



Effects of forest disturbance and habitat loss on avian communities in a Neotropical biodiversity hotspot



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ABSTRACT

Regenerating forests are increasingly ubiquitous in tropical landscapes. They hold great conservation potential and there is demand for assessments of their biodiversity value. Forest disturbance and forest loss often occur together, yet few studies attempt to disentangle their separate effects on biological communities. In the Ecuadorian Chocó, a biodiversity hotspot, we sampled understory birds in patches with increasing levels of disturbance (old-growth, selectively-logged, and secondary forests) within contiguous forest and in fragments. Species richness increased with disturbance but decreased with habitat loss, with a 75% reduction in endemic and threatened species in fragments compared to contiguous forest. This reduction in richness was most pronounced in secondary forest fragments, suggesting that disturbance and habitat loss interact synergistically to maximally reduce avian biodiversity. Species composition was strongly affected by habitat loss and, to a lesser extent, disturbance, with forest fragments and secondary forests presenting distinct communities dominated by generalists with medium-to-low sensitivity to anthropogenic disturbance and reduced proportions of endemics and endangered species. Capture rates also decreased (non-significantly) with habitat loss, and the relative abundance of dietary guilds varied in response to both habitat loss and disturbance. Our study shows that regenerating patches surrounded by contiguous forest can sustain high biodiversity levels and, when past habitat disturbance is mild, present similar communities to old-growth forests. In contrast, forest loss caused reductions in richness (especially in more disturbed patches), profound changes in community composition, and loss of species of conservation concern. These results underscore the importance of considering landscape context when evaluating the conservation value of disturbed forests.

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1. Introduction

Anthropogenic habitat modification in the tropics has generated intense concern because these regions suffer the highest rates of forest loss, fragmentation, and degradation (FAO, 2010) yet house most described and undescribed species (Joppa et al., 2011). On the other hand, reforestation and natural forest expansion have contributed to a global reduction in net forest loss in the last 20 years (FAO, 2010); e.g., secondary succession was estimated to replace one in every 6–7 ha of tropical forest cleared (Wright, 2005). While this rate does not offset the loss of primary forest, it calls attention to the potential that disturbed forests (here defined as forests that have been impacted by anthropogenic stressors such as fire, selective or extensive logging and are currently in regeneration) may hold for biodiversity and essential ecosystem

services. For example, disturbed forests may serve as species refugia and increase beta-diversity (Dent and Wright, 2009; Edwards et al., 2011), increase landscape connectivity (Stouffer and Bierregaard, 1995), preserve animal-mediated ecosystem processes (Schleuning et al., 2011), and sequester atmospheric carbon (Wright, 2005).

The value of disturbed forests as a conservation asset is vigorously debated (Wright, 2005; Barlow et al., 2007a,b; Dent and Wright, 2009; Didham, 2011; Gibson et al., 2011). Although recent studies have identified significant conservation benefits (Dent and Wright, 2009; Edwards et al., 2011), more information is needed to accurately gauge the conservation value of regenerating forests relative to primary forests. In particular, despite a large recent body of work on the effects of forest loss on biodiversity (reviews by Laurance and Bierregaard, 1997; Ewers and Didham, 2006; Fahrig, 2003), we know surprisingly little about how it interacts with habitat disturbance. Habitat disturbance and habitat loss are often correlated across landscapes (Harrison and Bruna, 1999; Laurance et al., 2002), yet very few studies have formally attempted to

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disentangle their independent and synergistic effects on biological communities or processes (Lees and Peres, 2006; Cornelius, 2008; Peters et al., 2008; Schleuning et al., 2011).

We examined changes in understory bird communities in response to both habitat disturbance and habitat loss (*sensu* Fahrig, 2003) in northwest Ecuador, at a transition zone between the Tumbesian and Chocó biogeographic zones, both characterized by high levels of endemism, diversity, and threat (Orme et al., 2005; Devenish et al., 2009). Birds are well suited for this as they are reliable indicators of broader biodiversity trends (Barlow et al., 2007a). The study took place within the Mache-Chindul Reserve, which contains some of the largest remaining tracts of primary forest in the region, but suffers from historical and ongoing deforestation. Human settlements in the study area consist mainly of small, traditional communities, and despite the presence of indigenous or long-standing (>200 years) populations, most land conversion occurred after the 1980s, with the advent of large immigration waves by mestizo ‘colonos’ (Sierra and Stallings, 1998). Deforestation and logging activities in the study region are largely non-organized and small-scale in nature, carried out by local landowners.

To examine the effects of intensity of habitat disturbance, we compared forest patches in three *habitat types*: (1) OG: old-growth forest, (2) SL: regenerating selectively-logged, and (3) CC: regenerating clear-cut (i.e., secondary) forests. To test for the effect of habitat loss, we compared patches in two *landscape types*: (1) contiguous forest (patches within a matrix of old-growth forest) and (2) fragmented forest (isolated patches within a matrix of pasture/agriculture). We sampled multiple replicates of each habitat type in each of the two landscape types to evaluate the following predictions: (a) richness and capture rates decrease with increasing disturbance (OG > SL > CC forest) and with habitat loss (contiguous forest > fragments); and (b) community similarity to contiguous OG forest (control treatment) decreases with intensity of habitat modification (highest for SL contiguous forest, lowest for CC fragments). In doing so, our broader objective was to assess the relative importance of habitat disturbance versus habitat loss on avian communities. If disturbance is more important, we expect that richness, capture rates, and community similarity will follow the pattern OG contiguous \geq OG fragmented > SL contiguous \geq SL fragmented > CC contiguous \geq CC fragmented. In contrast, if habitat loss is more important, we might expect OG contiguous \geq SL contiguous \geq CC contiguous > OG fragmented \geq SL fragmented \geq CC fragmented.

2. Methods

2.1. Study site

The study was conducted in a ~12000 ha area around Bilsa Biological Station (BBS; 79°45'W, 0°22'N, 330–730 m a.s.l.), a 3500-ha private reserve established in 1994 by Fundación Jatun Sacha and located within the larger Mache-Chindul Reserve (~120000 ha), Esmeraldas and Manabi Provinces, Ecuador (Fig. 1). Mean annual temperature is 23–26 °C; mean annual precipitation is 2000–3000 mm, with a January–June wet season and a July–December dry season, each presenting a peak in avian breeding activity (February–May and October–November; J. Karubian and L. Carrasco, unpublished data). BBS is comprised of a complex matrix of contiguous OG forest inter-digitated with SL or CC forests that were cut 19–30 years ago and abandoned to regenerate naturally. BBS contains some of the last large remnants of premontane wet forest in NW Ecuador and has been identified as critically important for the conservation of this megadiverse ecosystem (BirdLife International and Conservation International, 2005; Devenish et al., 2009). The surrounding areas within the Mache-Chindul Reserve have been extensively deforested for use

in small-scale agriculture and cattle ranching within the last 40 years (Charlat et al., 2000), resulting in a series of forest fragments with varying structural complexity. In this study, we use OG forest within BBS as our control treatment; however, given the size of BBS, it is possible that this site has been impacted by the reduced extent of overall forest in the region, such that extinctions have already occurred and ‘pristine’ avifauna is no longer present (Lees and Peres, 2006). As there is virtually no comprehensive baseline records that pre-date deforestation in this area, we cannot evaluate the extent of these effects.

2.2. Habitat characterization

We established 79 habitat sampling points at 200 m intervals along >15 km of existing trails within contiguous forest, covering ~1/3 of BBS (Fig. 1). Habitat type at each point was classified as OG (44 points), SL (16 points), or CC forest (19 points) based on knowledge of land use history and visual inspection of forest structure (canopy height, size of trees, understory density, etc.). To validate this classification, for each point we recorded the number of medium and large-sized trees (DBH of 10–50 cm within a 10 m-radius plot and with DBH \geq 50 cm within a 20 m-radius plot, respectively), canopy height (estimated visually), percent of canopy cover (100 – average of densiometer measures taken on four cardinal directions), and elevation (measured with a Garmin GPS unit). After variables were transformed as necessary to ensure normality, a discriminant analysis (DA) was employed to assess if habitat sampling points could be confidently assigned to habitat type categories based on these structural variables. In each site where birds were sampled, we recorded habitat variables (above) from each of three plots located at either extreme and in the center of our mist netting area; inter-plot distance was 100 m. The validated DA model previously built was then applied to bird sampling sites to objectively classify their predominant habitat type.

2.3. Bird sampling

Understory birds were sampled with ground-level mist-nets (12 × 2.5 m) in contiguous forest (BBS) and forest fragments around BBS. All sampling was conducted by LC, who has over a decade of experience working with the local avifauna; digital vouchers and genetic samples were collected. Sampling in BBS contiguous forest was carried out from October 2004 – August 2007 at 15 netting stations (Fig. 1) separated by ~1400 m on average (230–3200 m); this distance was similar for stations in the same (1479 ± 670 m, mean ± 1 SD) or different habitat types (1379 ± 680 m). All netting stations were surrounded by qualitatively similar habitat for at least 200 m in all directions from the center of the net lines with one exception, CC3, which was a patch of secondary forest approximately 200 × 200 m surrounded by OG forest on all sides (see Section 3). During each sampling session, eight mist-nets were setup along a 200-m linear transect and operated between 06:30–13:30 h for three consecutive days (one sampling session = three days). Sampling was rotated across netting stations, such that each station was sampled 5–8 times in total, and the total number of sampling sessions was similar across habitat types (OG, 33; SL, 32; CC, 34). Outside BBS, we sampled 13 forest fragments 3–48 ha in size (average ± 1 S.D. 20 ± 16 ha) located 0.6–7.7 km from BBS (average: 4.4 ± 2.2 km; Fig. 1, Supplementary material Table 1). Each fragment was sampled with eight mist-nets during a single sampling session (three days) between August 2010 and February 2011 or January 2012. Due to the lack of adequate cloud-free satellite imagery in the region, fragment area was measured directly, using GPS tracks obtained by walking the perimeter of fragments; we did not map unsampled fragments in the area. During exploratory analyses, we did not detect seasonality effects on species composition. Among

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