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Original article

Andean bird responses to human disturbances along an elevational gradient

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ABSTRACT

Understanding patterns of species diversity along environmental gradients is essential to the study of biodiversity. Numerous studies have found variation in species richness and composition of bird communities along elevational gradients, and several others described bird diversity changes following anthropogenic disturbances. Surprisingly, few studies have attempted to disentangle their separate effects on bird assemblages. Here, we explored variation in bird species richness and composition at different levels and types of disturbance along a 4000-m elevational range in the tropical Andes. Bird counts and disturbance measurements were conducted at 85 points distributed along the gradient within Cotapata National Park, Bolivia. Disturbances accounted for in our study correspond to the often overlooked 'moderate' levels of disturbance that occur in the Tropical Andes. Diversity patterns were described and compared with GLM models (for species richness) and CCA models (for species composition). We found that bird communities were structured by elevation and disturbance. Species richness decreased with both elevation and habitat openness. Anthropogenic disturbances also modified community composition within the same elevational ranges. We conclude that, whereas elevation remained the most important variable explaining bird species composition, disturbance explained species richness patterns to a higher extent.

1. Introduction

The tropical Andes are naturally complex and their topography, biogeographic heterogeneity and elevational gradient have shaped them into one of the most diverse ecosystems worldwide. Yet it is also one of the most endangered (Myers et al., 2000; Swenson et al., 2012), with habitat modification being the major threat to this region (Brooks et al., 2002). In the Bolivian Andes, natural heterogeneity has increased since pre-Columbian times due to anthropogenic disturbances that have produced new environmental gradients for wildlife to interact with. Understanding how natural and anthropogenic gradients interact to affect wildlife is central to conservation strategies for these complex landscapes (Cleary et al., 2005; Colorado, 2011; Swenson et al., 2012).

Wildlife–habitat relationships and community responses to environmental gradients have been studied extensively, and birds have been recognized as an ideal group to test hypotheses related to these topics (McCain, 2009). Birds are used in these type of studies because: (1) their taxonomy is well known, (2) survey methods are standardized, facilitating comparisons among studies, and (3) they are diverse and have evolved a broad range of strategies (ecological niches). Empirical studies have shown that bird species richness may decrease linearly with increasing elevation, or may show a mid-elevation peak (McCain, 2009; Wu et al., 2013). However, compositional changes in bird communities along elevations are still poorly understood (Acharya et al., 2011; Blake and Loiselle, 2000; Jankowski et al., 2009; Terborgh, 1971, 1977). Bird responses to anthropogenic disturbance seem even more difficult to predict (Borges and Stouffer, 1999; Rodewald and Yahner, 2001) as bird responses to different types and intensities of human-caused disturbances are species-specific (Forsman et al., 2010; Lee et al., 2005; Petit et al., 1999; Verhulst et al., 2004; Walters, 1998). Thus, any given combination of elevation and anthropogenic disturbance is likely to shape bird assemblages in different ways (Cleary et al., 2005; Nogues-Bravo et al., 2008). Surprisingly,

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to our knowledge, no studies have attempted to disentangle the separate effects of elevation and human disturbances on bird communities in the hyper-diverse tropical Andes.

In this study, we examine avian responses to anthropogenic disturbances along an elevational gradient within a protected area in the Andes of Bolivia: Cotapata National Park and Integrated Management Natural Area (hereafter Cotapata NP). Cotapata NP occurs within a region that is recognized for its high levels of endemism (Swenson et al., 2012) and is the most diverse national park in Bolivia, in terms or bird species per area (Balderrama, 2009). Due to the complex topography large human settlements in this landscape are uncommon, and most of the current human activities are localized. Here, we consider 'human disturbance' as temporal change in environmental conditions due to human activities, and we use four proxies to measure it: size of human settlements, amount of domestic animals (cattle), amount of waste, and presence of burn areas. Additionally, we measured two environmental variables that could result both from the elevational gradient and from the human activities in the area: vegetation cover and structural complexity (see *Environmental variables* for details). Disturbances accounted for in our study occur across the 4000-m elevational gradient of Cotapata NP and represent the most characteristic human-caused disturbances in the region.

Due to the strong temperature and humidity shifts along the elevational gradient of the park (Bach et al., 2007; Jones et al., 2011), we expected elevation to be the most important variable defining bird communities (McCain, 2009). Nevertheless, we also expected disturbances to modify communities, resulting in different assemblages at similar elevational ranges (Nogues-Bravo et al., 2008). Moreover, because natural disturbances such as landslides and treefall gaps are common in mountain forests, we expected human disturbances that resemble natural disturbances (i.e. small clearings) to be tolerated by most species whereas disturbances that do not resemble natural clearings (i.e. fires) might have a stronger effect on less resilient birds.

2. Materials and methods

2.1. Study area

We conducted our study in Cotapata NP (67°43′–68°02′W; 16°10′–16°20′S; Fig. 1), La Paz, Bolivia. Cotapata NP protects distinct vegetation types that develop between the high Andean plateau and the Andean foothills (5600–1000 m asl). The park is dominated by evergreen humid montane and cloud forests, with steep slopes and deep valleys, while natural grasslands occur at higher elevations (>3900 m asl). Small natural disturbances, such as landslides and treefall gaps, are common, as are scattered active and abandoned small agricultural clearings (~0.5–3 ha) within a forested matrix (Ribera, 1995; Sevilla Callejo, 2010). Climate is seasonal, with a long wet season that peaks in January and February and a two or three month dry season that peaks in June or July (Jones et al., 2011; Molina-Carpio, 2005).

To conduct our studies, we used all the existing hiking trails in the park as our sample routes because the complex topography makes it virtually impossible to access most areas within Cotapata NP (Fig. 1). Taken together, the trails extend across most of the park's gradient (~1000–5000 m asl), and traverse different levels of disturbance. Most of the trail network is narrow (between < 1 and 1.5 m wide), although some sections can be up to 3.5 m wide. Also, some sections of the trail network are pre-Inca: half are regularly used by local people and pilgrims, whereas the other half was reopened for this study. Thus, reopened trails constituted a long transect that crossed well-conserved forest across elevations whereas more actively use trails crossed disturbed areas across elevations. As described below, we measured human disturbances at determined points across elevations. For comparison purposes only, our higher level of disturbance would correspond to the 'moderate' level of disturbance in most studies (Gray et al., 2007; Lefevre et al., 2012). Therefore, human disturbance levels in our study range from relatively 'undisturbed' (the only impact being us opening a transect) to 'moderately disturbed' habitats (hereafter 'disturbed').

2.2. Bird surveys

Between April 2006 and April 2007, we recorded birds at 85 points (Fig. 1). We used a GPS unit (E-trex, Garmin®) to record UTM coordinates and an altimeter (KONUS®) to record elevation at each point. Because of the tortuous nature of the trails and complex topography, and based on our previous experience in this forest, walking was selected as a proxy for distance in the field; points were separated by 50 min walk from each other. The minimum linear distance (calculated using ArcView 3.2) between consecutive points was ~340 m (mean = 843.1 ± 507.5 SD), an appropriate distance to consider points independent and to detect the often overlooked small-scale (<1 km) shifts in environmental conditions that characterize tropical montane forests (Jones et al., 2011; McCain, 2009). We used non-fixed-radius 10-min point counts to sample birds (Blondel et al., 1981); counts were carried out by a single experienced observer accompanied by a field assistant. Each of the 85 points (replicates) was sampled six times throughout the year (approximately every two months) to account for seasonal variation. Similarly, each point was sampled at different times of the day (between sunrise and 11:30 and between 13:30 and 17:30) to help account for diurnal changes in bird activity. Because we wanted to make sure that registered birds were actually present in the small areas where disturbances were measured (see *Environmental variables*), we registered only birds detected visually; we noted the number of species and individuals at each point. Thus, when we heard a bird singing, we looked for the bird and registered it only if it was seen. Although we are aware that these types of surveys may undersample some groups, it has been suggested that employing identical methods using the same observer would produce comparable results (Woltmann, 2003). Moreover, we assessed the completeness of our counts at each point by calculating the expected species richness using the Jack1 richness estimator with the software EstimateS (Colwell, 2009), and ran all our analyses with both observed and estimated richness.

2.3. Environmental variables

We measured seven environmental variables in a 25-m radius circular area surrounding each point: elevation, vegetation cover, structural complexity, house density, waste, burn and cattle. Although vegetation cover and structural complexity can not be solely attributable to anthropogenic disturbances, they do decrease with disturbance. Thus, in combination with disturbance measurements (burn, cattle, human settlements and waste) they better describe the environmental changes caused by human activities in the evaluated points. Environmental variables were measured as follow: (1) elevation (to the nearest meter); (2) vegetation cover, estimated visually and expressed as percentage of surface covered by any type of vegetation and then categorized as follows: <20%, 20–40%, 40–60%, 60–80% and 80–100%; (3) structural complexity, based on the 'habitat heterogeneity hypothesis'(MacArthur and Wilson, 1967) we visually examined each point and categorized it as belonging to one of seven increasingly complex habitat