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Response of mixed-species flocks to habitat alteration and deforestation in the Andes

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ABSTRACT

Although a growing number of studies address how Neotropical birds respond to anthropogenic disturbance and deforestation, we continue to poorly understand responses of groups of interacting species, such as mixed-species flocks in the Andes. In this study, we examined how attributes at landscape (i.e., percentage of forest cover within 1-km^2) and local (i.e. structural complexity of microhabitat) scales shaped mixed-species flocks within five broadly-defined habitat types in the Northern and Central Andes. From 2007 to 2010, we systematically surveyed flocks along line transects in 97 1-km^2 plots distributed from Venezuela to Peru based on a stratified-random design. We recorded 220 avian species in 186 mixed-species flocks, with the greatest species richness and largest flocks detected in forested habitats. Understory insectivores were most closely associated with mature and secondary forests. Increasing forest cover promoted species richness and size of flocks, with particularly strong associations in successional habitats and shade coffee. Structural complexity was positively associated with flock size in early successional and silvopastoral habitats, where 20% increases in complexity doubled flock size. However, the opposite pattern was true in shade coffee and secondary forests. Encounter rates of flocks were poorly explained by simple metrics of forest cover and structural complexity. Unlike flocks reported in many lowland forests, Andean flocks tended to span all vertical strata, with fewer understory-specializing flocks (e.g. flocks led by *Basileuterus* warblers and *Chlorospingus* tanagers). Nonetheless, in such flocks, understory insectivores were most closely associated with mature and secondary forests. Our research supports the idea that managed habitats with overstory trees can contribute to flock conservation. Overall, our results further suggested that understory birds require the more forested of habitats (e.g., mature forest held almost twice as many understory specialists as other habitats), and may be less amenable to conservation with agroecosystems or working landscapes.

1. Introduction

The literature is rich with studies of how anthropogenic disturbance and deforestation affect ecological communities. Yet, we continue to have a relatively poor understanding of the responses of species interactions, especially groups of interacting species, to these adverse human activities. Certainly, studies have demonstrated that disturbance influences avifauna (Soulé et al., 1988; Harris and Silva-Lopez, 1992; Enoksson et al., 1995), and this has been especially well documented for boreal and temperate birds (Flather and Sauer, 1996; Jokimaki and Huhta, 1996; Bayne and Hobson, 1997). In the case of tropical birds, much of the research on fragmentation and deforestation has been conducted in Neotropical lowland ecosystems (e.g. Laurance and Bierregaard, 1997; Maldonado-Coelho and Marini, 2000, 2004). Comparatively few studies have focused on montane forests in the Andes, which is a region widely recognized as one of the worlds great centers of biodiversity (Rodríguez-Mahecha et al., 2004). Given that the high levels of species richness and endemism in this mountain range overlay with one of the greatest rates of deforestation among tropical forests (Whitmore, 1997; Wright, 2005), the Andes have been drawing international conservation attention.

Most studies of tropical fragmentation and deforestation have emphasized consequences to avian communities. For example, fragmentation often leads to disappearance of forest species, including understory insectivores. One of the factors that

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contributes to the sensitivity of forest birds to fragmentation is nest predation, and tropical tropical resident birds are known to be sensitive to high rates of nest predation in fragmented landscapes (Kattan, 1994; Renjifo, 1999, 2001). This is especially true for extinction prone insectivores which are highly vulnerable to fragmentation (Bierregaard et al., 1992; Karr, 1982; Sekercioglu et al., 2002; Renjifo, 1999; Kattan et al., 1994). Other factors associated with understory species loss of rainforest species from anthropogenic disturbances include diminished food supply and alteration of microhabitat conditions (see Sekercioglu et al., 2002; Powell et al., 2015a). The role of mutualistic interactions, however, has received scant attention.

The effects of deforestation and habitat degradation also can alter social systems such as mixed-species flocks (Maldonado-Coelho and Marini, 2004; Lee et al., 2005; Cordeiro et al., 2014). Mixed-species flocks are widespread in both temperate and tropical communities, and are reported to be negatively affected by habitat fragmentation and degradation in the Neotropics (e.g. Harper, 1989; Stouffer and Bierregaard, 1995; Develey and Stouffer, 2001; Maldonado-Coelho and Marini, 2004; Kumar and O'Donnell, 2007; Brandt et al., 2009). As the structure and dynamics of mixed-species flocks change in response to fragmentation, driven by alterations in habitat characteristics (e.g. degradation of microhabitats) and food availability (Maldonado-Coelho and Marini, 2000, 2004; Tellería et al., 2001), social systems can change as well. Frequency of occurrence and abundance of species within flocks as well as the propensity of a species to flock can all shift in sudden and profound ways. In particular, specific foraging guilds, such as understory insectivores that frequent flocks, may disappear entirely (Van Houtan et al., 2006; Goodale et al., 2013). Likewise, the disappearance of nuclear species due to disturbance could cascade into other community effects. Nuclear species are those that are present in most of the flocks, gregarious with conspecifics and noisy, and joined by solitary or pair-forming species (Greenberg, 2000). The loss of nuclear species may therefore change the structure and even lead to flock disappearance (Stouffer and Bierregaard, 1995; Thiollay, 1992, 1997, 1999; Van Houtan et al., 2006).

Despite being distinctive elements of montane forest bird communities in the Andes, no studies have examined the sensitivity of mixed species flocks to forest loss and degradation across regional or landscape scales. Many studies have shown how the combined effect of microhabitat, patch and landscape factors drive the distribution and patch use of animals (e.g. Levin, 1992; Dooley and Bowers, 1998; Lyra-Jorge et al., 2010), including birds (e.g. Jokimäki and Huhta, 1996; Saab, 1999; Sodhi et al., 1999; Lee et al., 2002; Luck, 2002; Buler et al., 2007; Coreau and Martin, 2007; Deppe and Rotenberry, 2008). However, most landscape studies of birds in the Neotropics have focused exclusively on forest patches (e.g. Kattan et al., 1994; Stouffer and Bierregaard, 1995; Renjifo, 1999), and very few studies have evaluated the simultaneous effect of multiple spatial scales (e.g. patch- and landscape-levels) on distribution of birds in several habitat types (but see Graham and Blake, 2001). Previous research in Andean and subandean forests has shown that attributes of the landscape strongly shape the composition and abundance of resident bird communities (Restrepo and Gomez, 1998; Renjifo, 1999, 2001). Given the high bird diversity and extensive levels of habitat degradation and deforestation in the Andes, understanding the effect of landscape context on habitat relationships is key to determining the conservation potential of different habitats.

In this study, we adopted a multi-scale approach to examine the extent to which mixed-species flocks respond to changes in landscape forest cover and in local habitat structure across a broad geographical range in the Andes. We hypothesized that the value of different habitats to mixed-species flocks (as indicated by abundance and diversity metrics) would be mediated by local and landscape-scale factors. In addition to this, we tested how specialist bird species such as understory insectivores that attend flocks are affected by habitat disturbance. To the best of our knowledge, this is the first multi-scale study to test for the effects of deforestation and habitat degradation on mixed-species flocks along a gradient of habitat types throughout the Northern and Central Andes.

2. Materials and methods

2.1. Study area

The study area encompassed the Northern and Central Andes, from Northern Colombia (±8°N, 73°W) to Northern Peru (±5°S, 78°W), including Ecuador. Ecosystems in the Andes are diverse, including deserts, open pampas, dry thorn forest, deciduous forest, rain forest, cloud forest, and paramo above 3000 m (Petit et al., 1995). The study area represented a range of altitudinal diversity, from tropical lowlands at 400 m to low-montane tropical forest at 2600 m.

We studied five broadly-defined habitat types in the Andes: shade coffee, pastures with isolated trees (hereafter termed "silvopastures"), early successional, secondary forest and mature forest.

Shade coffee (*Coffea arabica*) is planted under a layer of trees with canopy closure ranging from ~40% to 70%, typically represented by *Inga* spp. (Fabaceae), *Tabebuia* spp. (Bignoniaceae), *Cordia alliodora* (Boraginaceae), *Albizia* spp. (Fabaceae), and *Persea* spp. (Lauraceae). This habitat type is usually located between 800 and 2000 m of elevation and it is distributed virtually throughout our study area in the Andes.

Silvopastoral systems with grazed fields and mature overstory trees with a more open canopy compared to shade coffee (less than 50%), were included as a focal habitat type because they represent an increasingly popular land use that supports livestock, produces timber, and contributes to ecological restoration efforts by providing habitat for other species as well as improving soil conditions (Pomareda, 2000). While the overstory component of silvopastures structurally resembled the most open shade coffee farms, silvopastures generally lacked shrubs (i.e. woody plant of relatively low height which usually has several stems branching from near the base) and dense understory.

Early successional habitats were typically represented by second-growth habitats, with little or no tree development (<10 cm dbh), open canopy, and usually with poorly-developed shrub layer (<1 m height). Most successional habitat in the Andes results from natural disturbances (e.g., landslides) or abandoned agriculture/pasture, with our plots focusing on the latter.

Secondary forests represented naturally regenerating and riverine forests (i.e., not planted or otherwise intensively managed) in intermediate to advanced levels of structural (trees >10 cm dbh and <10 m height) and composition development (i.e. >12 years old). Secondary forests are typically originated in areas that were completely cut for agroforestry or silvopastoral activities.

Mature forests were structurally complex (high and dense canopy >10 m height, high basal area) and floristically diverse habitats with relatively little human use. Mature forests usually occurred in association with reserves and protected areas, where human extractive uses were largely prohibited.

2.2. Flock sampling

Data on composition, richness and abundance of mixed-species foraging flocks were recorded in 13 different regions (i.e.