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Review

Patterns and causes of understory bird declines in human-disturbed tropical forest landscapes: A case study from Central America

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ABSTRACT

Tropical forest understory birds are declining globally for unknown reasons, indicating an urgent need to understand the causes. We review and synthesize studies investigating causes of these declines focusing on the Sarapiquí region of the Caribbean slope of Costa Rica. We discuss evidence for five potential causes of population declines motivated by current understanding of the effects of fragmentation, disturbance of remnant forests, climate change, and their possible interactions: (1) reduced forest area increases the probability of stochastic extirpation; (2) reduced connectivity among forest patches decreases population rescue opportunities; (3) degradation of preferred microhabitats due to, for example, abundant large mammals, jeopardizes specialized birds' foraging opportunities; (4) high nest predation rates reduce productivity below replacement levels; and (5) changes in macro- and microclimate increase energetic demands and reduce survival. Our review documents how tropical forest loss and degradation likely impact understory birds through a variety of direct, indirect, and interrelated causes spanning multiple temporal and spatial scales and levels of biological organization. We propose that the processes affecting understory birds in the Sarapiquí region may be broadly representative of threats experienced by rainforest understory birds pantropically. Effective conservation will require consideration of such diverse and interacting factors.

Contents

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1. Introduction

Tropical communities are threatened globally (Newbold et al., 2014). Effective conservation of tropical species requires determining why their populations are declining and identifying the ecological and life history traits associated with persistence or loss. Although many correlates of extinction risk have been identified such as habitat fragmentation (Haddad et al., 2015), mechanistic studies of declines are surprisingly infrequent. Considerable recent interest has focused on avian declines in particular. While we recognize that tropical forests are losing their avifaunas, the causes of these extirpations are poorly understood (Sodhi et al., 2004, 2011). The biodiversity stakes are high because these communities are diverse and provide essential ecosystem services such as insect control (Blake and Loiselle, 2009; Maas et al., in preparation; Şekercioğlu, 2006; Terborgh et al., 1990).

Insectivorous birds have emerged as a guild of particular concern in tropical rainforest understory (Robinson, 1999, 2001; Şekercioğlu et al., 2002; Sigel et al., 2006, 2010). Many of these species possess traits that increase sensitivity to disturbance including having large territories (and thus, low population density and large area requirements), poor dispersal capabilities, and preferences for old growth or interior forest habitat (Lees and Peres, 2008, 2010; Robinson, 1999; Şekercioğlu and Sodhi, 2007; Şekercioğlu et al., 2002; Sodhi et al., 2004; Stouffer and Bierregaard, 1995). Microhabitat specialization resulting from diet and/or foraging specialization is also common in this guild, including reliance on dense understory vegetation, sparse leaf litter, or particular types of arthropods or fruits (Fitzpatrick, 1980; Marra and Remsen, 1997; Michel et al., 2015, in press; Sherry, 1984; Stratford and Stouffer, 2013). Nest type and placement by many of these birds (e.g., open-cup, ground, and pendulous nests) may elevate predation risk from a variety of predators (Oniki, 1979; Sieving, 1992; Sigel et al., 2010; but see Sigel et al., 2006; Young et al., 2008). Finally, the tropical forest understory guilds contain many small-bodied birds (Karr, 1971) that must feed frequently due to high mass-specific metabolic rate exacerbated by large surface area to body mass ratio (Calder, 1974). A consequence of such physiological traits is sensitivity to climatic change (Canaday, 1997; Karr and Freemark, 1983; Stratford and Robinson, 2005) and thus greater vulnerability to extinction (Boyle and Sigel, 2015; Owens and Bennett, 2000).

Here we take advantage of a well-studied tropical region, the Sarapiquí River watershed on the Caribbean slope of Costa Rica, as a case study to examine the causes of understory bird population declines in fragmented and otherwise disturbed tropical forests. Given the correlates of avian declines listed above and this region's ecological history, five core hypotheses (grouped into four categories) emerge as likely causes of decline: (1a) Loss of intact old-growth forest has reduced available habitat for bird species with strong preferences for this habitat type. (1b) Fragmentation also prevents dispersal-limited understory birds from moving between isolated habitat patches. (2) Microhabitat availability has declined even within intact forest; specifically, increased abundance of collared peccaries (*Pecari tajacu*, a native omnivorous mammal) has reduced an important microhabitat (dense liana tangles) needed by many specialized insectivores, including mixed-species flock participants. (3) Nest predation by a specialized predator, the bird-eating snake (*Pseustes poecilonotus*) has disproportionately impacted ground/understory nesters in connected forest more than in fragments or contiguous forest. (4) Physiological stressors linked to changing temperature and rainfall regimes are resulting in declines of small-bodied birds. In the following sections we review evidence from the Sarapiquí region of Costa Rica for each of these hypotheses, and consider each of these causes in a broader tropical perspective. Finally, in order to develop comprehensive conservation recommendations, we interpret causes in terms of their associated spatio-temporal scales and levels of biological organization.

2. Methods

We reviewed published literature by searching Web of Science, Google Scholar, Science Direct, and the Searchable Ornithological Research Archive. Search terms included combinations of the following: Sarapiquí, Costa Rica, forest, rainforest, disturb*, fragment*, climate change, avian, understory, bird*, decline, mechanism, cause*. We supplemented these searches with targeted efforts to locate references recommended by colleagues or otherwise identified during the literature search.

We assessed recent (1997–2012) land use in the Sarapiquí River watershed through analysis of land cover datasets in ArcMap 10.1 (ESRI, Redlands, CA). We merged the 1997–2000 Land Use dataset from the Earth Observation Systems Laboratory and Fondo Nacional de Financiamento Forestal (http://cro.ots.ac.cr/en/laselva/gis/laselva_gis/index.html) with the 2012 MODIS Land Cover type dataset (MCD12Q1). The MCD12Q1 data product was obtained through the online Data Pool at the NASA Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov/data_access). Additional spatial data layers (rivers, reserve boundaries, and a digital elevation model) were obtained from the La Selva Biological Station Geographic Information Systems Laboratory (http://cro.ots.ac.cr/en/laselva/gis/laselva_gis/index.html).

3. Causes of understory bird decline

3.1. Sarapiquí land use history, avifauna, and regional context

The Sarapiquí region was historically covered by tropical wet forest, receiving approximately 4000 mm of rain annually (Holdridge, 1967). This forest cover declined to approximately 70% by 1963, and ~55% today (Read et al., 2001; Fig. 1). Mature forest loss slowed following a 1996 ban on deforestation, but agricultural expansion into pasture and secondary forest interferes with forest regeneration (Fagan et al., 2013). The remaining mature forest is largely restricted to ecological reserves, including Braulio Carrillo National Park, which encompasses 47,000 ha of primarily old-growth forest that extends up to ~3500 masl (McDade and Hartshorn, 1994), La Selva Biological Station (hereafter La Selva), Tirimbina Biological Reserve (hereafter Tirimbina), and several