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Forest loss increases insect herbivory levels in human-altered landscapes

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A B S T R A C T

Insect herbivory has been observed to be affected by habitat loss and fragmentation, although the mechanisms by which these anthropogenic disturbances affect this process are not well understood. To aid in clarifying this issue, we assessed the relation between forest cover and leaf damage caused by herbivorous insects on a representative tropical forest understory plant family, the Rubiaceae. We measured leaf area loss of Rubiaceae plants in 20 forest sites located in the Brazilian Atlantic forest, and also tested whether variation in forest cover, abundance of insectivorous birds (predators) and of Rubiaceae plants (resources) could explain the observed variation in leaf damage. Herbivory levels varied between 2.6 and 12.5 percent leaf area lost and increased with decreasing forest cover, whereas the other explanatory variables did not provide additional explanatory power. Therefore, forest loss appears to be the main driver of changes in local herbivory, and ecological processes such as top-down and bottom-up control may not account for the deforestation-related increase in herbivory levels. Other mechanisms, for example leaf quality and/or the influence of the adjoining land uses, have to be explored in future studies.

1. Introduction

Humans have already modified a major portion of the planet (Ellis, 2011), resulting in unprecedented rates of species extinction (Säterberg et al., 2013). Habitat loss is a major human driver triggering species loss, with particularly severe impacts in tropical forests where most of the world's biota is concentrated (Fahrig, 1997). Today a large part of biodiversity is located in human-altered landscapes, with 70 percent of forests worldwide located within 1 km or less from an anthropogenic edge (Haddad et al., 2015). In addition to the massive conversion of natural habitats, the structure and composition of landscapes have also been changed, with the fragmentation of a previously continuous habitat resulting in more and smaller patches, with more edge-affected habitats and decreased connectivity among the patches. As a result, biodiversity patterns have been reassembled, including novel combinations of species and different abundance arrangements (McKinney and Lockwood, 1999; Tabarelli et al., 2010). Such shifts in community structure cause the disruption of ecological interactions, some of which have the potential to affect ecosystem properties and functioning (Cardinale et al., 2012; De Coster et al., 2015; Mitchell et al., 2015; Valiente-Banuet et al., 2015).

Insect herbivory is an ecological interaction that plays a key role in ecosystem functioning, affecting growth and survival both of insect (Wirth et al., 2008) and plant species (Duwyn and MacDougall, 2015) and possibly modifying plant community composition (Coley, 1983; Hulme, 1996). Thus, this ecological process is a key driver of forest ecosystem functioning: as leaf consumption by herbivores affects tree growth, it will start negatively affecting tree health and fecundity, inhibiting regeneration and modifying ecosystem structure (Wirth et al., 2008; Allan and Crawley, 2011). A recent global analysis indicated that habitat loss and its consequent fragmentation lead to a widespread disruption of this trophic interaction, although the observed effects are largely species and context-dependent (Martinson and Fagan, 2014). Indeed, studies have shown that herbivory levels can be positively

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(Arnold and Asquith, 2002; Elzinga et al., 2005) or negatively affected by fragmentation (Fáveri et al., 2008). However, no changes in herbivory levels in human-altered landscapes were also reported in other studies (De la Vega et al., 2012; Souza et al., 2013; Peter et al., 2014). For example, herbivory may increase near habitat edges (Urbas et al., 2007; Guimarães et al., 2014), but such patterns are not consistent (Benítez-Malvido and Lemus-Albor, 2005) and depend, among other things, on the nature of herbivory (Rosetti et al., 2014) and on the plant species considered (Fáveri et al., 2008). On the other hand, whereas forest fragmentation has been also observed to reduce herbivory levels in tropical (Fáveri et al., 2008; Ruiz-Guerra et al., 2010; De la Vega et al., 2012) and temperate (Valladares et al., 2006) forests, some studies detected no relation between herbivory levels and patch size (Souza et al., 2013; Maguire et al., 2015). Different relationships between insect herbivory patterns and habitat fragmentation suggest that multiple proximate mechanisms may be needed to explain these patterns (Martinson and Fagan, 2014).

Among the main mechanisms known to influence insect herbivore populations and consequently herbivory patterns are bottom-up and top-down controls, which are associated with the relative importance of plant resources and predators, respectively (Säterberg et al., 2013). The abundance and composition of both predators and plant resources are often changed in human-altered landscapes (Foley et al., 2005). Regarding top-down controls, decades of studies have shown that potential predators of herbivorous insects such as birds, especially the most specialized species, can have their diversity reduced in fragmented landscapes (see Ferraz et al., 2012; Morante-Filho et al., 2016). Indeed, the loss of species or significant decreases in local abundances of insectivorous birds is known to trigger trophic cascades, in which the loss of predatory birds leads to an increase of herbivore populations, hence increasing herbivory levels (Van Bael et al., 2003; Peter et al., 2015).

Habitat loss and fragmentation can also influence bottom-up effects by changing the plant (resource) availability and distribution (Urbas et al., 2007). The increasing number of small patches and edge-forest habitats in fragmented landscapes tend to be dominated by pioneer and generalist plants, with a concomitant decreasing representation of those plants typical of undisturbed forest (Laurance et al., 2006). Release from resource limitation and dietary restrictions at forest edges may favor generalist herbivores such as leaf-cutting ants (Urbas et al., 2007; Falcão et al., 2011) and thus increase herbivory. In addition, pioneer plants are characterized by fast-growing and short-lived leaves that offer little protection against herbivores (Coley and Barone, 1996). In contrast, low levels of herbivory on forest-specialist plants such as shade tolerant species can be expected due to low resource availability for specialist herbivores (Guimarães et al., 2014). Thus, given the complex nature of the plant-insect trophic interactions and the interplay among different variables known to affect herbivory levels, there is a dire need to unravel the relative importance of proximate causes determining herbivory levels in human-altered landscapes.

To contribute to this discussion, we assessed how landscape-scale forest cover affects insect herbivory levels, exploring potential proximate causes influencing the observed pattern. The study was conducted in forest patches within the Brazilian Atlantic forest, a biome with outstanding levels of species richness and endemics (Mittermeier et al., 1999). Herbivory was measured on a selected group of highly diverse, understory, shade-tolerant species characteristic of the native tropical forests, the Rubiaceae family (Chiquieri et al., 2004). Previous knowledge of biodiversity patterns has shown that Rubiaceae species are sensitive to landscape-scale forest loss (Andrade et al., 2015), with a significant decrease in species richness and abundance in patches located in more deforested landscapes. Many Rubiaceae species are known to contain high levels of alkaloid and quinines in their leaves, a situation likely to narrow the range of potential herbivores to those more specialized (Wink, 1992). In this study we use Rubiaceae plants found in the Brazilian Atlantic forest to assess how top-down and bottom-up effect associated with forest fragmentation may influence their associated herbivory levels.

In particular, we assessed (1) how predators (insectivorous birds) and resource availability (abundance of Rubiaceae plants) vary with forest cover reduction, (2) whether and how herbivory levels are related to the amount of remaining forest on the landscape scale, and (3) if such herbivory levels can also be explained by the variation in the abundance of predators and plant resource, representing top-down and bottom-up control, respectively. As many species from the family Rubiaceae are known to contain high levels of alkaloid and quinines in their leaves (Wink, 1992), based on the bottom-up hypothesis we would expect that a decrease in plant resources may lead to a decreased local abundance of more specialized herbivores and, consequently, lower herbivory levels. Conversely, forest cover loss has been shown to lead to a local decrease in species diversity of insectivorous birds (Morante-Filho et al., 2015), which could relax the top-down control of insects, ultimately resulting in higher herbivory levels (Sanz, 2001). If bottom-up control is predominant, a decrease in herbivory would be expected in more deforested landscapes due to a decrease in plant resource abundance, whereas the opposite pattern would be expected if top-down control is more important. Alternatively, we also explore whether these factors combine to determine herbivory levels by examining their potential interaction effects.

2. Methods

2.1. Study sites

We performed this study in Atlantic forest patches in southern Bahia, North-eastern Brazil, a region originally covered by lowland wet forest. These forests are characterized by a clear stratification into lower, canopy and emergent layers, abundant epiphytes, ferns, bromeliads and lianas, and a great diversity and high level of endemism of tree species (Thomas et al., 1998). Average annual temperature is 24 °C and mean annual precipitation is 2000 mm, with no marked seasonality (Mori et al., 1983).

Using recent satellite images (QuickBird and WorldView, from 2011; RapidEye, from 2009 to 2010) and an intense process of ground-truthing, we mapped the land-use of 3500 km^2 of the region including the municipalities of Belmonte, Una, Santa Luzia and Mascote (15° 28′S and 39° 15′W). We produced maps on a 1:10 000 scale, which is adequate for identifying land cover patches based on the visual inspection of differences in color, texture, shape, location, and context. This region contains a representative amount of forest tracts, which occupy nearly 80 percent of the landscape and all of which have similar soil, topography, and floristic composition (Fig. 1). The predominant matrix is pasture, corresponding to almost 80 percent of the non-forested area, followed by shade cacao plantations, eucalypt and rubber tree plantations, and agriculture, which together account for another 15 percent of the non-forest cover.

2.2. Site selection and estimates of forest cover

We randomly selected 20 forest sites within the region to conduct our surveys (see details in Morante-Filho et al., 2015). We adopted the sample site-landscape approach (Fahrig, 2013), in which the response variables were evaluated within each forest site and landscape attributes were measured within a specific area