Edge-induced narrowing of dietary diversity in leaf-cutting ants

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Abstract

Much of the ecological alteration faced by human-modified Neotropical forests can be assigned to edge effects, including the proliferation of some voracious herbivores such as leaf-cutting ants. However, the underlying mechanisms/impacts of tropical forest edge on herbivores performance and their foraging behaviour (e.g. dietary diversity) have rarely been investigated. The goal of this study was, therefore, to determine whether and how the annual diet (i.e. species richness, diversity and the relative proportion of pioneer versus non-pioneer species of plant materials) of *Atta cephalotes* colonies differs in the forest edge versus the interior zone of a large remnant of Atlantic forest in northeastern Brazil. Among the key results was a strong habitat effect on dietary diversity (explaining *ca*. 40–50% of the variation), which, in edge colonies, decreased approximately by one fourth compared to interior colonies (inverse of Simpson's index: 3.7 ± 0.84 versus 4.99 ± 0.95). There was a predominance of leaf fragments collected from pioneer species in the diet in both habitat (86% in edge and 80.4% in interior). Edge colonies collected proportionally more fragments from pioneer species than colonies located in the forest interior. Our results are the first to demonstrate an edge-mediated relaxation of dietary restrictions in leaf-cutting ants. These findings render robust support to previous evidence indicating the reduction of bottom-up forces as a key factor explaining both edge-induced hyper-abundance and increased herbivory of leaf-cutting ants in human-modified Neotropical landscapes.

Keywords: *Atta cephalotes*, bottom-up control, Brazilian Atlantic forest, diet breadth, edge effects, foraging behaviour, fungus-culturing, herbivory, pioneer trees

Introduction

Forest fragmentation and edge creation from deforestation have been ranked among the most pervasive and disturbing results of present-day human land use dynamics (Whitmore,

1997) and an ever-increasing proportion of the forested tropical landscape is in close proximity to edges (Broadbent *et al.*, 2008). Much of the ecological degradation faced by fragmented forests (e.g. species loss, biomass collapse, disruption of species interactions) can be assigned to edge effects (Laurance *et al.*, 2002), such as altered microclimatic conditions (Williams-Linera *et al.*, 1998) and increased wildfire susceptibility (Cochrane & Laurance, 2002), which lead to increases in tree mortality (Nascimento & Laurance, 2004), changes in communities composition and structure (Harper *et al.*, 2005),

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and acceleration of forest dynamism (Laurance, 2002). In terms of their tree assemblages, edge-influenced forests are strongly impoverished in species composition, life history traits and functional diversity (Girão *et al.*, 2007; Tabarelli *et al.*, 2008), which goes along with a pronounced proliferation of pioneer trees (Oliveira *et al.*, 2004; Santos *et al.*, 2008; Tabarelli *et al.*, 2008).

This increased abundance of pioneer trees may, in turn, promote herbivore populations because these tree traits are likely to be a more attractive, less defended food source for herbivores than shade-tolerant species (Coley & Barone, 1996). In fact, a recent review devoted to plant-herbivore interactions along the forest edge revealed robust evidence for a pronounced positive edge effect on herbivore densities, especially for generalist herbivores (Wirth *et al.*, 2008). However, the underlying mechanisms and the impact of tropical forest edge on herbivory levels, herbivore performance or foraging behaviour have rarely been investigated (Bentez-Malvido & Lemus-Albor, 2005; Urbas *et al.*, 2007) in spite of the importance of these processes for the organization of plant communities and ecosystem function (Hulme, 1996). To give an example, to our knowledge, there is no study available to date on how forest edge influences the dietary diversity of tropical herbivores.

The purpose of this study was to determine if and how the diet of leaf-cutting ants (LCA), as prominent ecosystem engineers in the Neotropics, is affected by proximity to forest edge. LCA are highly polyphagous (Rockwood, 1976) and are among those herbivores that hugely and persistently benefit from edges (Wirth *et al.*, 2008; Meyer *et al.*, 2009). For example, the colony density of *Atta cephalotes* was about six times higher in the first 100-m edge zone than in the >100-m forest interior of Brazilian Atlantic forest (Wirth *et al.*, 2007), and colonies located at the forest edge removed about twice as much leaf area from their foraging grounds as interior colonies (Urbas *et al.*, 2007). The reasons for these edge-induced phenomena are not yet fully understood, but the relaxation of bottom-up control (i.e. increased resource availability) has frequently been suggested to account for hyper-abundant LCA in anthropogenic habitats and early successional forests (Fowler, 1983; Farji-Brener, 2001; Urbas *et al.*, 2007). These habitats are dominated by pioneer plant species, which are known as preferred food plants of LCAs (e.g. Farji-Brener, 2001; Wirth *et al.*, 2003). We, therefore, hypothesized that, if edge colonies of LCA indeed benefit from the higher proportion of pioneers in this habitat (Oliveira *et al.*, 2004; Santos *et al.*, 2008), diet breadth should be reduced compared to colonies of the forest interior. In detail, we compared (i) species richness and diversity and (ii) the relative proportion of pioneer versus non-pioneer species of plant materials harvested by *A. cephalotes* colonies in the forest edge versus the interior zone of a large remnant of Atlantic forest in northeastern Brazil.

Methods

Study site

This study took place at Usina Serra Grande, a private sugar-cane landholding in the State of Alagoas, northeastern Brazil (8°30'S, 35°50'W) within the most threatened region of the Atlantic Brazilian forest (Silva & Tabarelli, 2000). The forest cover is assigned to a unique biogeographic zone of the Atlantic forest biota – the Pernambuco Center of Endemism, an 80-km-wide strip of tropical forest that once covered

56,400 km^2 of area along the Brazilian Atlantic coast (Santos *et al.*, 2007). The landscape still retains ∼9000 ha of forest in a set of fragments of variable sizes, embedded in a uniform, old (at least 60 years) and stable matrix of sugar-cane monoculture. The largest fragment, locally named Coimbra Forest, covers 3500 ha of largely well-conserved lower montane wet forest (Veloso *et al.*, 1991) and is the single largest remnant of Atlantic Forest in Northeast Brazil. Despite the obvious limitations of the landscape configuration available to us (i.e. only a single, unreplicated tract of forest), the 40 km of Coimbra Forest perimeter represent a relatively stable environment particularly suitable for assessing the long-term effects of edge creation, as reflected by a number of published studies (e.g. Oliveira *et al.*, 2004; Girão *et al.*, 2007; Santos *et al.*, 2008). The Coimbra Forest is situated on a low altitude plateau (300–400 m above sea level) covered by two similar classes of dystrophic and clay-laden soils, yellow-red latosol and yellow-red podzol according to the Brazilian system of soil classification (IBGE, 1985). Annual rainfall is *ca.* 2000 mm, with a 3-month dry season (<60 mm month^{-1}) from November to January (Oliveira *et al.*, 2004). The vegetation largely consists of well-conserved, old-growth forest and has been classified as lower mountain wet forest, with Leguminosae, Lauraceae and Sapotaceae as the richest families in terms of tree species (Grillo *et al.*, 2006). The forest is surrounded by plantations of sugar cane and the edge zone has been shown to be largely dominated by pioneer species, which represented over 90% of the adult trees at the edge and 27% in the forest interior (Grillo *et al.*, 2006). The forest has been strictly protected against disturbances, such as wildfires and logging (Santos *et al.*, 2008), which has guaranteed the stability of forest borders (most forest edges in the area are at least 60 years old). A detailed description of the geomorphology, remaining vegetation, and floral and faunal composition of the area can be found in Pôrto *et al.* (2006).

Atta cephalotes

Atta cephalotes (L) is a leaf-cutting ant of Neotropical forests, with a continuous distribution from Mexico to Bolivia and an additional disjunct occurrence in Northeast Brazil (Corrêa *et al.*, 2005). We chose *Atta cephalotes* for this study because (i) it occurs in both forest interior and edge habitats and (ii) its foraging activities are relatively easy to monitor due to their single-mounded and conspicuous nests (cf. Urbas *et al.*, 2007; Almeida *et al.*, 2008). Along the edge of Coimbra Forest, the density of *A. cephalotes* colonies increased in a 100-m edge zone (1.70±2.83 ha^{-1}) and sharply drops by a factor of about six towards the forest interior (0.30±1.41 ha^{-1}: Wirth *et al.*, 2007).

Study design

We evaluated the influence of forest edge on diet breath for ten adult colonies of *A. cephalotes*, five at the forest edge (hereafter referred to as edge colonies) and five in the forest interior (interior colonies). Edge colonies were chosen within 100 m of the forest border along different portions of the 40-km perimeter of the Coimbra Forest. The distance among the studied edge colonies was 2.0±1.4 km (mean±SD). Interior colonies were located more than 200 m from the forest margin, with inter-colony distances averaging 1.1±0.4 km. We selected evenly-sized colonies across the two habitats, so that nest surface areas of edge and interior colonies did not differ from each other (79.0±44.7 m^2 and 92.4±24.26 m^2, respectively;

$t = 0.59$, df $= 8$, $P = 0.57$). The same nest size suggests that colonies were approximately even aged (Bitancourt, 1941). Colony size distribution of the colonies is fully representative for colonies of the local leaf-cutting ant population assessed in previous studies (Corrêa et al., 2010).

Diet composition and dietary diversity

To estimate the diversity of the plant material harvested by *Atta cephalotes* colonies, we collected samples of the plant particles carried into their nests. Each survey of harvested food plants was conducted during a single observation day around the colony-specific time peak of daily activity (around midnight: Urbas et al., 2007) to increase representativeness of the samples (Wirth et al., 2003). In a sampling night, the laden ants passing a fixed point close to the entrance of each foraging trail of each colony were collected for 1 min with a small recharge-able vacuum cleaner (Black & Decker V1250). After collection, the vacuum cleaner was shaken gently to induce the ants to drop their loads and release them. To account for seasonal patterns in LCA harvest behaviour, sampling was repeated in bimonthly intervals for the duration of one year over from July 2002 until May 2003, thus resulting in six samples per year per colony. One interior colony died during the study and was, therefore, excluded from the analysis.

The collected material was then divided into fragments of leaves and nongreen materials, which typically comprised less than 10% of the overall harvest (Shepherd, 1985). Leaf fragments were separated into morphospecies based on morphological characters, such as surface texture, colour, pubescence and venation pattern, and counted per species. Where achievable, morphospecies were later identified to the lowest possible taxonomic level by taxonomists of the UFPE herbarium (see Acknowledgement) and, judging from herbarium specimens, collected at the study site (Oliveira et al., 2004; Grillo et al., 2006). However, since fragments harvested by *Atta* ants are usually below 1 cm^2 (Wirth et al., 2003) and the diversity of food items was high, species identification was extremely difficult/incomplete. Therefore, to compare dietary diversity in the diets of edge and interior colonies, we employed a morphospecies approach, as has been previously used in comparative ecological studies, in which species diversity was high and identification difficult (e.g. Garrettson et al., 1998; Condit et al., 2002). As a control for potential biases, we used the subset of taxonomically identified species to check whether morphotyping adequately reflected the floristic differences among colony diets; we thus present findings for both a maximum and a conservative number of food species.

To determine the relative proportion of pioneer species of plant materials harvested by *A. cephalotes* colonies, the iden-tified plants species were assigned to mutually exclusive cate-gories of regeneration, which represent distinct functional groups, pioneer or shade-tolerant species, according to defi-nitions provided by Hartshorn (1978) and information on life-history traits provided by Oliveira et al. (2004) and Grillo et al. (2006). Based on this information, we were able to assign 71 of a total of 78 identified species to one of these two categories.

To express the diversity of plant species in the ant diet, we used the inverse of Simpson's index, "D" (Krebs, 1999):

$$D = \frac{1}{\sum\limits_{j=S}^{S} (p_i)^2}$$

where S is the number of species, and p_i is the proportional abundance of species i in the diet. The inverse of this index is especially useful for diet comparisons since, in this case, it gives the number of 'equally-used' items that present the same level of diversity (Krebs, 1999). The value increases with both the specific richness of the diet and the equitability of those species (rarely eaten species contribute less to D than commonly eaten species).

Statistical analysis

The effects of the habitat (forest interior and edge) and the observed month (July, Sept., Nov., Jan., March, May) on dietary species richness and diversity were studied using a repeated-measure ANOVA with habitat, as a between-group factor, and month, as a within-group factor. In addition, we compared floristic similarity in species composition between colony habitats using ANOSIM tests of Bray-Curtis similarity measures. For this, we pulled the data from the six different sampling periods together for each nest. Species abundance data were square root-transformed and standardized (sensu Clarke & Gorley, 2001) in order to avoid any bias resulting from highly abundant species and differences in sample sizes (i.e. fragment density per colony). The frequencies of pioneers and shade-tolerant species in the ant diet were compared using χ^2 tests. Normality of the residuals and homogeneity of variances were checked via Shapiro-Wilk and Levene tests, respectively. All procedures are properly described in Zar (1999); analyses were carried out using STATISTICA v. 6.0 (StatSoft Inc., 2001) and Primer (Clarke & Gorley, 2001).

Results

We sampled a total of 9538 leaf fragments belonging to 329 morphospecies in the annual diet of the studied *Atta cephalotes* colonies ($n = 9$). The number of harvested morphospecies per colony and month ranged from 9 to 19.75 during one year with no significant habitat-related differences ($F_{1,7} = 0.47$, $P = 0.51$; fig. 1a). On average, a colony foraged on ca. 14 host plant morphospecies per month. Dietary species richness varied markedly throughout the year (effect of sampling month; $F_{5,35} = 8.47$, $P < 0.001$); for both edge and interior colonies, it clearly peaked in the dry season during November and January (fig. 1a).

In contrast to the absolute number of harvested species, dietary diversity of colonies (i.e. taking relative species abundance into account) was influenced by the forest habitat. Using the reciprocal of Simpson's index, harvest diversity of edge colonies was 3.7 ± 0.84 (mean $\pm$ SD) equally-used species per month, which was generally and significantly lower than in interior colonies (4.99 ± 0.95) with no significant variation across months (habitat: $F_{1,7} = 5.76$, $P = 0.0474$; sampling month: $F_{5,35} = 1.29$, $P = 0.291$; fig. 1b). This means that, at the edge of the forest, ants focussed their harvesting on a smaller number of species compared to the forest interior, where diet breadth was wider. The interaction between habitat and time was nonsignificant for both dietary richness and diversity of harvested morphospecies.

The diet among *A. cephalotes* colonies was floristically more similar within edge (18.69 ± 7.61) and interior (20.4 ± 3.08) habitats than between habitats (14.75 ± 5.13). These similarity patterns were corroborated by ANOSIM, which uncovered a strong habitat effect on the floristic similarity of dietary
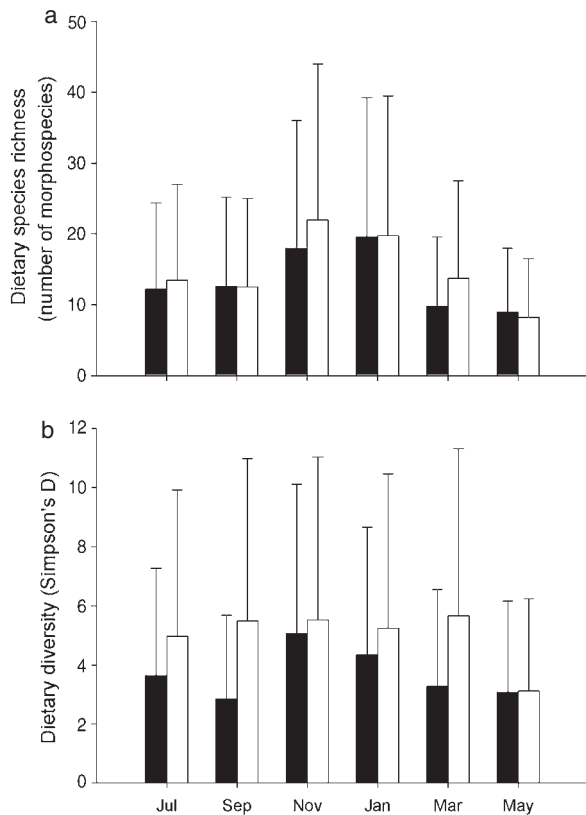
Fig. 1. Estimated monthly means (±SD) of the number of (a) morphospecies harvested, and the (b) inverse of Simpson´s index 'D', i.e. equally utilized species harvested of *Atta cephalotes* colonies at the edge (gray boxes; $n=5$) and interior (light boxes; $n=4$) of a remnant of the Atlantic forest in Northeast Brazil (■, edge; □, interior).

Discussion

Our study is the first to address edge effects on diet breadth of leaf-cutting ants. It clearly demonstrated that the diversity of food plants used by colonies living at the forest edge of a large remnant of the Atlantic forest is reduced as compared to colonies in forest interior habitats. Considering earlier findings on the foraging behaviour of LCA in edge-affected forests (e.g. smaller foraging areas: Urbas *et al.*, 2007), we can reasonably conclude that the well-documented proliferation of pioneer tree species in edge habitats (e.g. Laurance *et al.*, 2002; Oliveira *et al.*, 2004) is the ultimate cause behind such marked narrowing in diet breadth. In consequence, these results complement previous evidence indicating the reduction of bottom-up forces as key factor explaining both edge-induced hyperabundance (Wirth *et al.*, 2007; Meyer *et al.*, 2009) and increased (per colony) herbivory (Urbas *et al.*, 2007; Wirth *et al.*, 2008) of LCA in fragmented landscapes.

Our findings did not reveal habitat difference in the species richness of annual LCA diets, i.e. edge and interior colonies harvested similar numbers of food species throughout the year. However, when considering the relative contribution of each species in the measure of dietary diversity, the colonies differed in relation to their location in the forest. As colonies approach the edge, their dietary diversity decreased approximately by one fourth compared to the interior value. Moreover, around 40–50% of the variation in leaf diet was explained by habitat. As a causal mechanism, we suggest the palatable forage hypothesis (Farji-Brener, 2001), which states that pioneer tree species show less physical and chemical antiherbivore defence than shade-tolerant ones (Coley & Barone, 1996) and are more palatable to LCA (Wirth *et al.*, 2003). For example, terpenoids are plant defensive compounds well known to repel ant workers and inhibit the growth of their fungal symbionts (Howard *et al.*, 1988). At the study site, terpenoids have been shown to completely lack in dominant food plants of colonies in the forest edge zone, where they were less frequent compared to the forest interior site (Urbas, 2004).

The above mechanism is supported by the additional finding that edge colonies collected proportionally more leaf fragments from pioneer species than colonies located in the forest interior. Previous studies have already documented that leaf resources exploited by LCA depend on the abundance of preferred (or higher ranked) species and, as their abundance increases, dietary diversity decreases (Shepherd, 1985; Rockwood & Hubbell, 1987; Vasconcelos & Fowler, 1990; Vasconcelos, 1997). In fact, of 134 tree species identified at the study site, Oliveira *et al.* (2004) found twice as many pioneer species along the edge as compared to the forest interior (83 versus 37%), and pioneers represented over 90% of the stems of adult trees at the edge (versus 27% in the interior: Grillo *et al.*, 2006).

Our results also point to the obvious lesson that species richness is an imperfect/misleading proxy for dietary responses to environmental changes in leaf-cutting ants and, probably, other generalist herbivores. LCA are notorious for their high degree of polyphagy; but, in effect, the bulk of harvested plant material is dominated by a few highly preferred resources (Rockwood, 1973; Blanton & Ewel, 1985). To give an example, in the annual harvest of *Atta colombica* in Panama, the seven top-ranked species were exploited just as much (51% of all foraging days) as all other 45 food species together (Wirth *et al.*, 2003). To date, these aspects of leaf-cutting ant foraging behaviour are best explained

morphospecies among colonies ($R=0.52$, $P=0.008$). An additional ANOSIM evaluation of habitat effects with a subset of taxonomically identifiable food items (78 species from 41 families and 55 genera; see supplementary material) revealed similar findings ($R=0.43$, $P=0.016$) and confirmed that morphotyping seemed to adequately reflect the floristic differences among colony diets.

From those food species that could be assigned to a particular regeneration strategy ($n=71$), a significant majority were pioneers in both edge (74.6%; $\chi^2=35.51$, df=1, $P<0.0001$) and interior colonies (66.2%; $\chi^2=14.9$, df=1, $P=0.0002$) with no significant differences between habitats ($\chi^2=1.22$, df=1, $P=0.3579$). When considering the number of leaf fragments collected from these species, the predominance of pioneer species in the diet turned even higher in edge (86%; $\chi^2=2630.02$, df=1, $P<0.0001$) and interior (80.4%; $\chi^2=872.08$, df=1, $P<0.0001$). Such more quantity-based analysis also revealed significant differences in the proportion of fragments harvested from pioneer and shade-tolerant species between habitats ($\chi^2=19.29$, df=1, $P<0.0001$), where edge colonies collected proportionally more fragments from pioneer species (2177 versus 353) than colonies located in the forest interior (948 versus 231).

by suggestions of Shepherd (1985) and Pyke (1984), who hypothesized that optimal foraging is achieved by constantly taking samples of all potential leaf sources, thus tracking variable distributions of substrate patches in time and space.

Hyper-abundance of LCA in small fragments (Rao, 2000) or edge habitats (Wirth *et al.*, 2007; Meyer *et al.*, 2009) has been attributed to the release of resource limitation (i.e. top-down forces) (Rao, 2000; Terborgh *et al.*, 2001). Such effects have also been shown at the study site, where edge colonies experienced significantly fewer attacks by parasitic phorid flies than interior colonies (Almeida *et al.*, 2008). Recently, we proposed an additional mechanism to explain this increased LCA colony density in edge affected habitats via the attenuation of bottom-up forces (Urbas *et al.*, 2007; Wirth *et al.*, 2007, 2008; Meyer *et al.*, 2009; Silva *et al.*, 2009). Briefly, we argued that anthropogenically created forest edges lead to reduced foraging areas and increased herbivory rates per colony (Urbas *et al.*, 2007), ultimately promoting an increase in LCA populations (Wirth *et al.*, 2007; Meyer *et al.*, 2009) via a pronounced proliferation of pioneer trees (Oliveira *et al.*, 2004; Santos *et al.*, 2008). As pioneer tree species show less anti-herbivore defence than shade-tolerant ones (Coley & Barone, 1996), they are more palatable to LCA (Wirth *et al.*, 2003). The present findings can be fully integrated into this general concept of bottom-up induced hyper-abundance of LCA as edge proximity clearly reduced dietary diversity of the colonies, thus adding further support to this resource-driven perspective.

If the above interpretation of relaxed top-down and bottom-up control of LCA populations in edge habitats holds, we expect a synergism between anthropogenic edge creation and engineering impacts of LCA leading to detrimental consequences for human-modified Neotropical forests as outlined briefly in the following. Fragmentation and the consequent increase of edge habitats in tropical forests are widespread (Whitmore, 1997; Broadbent *et al.*, 2008) and support more LCA colonies (Rao, 2000; Wirth *et al.*, 2007; Meyer *et al.*, 2009; Silva *et al.*, 2009). This increase in colony density may alter both the floristic and functional signature of plant assemblages via two mechanisms: increased herbivory rates (Urbas *et al.*, 2007) and the creation of canopy gaps above nest, which drastically change the light climate (Meyer, 2008; Corrêa *et al.*, 2010), reduce the density of shade-tolerant species around the nests (Corrêa *et al.*, 2010) and increase the performance of large-seeded seedlings (Meyer, 2008). Such changes on plant species regeneration across the borders of the Coimbra Forest are still apparent during the decade subsequent to nests abandonment (Bieber *et al.*, in press). Thereby, LCA may amplify the impacts of forest fragmentation, which drive natural system towards early successional characteristics (Tabarelli *et al.*, 2008). To place the present study in this context, we conclude that edge creation implies the relaxation of LCA resource limitation and ultimately promotes high colony density, which, in turn, reinforces the deleterious effects of forest fragmentation.

Acknowledgements

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