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Research Letters

Habitat fragmentation narrows the distribution of avian functional traits associated with seed dispersal in tropical forest

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A B S T R A C T

Land-use change influences biodiversity in non-random ways, affecting some species and functional groups more than others, with potential implications for the loss or degradation of important ecological processes, such as seed dispersal. Here we investigate the effect of patch-size reduction on the composition and functional richness (FRic) of avian communities in Atlantic Forest fragments, focusing on morphological traits associated with seed dispersal in frugivorous birds. We found that FRic of three key traits—hand-wing index, body mass and gape width—decreased with patch size reduction, because species with larger values for morphological traits were lost through local extinction. The relative absence of large-gaped and more-dispersive frugivores in small forest fragments has important implications because these species play a pivotal role in seed dispersal, carrying higher seed loads for longer distances, and consuming larger-sized seeds that cannot be dispersed by smaller-gaped frugivores. Our results highlight the importance of preserving large or interconnected habitat patches, and promoting habitat restoration of cleared areas, to ensure that sufficient avian functional diversity is maintained to supply the full range of seed dispersal services required by tropical forests, both currently and in future.

Introduction

The conversion of tropical forests to anthropogenic land uses is driving the rapid loss and fragmentation of natural habitat into smaller patches, with deleterious consequences for biodiversity (Laurance et al., 2014; Taubert et al., 2018). However, the effects are non-random because species vary widely in their responses to habitat fragmentation, with negative impacts increasing for large, forest-dependent or dispersal limited species (Bregman et al., 2014; Coelho et al., 2016). A combination of area effects and edge effects (Pfeifer et al., 2017), as well as changes in physical conditions of the forest fragments and their surroundings, determine which species are able to survive and colonize those modified areas (Magnago et al., 2015). Because the sensitivity of species to land-use change is influenced by their traits (Burivalova et al., 2015), habitat fragmentation does not merely affect species richness, but also the structure, composition and functional diversity of species assemblages (Uezu and Metzger, 2011; Magioli et al., 2015; Bregman et al., 2016). However, the implications for ecological processes remain poorly understood.

Recent studies have reported a decrease in the functional integrity of bird communities, and the abundance of their constituent species, in tropical forests (De Coster et al., 2015; Coelho et al., 2016). In particular, species with particular ecological and physical traits, such as large body mass and frugivory, are often

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the most impacted (Galetti et al., 2013; Burivalova et al., 2015). A range of mechanisms may increase local extinction of these traits in small habitat patches, including low population density, large area requirements, and reduced likelihood of recolonization for larger species (Tobias et al., 2013), as well as hunting and interspecific competition for food resources, both of which can significantly increase in forest fragments (Bregman et al., 2015, 2016).

Non-random extinctions mediated by body size and dietary niche have important implications for ecological processes (Burivalova et al., 2015; Bregman et al., 2016). In particular, the loss of frugivorous species from tropical forests is potentially disastrous because more than 90% of woody plant species are dispersed by animals (zoocoric; Jordano, 2016), with birds particularly important, especially when other large vertebrates have been extirpated (Holbrook et al., 2002). Moreover, the long-term resilience of tropical forests, and their ability to regenerate, relies on the continued presence of frugivores that can transfer seeds from remaining forest into adjacent disturbed habitats (Alexandrino et al., 2016; Pizo, 2007). Yet, we still have only a limited understanding of how land-use change effects the structure and functioning of seed-disperser communities in fragmented tropical forests.

In this investigation, we assess how reduction in forest patch size affects the composition of morphological traits and functional richness of frugivorous bird assemblages. We focused on survey data from forest fragments in the Atlantic Forest of Brazil, an area famed for habitat fragmentation and the consequent loss of biodiversity (Brooks et al., 1999). Given that biodiversity tends to decline in association with habitat patch size in tropical forests (Bregman et al., 2014; Magioli et al., 2015; De Coster et al., 2015), we predict that functional richness of frugivore assemblages will decrease in line with patch size. We also explore the association between habitat patch size and the occurrence of key traits associated with seed dispersal—including beak shape and wing shape—both of which can provide insight into the size of seeds consumed by frugivores and the distance seeds are likely to be dispersed (see Bregman et al., 2016; Pigot et al., 2016).

Material and methods

Study area

We focused on the southeastern sector of the Brazilian Atlantic Forest, a region that has undergone dramatic human-modification such that only ca. 12% of the original forested habitat remains, much of which is divided into forest fragments smaller than 50 ha (Ribeiro et al., 2009). The Atlantic Forest as a whole is a biodiversity hotspot supporting approximately 688 bird species, of which ~30% are endemic (Goerck, 1997). Many regional bird species have been negatively affected or even extirpated by forest loss and fragmentation (Brooks et al., 1999; Pereira et al., 2014).

Bird assemblage database

We created a database of bird assemblages using data collected through field surveys of Atlantic Forest habitat patches between 1990 and 2014. We searched for indexed papers on Web of Science, Google Scholar and SciELO, and also used online search engines to look for relevant gray literature including non-indexed papers, management plans of protected areas, theses, dissertations and monographs. We searched in English using the following keywords (bird* OR avian) AND (Atlantic Forest OR forest OR fragment OR remnant OR community*). We also conducted the same searches translated into Portuguese. Any study restricted to a particular subset of the bird community, whether defined by ecology (e.g. understory species) or taxonomic groups (e.g. Passeriformes), were discarded. Because we are concerned with the impacts of fragmentation on seed dispersal in tropical forests, we restricted our dataset to species that were both frugivorous and forest-dependent. Frugivores were classified as species with >10% of their diet consisting of fruit, berries and seeds (Wilman et al., 2014), since species classified as omnivorous can act as important seed dispersers in modified areas (Pizo, 2007). Seed predators such as Tinamidae and Psittacidae were excluded, following Bregman et al. (2014). Forest-dependent species were classified based on Parker et al. (1996).

The final dataset contained a total of 33 studies supporting a total complement of 157 frugivorous forest-dependent bird species (see supplementary data 1, supplementary data 2, Table S1). This produced data on frugivore assemblages in 48 areas, covering a wide gradient of latitude (19°28′–29°28′ S), longitude (40°32′–53°47′ W), elevation (30–1059 masl), and patch sizes (mean = 6169 ha [2.59–185,000 ha]; Fig. 1). Many of our assemblages are directly related to surveys in habitat fragments whereas other surveys were conducted in forests embedded in a non-habitat agricultural matrix (i.e., sugarcane and pasture) as forest patches. Some of our study sites (indicated in supplementary data 1) lie within the Serra do Mar forest continuum, the largest remnant of the Atlantic Forest (>1,000,000 ha overall, but subdivided by roads and associated habitat clearance). In these cases, the size of study plots does not represent the actual patch size of the forest, so we assigned an arbitrary patch size of 500,000 ha, following Ribeiro et al. (2009).

Morphological traits

We collected data on four biometric traits – body mass, gape width, wing length, and first-secondary length (supplementary data 2, Table S2) – each capturing different dimensions of the ecological niche related to seed dispersal. Body mass is a standard ecological trait and at least partly reflects the amount of fruits that can be consumed, and seeds dispersed, by frugivorous organisms (Jordano and Schupp, 2000). Gape width provides an estimate of the upper limit to seed size that can be swallowed and, consequently, dispersed by a bird (Wheelwright, 1985). Wing length (WL) and first-secondary length (FSL) in combination provide an estimate of wing shape related to dispersal (Dawideit et al., 2009). Specifically, following Claramunt et al. (2012), we calculated hand-wing index (HWI) using the equation $HWI = 100 \times (WL - FSL)/WL$, where WL is the distance from the carpal joint to the tip of the longest primary feather, and FSL is the distance from the carpal joint to the tip of the first secondary feather. HWI is a standard index of flight and dispersal ability in birds, and thus potentially reflects the potential for long-distance seed dispersal, which in turn is crucial role for metacommunity dynamics and seed dispersal in fragmented forests (Hamilton, 1999).

We compiled body mass data for all study species based on published literature (Dunning, 2007; Wilman et al., 2014). The other three biometric traits were measured from specimens at several museum collections, including the Natural History Museum, Tring, UK, and in the Zoology Museum of University of São Paulo, Brazil. When possible, we measured four adult individuals of each species (two males and two females), and used average values at species level in our analyses. In total, we compiled a complete dataset of four biometric traits for all bird species in our sample. We note that HWI was only very weakly associated with body mass (Pearson's correlation: $r = -0.01$) and gape width ($r = -0.12$), while gape width was partially correlated with body mass ($r = 0.48$).