Long-term monitoring finds declining abundances of most bird species across three habitats in the Tropical High Andes

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ABSTRACT

There is a long history of using birds as indicators of environmental threats that may result in major changes in ecosystem conditions. We use an 11-yr constant effort mist netting data set from the Ecuadorian Andes to assess the population trends of resident bird species in three high elevation habitats. These habitats included native, mature secondary, subtropical moist broadleaf forest; mixed native and non-native forest; and native montane shrubland. Results indicate that bird populations across these three habitats have been declining an average 2.8%/yr, and this decline is significant. Capture rates declined for 79% of the 38 species that met our inclusion criteria [declined in at last 1 habitat? Each habitat?]. When species were grouped by diet, body size, primary habitat occupied, or habitat breadth, no particular group of species showed significant differences in rates of decline [and no group show significant INCREASE!]. We believe that to operate at such a scale habitat change must be occurring through the abiotic environment, reducing habitat quality for component biota. We focus discussion on climate change and other possible mechanisms behind these declines in species’ abundances, but also note that there may be synergistic effects linking climate change with other anthropogenic impacts on these bird populations.

KEY WORDS:

INTRODUCTION

Many biodiversity hotspots suffer from anthropogenic transformation of forests and other native habitats that threatens the survival of multiple species (Orme et al. 2005). Like other major hotspots, the Tropical Andes region has suffered extensive habitat loss because of inappropriate land use. Ranking first among the world’s 25 hotspots of diversity and endemism (Myers et al. 2000), the Tropical Andes harbor the greatest concentration of restricted-range bird species in South America (Stotz et al. 1996, Stattersfield et al. 1998), and have one of the highest concentrations of the world’s threatened bird species (Stotz et al. 1996). Habitat has been lost to the burning of grasslands to benefit cattle, urbanization, road building, deforestation, the cultivation of exotic trees, and other causes.

Global climate change, including related largescale weather patterns such as El Niño Southern Oscillation, also affects birds and their habitats (Root et al. 2003, Hannah et al. 2007, IPCC 2007). The Tropical Andes is expected to be one of the regions most affected by climate change in the current century (Thomas et al. 2004, Malcolm et al. 2006, Higgins 2007, Gonzalez et al. 2010, Beaumont et al 2011, Bush et al. 2011). Most analyses of the effects of climate change on birds have focused on impacts on elevational (Sekercioglu et al. 2008; Tingley et al. 2009, 2012; Lenoir and Svenning 2015,) and geographic ranges of species (e.g. La Sorte and Thompson 2007, Chen et al. 2011, Graham et al. 2011), or the phenology of ecological phenomena (e.g. Both et al. 2006, Thackeray et al. 2016). Climate change has also been shown to alter community composition and dynamics (Root et al. 2003; La Sorte and Thompson 2007; Blake and Loiselle 2015, 2016; Freeman et al. 2018), but much less is known about how climate change may impact the population size of avian species (Latta et al. 2011, Freeman et al. 2018).

Birds are excellent indicators of the impacts of anthropogenic disturbances, including climate change (Morrison 1986, Niemi and McDonald 2004), and have been used to monitor environmental quality in diverse situations (Ormerod and Tyler 1993, Canterbury et al. 2000, Mulvihill et al. 2008, Durant et al. 2009). The wide use of bird taxa as indicators is appropriate because: (1) many bird species are tightly tied to particular habitats; (2) birds occur in almost all habitats and across broad disturbance gradients; and (3) most birds are relatively short-lived so shifts in abundance and diversity will appear relatively quickly in the population (Browder et al. 2002). Thus, avian indicators are highly useful in assessing the condition of the environment, and as early-warning signals to detect how ecological changes may be impacting habitats (Niemi and McDonald 2004).

Several approaches are available to study changes in bird populations in the Tropical Andes. To date, most studies have relied on comparisons of species richness or abundance (Renjifo 2001, Latta et al. 2011, Tinoco et al. 2013), thus limiting our ability to predict the long-term effects of habitat disturbance on populations. Species-specific survival estimates also have the potential to inform population trends, but survival estimates require large amounts of long-term data (Ruiz-Gutiérrez et al. 2012), so survival estimates have been published for only 28 species from the Tropical Andes (Tinoco et al. 2019). When data are collected using a consistent, constant effort monitoring method, long-term data sets can be the most informative in terms of understanding changes in bird populations related to anthropogenic disturbances and climate change. Although generally unavailable from tropical montane sites, these may offer the best opportunities for understanding the pace of change in communities and populations (Latta et al. 2005, 2011; Scridel et al 2018).

Here we use birds as indicators of change in habitats in the Tropical Andes. We utilize an 11-yr, constant effort mist netting data set from the High Andes of southern Ecuador to assess changes in abundance of resident bird species in three habitats across a gradient of disturbance. These habitats include minimally altered, native, montane cloud forest or *bosque altoandino*, mixed native and non-native forest, and early successional shrub recovering from cattle grazing. In each habitat, we explore species-specific population trends of birds. We also explore potential explanatory patterns of population trends by classifying birds captured in mist nets into groups based on body mass, diet, primary habitat occupied, and habitat breadth, in order to suggest mechanisms responsible for changes in avian abundance. We discuss our findings in the context of anthropogenic disturbances affecting the region.

METHODS

Study Site

Our study was conducted in the Llaviuco Valley (02.840S, 79.160°W) of Cajas National Park, and the adjacent 2700 ha Mazán Reserve (02.870°S, 79.120°W) in the High Andes of Azuay province, Ecuador (Fig. 1). These areas are of global importance for biodiversity conservation (Astudillo et al. 2015), have been designated together as an Important Bird Area (Freile and Santander 2005), and are part of UNESCO’s Macizo del Cajas International Biosphere Reserve. Cajas National Park and Mazán are both managed by ETAPA-EP (Empresa Pública Municipal de Teléfonos, Agua Potable y Saneamiento Ambiental), a local public department that serves the city of Cuenca, Ecuador.

We placed three sampling sites in areas with unique habitat types. These included: (1) native, mature secondary, subtropical moist broadleaf forest (NATIVE) located in Mazán; (2) mixed native and non-native forest (MIXED) also located in Mazán; and (3) native montane shrubland (SHRUB) located in Llaviuco Valley.

The mature secondary moist broadleaf forest (NATIVE) is at an elevation of 3200 m asl. Tree species common in this area include *Hedyosmum cumbalense*, *Symplocos quitensis*, and *Myrcianthes* sp*.*, with an understory composed mainly of *Miconia bracteolata*, *Viburnum triphyllum*, and *Oreopanax avicenniifolius*. The canopy reaches 10–15 m in height. Measures of the vegetation structure at this sampling station obtained in 2007 and 2013 reveal little change with a percent canopy cover of 70.8±16.6% in 2007 (all values are expressed as means ± SD) and 71.0±15% in 2013, a density of trees (DBH > 9 cm) of 83/ha in 2007 and 85/ha in 2013, and a shrub density of 3.3±1.3 individuals/m2 in 2007 and 5.4±1.5 individuals/m2 in 2013. Limited selective logging occurred at this site >30 years ago, but the reserve is now under strict protection that allows only select scientific activities.

The mixed non-native forest (MIXED) is at an elevation of 3100 m asl and is characterized by mixed stands of mature *Eucalypthus globulus,* *Pinus patula*, and remnant native species. These introduced species were planted >30 years ago and now have a height of 15-20 m. Species common in the understory include *Rubus* sp. and *Baccharis* sp., with little or no regeneration by the non-native overstory species. The vegetation structure at this location remained similar from 2007 to 2013, with a canopy cover of 64.8±20.0% in 2007 and 65.4±15% in 2013, a tree density (DBH > 9 cm) of 84/ha in 2007 and 94/ha in 2013, and a shrub density of 2.6±0.6 individuals/m2 in 2007 and 4.6±0.9 individuals /m2 in 2013.

The native montane shrubland site (SHRUB) is in Llaviuco Valley at an elevation of 3150 m asl. Common shrub species include *Barnadesia arborea*, *Brachyotum* sp., *Rubus floribundus*, and *Salvia corrugata*. The canopy is low (<3 m), with only isolated taller trees. Sampling of vegetation structure in the years 2007 and 2013 indicate that while the habitat continued to be characterized as a shrubby grassland, there was an increase in canopy cover (16.6±23.4% in 2007 to 33.2±24.2% in 2013), abundance of trees (8/ha in 2007 to 23/ha in 2013), and density of shrubs (1.5±0.6 individuals/m2 in 2007 to 3.1±1.0 individuals/m2 in 2013). While the native forest in the Llaviuco Valley was cleared for cattle ranching in the historical era, since being incorporated into Cajas National Park in 1996 the cattle have been removed and the vegetation has naturally reestablished.

The study area receives 1200-1500 mm of rain annually in a bimodal pattern; a main rainy season January-June, a dry season July-September, and a secondary rainy season October-December (Celleri et al. 2007). Mean monthly temperatures range is 5-12°C.

Sampling protocol

We established in 2006 a long-term bird monitoring program using standardized methods of constant effort mist netting (e.g., Ralph et al. 2004, Latta et al.2005) to monitor bird populations so that comparisons could be made across space and time. Each of our three sites was sampled three times annually (2006 to 2016) to cover the climatic seasonality of the study area; we sampled during the main wet season (21 March – 6 May), the dry season (19 July – 9 September), and the secondary rainy season (30 October – 20 December).

At each of the three sites we captured birds by randomly placing 20 mist-nets (12 m x 3 m x 30 mm mesh) either along or perpendicular to existing paths or small vegetation gaps. The distance between nets varied, but together they extended over ~550 m in total distance. At each site nets were open for two continuous days, from dawn to 17:00 on day 1 and dawn to 11:00 on day 2. All captured birds were identified to species, sexed, and aged (hatching year, adults) using plumage characteristics (Ridgely and Greenfield 2001). All birds were uniquely banded with a numbered aluminum band.

Mist net schedules and locations were determined in order to avoid the potential for net shyness or net avoidance (Karr 1981). Birds may learn through experience the placement of mist nets (Karr 1981), but net shyness is largely avoided by the presence of large gaps in net arrays (Ralph et al. 2004), and by reducing the number of days of continuous mist netting to no more than three days (Burton and DeSante 2004, Faaborg et al. 2004). Many previous studies have shown avoidance of nets by previously captured birds may last from no more than a few days (Nur and Geupel 1993, Ballard et al. 2004) to a week (DeSante et al. 2004), or rarely a month (Faaborg et al. 2004), but no evidence suggests that birds avoid nets for longer periods of time (Ralph et al. 2004).

Mist nets are subject to several biases (Ralph and Scott 1981, Karr 1981, Remsen and Parker 1983). For example, in some habitats nets do not sample all strata of the vegetation, very small or very large birds may be ineffectively sampled, and nets may overestimate the abundance of species that travel widely in search of food over that of more sedentary foragers (Remsen and Parker 1983, Remsen and Good 1996). While recognizing these potential biases, in this study we minimize these problems because we limit analyses of net-capture frequencies to comparisons within species over time. Thus, we assume capture rate is proportional to the abundance of the species, and that the relationship between capture rate and abundance does not vary with time (Remsen and Good 1996, Silkey et al. 1999).

We classified birds captured in mist nets into groups based on body mass, diet, primary habitat occupied, and habitat breadth. Body mass was determined by reference to published data on Ecuadorian birds (Toral 1996, Ridgely and Greenfield 2001, Dunning 2007, Latta et al. 2011) and our unpublished data. Birds were grouped by diet on the basis of principal food items consumed (Ridgely and Greenfield 2001; pers. obs.) as insectivores, nectarivores, granivores, frugivores, carnivores, and omnivores. We assigned all species to a single preferred habitat on the basis of Stotz et al. (1996). For species whose primary habitat was not represented at Cajas National Park or the Mazán Reserve, we selected the next most preferred habitat recognized by Stotz et al. (1996) that was present. Habitats can also be seen as an indication of elevational preferences, as habitat changes with elevation in the Andes. Habitats, from relatively low to relatively high elevation, were montane evergreen forest (F), montane shrub and secondary forest (N), forest edge (E), high elevation dwarf or elfin forest (D), and *páramo* grasslands (P). Habitat breadth was also derived from Stotz et al. (1996) and was expressed as the number of habitats occupied by the species across its range, with more specialized species occupying fewer habitats.

Statistical Analyses

Our data set consists of count data with correlation resulting from repeated measurements on the same species accross sites within years, and within sites between years. We fit a generalized linear mixed model (GLMM) to model capture rate as a function of time and habitat type. We also modeled capture rate as a function of time and diet categories, time and body-mass classes, time and preferred habitat, and time and habitat breadth. All models included random intercepts and slopes for each species nested within each habitat. An example model structure in shown in Appendix 1.

We evaluated whether our count data was best modeled using Poisson, zero-inflated Poisson, negative binomial, and zero-inflated negative binomial error distribution, both with and without a one-year time lag autoregressive (AR-1) correlation structure. AR-1 models include the response variable at the previous time point as a predictor for the current time point; that is, the observed capture rate at time *t* is used to predict the capture rate at time *t* + 1. (Akaike 1974)aan AR-123

We assessed the sensitivity of parameter estimates to inclusion of rare species by fitting the model both with and without these species. Rare species were iteratively excluded from model-fitting; species were dropped in order from fewest years captured to most years captured. The population-level parameter estimates and species-level best linear unbiased predictors (BLUPs) were stable across these models.

All models were fit in R version 4.05 (R Core Team 2021) in glmmTMB version 1.0.2.1 (Brooks et al. 2017). AIC calculations were done using the *AICtab* function in bbmle (Bolker and R Core Team 2020).

RESULTS

Through 4708 total captures, we banded 3600 individuals of 70 species. The total number of unique species varied by site (SHRUB=58, MIXED=48, NATIVE=48) and by year, and ranged from 52 (in 2007) to 37 (2016).

We then fit our model allowing the habitats to have different rates of decline; there were no significant differences between the habitats. AIC and BIC identified the simpler model (in which all habitats share a time effect) as the better model (Table 1).

Using this model, we estimated that the baseline (time = 0 = March 2006) capture rate/1,000 net hours is 7.191 (95% CI (5.383, 9.606)) in native shrub (SHRUB), 5.820 (95% CI (4.226, 8.015)) in mixed non-native forest (MIXED), and 4.423 (95% CI (3.153, 6.206)) in mature secondary forest (NATIVE). We estimated a 2.8% (95% CI (0.9%, 4.6%)) decrease in capture rate between years across all species and all habitats. This means that the population, as a whole, is estimated to have a significant year-to-year decrease in capture rates of 2.8%.

Out of 70 unique species in our three study sites, 38 met our inclusion criteria of being captured in at least 4 of 11 yr (Table 2). Among these 38 species, we found that the vast majority of species have non-significant, but decreasing point estimates (Figure 1; Appendix 3), with three species having significant negative population trends. These species include the Mountain Velvetbreast (*Lafresnaya lafresnayi*), Sapphire-vented Puffleg (*Eriocnemis luciani*), and Black-tailed Trainbearer (*Lesbia victoriae*). Plots of observed and predicted capture rates for these three species (Figure 2a, b, c) show these significant declines.

Our data also showed only 9 species with non-significant, increasing point estimates (Figure 1, Appendix 3). These species include (*E. luciani* in secondary forest (2.1% increase per year), *Margarornis squamiger* in secondary forest (1.5% increase per year), *Metallura baroni* in secondary forest (1.2% increase per year), *Catamenia inornata* in secondary forest (0.8% increase per year), *Ochthoeca frontalis* in secondary forest (0.8% increase per year), *Diglossopis cyanea* in secondary forest (0.5% increase per year), *Metallura tyrianthina* in secondary forest (0.3% increase per year); *M. tyrianthina* in primary forest (2.5% increase per year); *Hellmayrea gularis* in introduced forest (1% increase per year), *Troglodytes solstitialis* in introduced forest (0.4% increase per year).

Finally, we found no evidence to suggest that capture rates are changing differently for different ecological groups of bird species. For example, there was insufficient statistical evidence to suggest that capture rates are changing differently for birds with different diets (Figure 3A), as diet groups shared the estimated 2.83% (95% CI: 0.9-4.7%) decrease in capture rate from year to year. Similarly, we found no statistically significant difference in how the capture rates change with time for the three body size groups (Figure 3B), or birds occupying different primary habitats (Figure 3C), or species with broader or narrower habitat breadth (Figure 3D). In all cases, all groups were found to share the decrease in capture rates of 2.8% (95% CI: 0.9-4.7%) per year.

DISCUSSION

Our results indicate that bird populations across three habitats in the High Andes of southern Ecuador have been declining an average 2.8%/yr over an 11 yr sampling period. Furthermore, although uncertainty exists around some species level estimates, capture rates declined for 79% (30 of 38) of the species meeting our inclusion criteria of having been sampled in at least 4 discrete years. When grouped by diet, body size, primary habitat occupied, or habitat breadth, no particular group of species showed significant differences in rates of decline. While natural variation over time in the abundance of birds is to be expected, evidence suggests there are normally considerable interspecific differences in the direction and magnitude of population change (Blake et al. 1994; Ballard et al. 2003; Stouffer et al. 2011, 2020; Boyle and Sigel 2015; Blake and Loiselle 2016). We believe that long-term monitoring has not previously documented a generalized decline of such a large and diverse set of bird species, as seen here, in either the High Andes or elsewhere.

Anthropogenic changes in land use within our study areas could explain some population trends. In particular, the native montane shrubland site (SHRUB) saw modest increases in canopy cover, tree abundance, and shrub density but these changes could account for decreases in abundance of some species such as *Lesbia victoria* which thrives in urban dry valleys of the region (Tinoco and Astudillo 2007). Similarly, 7 of the 9 species (78%) showing non-significant increases in population occurred in this habitat where recovery of native shrubs after disturbance was most pronounced. However, management practices at all of our study sites eliminated chances for anthropogenic degradation of habitat, and we never observed any overt disturbances to habitat. Thus, local changes in land use are not likely to account for the broad declines in abundance we observed.

Outside of our study sites, we have few data on how habitat may have changed in the immediate area during the years of this study. Although the High Andes have suffered centuries of loss of native habitats (White and Maldonado 1991, Hofstede et al. 2002), Gaglio et al. (2017) found that in the highlands of Central Ecuador, overall coverage of natural ecosystems increased slightly during 2000–2014, with afforestation rates of 0.28%/yr at the highest elevations. Combined with findings that forest protected areas are effective in reducing deforestation in Tropical Andean forests of Ecuador (Cuenca et al. 2016), the evidence suggests that anthropogenic loss of habitat was not a widespread problem during the monitoring period. Looking beyond the years of this study, the time scale of habitat loss would also seem to eliminate the possible occurrence of community-level dynamics such as an extinction debt (Tilman et al. 1994). Deﬁned as a time-delayed but deterministic extinction of specialists from a habitat as the community equilibrates after habitat alteration (Tilman et al., 1994), an extinction debt is unlikely here since Ecuadorian forests and grasslands have been impacted by human activities for centuries (White and Maldonado 1991).

Beyond habitat, the ecology of the birds themselves may potentially explain patterns in population trends. However, we found no evidence species declining in abundance shared any particular ecological correlates of risk, lived in unique places, differed systematically in their ecology, or were subject to specific threats. For example, there was no significant difference in rates of decline among sampled habitats (Fig. X), even when the habitats were as different as mature secondary forest, mixed non-native forest, and native shrub. Declining species were not dietary specialists dependent on a single limited resource (Fig. X), fruit or nectar for example, nor were they only specialists occupying narrowly defined niches (Fig. X). Declining species were not primarily larger-bodied victims of hunting (Gage et al. 2004, Keane et al. 2005), or smaller-bodied species subject to environmental stochasticity and temporal variation in food supply (Fig. X; Cook and Hanski 1995). While stochastic impacts might be more broadly hypothesized as responsible for negative population trends, our data indicate population declines were not sudden and precipitous as might be expected of stochastic events (LaDeau et al. 2007, Robinson et al. 2010). In contrast, our data show a pattern of substantial annual variation in abundance amounting to persistent long-term declines (Fig.Ya-c).

It is, in fact, this universal decline of the majority of species that is the most important and unique finding of our study. While long-term monitoring of birds using mist nets remains an unusual accomplishment in the Western Hemisphere (Latta et al. 2017; Faaborg et al. 2013; Blake and Loiselle 2015, 2016; Stouffer et al. 2020), in previous studies there were “winners” and “losers” in that some species increase in capture rates while other species decline (Blake and Loiselle 2015; Latta et al. 20011, 2017). To operate at such a scale, we believe that habitat change must be occurring through the abiotic environment, reducing habitat quality for component biota. For example, habitat change may increase foraging and activity costs, and decrease the energy available to birds for reproduction and other vital needs, potentially causing fitness impacts (Shankar et al. 2019). Climate change-driven impacts occur on such large scales and may be more frequent in tropical mountains because montane species often exhibit a high degree of habitat specialization and unique ecological traits. As a result, the disruption of biotic processes and interactions may be more likely (Reif and Flousek 2012, Reif et al. 2015, Mahon et al. 2016, Pacifici et al. 2017, Scridel et al. 2017, Scridel et al. 2018), affecting fitness and population size of many species.

Past studies have shown a variety of impacts of climate change and largescale weather patterns (e.g., El Niño Southern Oscillation) on tropical montane birds (Sillett et al. 2000, Mazerolle et al. 2005, LaManna et al. 2012). These studies frequently pair historical surveys with a more recent census to derive results in terms of species distributions (e.g., Root et al. 2003, Tingley et al. 2009, Forero-Medina et al. 2011, Freeman and Class-Freeman 2014, Freeman et al. 2018), community structure (Latta et al. 2011), or abundance trends (Latta et al. 2011, Freeman et al. 2018). For example, Freeman et al. (2018) paired data from 9-10 day expeditions separated by 32 years (1985-2017) to show that most species above 1200 m asl at their Peruvian site declined in both range size and abundance, with several previously common mountaintop residents disappearing entirely. Similarly, climate change was invoked to explain differences between bird communities in our Mazán study sites when capture rates were compared between two time periods: 1994–95 and 2006–07 (Latta et al. 2011). In that study, species preferring higher-elevation habitats declined more than lower-elevation species, consistent with the possibility that species may be moving up in elevation as a result of climate change, or may be perishing as habitats dry with increased temperatures (Foster 2001, Barnett et al. 2005, Hannah et al. 2007, Sekercioglu et al. 2008, Graham et al. 2011).

While it is reasonable to conclude that the observed decline in species’ capture rates and abundances in this study is a result of global climate change, our study leaves open the mechanism behind those declines. As mentioned above, mechanisms may be revealed by demographic rates such as reproductive success and survival, and several studies have indicated that fluctuations in climate influence demographic rates in montane birds in the Northern Hemisphere (Crick et al. 1997, Laaksonen et al. 2006, Scridel et al. 2018). But long-term studies assessing reproductive success or survival of tropical mountain birds in relation to climate change are rare (Scridel et al. 2018). One of the only such studies (Tinoco et al. 2019) calculated apparent survival rates of birds using the same 11 yr capture–recapture dataset from the three habitats in this study. After fitting mark–recapture models for 28 species with habitat as a covariable, no significant differences in survival rates were found, either among habitats, or among species grouped by habitat specialization. While lower survival estimates may have been expected in the human-impacted non-native forest, the lack of pattern in the data may be the result of a homogenization of survival rates resulting from more widespread impacts of climate change. Date were too sparse, however, to analyze a time effect.

An additional, more specific, mechanism behind avian population declines may be associated with climate impacts on resources through a bird’s energy budget. Recent work on hummingbird energy budgets in North America indicate that the most important factor influencing variation in daily energy expenditures is resources, not temperature, and that this increase is related to decreased nectar availability rather than temperature *per se* (Shankar et al. 2019). With climate change, the indirect energetic costs of changes in plant or insect phenologies (Scridel et al. 2018), or shifting resources (Shankar et al. 2019), could have greater impacts on energy budgets than direct costs such as thermoregulation. Our finding that declining capture rates (Figure 1; Appendix 3), were significant for three hummingbird species (Mountain Velvetbreast (*Lafresnaya lafresnayi*), Sapphire-vented Puffleg (*Eriocnemis luciani*), and Black-tailed Trainbearer (*Lesbia victoriae*)) may support this hypothesis, but more study is needed.

Finally, it is important to note that there may be synergistic effects linking climate change with other anthropogenic impacts on these bird populations. Climatic disruption may act as a systemic threat, but mechanisms driving transformation of ecosystems can be complex with multiple stressors such as pathogens (Bergstrom et al. 2015, Kilpatrick and Wheeler 2019), changes in insect abundance (Scridel et al. 2018, Lister and Garcia 2018), or anthropogenic land use (Sirami et al. 2017) possibly acting cumulatively. For example, Scridel et al. (2018) found evidence of responses of montane bird populations to climatic events such as extreme weather and temperature regimes, as well as land use change. Although very few studies truly integrate climate change and land use (Sirami et al. 2017), a variety of taxa may respond more to climate change than to land use in terms of species distributions (Lavergne et al. 2006, Hockey et al. 2011, Kampichler et al. 2012, Fox et al. 2014). However, little is known about how synergistic effects of climate, land use, or other stressors may affect underlying mechanisms affecting bird abundances.

Conclusion

Our finding that the majority of bird species are declining in our High Andes study sites suggests the potential for transformation of ecosystem identity (Keith et al. 2013). While we emphasize that we do not have evidence for avian declines from other sites in the High Andes, long-term data are scarce from any habitat in the hemisphere, so patterns from representative sites need to be strongly considered. While our results point to population declines since 2006 rather than extirpations, some detrimental ecosystem changes may result not only from loss of species, but also from loss of individuals from the system (Gaston and Fuller 2007, Keith et al. 2013). The identity, number and diversity of organisms within a system control its functioning, and reductions or eliminations will often result in an eroded provision of ecosystem goods and services (Buytaert et al. 2011, Lindenmayer and Sato 2018, Cardinale et al. 2012). This is particularly concerning in the decline of Tropical Andean bird populations since birds serve functional roles as predators, pollinators, scavengers, and seed dispersers, and their decline could have cascading effects on ecosystem function and many ecosystem services (Whelan et al. 2008, Sekercioglu 2012). The consequences of rapidly changing global climatic conditions on these tropical mountain forests and grasslands is of high concern, but combined with ongoing severe threats from anthropogenic impacts such as logging, grazing, and agricultural expansion in the region, human-accelerated environmental change appears to be precipitating a potential transformation of this ecosystem.

Additional studies monitoring reproductive success and survival of montane birds would be useful in order to better understand natural variation in population size and the demographic mechanisms that underpin changes in species’ abundance. More intensive, long-term studies would enhance our understanding of the key factors that determine population trends and elucidate more complex mechanisms, such as energetic and phenological effects (Scridel et al. 2018, Shankar et al. 2019), pathogens (Kilpatrick and Wheeler 2019) and habitat destruction (Kattan et al. 1994, Sirami et al. 2017), that may interact with climate factors and play a role in population change (Scridel et al. 2018).

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