



## Research paper

# Deforestation drives functional diversity and fruit quality changes in a tropical tree assemblage



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## ABSTRACT

Functional traits associated with plant-animal interactions are essential for forest functionality, given that a higher diversity of fruit traits is likely to maintain a more diverse assemblage of frugivores and consequently promote the seed dispersal function. Yet, shade-intolerant species tend to persist in human-modified landscapes in the long term, which in turn is expected to reduce fruit trait diversity. Here we evaluate how forest cover at the landscape-scale influences the functional diversity of fruit traits, considering the zoochoric tree community and two regeneration strategies separately (shade-tolerant and shade-intolerant species). We sampled 20 forest remnants in the Brazilian Atlantic Forest, located in landscapes with forest cover ranging from 2 to 93%. In each remnant, we established five plots of 25 × 4 m and marked all trees ≥ 5 cm diameter at breast height (DBH). We compared morphological and chemical attributes of fleshy fruits directly related to the attraction of frugivores, and evaluated the similarity of the zoochoric tree assemblage composition along the forest cover gradient, taking into account the two regeneration strategies. We calculated four functional indices (richness, evenness, divergence, and community-level weighted means of trait values) and used either linear models or spatial mixed linear models to evaluate the effects of forest cover on functional diversity. Our main results revealed that forest cover loss has negatively affected fruit functional diversity for the overall zoochoric community. Forest cover loss also affected functional richness and functional evenness for total and shade-tolerant species, and was positively correlated with the content of protein and lipid in fruits of shade-intolerant species. Additionally, sites exhibiting a lower amount of forest cover showed greater compositional similarity among shade-intolerant species but reduced similarity among shade-tolerant species. We conclude that patterns of species reassembly triggered by landscape-scale deforestation decreases the capacity of the remaining forest for provisioning food resources for frugivore assemblages. The maintenance of shade-tolerant species is pivotal in deforested areas, since their fruit quality is not offset by shade-intolerant species. This is particularly important, mainly because shade-intolerant species are those still persisting in disturbed forests; however, their presence will not provide the same food quality supplied by those species lost.

## 1. Introduction

Habitat loss and fragmentation are considered the major drivers of species extinction rates in tropical forests, becoming a great challenge for biodiversity conservation (Fahrig, 2013; Hanski, 2015). The conversion of once large tracts of continuous forests mainly to agriculture and pasture, in addition to selective logging, hunting, and other human disturbances, seriously threatens natural habitats and consequently affects the persistence of native species of fauna and flora (Rudel et al.,

2009; Canale et al., 2012). A great number of studies has assessed the effects of habitat loss and fragmentation on species diversity in tropical forests (Pardini et al., 2010; Laurance et al., 2011; Arroyo-Rodríguez et al., 2013; Morante-Filho et al., 2015). Thus, understanding the influence of species loss on species interactions and ecosystems services is critical for conservation actions (Dobson et al., 2006; Valiente-Banuet et al., 2015).

Tree assemblages play key roles in forest ecosystem structure and functioning, yet they are facing unanticipated changes in human-

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modified landscapes (Laurance et al., 2000; Girão et al., 2007; Santos et al., 2008). Empirical evidence suggests non-random floristic transitions, in which sensitive species such as emergent, shade-tolerant, and large-seeded trees are more likely to be reduced in fragmented forest landscapes (Silva and Tabarelli, 2000; Benchimol and Peres, 2015), whereas generalist and disturbance-loving pioneer species become dominant (Tabarelli et al., 2012). Anthropogenic disturbances, including overhunting, fire and intensive logging, are likely to synergistically interact with forest fragmentation, inducing a turnover in floristic species composition (Michalski et al., 2007; Benchimol and Peres, 2015). Patterns of species replacement in highly disturbed forests seem to be dominated by small-seeded, light-wooded, fast-growing, and short-living trees, a phenomenon termed floristic homogenization (i.e. reduced beta-diversity or increased species similarity) (Lôbo et al., 2011; Poulsen et al., 2013). The traits of the newcomers greatly favor the dispersal of their seeds, which in turn may accelerate forest dynamics and reduce carbon stocks (Bello et al., 2015; Peres et al., 2015). In fact, biodiversity erosion can lead to higher vulnerability of specific functional groups of plants and animals, and induce the loss of whole groups (Elmqvist et al., 2003; Cardinale et al., 2012). Thus, drastic changes in specific functional traits can functionally affect forest dynamics (Tilman et al., 1997; Banks-Leite et al., 2014).

Changes in functional attributes experienced by tree assemblages in tropical forests might affect resource availability for frugivorous species (Aizen and Feinsinger, 1994; Laurance et al., 2003). Non-random patterns of fruit consumption suggest a phenotypic selection of fruit traits associated with seed dispersal (Jordano, 1995; Lomáscolo et al., 2010; Sobral et al., 2010). For instance, fruit traits such as morphology and nutritional contents are important to attract a variety of frugivorous animals and are directly related to seed dispersal (Gautier-Hion et al., 1985; Jordano, 2000; Galetti et al., 2011). Additionally, variation in fruit size has important implications for the evolution of plant-animal interactions, determining which species are able to consume and disperse seeds (Wotton and Kelly, 2011). Furthermore, the selection of fruits with high pulp-to-seed ratios are responsible for evolutionary selection pressures towards large amounts of pulp (Blendinger et al., 2016).

Functional traits associated with plant-animal interactions might be essential for forest functionality (Fontaine et al., 2006; Girão et al., 2007). This is because a higher diversity of fruit traits may sustain a more diverse assemblage of frugivores (Pizo, 2002; Galetti et al., 2011), thus maintaining the evolutionary links between plants and the potential dispersal vectors, ultimately influencing the colonization patterns in forest patches (Duarte et al., 2011). However, long-term species persistence in human-modified landscapes is biased towards a smaller subset of disturbance-adapted assemblages (Tabarelli et al., 2012), ultimately leading to floristic homogenization (Arroyo-Rodríguez et al., 2013) and reduced phylogenetic diversity (Santos et al., 2014; Andrade et al., 2015). Consequently, fruit trait diversity might also be reduced in those anthropogenic landscapes. However, studies assessing functional diversity based on fruit traits in disturbed habitats have mostly focused on fruit morphology, mainly fruit and seed size (Mayfield et al., 2006; Flynn et al., 2009; Magnago et al., 2014) or seed mass (Laliberté et al., 2010; Benchimol and Peres, 2015), overlooking other crucial traits related to frugivorous attraction such as fruit nutritional contents.

Here, we test the hypothesis that forest cover reduction at the landscape-scale alters fruit traits related to frugivorous attraction, inside the forest remnants. For this, we calculate the functional diversity of fleshy fruit traits in 20 remnants of the Brazilian Atlantic Forest hotspot, considering both the overall zoochoric tree community and two regeneration strategy types (shade-tolerant and shade-intolerant species). We first compared the distribution of each specific fruit trait and tree species composition between both regeneration strategy types, and thus examined their responses to forest cover reduction. Previous studies on the same landscapes showed a decrease in richness and abundance of the overall tree community (Rocha-Santos et al., 2017),

mainly due to the decrease of shade-tolerant species (Pessoa et al., 2017). We further assessed whether the changes in tree diversity resulting from forest cover loss are leading to modifications in the functional diversity of fleshy fruits. Specifically, we predicted that (1) shade-tolerant and shade-intolerant species may diverge in their responses to forest loss, given their distinct vulnerability to human disturbances (Püttker et al., 2015); (2) highly deforested areas may exhibit stronger changes in morphological and nutritional resources, including an increased dominance of small-fruit species containing small seeds and exhibiting poor nutritional contents (Moermond and Denslow, 1985; Silva and Tabarelli, 2000; Tabarelli and Peres, 2002); and (3) the loss of shade-tolerant species in highly deforested areas may affect functional diversity, compromising the resources available for frugivorous species.

## 2. Materials and methods

### 2.1. Study area

The present study was conducted in 20 forest remnants of the Brazilian Atlantic Forest in southern Bahia between 15°0′–16°0′S, 39°0′–39°30′W (Fig. 1), embedded within different land-use matrices, such as pasture, agricultural lands, and forestry uses like shade-plantations of cacao (*Theobroma cacao*), rubber trees (*Hevea brasiliensis*), or *Eucalyptus* sp. Because it contains a significant fraction of the overall biological diversity of Brazil, including high levels of endemism, richness and the occurrence of rare species, the region is currently considered one of the world's 35 biodiversity hotspot (Martini et al., 2007). The region is classified as Southern Bahian Wet Forest, and mostly exhibit a structure of tropical forests, with an emergent canopy, sub-canopy and herbaceous layers (Thomas et al., 1998). The study area is located between the Jequitinhonha and the Contas rivers, where forest remnants exhibit similar soil types, topography, and floristic composition (Thomas et al., 1998; Thomas, 2003). Deforestation in this region occurred at about the same time, starting in the mid 1980s, increasing during the cocoa crisis of the 1990s (Rocha-Santos et al., 2017). The regional climate, according to Köppen classification, is the type Af, hot and humid without a dry season (Gouvêa, 1969). The average annual temperature is 24 °C and the mean annual precipitation is 2000 mm, classified as weakly seasonal, and the elevation ranges from 100 to 350 m (Thomas et al., 1998).

We adopted a hybrid patch-landscape approach (Tischendorf and Fahrig, 2000) and undertook the sample site selection based on high-resolution satellite images (RapidEye from 2009 to 2010, QuickBird and World View from 2009 to 2011). We mapped land-use by manually digitizing 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 validation, we mapped the vegetation and land-use over an area of 3470 km<sup>2</sup>, including the municipalities of Una, Canavieiras, Mascote and Belmonte. We excluded demanding access, indigenous lands and highly mountainous forest sites. The remnants were at least 1 km distant from each other to reduce overlapping among remnants. A previous study at the same studied sites tested the effect of forest cover on tree diversity at those different spatial scales, and showed that trees best responded to the effects of habitat (i.e., exhibited higher amount of variation explained) at 1000 m (Rocha-Santos et al., 2017). Based on this mapping and on field investigations, we identified 48 potential remnants surrounded by different amounts of native forest cover, and ended up with 20 remnants in landscapes showing a wide gradient of forest cover from 2 to 93% (Fig. 1). Sample sites were at least in medium to advanced stages of secondary succession and were variable in size, but only forest sites larger than 3 ha were included.

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