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Habitat structure and food resources for wildlife across successional stages in a tropical forest

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ABSTRACT

Tropical forests are experiencing an increase in the proportion of secondary forests as a result of the balance between the widespread harvesting of old-growth forests and the regeneration in abandoned areas. The impacts of such a process on biodiversity are poorly known and intensely debated. Recent reviews and multi-taxa studies indicate that species replacement in wildlife assemblages is a consistent pattern, sometimes stronger than changes in diversity, with a replacement from habitat generalists to old-growth specialists being commonly observed during tropical forest regeneration. However, the ecological drivers of such compositional changes are rarely investigated, despite its importance in assessing the conservation value of secondary forests, and to support and guide management techniques for restoration. By sampling 28 sites in a continuous Atlantic forest area in Southeastern Brazil, we assessed how important aspects of habitat structure and food resources for wildlife change across successional stages, and point out hypotheses on the implications of these changes for wildlife recovery. Old-growth areas presented a more complex structure at ground level (deeper leaf litter, and higher woody debris volume) and higher fruit availability from an understorey palm, whereas vegetation connectivity, ground-dwelling arthropod biomass, and total fruit availability were higher in earlier successional stages. From these results we hypothetize that generalist species adapted to fast population growth in resource-rich environments should proliferate and dominate earlier successional stages, while species with higher competitive ability in resource-limited environments, or those that depend on resources such as palm fruits, on higher complexity at the ground level, or on open space for flying, should dominate older-growth forests. Since the identification of the drivers of wildlife recovery is crucial for restoration strategies, it is important that future work test and further develop the proposed hypotheses. We also found structural and functional differences between old-growth forests and secondary forests with more than 80 years of regeneration, suggesting that restoration strategies may be crucial to recover structural and functional aspects expected to be important for wildlife in much altered ecosystems, such as the Brazilian Atlantic forest.

1. Introduction

Tropical forests have already lost about 6 million km^2 (35%) of their area due to human action (Wright, 2010). Although natural regeneration occurs in a significant extension of cleared areas, deforestation of old-growth forests is still widespread, leading to an increase in the proportion of secondary forests (FAO, 2010; Wright, 2010). Today over half of the remaining tropical forests are secondary or otherwise degraded, and the proportion of these secondary vegetation continues to increase (Wright, 2010). However, the impacts of such a process on wildlife are poorly known, since the value of secondary forests to wildlife conservation and long-term maintenance of ecological processes is still poorly understood (Bowen et al., 2007; Chazdon et al., 2009a; Gardner et al., 2007), and strongly debated. Some authors argue that natural regeneration could mitigate the effects of old-growth forest loss (Dent and Wright, 2009; Wright and Muller-Landau, 2006a, 2006b), while others suggest that secondary forests do not have the same conservation value of old-growth forests (Brook et al., 2006; Gardner et al., 2007; Gibson et al., 2011; Laurance, 2007).

Studies assessing wildlife recovery during tropical forest regeneration indicate that the most common species at the beginning of this process are habitat generalists or species typical of open physiognomies or biomes, which are rare or absent in old-growth forests (Bowen et al., 2007; Lawton et al., 1998; Pardini et al., 2009). On the other hand, a large number of species that are common in old-growth forests are rare or absent in secondary vegeta-

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tion (Barlow et al., 2007a; Bowen et al., 2007; Chazdon et al., 2009a; Dunn, 2004; Pardini et al., 2009) and are commonly restricted to forested biomes at larger spatial scales (Pardini et al., 2009). Therefore, although species richness in young forests may often be comparable to that in old-growth areas, species composition changes substantially during regeneration (Dunn, 2004; Pardini et al., 2009).

Nevertheless, the ecological processes underlying changes in composition or structure of wildlife assemblages during succession have been rarely investigated (Gardner et al., 2009). These processes should be related to the structural, functional, and floristic changes that occur during regeneration, such as the increase in plant biomass (linked to the increase in basal area and canopy height), the decrease in net primary productivity, and changes in plant species composition (Brown and Lugo, 1990; Clark, 1996; Guariguata and Ostertag, 2001), which should lead to changes in habitat structure and food resources for wildlife (e.g. Jayapal et al., 2009). In particular, vegetation structure (e.g. Dial et al., 2006; Hopkins, 2011; Lambert et al., 2006; Malcolm, 1997; Pardini et al., 2005), as well as the structure of the leaf litter (e.g. Naxara et al., 2009; Sayer et al., 2010; Van Sluys et al., 2007; Vonesh, 2001) and woody debris (e.g. Grove, 2002; Lambert et al., 2006; Naxara et al., 2009; Vonesh, 2001) are important habitat features to several wildlife groups. Besides these structural aspects, the availability of arthropods and fruits – important food resources to several vertebrates (e.g. Caldwell and Vitt, 1999; Durães and Marini, 2005; Herrera et al., 2002; Pinotti et al., 2011; Tutin et al., 1997) – should also change during regeneration.

Thus information on how regeneration changes aspects of habitat structure and food availability, although scarce (but see DeWalt et al., 2003), is essential to clarify the ecological processes underpinning the changes usually observed in wildlife composition, as well as to support restoration techniques aiming at the conservation or recovery of wildlife (Prach and Walker, 2011; Walker et al., 2007). This type of information is of particular importance in severely exploited tropical forests, such as the Brazilian Atlantic forest. The second largest South American rainforest, the Atlantic forest is inserted in the most populous Brazilian region, the Atlantic coast, home to 61% of the Brazilian population in an area of about 15% of the country (SOS Mata Atlântica and INPE, 2009). It has been intensely exploited since the arrival of Europeans in the 16th century (Dean, 1995), and currently only 11.4–16% of its original area remains, mostly in small fragments of secondary forest (Ribeiro et al., 2009). Recently, efforts are being made for the restoration of altered landscapes in this biome (e.g. Wuethrich, 2007). However, for these initiatives to be effective also for wildlife, information on the recovery of important aspects of habitat structure and food availability is essential.

Here we investigate the existence of consistent patterns of variation in habitat structure and food availability in a mosaic of forests in different successional stages inserted in the largest continuous tract of Brazilian Atlantic forest, comparing 28 sampling grids in mid secondary, late secondary, and old-growth forest patches. We discuss our findings pointing out hypotheses on the implications for commonly observed changes in composition of animal assemblages during tropical forest regeneration, and for the recovery of wildlife through natural regeneration in intensively exploited ecosystems.

2. Materials and methods

2.1. Study area

Our study was carried out in the Morro Grande Forest Reserve (23°39′–23°48′S, 47°01′–46°55′W), located in the Cotia municipality, São Paulo State, Brazil (Fig. S1-A). The Reserve encompasses 9400 ha of continuous Atlantic forest, comprising patches in different successional stages after clear cut and small-scale agriculture and cattle ranching, and by old-growth patches that were not clear cut during the period of more intensive exploitation in the region, from the 17th century until the 1930s, when the area was expropriated and cleared patches could start regenerating (Metzger et al., 2006). In its southern portion, the Reserve is connected to the largest continuous area of Atlantic forest in Brazil, the Serra do Mar sub-region (Ribeiro et al., 2009). The altitude varies from 860 to 1075 m, the climate is Cfb, temperate warm and wet (Köppen, 1948), and the average monthly temperature and precipitation vary from 16.5 to 20.5 °C and 43 to 77 mm in the cool–dry season (April to September), and from 20.7 to 23.5 °C and 125 to 196 mm in the warm–wet season (October to March) (Metzger et al., 2006). The forest is classified as "Dense Mountain Rain Forest", and the most representative botanic families are Myrtaceae, Lauraceae, Fabaceae and Rubiaceae (Catharino et al., 2006). Detailed abiotic and historic data of the study area are found in Metzger et al. (2006).

2.2. Sampling design

Through the interpretation of aerial photographs and ground-truthing through the checking of 64 sites in the field, we mapped land cover in a buffer of 1 km from the access roads in the Reserve, classifying the native vegetation into successional stages as defined by Brazilian law (Supplementary data). From the total area mapped, 62.4% is in mid secondary stage, 12.3% in patches in late secondary stage, and 10.1% in patches of old-growth forest. The last are represented by areas that were not clear cut since the 17th century, and were considered control areas (see also Supplementary data). Sampling grids were located in the eight largest late secondary patches (6.1–164.8 ha), in the ten largest old-growth patches (7.4–90.8 ha), and randomly in 10 points in mid secondary stage (since forests at this stage are connected and not fragmented in patches), totaling 28 grids. We kept a minimum distance of 500 m among grids, of 100 m from each grid to open areas or areas in other successional stages, and of 50 m from each grid to water bodies. For each successional stage, half of the grids were located in the north and half in the south of the Reserve (Fig. S1-A). Detailed information about the mapping of successional stages and the location of sampling grids is found in the Supplementary data.

2.3. Data collection

Grids were 100 × 70 m (0.7 ha, Fig. S1-B), an appropriate size to encompass small-scale heterogeneity within successional stages, while still maintaining at least a 100-m distance to forests at different successional stages. All datasets were collected in the warm–wet season, and for each of them, all grids were sampled simultaneously or within a short period of time (maximum 25 days), in order to prevent bias due to seasonal variation across sampling grids. Data on habitat structure were collected in January 2008, on ground-dwelling arthropods in three sampling sessions in the warm–wet season 2007–2008 (November–December 2007, February–March 2008 and March–April 2008, in each of which all grids were sampled, except three grids in the last session, see below), on trunk-dwelling arthropods in February 2009, and on fruits in January 2009. In three of the 28 grids (one in each successional stage, Fig. S1-A), we were unable to complete samples after mid March 2008 for security reasons. Thus, data from one of the three planned samplings of ground-dwelling arthropods, as well as data from the sampling of trunk-dwelling arthropods and fruits are missing in these three grids.