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Research Letters

Matrix and area effects on the nutritional condition of understory birds in Amazonian rainforest fragments

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ABSTRACT

Forest fragmentation, a result of deforestation, not only decreases the amount of habitat available for wildlife, but also increases the isolation of the remaining fragments and the area of edges surrounding them. Also, deforestation often leads to the creation of a dynamic regenerating matrix where cleared land is subsequently abandoned. Here we examine the effects of fragmentation and landscape change on the nutritional condition of Amazonian rainforest birds at the Biological Dynamics of Forest Fragments Project, near Manaus, Brazil. We analyzed ptilochronology-based measurements of feather growth rate in 12 species living in fragments within a dynamic landscape over 21 years. Ptilochronology serves as an index of nutritional condition by revealing energy available for maintenance over 1–2 weeks while the feather is grown, allowing intraspecific comparison across treatments. Feather growth rate decreased in fragments surrounded by young second-growth borders but increased as fragment size and age of adjacent second-growth vegetation increased. Results from this simple, yet informative, measure of nutritional condition reveal physiological impacts of land cover change, including the response of birds to changes occurring at both local and landscape levels. Our results highlight the importance of looking beyond presence/absence data to describe fragmentation effects, and support the value of landscape-scale approaches for the conservation of tropical forest biodiversity.

Introduction

Habitat loss and degradation rank among the most significant threats to global biodiversity (Barlow et al., 2016; Foley et al., 2005). Habitat loss often leads to fragmentation, which not only decreases the amount of habitat available for wild species, but at the same time increases the isolation of the remaining fragments, as well as the amount of edges around them (Kupfer et al., 2006; Lindenmayer and Fischer, 2006). Although evidence suggests the effects of fragmentation per se are not always as negative as previously thought (Fahrig, 2017), long-term experiments of habitat fragmentation demonstrate that reduced area, increased isolation, and increased proportion of edge habitat all have important negative implications on biodiversity and ecological processes (Haddad et al., 2015).

Following fragmentation, normal abiotic conditions are significantly altered, especially at or near edges (Haddad et al., 2015; Harper et al., 2005; Lindenmayer and Fischer, 2006; Lovejoy et al., 1986; Murcia, 1995). Physical conditions near edges are typically hotter and drier than in forest interiors, which can affect forest structure, alter food resources and favor non-forest species (Haddad et al., 2015; Lovejoy et al., 1986; Murcia, 1995; Pfeifer et al., 2017; Saunders et al., 1991). Similarly, invasive species, predators, and brood parasites can all be attracted to edges, altering species interactions (Murcia, 1995; Saunders et al., 1991; Stratford and Robinson, 2005). The size of a fragment is also an important feature affecting the establishment of territories and significantly reducing the number of individuals that can share a single fragment (Johnson et al., 2011; Stratford and Robinson, 2005). Additionally, as the area of a given fragment decreases, so does the amount of core habitat that is unaffected by the surrounding environment (Gascon et al., 2000; Haddad et al., 2015; Kupfer et al., 2006). Fragment shape,

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position in the landscape, and connectivity to other fragments also play an important role affecting within-fragment dynamics, highlighting the importance of landscape-scale approaches to understanding the effects of habitat fragmentation (Haddad et al., 2015; Laurance, 2008).

Consequently, even when birds are able to persist in fragments they may still suffer from alterations that reduce habitat quality (Barlow et al., 2016). Because of this, forest fragments are often lacking sensitive species that cannot tolerate area or edge effects (Stratford and Stouffer, 1999). Nonetheless, certain species can persist in fragments, although they may be affected in subtle but important ways that can ultimately affect their long-term fitness and survival (Fahrig, 1997). For this reason, it is important to move beyond simply noting presence or absence of a particular species in fragments in favor of revealing processes involved in long-term persistence, including breeding success, survival, and physical condition (Johnson, 2007).

Feathers serve a variety of vital functions in the lives of birds; they are essential for body insulation, flight performance, and social communication (Stettenheim, 1976). Because of their importance, maintaining a complete, functioning set of feathers is crucial. When feathers are lost or damaged, replacements are rapidly grown, and natural selection is thought to favor the expenditure of energy and nutrients for high-quality feathers (Dawson et al., 2000). However, feathers are costly structures, made up of more than 90% protein which, depending on the species, can be up to 12% of an individual's body mass (Murphy, 1996). Therefore, both the rate of feather growth and the amount of material put into each feather can be adjusted to compensate for reduced resources or energetic demands of other activities (Grubb, 1989, 2006; Murphy et al., 1988).

Feathers are composed of alternating dark and light growth bars, with a pair of dark-light bars corresponding to a 24-hour period of feather growth (Michener and Michener, 1938). The measurement of growth bars, a technique known as ptilochronology (Grubb, 1989), has been used as an indirect measure of the nutritional condition of birds during the period of feather growth. Under good conditions, birds grow their feathers faster, which results in wider growth bars; under adverse conditions, feather growth can be reduced, resulting in narrower growth bars (Grubb, 1989, 2006). Consequently, the width of growth bars on feathers gives a day-by-day record of the nutritional regime under which a bird has lived, providing information about the bird's nutritional condition and the quality of its habitat. Since the discovery of ptilochronology as a biomarker, the technique has been applied to various ecological questions, generally giving satisfactory results as a metric of habitat quality (Brown et al., 2002; Grubb, 2006; Strong and Sherry, 2000; Talloen et al., 2008; Vangestel and Lens, 2011; Yosef and Grubb, 1992).

The effects of habitat fragmentation on the nutritional condition of birds were revealed by ptilochronology in two common species at the Biological Dynamics of Forest Fragments Project (BDFFP), the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) and the White-crowned Manakin (*Dixiphia pipra*). Stratford and Stouffer (2001) showed that although these birds might not have significant long-term changes in their abundance, they may still suffer the physiological consequences related to fragment size. A few years later, Stouffer et al. (2006) highlighted how landscape change, especially second-growth regeneration along edges and in the matrix, positively affected bird abundance and recolonization of previously isolated fragments. Understory birds at the same site also increasingly used fragment edges as second-growth vegetation developed over 12–30 years, although with considerable differences among bird guilds (Powell et al., 2013).

In light of the important effects of the landscape on processes occurring inside the fragments, we wanted to understand the role of edge and matrix second-growth vegetation on the nutritional condition of birds in forest fragments. We measured feather growth rate in 12 species of birds living in fragments within a dynamic landscape over 21 years at the BDFFP. We expected to find lower nutritional condition in birds from smaller fragments compared to larger fragments and continuous forest. We also expected to see reduced nutritional condition in fragments surrounded by young vegetation at their edges (hereafter border), or in the matrix (hereafter second-growth), but we hypothesized that negative effect to be lost as this vegetation matured.

Methods

Study area

The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP) study area, in central Amazonia, approximately 80 km north of Manaus, Brazil. The BDFFP is the world's largest-scale and longest running study of habitat fragmentation. The current landscape consists of a mix of eleven forest fragments of different sizes (five 1 ha, four 10 ha, and two 100 ha), surrounded by second growth forest at different stages of regeneration, embedded in a primary *terra firme* forest that extents for hundreds of kilometers to the north, east, and west (Gascon and Bierregaard, 2001). Forest fragments were isolated in the early 1980s (except one isolated by 1991), and vegetation around them has been periodically cut to maintain fragment isolation. The study area corresponds to a lowland tropical moist forest (50–100 m elevation), with temperatures ranging from 19 to 39 °C, and total annual rainfall from about 1900 to 2500 mm (Gascon and Bierregaard, 2001; Laurance, 2001). Precipitation is common in every month, however there is a distinct dry season between June and October (Gascon and Bierregaard, 2001; Laurance, 2001). Day length remains generally constant throughout the year, with the difference in day length between the longest and shortest days of the year being approximately 18 min (De Oliveira and Mori, 1999). Canopy height is about 35–40 m, with emergent trees sometimes exceeding 50 m (Gascon and Bierregaard, 2001).

Bird sampling and feather collection

Birds were captured using mist nets (NEBBA type ATX, 36-mm mesh, 12 × 2 m), with the bottom of the nets at ground level. The number of nets varied depending on fragment size. In 1-ha fragments, one line of 8 end-to-end mist nets was used. In the 10-ha fragments, one line of 16 nets was used. Three lines of 16 nets were used in the 100-ha fragments, and four lines of 16 nets were used at the continuous forest sites. Also, three or four sets of 4 mist nets were used along the borders at each of the fragments. Each net lane was sampled for a day at the time, usually at no less than one month intervals, from 0600 to 1400 h.

The outermost right rectrix (R6) was collected from each banded bird and placed in individual paper envelopes. Feathers that were still growing were pulled if a minimum of ten consecutive growth bars were visible. Feather samples come from this systematic sampling of all fragments that has taken place in discrete time intervals: 1991–1992, 2000–2001, and 2007–2012. We included feathers from 12 species that belong to six different foraging guilds and differ in their sensitivity to fragmentation and landscape change, based on previous research at the BDFFP (Table 1). Sample size limited the species we could analyze; we only included species with feathers collected in every fragment size and time interval.