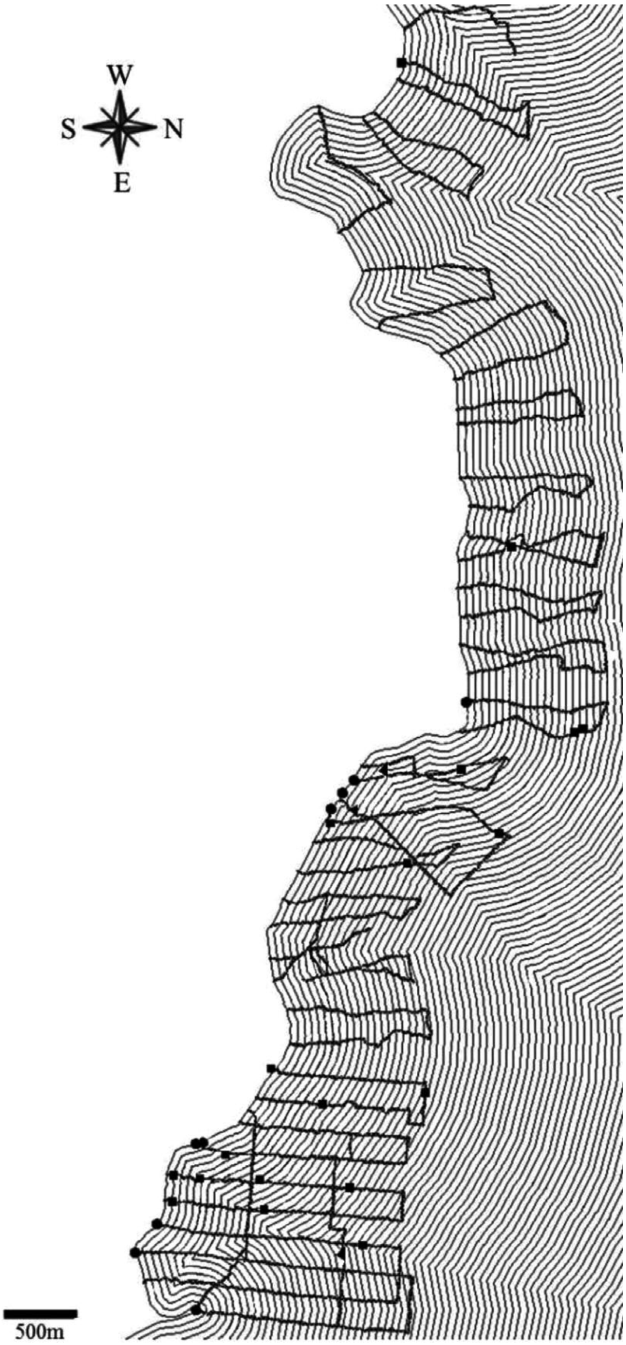

Figure 1. Schematic overview of mapped *Atta* colonies along all transects (black lines) surveyed in this study. Triangles stand for *A. cephalotes*, squares for *A. sexdens* and circles for *A. laevigata*. Parallel lines indicate the 50-m distance zones from the forest border as used for density analysis.

Overall we recorded 31 adult colonies of *Atta* spp. along transects, resulting in an average colony density of 0.12 colonies ha^{-1}. The most abundant species was *A. sexdens* (L.), which accounted for 61.3% of all colonies.

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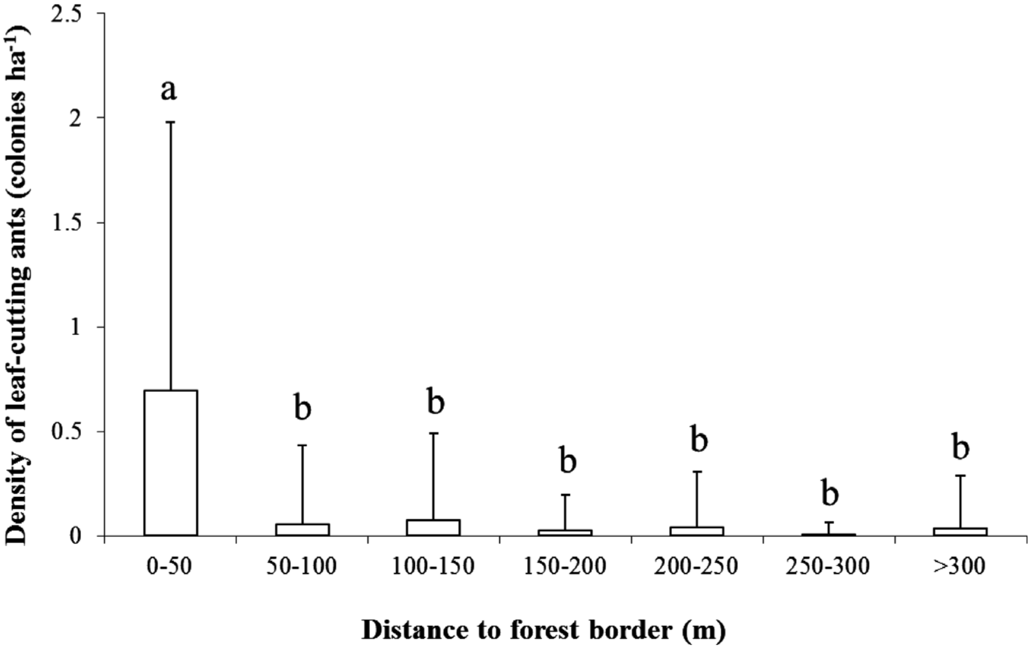

Figure 2. Mean colony density (+ SD) of leaf-cutting ants (*Atta* spp.) in seven distance zones paralleling the forest border at the Biological Dynamics of Forest Fragments Project (BDFFP) in central Amazonia, Brazil. Different letters indicate significant differences ($P < 0.05$) among distance zones. The number of sample areas was 45 for each distance zone up to 300 into the forest; the distance zone > 300 m into the forest was sampled 612 times.

The other two species found in the area were *A. laevigata* (Smith) and *A. cephalotes* (L.), which accounted for 29% and 9.7% of the colonies, respectively. Altogether, the three species showed an almost 20-fold increase of colony density within the first 50 m of the forest as compared to edge distances >50 m into the forest (Figure 2). Colony density within the first 50 m was 0.69 ± 1.29 ha^{-1} and significantly higher than densities within other distance zones ($Z = -3.87$, $P < 0.001$). In the forest interior (>50 m distant to the border), colony density averaged 0.04 ± 0.26 ha^{-1} and was, thus, more than an order of magnitude lower than the respective values previously recorded in the Atlantic forest (1.01 ± 2.58 ha^{-1}, Wirth *et al.* 2007). *Atta laevigata* was only found in close proximity to the physical forest edge, while the other two species were found throughout the forest. Moreover, colonies were significantly ($Z = 3.80$, $P < 0.001$) more abundant in the close vicinity of understorey foot trails with an average density of 0.12 ± 0.54 ha^{-1} vs. 0.04 ± 0.33 ha^{-1} away from them. Our model, although based on only two spatially related variables, explained 39% of the variation in colony density.

The distribution of *Atta* colonies across the BDFFP landscape was in accordance to our expectations and suggests that edge-related proliferation of *Atta* spp. may be a widespread phenomenon as LCAs benefit from forest fragmentation overcoming landscape singularities regarding matrix type, forest cover and historic human disturbances (i.e. aging vs. newly fragmented landscapes). Our results also indicate that small-scale disturbances, such as those by foot trails, are enough to trigger a positive response in colony numbers. In fact, while colony density in the Amazon showed a >17-fold increase within the first 50 m, it rose almost three-fold close to foot trails as well. Finally, the BDFFP findings suggest that some *Atta* species (e.g. *A. laevigata*), although able to inhabit undisturbed forests, are in fact poorly adapted to this habitat, while having a high potential to proliferate across edge-affected habitats.

Although we merely obtained a snapshot of the colony distribution in the BDFFP landscape, it is likely that such increased abundance along forest edge zones persists or even increases as already documented in the Atlantic forest (Meyer *et al.* 2009), as well as across Amazonian secondary forest patches (Vasconcelos & Cherrett 1995) and at roadsides (Vasconcelos *et al.* 2006). Apart from nesting site preferences of founder queens for open habitats (Vasconcelos 1990), LCA proliferation has been proposed to result from relaxation of food limitation, via increased abundance of palatable pioneer plants (i.e. bottom-up regulation; Farji-Brener 2001, Urbas *et al.* 2007), and population control through predators and parasites (i.e. top-down regulation; Almeida *et al.* 2008, Terborgh *et al.* 2001). Accordingly, cross-forest differences in colony density or proliferation level (e.g. Atlantic vs. Amazonian forest) may be largely governed by differences in population controls. Much of the Atlantic forest landscape now consists of relictual and edge-dominated forest (<15% of forest cover), in

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which edge-affected habitats support pioneer-dominated plant assemblages; i.e. nearly 80% of tree species and stems (Santos *et al.* 2008); these landscapes have also experienced complete extirpation of medium- and large-sized vertebrates as forest conversion into human-modified landscapes dates back to the 16th century (Silva & Tabarelli 2000). In the opposite extreme of alteration, the BDFFP landscape is still largely dominated by pristine forests (>90% of forest cover) with their old-growth (less palatable) flora and the whole spectrum of baseline fauna (Laurance *et al.* 2002, Stouffer & Borges 2001). It is thus a plausible consequence that colony density is still lower in this Amazonian landscape than in the Atlantic forest interior (Wirth *et al.* 2007), but this cross-forest difference is likely to diminish as edge-affected habitats encroach pristine forest, suitable nesting sites become more frequent, pioneer plants proliferate and defaunation proceeds (Laurance *et al.* 2002).

Leaf-cutting ants (species of *Atta* and *Acromyrmex*) are prevalent herbivores cutting up to 15% of the standing leaf crop in their foraging areas (Urbas *et al.* 2007), which, in the case of tropical forests, alters light availability and promotes environmental heterogeneity (Farji-Brener & Illes 2000, Wirth *et al.* 2003). Additionally, LCA activities alter soil and microclimate properties with tangible effects on plant recruitment and the successional trajectory of forest patches (Bieber *et al.* 2011, Corrêa *et al.* 2010, Farji-Brener & Illes 2000, Meyer *et al.* 2011). With LCA proliferation such activities and their cascading impacts are likely to affect the functioning of human-modified landscapes through unprecedented rates and via new ecological roles. We therefore urge further studies to explore the forces driving ant proliferation and its consequences, the plurality of possible outcomes, and the shifting ecological role played by LCAs (i.e. traditional vs. novel roles) as landscape alterations by human populations proceed.

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