



Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest

Bruno K.C. Filgueiras^{a,*}, Luciana Iannuzzi^b, Inara R. Leal^c

^a Programa de Pós-Graduação em Biologia Animal, Universidade Federal de Pernambuco, Recife, PE 50670-901, Brazil

^b Departamento de Zoologia, Universidade Federal de Pernambuco, Recife, PE 50670-901, Brazil

^c Departamento de Botânica, Universidade Federal de Pernambuco, Recife, PE 50670-901, Brazil

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ABSTRACT

Habitat loss and fragmentation have turned into the most important threats to biodiversity and ecosystem function worldwide. Here we investigate the effects of habitat fragmentation and drastic changes in tree communities on dung beetle richness and community structure. This study was carried out in a severely fragmented 670-km² forest landscape of the Atlantic Forest of north-eastern Brazil. Sampling was carried out in 19 forest fragments between September 2007 and March 2008 with the use of pitfall traps and flight interception traps. A total of 5893 individuals and 30 species of dung beetle were collected. Fragment area and isolation were the most significant explanatory variables for predictable and conspicuous changes in dung beetle species richness. Smaller and isolated fragments presented lower number of species, but fragments with lower tree species richness and lower proportion of shade-tolerant species were also considerably impoverished in terms of dung beetle species richness. The body mass of dung beetles were explained by fragment area and the percentage of emergent trees with smaller and less stratified fragments being dominated by small-bodied dung beetles. An ordination analysis segregated dung beetle communities between small fragments (<100 ha) and the control area. Seventy-seven percent of the species were recorded in the control area and 22% of all species were unique to this habitat. Our findings indicate that large fragments in the Atlantic Forest appear to consist in a sort of irreplaceable habitats for particular groups of dung beetle species, as well as for the integrity of their communities.

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1. Introduction

Habitat loss and fragmentation are drastic processes in tropical forests and have a pervasive, disruptive impact on biodiversity (Laurance et al., 2002; Ewers and Didham, 2006). Fragmentation *per se* is a landscape level phenomenon, which not only reduces habitat size and quality but also increases isolation and creates ecological boundaries that differ significantly from true core habitat (Fahrig, 2003). As a consequence, habitat fragmentation promotes decline in total number of species in the landscape, while increments the risk of local extinctions (Ewers and Didham, 2006). For example, habitat loss and fragmentation promote rapid, drastic, and persistent changes in the functional signature of tropical tree communities (Laurance et al., 1998; Tabarelli et al., 2008). Small fragments and forest edges of large fragments (i.e., fragmentation-affected habitats) are expected to exhibit species-poor tree communities and may be impoverished in terms of emergent (Laurance et al., 2000; Santos et al., 2008), shade-tolerant (Oliveira et al., 2004; Santos et al., 2008), vertebrate-pollinated (Girão et al.,

2007) and large-seeded trees dispersed by vertebrates (Silva and Tabarelli, 2000; Melo et al., 2006). As emergent trees and shade-tolerant species are critical sources of fruits, flowers, and shelter for animals, their decline in fragments is likely to cascade over higher trophic levels (Laurance et al., 2000).

Like tree species, dung beetle communities are also influenced by human disturbances, such as habitat fragmentation (Klein, 1989; Estrada et al., 1999; Feer and Hingrat, 2005; Nichols et al., 2007; Gardner et al., 2008; Larsen et al., 2008). Area loss and isolation are recognised to have a drastic effect, reducing species richness and abundance of dung beetle communities (Larsen et al., 2008), with clear impacts on beetle-mediated services such as secondary seed dispersal (Chapman et al., 2003) and nutrient recycling (Bornemissza and Williams, 1970). Changes in the structure of dung beetle communities usually encompass shifts in species richness, abundance and guild structure relative to daily activity, diet and resource-relocating behaviour (Andresen, 2005). Such characteristics make dung beetles indicators of natural or anthropogenic environmental disturbances in tropical forests (Halfpeter and Favila, 1993; Davis et al., 2001). Additionally, dung beetles are abundant and diverse in the tropics (Philips et al., 2004), where their communities respond to soil type (Osberg et al., 1994),

* Corresponding author. Tel.: +55 81 2126 8853.

E-mail address: bkcfilgueiras@gmail.com (B.K.C. Filgueiras).

microclimate (Lumaret et al., 1992) and the abundance of food sources (Estrada et al., 1999; Filgueiras et al., 2009; Nichols et al., 2008, 2009).

A vast number of studies have also documented the influence of vegetation type on dung beetle communities (Estrada et al., 1998; Davis et al., 2001; Andresen, 2005; Davis and Philips, 2005; Scheffler, 2005; Gardner et al., 2008). Most studies, however, have primarily compared dung beetle communities in forest habitats vs. other components of human-modified landscapes. For example, Gardner et al. (2008) found that the total species richness and abundance of dung beetles was significantly lower in planted forests as compared to primary forest. Such reorganization of dung beetle communities following habitat change is frequently assumed to result from altered vegetation structure (Gardner et al., 2008), but the role played by different attributes of vegetation structure remain unexplored. As vegetation type is an important factor determining the organization of dung beetle communities in tropical rainforests (Halffter and Arellano, 2002; Andresen, 2005), the use of functional groups of tree species may demonstrate what types of habitats are favourable to forest dung beetles and how such variable shape dung beetles communities.

Although several studies have examined fragmentation-related effects on dung beetles (Nichols et al., 2007; Larsen et al., 2008), few studies addressed simultaneously the influence of fragment, landscape and vegetation attributes on dung beetle communities. Therefore, the primary aim of this study was to examine how dung beetle communities respond to habitat fragmentation and its related shifts in the functional signature of tree communities in hyper-fragmented landscape of Atlantic Forest. Namely, we sought to determine whether dung beetles are influenced by (a) fragment area and isolation, (b) tree density, (c) tree species richness, and percentage of (d) shade-tolerant and (e) emergent trees.

2. Methods

2.1. Study area

The study was carried out at Usina Serra Grande, a large private sugar-cane landholding in the State of Alagoas in north-eastern Brazil (8°30'S, 35°50'W) (Fig. 1). The Serra Grande landscape is located within the most threatened region of the Brazilian Atlantic Forest (Silva and Tabarelli, 2000; Lopes et al., 2009). The massive destruction of the Atlantic Forest started with the arrival of the first European colonizers in the 16th century, and since that time about 88% of the natural vegetation in this formation has been modified or replaced by anthropogenic environments (Tabarelli and Gascon, 2005). We selected a large, hyper-fragmented landscape (667 km²; 9.2% of forest cover), containing 109 forest remnants (ranging in size from 1.67 to 3500 ha), all of which entirely surrounded by a uniform and stable matrix of sugar-cane monoculture (Silva and Tabarelli, 2000; Santos et al., 2008). The largest fragment, Coimbra Forest (3500 ha) is the best preserved patch of forest in the region, still supporting ecological groups that are believed to inhabit more continuous and undisturbed tracts of Atlantic Forest, such as large-seeded trees and frugivorous vertebrates (Santos et al., 2008). The Serra Grande landscape is therefore a useful landscape for assessing persistent and long-term effects of habitat loss and fragmentation as reflected by a number of published studies (e.g., Oliveira et al., 2004; Girão et al., 2007; Santos et al., 2008; Lopes et al., 2009).

The Serra Grande landscape 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). The vegetation consists of lower mountain rain forest, with

Leguminosae, Lauraceae, Sapotaceae, Euphorbiaceae, Chrysobalanaceae and Lecythidaceae as the richest families in terms of tree species (Grillo et al., 2006).

2.2. Dung beetle communities

Sampling of beetles from the subfamily Scarabaeinae was carried out between September 2007 and March 2008 in 19 focal fragments (10–3500 ha), in which tree communities had been previously surveyed (Oliveira et al., 2004; Santos et al., 2008). Fragments were surveyed once during this period, but to avoid seasonality effects on dung beetle community, trapping was carried out in the same season. In Serra Grande landscape, annual precipitation is 2000 mm (ranging from 20 to 155 mm per month, www.inpe.br), with a dry season (<60 mm/month) occurring from November to January (Oliveira et al., 2004) and with the wettest period between April and August (Pimentel and Tabarelli, 2004).

We established ten sets of pitfall traps (spaced 20 m apart) (Andresen, 2005) per fragment, and each set was composed by four traps arranged in a square (placed 10 m apart) and disposed within a 200-m transect in the geographic centre of each fragment. Three traps were baited – human faeces (~30 g), fermented banana (~30 g), and decomposing bovine spleen (~30 g) – and one non-baited trap was used as the control. The traps were made up of plastic containers (15 cm in diameter by 13 cm in height) with a bait-holding recipient (3 cm in diameter by 4.8 cm in height) when using human feces or fermented banana as bait. For the decomposing bovine spleen, an iron support in the shape of an inverted “U” was used, containing protection for the bait. Each fragment also had a flight interception trap (FIT) (2 m in width by 1.5 m in height), which was also located in the center of the fragment but supporting reduced vegetation density to enhance beetle capturing. FIT has been adopted to complement pitfalls and provide a more complete sampling of dung beetle communities (Hill, 1996). Below the trap, trays containing a water and detergent solution were placed to capture the insects that fell after making contact with the flight interception trap. Forty-eight hours after installing the traps, dung beetles were collected and sent to Dr. Fernando Vaz-de-Mello (University of Mato Grosso, Brazil) for identification.

Beetle guild composition was characterized in terms of two ecological attributes: diet (coprophagous, necrophagous, saprophagous and generalist) and resource-relocating behaviour (tunneler, roller and dweller). Only dung beetle species with more than 20 individuals sampled were assigned into diet categories: coprophagous, necrophagous or saprophagous if >70% of individuals were captured in coprophagous, necrophagous or saprophagous traps, respectively (Andresen, 2005). Species in which at least 70% of the individuals were collected in both copro- and necrotraps were considered generalists. Furthermore, to obtain body mass estimates for each species, samples of 1–25 specimens were dried at 60 °C and weighed on a scale with an accuracy of 0.0001 g.

2.3. Fragmentation metrics

All 19 forest fragments were examined in terms of area and isolation (Table S1). A proximity index was generated to estimate the level of fragment isolation from other fragments (Gustafson and Parker, 1992). The index was calculated for each patch using area (S) and nearest neighbour distance (n) of that patch and each k neighbouring patches whose edges are within of specific buffer: $PX = \sum (S_k/n_k)$. Proximity index is large when the patch is surrounded by larger and/or closer patches, and decreases as patches become smaller and/or sparser. This index distinguishes sparse distributions of small habitat patches from clusters of large patches (Gustafson and Parker, 1992). This metric is biologically realistic

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