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The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure

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ABSTRACT

Habitat loss is one of the primary drivers of change in forest biodiversity and ecosystem function worldwide. The synergetic effects of habitat loss and fragmentation might lead to profound impacts on forest structure and composition, conducting forest fragments towards early successional stages (retrogressive succession). In this study, we tested this hypothesis by evaluating how landscape-scale forest loss affects the forest structure. We sampled forest structure descriptors in 40 forest sites in landscapes ranging from 3 to 100% forest cover. Forest cover was negatively related to most of the structural variables, generally in a non-linear manner. In contrast, dead trees and logging were ubiquitous and not related to forest cover. The forest remnants in more deforested landscapes retain early successional forest attributes, with tree assemblages that are less dense, shorter, thinner, with an overall basal area loss, and with increasing canopy openness. This structural degradation indicates that landscape-scale forest loss strongly determines the trajectory of the local forest structure, pushing forests to a retrogressive succession process, which is more likely to occur in deforested landscapes and can lead to functional forest erosion. Our findings indicate that remnants within deforested landscapes may suffer recruitment limitation, primarily of large trees. Additionally, the forest structure characteristics were more severely degraded in landscapes with less than 40% forest cover. In the face of these results, the recommendation is to avoid the reduction of forest cover below this threshold, at which point structural erosion becomes more severe, with predictable negative consequences on biodiversity and ecosystem service maintenance.

1. Introduction

The negative responses of native biota to habitat loss have been largely reported over the last few decades, which is an issue of special concern in tropical forests because they harbor more than 60% of the world's terrestrial species (Brooks et al., 2002; Gardner et al., 2009; Wright and Muller-Landau, 2006). Currently, most of the biota in tropical regions is present in anthropogenic landscapes, in which historical deforestation has reduced large forest tracts that were once continuous into a myriad of small patches that are often isolated from one another by other human-modified land uses (Ribeiro et al., 2009; Wright and Muller-Landau, 2006). Several studies have shown that habitat loss leads to a reduction on species diversity of plants and animals (Andrén, 1994; Bender et al., 1998; Lindenmayer et al., 2005; Montoya et al., 2010).

More recently, researches have highlighted the non-linearity of individual species and entire assemblage responses to habitat loss in the landscape (Banks-Leite et al., 2014; Lima and Mariano-Neto, 2014; Morante-Filho et al., 2015; Rigueira et al., 2013), which may also be associated with a regime shift in the ecosystem (Pardini et al., 2010). Theoretically, there is an extinction threshold at which species losses sharply increase with habitat cover reduction (Fahrig, 2003). Additionally, the extinction probability as deforestation proceeds may be influenced by the habitat configuration, once smaller patches are more likely to harbor non-viable populations and local extinctions are not offset by migrants as isolation effects increase (Andrén, 1994; Villard and Metzger, 2014).

Landscape deforestation, by increasing forest edges amount and number of fragments and decreasing fragment size (Fahrig, 2003) can trigger local modifications of the forest structure in the remaining patches (Kapos, 1989; Matlack, 1993; Murcia, 1995; Saunders et al., 1991). For example, edge effects change the microclimatic conditions, causing tree damage and mortality particularly for emergent and large trees, and also influencing seed predation, germination and establishment, increasing plant species turnover (Fleury and Galetti, 2004, 2006; Oliveira et al., 2004, 2008; Santos et al., 2008). The death of

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emergent and large trees affects the mean tree diameter, height and basal area, reduces forest biomass and increases the number of canopy gaps, which alter light input into the forest interior (Laurance et al., 2011; Magnago et al., 2015b; Nepstad et al., 1999; Pinto et al., 2010). Moreover, habitat loss and fragmentation can cause the elimination of important animals and the breakdown of animal–plant interactions as a consequence (Cordeiro and Howe, 2003; Jorge et al., 2013). In fragmented landscapes, defaunation tends to occur at higher rates because of the accessibility of these areas to hunters and other synergistic habitat loss effects (Galetti and Dirzo, 2013; Laurance et al., 2011). Seed dispersal, seed predation and seedling trampling are among some of the reported interactions that are compromised in defaunated forests, all of which result in cascading effects on plant regeneration (Jorge et al., 2013; Wright and Duber, 2001).

In addition, those smaller fragments within more deforested landscapes may be subject to the strong negative effects of selective logging, primarily because of the high vulnerability and accessibility of fragments (Echeverría et al., 2007; Liu and Slik, 2014). Large and emergent trees are more subject to logging because they normally have hardwood and more wood volume and therefore more economic value (Oliveira et al., 2004). With increases in large tree deaths, more light input and the scarcity of large fruit dispersion in fragmented landscapes, it is predictable that the loss of one large and emergent tree can be compensated for by many small trees (Laurance et al., 1998; Oosterhoorn and Kappelle, 2000), however this change is not able to replace the carbon stock (Bello et al., 2015). The result of these emerging processes is a profound alteration in the forest structure and species composition, driving forest fragments towards early successional stages, or the so-called retrogressive succession (Santos et al., 2008; Tabarelli et al., 2008).

Forest structural changes triggered by the aforementioned disturbances negatively affect biota and can also reduce the potential for carbon storage and hydrological forest cycles (Bello et al., 2015; Wright, 2010). Given that the vegetation structure is usually the primary local component used to describe habitat quality (Banks-Leite et al., 2013), the relation between forest cover loss and vegetation structure in the remnant area can have important implications for understanding the mechanisms driving biota persistence in disturbed landscapes. The forest structure affects fauna mobility (McElhinny et al., 2006) and resource availability (DeWalt et al., 2003; Palomares, 2001), shaping the diversity patterns of many taxonomic groups that can affect the whole forest dynamic (Tews et al., 2004). Overall, forest remnants with greater structural complexity or structural heterogeneity are positively related to bird diversity (Rosenvald et al., 2011; Watson et al., 2004), the presence of primates (Arroyo-Rodrıguez et al., 2007), the abundance of small mammals (Pardini et al., 2005), and arthropod diversity (Wettstein and Schmid, 1999).

Given the importance of forest structure on biodiversity maintenance and the paucity of studies at the landscape scale, this study attempts to investigate the influence of forest loss at the landscape scale over forest structural characteristics in a quantitative manner. We also evaluated whether the relation between forest loss and forest structure is linear or if it exhibits a threshold value. To accomplish this goal, we measured the vegetation structural descriptors, the intensity of logging, and the number of dead trees in 40 forest sites across a forest cover gradient (3–100%). We believe that in deforested landscapes the forest fragments will be subjected to retrogressive succession, leading to forest structure shrinkage. Therefore, we predict that the forest cover loss will lead to an increase in the number of dead trees and logging and a reduction in the mean diameter, height, basal area, and density of large trees. Given these changes, we also expect that landscape scale deforestation will lead to an increase in canopy openness, and with more light available, there is a higher density of lower stratum foliage and tree density, particularly because of the increase in small, shade-intolerant individuals at sites with a lower amount of forest cover at the landscape scale.

2. Methods

2.1. Study area

We conducted this study in the Atlantic Forest of southern Bahia between 15°0′–16°0′S and 39°0′–39°30′W. We selected lowland forest fragments that show similar floristic composition, soil type, and topography (Thomas et al., 1998). We avoided sampling montane, sand areas, and the central tabuleiro forest, according to Thomas (2003). The regional climate according to the Koppen classification is hot and moist, without a distinct dry season (Gouvêa, 1969). The mean annual temperature ranges from 23.0 to 24.4 °C, and the average rainfall ranges from 1072 to 1656 mm year^{-1} (WorldClim database; Hijmans et al., 2005). The dominant natural vegetation is classified as a Tropical Lowland Rainforest, which is characterized by a clear vertical stratification in the understory, a canopy (trees 25–30 m high) and emergent layers (trees reaching up to 40 m) (Faria et al., 2009; Thomas et al., 1998). Southern Bahia has one of the highest diversities of wood species in the world (Martini et al., 2007; Thomas et al., 1998).

2.2. Sampling design

The sample site selection was based on the mapping of satellite images (RapidEye from 2009 to 2010, QuickBird and World View from 2009 to 2011). The mapping was performed by manually digitizing the land cover features as visually interpreted at a scale of 1:10,000, which is adequate for identifying patches based on differences in color, texture, and shape.

After intensive ground-truthing, we mapped the vegetation and land use over an area of 3500 km^2. Based on this mapping and on field investigations, we identified 58 potential sampling sites that are located in the forest remnants and surrounded by different amounts of native forest. We performed a stratified sampling of 40 selected sites, maintaining the maximum variation in the amount of forest in the landscape (Fig. 1).

2.3. Vegetation structure

We established 155 sampling plots of 20 $\times$ 4 m in 39 forest sites (4 plots/site, except one site with 3 plots) and 105 extra sampling plots of 25 $\times$ 4 m in 21 forest (5 plots/site), covering 2.29 ha. These extra plots were collected in a different vegetation study occurring during our own study and were installed in a subset of 20 forest sites included in the range of our previous 39 sites, and uniformly distributed along the gradient of forest cover. The mean sampled area at each site was 572 $\pm$ 252 m^2 (mean $\pm$ SD). Because of the different sample sizes, prior to the analyses we performed linear regressions without the inclusion of the 5 extra plots and the patterns found were maintained. Therefore we opt to include the extra plots to increase sample size and model adjustments. Sampling plots were placed in the center of each site to minimize the edge effects, maintaining a minimum distance of 50 m between plots. Within each plot, we counted and measured the diameter at breast height (DBH) and the heights of all trees with a DBH ≥ 5 cm and with the main trunk totally or partially located within the plot area. We measured the foliage vertical stratification profile by using a technique adapted from Malcolm (1995). The vertical profiles were recorded in three points that were randomly located within each plot by estimating the length (cm) occupied by foliage in an imaginary vertical line in six forest strata (each 5 m interval until 30 m height; see Faria et al. (2009) for further details). We used the mean length value occupied by foliage in each stratum for later analyses. We also estimated the percentage of canopy openness inside the vegetation plots by using hemispherical photographs (Nikon Coolpix4300 digital camera equipped with hemispherical fish-eye lens). Photographs were taken 1.5 m from the ground and analyzed with GLA Gap Light Analyzer software.