






Bird extirpations and community dynamics in an Andean cloud forest over 100 years of land-use change

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Abstract: Long-term studies to understand biodiversity changes remain scarce—especially so for tropical mountains. We examined changes from 1911 to 2016 in the bird community of the cloud forest of San Antonio, a mountain ridge in the Colombian Andes. We evaluated the effects of past land-use change and assessed species vulnerability to climate disruption. Forest cover decreased from 95% to 50% by 1959, and 33 forest species were extirpated. From 1959 to 1990, forest cover remained stable, and an additional 15 species were lost—a total of 29% of the forest bird community. Thereafter, forest cover increased by 26% and 17 species recolonized the area. The main cause of extirpations was the loss of connections to adjacent forests. Of the 31 (19%) extirpated birds, 25 have ranges peripheral to San Antonio, mostly in the lowlands. Most still occurred regionally, but broken forest connections limited their recolonization. Other causes of extirpation were hunting, wildlife trade, and water diversion. Bird community changes included a shift from predominantly common species to rare species; forest generalists replaced forest specialists that require old growth, and functional groups, such as large-body frugivores and nectarivores, declined disproportionately. All water-dependent birds were extirpated. Of the remaining 122 forest species, 19 are vulnerable to climate disruption, 10 have declined in abundance, and 4 are threatened. Our results show unequivocal species losses and changes in community structure and abundance at the local scale. We found species were extirpated after habitat loss and fragmentation, but forest recovery stopped extirpations and helped species repopulate. Land-use changes increased species vulnerability to climate change, and we suggest reversing landscape transformation may restore biodiversity and improve resistance to future threats.

Keywords: Andean cloud forests, community shifts, local extinctions, population extirpations

Extirpaciones de Aves y las Dinámicas Comunitarias en un Bosque Nuboso Andino durante más de Cien Años de Cambios de Uso de Suelo

Resumen: Los estudios a largo plazo para entender cambios en la biodiversidad todavía son escasos – especialmente en las montañas tropicales. Examinamos los cambios en la comunidad de aves del bosque de San Antonio en los Andes colombianos, desde 1911 hasta 2016. Evaluamos los efectos pasados del cambio en el uso del suelo y analizamos la vulnerabilidad de las especies ante la disrupción climática. La cobertura del bosque disminuyó del 95% al 50% para el año 1959, y 33 especies de bosque fueron extirpadas. Desde 1959 y hasta 1990, la cobertura permaneció estable y se perdieron 15 especies más – un total del 29% de la comunidad de aves de bosque. A partir de ahí la cobertura del bosque incrementó en un 26% y 17 especies recolonizaron el área. La principal causa de las extirpaciones fue la pérdida de conectividad con los bosques adyacentes. De las 31 (19%) especies de aves extirpadas, 25 especies tienen una distribución periférica a San Antonio, principalmente en las tierras bajas. La mayoría de las especies aún tenían presencia regional, pero las conexiones rotas entre los bosques limitaron su recolonización. Otras causas de las extirpaciones fueron la caza, el mercado de fauna y el desvío de cursos de agua. Los cambios en la comunidad de aves incluyeron una transición de especies predominantemente comunes a

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Article impact statement: 100 years of land-use change have produced bird extirpations and abundance declines in an Andean mountain site. Paper submitted July 1, 2018; revised manuscript accepted September 23, 2019.

especies raras; las especies generalistas de bosque reemplazaron a las especies especialistas que requieren bosques maduros y los grupos funcionales, como los grandes frugívoros y nectarívoros, declinaron desproporcionadamente. Todas las aves dependientes del agua fueron extirpadas. De las 122 especies que permanecen en el bosque, 19 son vulnerables a la disrupción climática, diez han disminuido en abundancia y cuatro se encuentran amenazadas. Nuestros resultados muestran una pérdida inequívoca de especies y cambios en la estructura y abundancia de la comunidad de aves a escala local. En general, encontramos que las especies fueron extirpadas después de la pérdida y fragmentación del hábitat, pero la recuperación del bosque detuvo las extirpaciones y ayudó a las especies a recolonizar. Los cambios en el uso de suelo incrementaron la vulnerabilidad de las especies ante el cambio climático, por lo que sugerimos que revertir la transformación del paisaje podría restaurar la biodiversidad y aumentar la resistencia a futuras amenazas.

Palabras Clave: bosques nubosos andinos, cambios en la comunidad, extinciones locales, extirpaciones poblacionales

摘要: 目前,关于生物多样性变化的长期研究还很少见,特别是在热带山区。我们研究了哥伦比亚安第斯山脉圣安东尼奥地区一个云雾林在 1911-2016 年间的鸟类群落变化。本研究评估了过去土地利用变化的影响和物种对气候变化的脆弱性。1911-1959 年,该地区森林覆盖率由 95% 下降到 50%,33 种森林物种局部灭绝。1959-1990 年,森林覆盖率保持稳定,但仍有 15 种鸟类绝迹,占森林鸟类群落总数的 29%。此后,森林覆盖率增加了 26%,且有 17 个物种在该地区重新定殖。物种局部灭绝的主要原因是相邻森林之间的连接被破坏。在 31 种 (19%) 灭绝的鸟类中,25 种在圣安东尼奥周围也有分布,且主要在低地地区。这些鸟类大多仍有区域性分布,但森林连接被破坏限制了它们重新定殖。局部灭绝的其它原因还包括狩猎、野生动物贸易和引水工程。鸟类群落的变化包括占优势的鸟种从常见种向稀有种转变;森林中的广幅种取代了需要原始林的狭域种;而包括大型食果动物和食蜜动物在内的功能群则不成比例地减少。所有依赖水体的鸟类都消失了。在残余的 122 种森林物种中,19 种易受到气候变化的影响,10 种种群数量已大量下降,还有 4 种受到胁迫。我们的研究结果展现了局部尺度上明确的物种灭绝和种群结构及数量变化。一般来说,栖息地丧失和破碎化会导致物种局部灭绝,但森林恢复可以阻止灭绝,并帮助物种重建种群。土地利用变化增加了物种对气候变化的脆弱性,我们认为逆转景观改造有助于恢复生物多样性,并提高物种对未来威胁的抵抗力。【翻译:胡怡思;审校:聂永刚】

关键词: 局部灭绝,群落转变,种群灭绝,安第斯云雾林

Introduction

Assessing the effects of drivers of change on local biotic assemblages is a major challenge (Brook et al. 2008). In the tropics, habitat loss and fragmentation have extirpated species and caused declines of functional groups (Sekercioglu et al. 2004; Sodhi et al. 2004). These historical legacies may influence future species responses to environmental change and have far-reaching effects for the provisioning of ecosystem services (Bregman et al. 2014; Essl et al. 2015). The effects of climate disruption are complex (Pimm 2009). Globally, most species extinctions are predicted in tropical mountains—through upward range shifts due to rising temperatures or disruption of habitat conditions (Sekercioglu et al. 2008; Anderson et al. 2013; Helmer et al. 2019). Such places hold many endemic species (Hazzi et al. 2018) and the interactions with further land-use change could worsen declining trends (Oliver & Morecroft 2014).

Long-term studies provide evidence for temporal changes in community composition and structure that one can relate to their underlying causes. Such studies remain rare for Neotropical bird communities, and the drivers of change may not always be apparent (Blake & Loiselle 2015; Rosselli et al. 2017). Moreover, most work has been in lowlands (e.g., Laurance et al. 2011). Here, we documented changes over a century to the

bird community in the cloud forest of San Antonio, a mountain ridge in the western Andes of Colombia. We used data from bird surveys conducted from 1911 to 1990 and surveyed the site in 2016. We extended our survey into the nearby buffer zone of the Farallones de Cali National Natural Park, where the forest is continuous, to evaluate changes at a regional level.

Our unusually long-term data set allowed assessment of the conservation significance of species losses and gains. Species losses occur after habitat loss and may continue after forest fragmentation according to an “extinction debt” (Haddad et al. 2015; Halley et al. 2016). Delayed extinctions occur for tropical birds (Shaw et al. 2013; Boyle & Sigel 2015), but what happens when forest cover recovers? Species losses may continue or stop. Does the recovered forest hold a “species credit” (Latta et al. 2017) that allows some locally extirpated species to recolonize? Furthermore, local dynamics depend on habitat configuration at landscape and regional scales (Opdam & Wascher 2004). We asked whether species with peripheral populations were more likely to be extirpated with the loss of connectivity from San Antonio to adjacent forests (Terborgh & Winter 1983; Nathan et al. 1996).

Although biodiversity loss at a global scale is well understood (Pimm et al. 2014), there is controversy at the

local level. Recent studies contend that species losses can be compensated for by increasing numbers of other species. The result is no net loss at local scales (Gonzalez et al. 2016). Cardinale et al. (2018) disputed the generality of that conclusion because most of these studies lack appropriate baselines and considered only species richness (Hillebrand et al. 2018). We evaluated how community structure and abundance changed over time, assessed trends for functional groups, and provided measures of functional homogenization (Clavel et al. 2011).

Finally, it is critical to understand how habitat loss and climate disruption intersect (Pimm 2008, 2009). If habitat loss exterminates vulnerable species; they cannot then succumb to climate change (or they may remain in a perilous state and be extirpated later). If habitat loss extirpates lowland species, which is where land-use change is greater, montane species are spared. Montane species are more vulnerable to climate disruption, so for them the impacts of land-use change and climate will be additive (Brook et al. 2008).

Our work addressed 3 key topics for conservation that transcended our case study of biodiversity changes in a tropical mountain bird community. We asked whether local species losses are offset by species additions (no net biodiversity loss); whether regional habitat loss influences species extirpations; and evaluated species vulnerability to future climate change.

Methods

Study Area and Historical Data Sources

The San Antonio mountain ridge is 8795 ha. Elevations range from 1700 to 2250 m, and it extends 25 km north-east from the Farallones de Cali massif (4100 m elevation). San Antonio is at the intersection between the humid Pacific lowlands, the drier Cauca Valley, and the high Andean forests of Farallones de Cali (Fig. 1).

We assembled data from 5 bird surveys conducted in the 20th century. Results of the first provide a pre-disturbance baseline and are from an expedition led by Frank M. Chapman (1917) to Colombia from 1911 to 1915. Their collecting efforts aimed to obtain a complete inventory of birds present at each site to evaluate species biogeographical limits (Kattan et al. 2016). The second data source is Mervin G. Palmer's 1907–1908 collection of 104 species (obtained from <http://www.vertnet.org>). Chapman (1917) wrote, "[Our] collections . . . in connection with those of Palmer, are believed to contain a large proportion of the birds which occur in this locality."

The third data source corresponded to a midcentury peak-disturbance period after construction of the Cali to Buenaventura road from 1920 to 1940. Alden H. Miller conducted a 1-year study in 1959 that provided de-

tailed natural history accounts and qualitative abundance estimates for most species recorded (Miller 1963). The latter 2 sources are from a period after long-term forest fragmentation. M. Giraldo surveyed the site in 1985 (unpublished data), and Kattan et al. (1994) conducted surveys from 1989 to 1990.

Contemporary Bird Surveys

We resurveyed birds in 2 fragmented-forest areas at San Antonio divided by the Cali-Buenaventura road: Cerro de la Horqueta and the area known as Km-18. To evaluate the changes at the regional scale, we surveyed the La Teresita area in the buffer zone of the Farallones de Cali National Natural Park (Fig. 2). Here, the forest was extensive (>100,000 ha) and had elevational continuity up to 4,100 m.

We visited the 3 localities 4 times from May 2015 to February 2016. A sampling session consisted of 3 consecutive days; 2 observers sampled each site simultaneously (Forcey et al. 2006). Observations were made at 13 point-count stations separated by >150 m that covered edge and forest interior at each of the 3 sites. Counts lasted 10 minutes and had a fixed radius of 25 m (Ocampo-Peñuela & Pimm 2015). We complemented our efforts with survey data from San Antonio (J. Orejuela-Gartner et al. [2007], C. Montealegre-Talero [2009, unpublished data]), an exploratory survey at the locality of Monteguadua in the buffer zone of the Farallones de Cali National Park and eBird data for San Antonio (Cornell Lab of Ornithology 2017).

Species Classification

We classified birds as forest specialists, forest generalists, and nonforest species. Specialists live only in old-growth forest interior and edges. Generalists are associated with early and late second-growth forest and edges. Nonforest species inhabit open areas with scattered trees. We also assigned species to functional groups based on Kattan et al. (1994) and Renjifo (1999) with some modifications (Supporting Information).

We also classified birds into core or peripheral species based on their biogeographical distribution (Andes, Pacific, or Cauca Valley) and elevational center of abundance (Stotz et al. 1996; Renjifo 1999). Core species had lower montane (1000 to 1700 m) to middle montane (1700 to 2500 m) Andean distribution. Peripheral species had lowland (0–1000 m) and upper montane (>2500 m) centers of abundance. We considered birds that occur on the Pacific coast and in the Cauca Valley peripheral species.

Changes in Community Composition

We compiled data on the historical core avifauna (i.e., birds regularly breeding in or migrating to the area

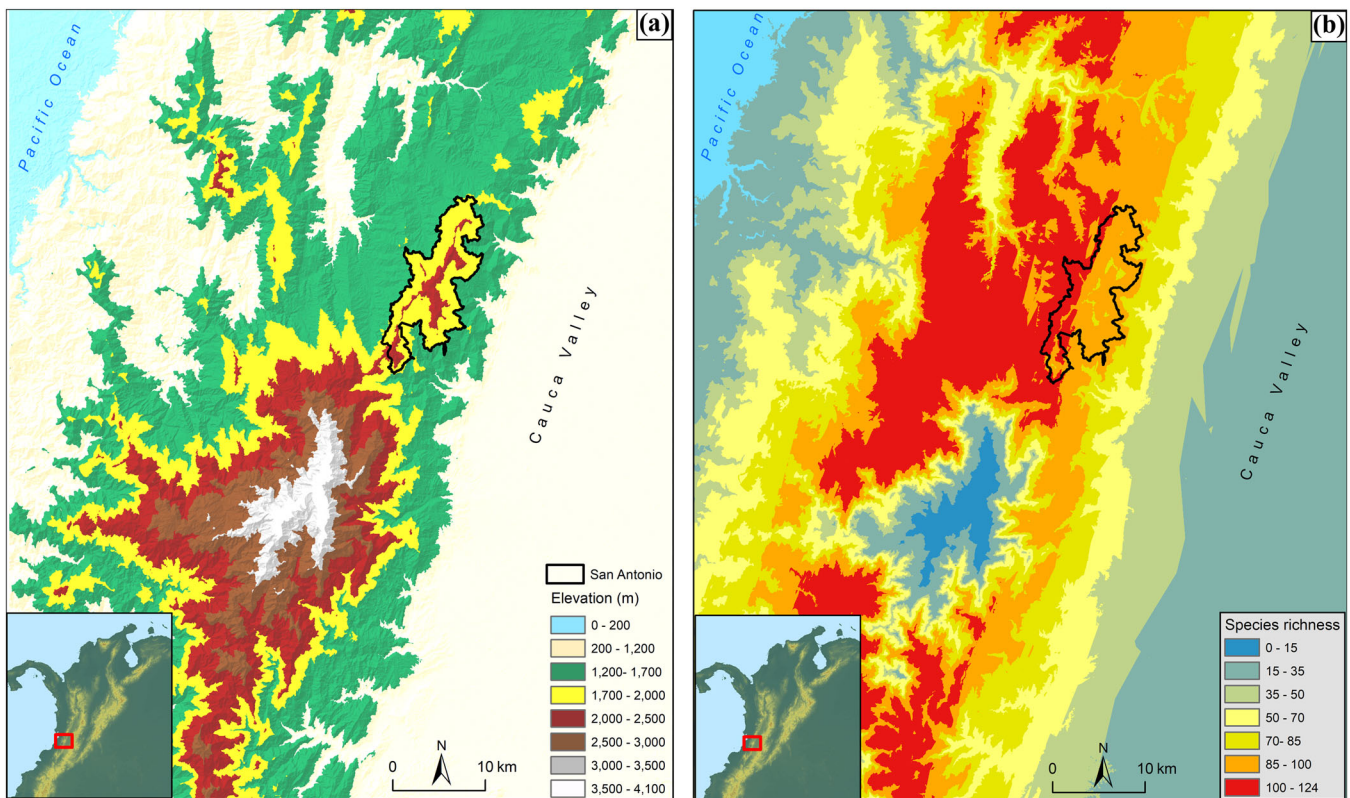


Figure 1. (a) San Antonio is a mountain ridge extending north-northeast of the Farallones de Cali massif in the western Andes of Colombia and (b) forest bird species richness in the area.

excluding vagrants [Remsen 1994]) as a baseline to evaluate extinctions and colonizations. We assessed individuals individually from each survey. In case of doubt (e.g., low detectability), we conservatively considered species as present. If a species was not recorded in a historical survey, but it was recorded in a later survey, we considered the species to have been present. Our criteria may underestimate the number of recolonizations that occurred, but they kept our estimates of species extirpations low. We classified species as extirpated up to 2016 if there were fewer than 5 records the previous 10 years.

We calculated the richness-based species-exchange ratio (SER_r) (Hillebrand et al. 2018) as a measure of how many species are exchanged between surveys: $SER_r = (S_{imm} + S_{ext})/S_{tot}$, where S_{imm} is newly immigrated species, S_{ext} is extirpated species from the previous survey, and S_{tot} is total number of species across both surveys. We calculated the proportion of forest specialists to forest generalists as a measure of functional homogenization (Clavel et al. 2011).

Abundance Changes

To obtain population trends, we compared results of the different sampling methods by assigning species to 5

categories of relative abundance in each survey (Curtis & Robinson 2015; Rosselli et al. 2017; Freeman et al. 2018): abundant, common, fairly common, uncommon, and rare. We estimated population trends for 1911–1990 (forest loss and species extirpations) and 1990–2016 (forest recovery and species recolonizations) and historical population trends for each bird species after 100 years (details in Supporting Information).

Our criterion for a difference in relative abundance was a shift in at least 2 categories from the historical to the contemporary (e.g., from fairly common to rare). Otherwise, the population was considered stable (e.g., from fairly common to uncommon). This makes our estimates conservative and less likely to reflect small changes in abundances that may arise from the natural variation in populations and from methodological artifacts.

We compared changes in relative categories for the forest bird community by summarizing information in the historical surveys (1911–1959, representing an estimate for the early to mid-20th century) and contemporary surveys (2007–2016, an estimate for the 21st century). We did so to make our estimates more robust because few species had relative abundance categories in all surveys. We conducted a chi-square test to evaluate whether the abundance distribution differed between both periods.

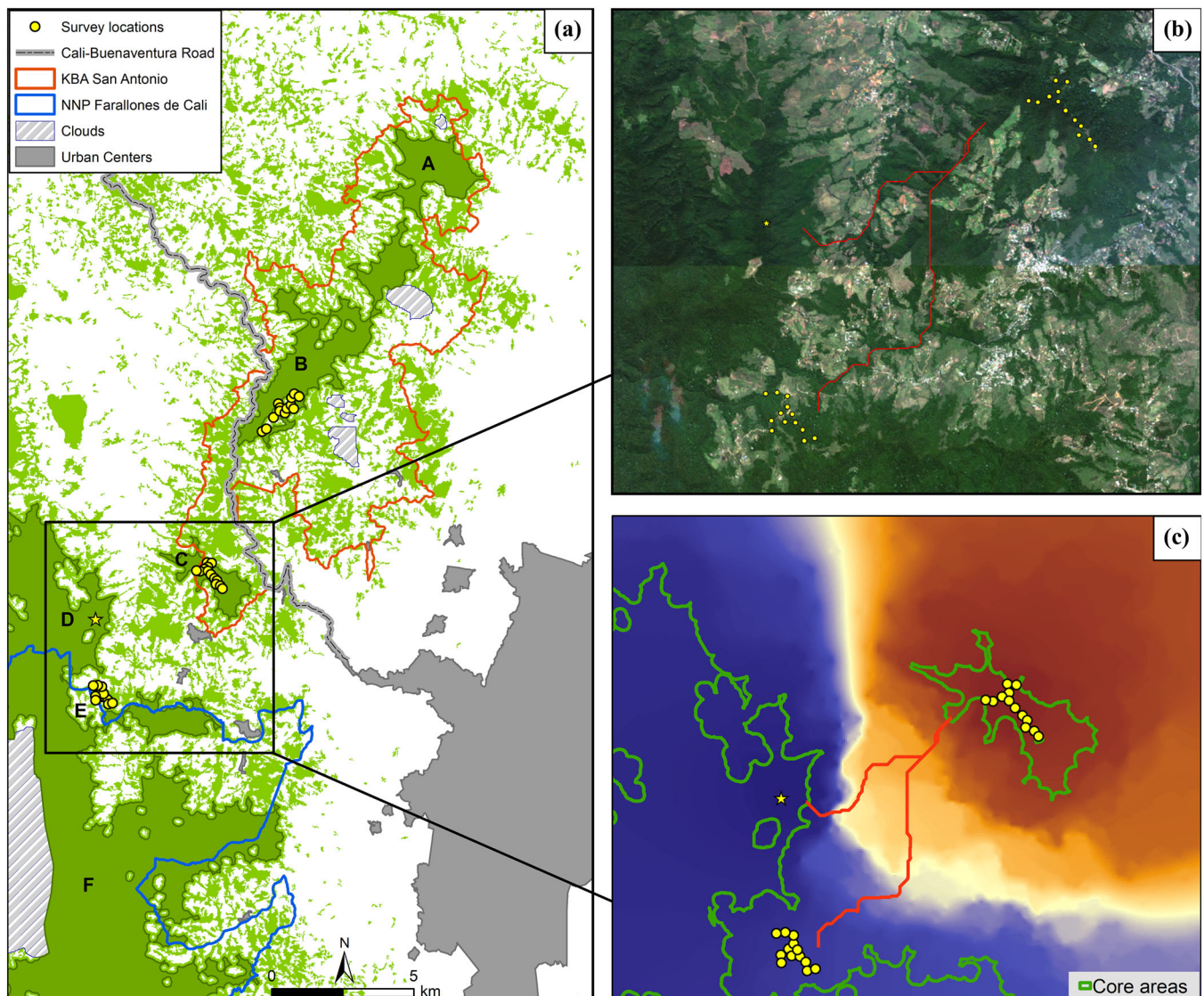


Figure 2. Loss of forest connectivity at the landscape level: (a) forest cover in 2016 based on a supervised forest and nonforest classification of 5-m resolution satellite imagery (A–F, core forest areas of at least 100 ha; A, Chibcoral-Dapa; B, Km-18; C, Cerro de la Horqueta (San Antonio summit); D, Monteguadua; E, National Natural Park Farallones de Cali; circles, point-count surveys; star, 1-day inventory at Monteguadua); (b) close-up of satellite imagery showing least-cost paths through forest between core areas C and E in a largely fragmented area, and (c) movement barrier arising from limited forest pathways between core areas C and E based on a model of landscape connectivity that analogizes dispersal to current flow in an electric circuit (see Methods).

Forest-Cover Changes

We combined multiple sources to estimate forest-cover changes between 1911 and 2016. We assumed a pre-disturbance baseline of ~95% forest cover in 1911 (Chapman 1917), which was before the construction of the Cali-Buenaventura road. For the mid-century peak-disturbance time, we digitized a 1977 land-cover and land-use map (scale 1: 10,000, plate 299-II-B-I) of the Agustin Codazzi Geographical Institute of Colombia, based on aerial photographs. This map covered the southern portion of San Antonio (28%), where the historical and con-

temporary surveys were conducted. It is representative of Miller's survey in 1959 because forest cover remained stable through the mid-20th century (Kattan et al. 1994). To obtain current forest cover, we performed a supervised forest versus nonforest classification, a mosaic of RapidEye Ortho Level 3A imagery at 5-m resolution from 22 November 2016 (tile_1840707) and 25 July 2015 (tile_1840607) (details in Supporting Information). We then determined forest-cover changes by comparing the 1911 baseline with the forest values of 1977 and 2016 maps.

Regional Changes

We detected core forest areas of at least 100 ha (Bregman et al. 2014) in our 2016 forest-cover map (Supporting Information). We analyzed connectivity between them with a model that analogizes the movement of organisms in the landscape to current flow in an electric circuit. Core areas connected through multiple forested pathways possess less resistance to movement (i.e., electric flow) than others with few available routes. We performed these computations with Circuitscape 4.0 (McRae et al. 2008) and all spatial analysis with ArcGIS 10.4.1.

To investigate geographical patterns of change in species richness, we overlapped species ranges of the historical forest avifauna refined by their elevational amplitude (the difference between the maximum and minimum elevations). Distribution maps were from Birdlife International (2016) and rasterized to a resolution of 30 m (900 m²) per cell size. We also created richness maps for persisting and extirpated species and divided their values on a per-pixel basis by the richness values of the historical forest avifauna. These ratios were used to visualize geographical patterns of change.

Vulnerability to Climate Disruption

We assessed whether the 122 forest species that remained are vulnerable to climate disruption based on their degree of specialization and past population trends. We grouped them into 1 of 6 combinations of declining versus stable abundance, 4 degrees of specialization (habitat specialist, narrow elevational range, both habitat specialist and narrow elevational range, neither habitat specialist nor narrow elevational range). We used a chi-square test to determine whether there were significant differences among numbers observed. We tested whether body mass and size of the elevational range affected population density with an unweighted least squares multiple regression.

We did not model the elevational shifts to predict whether species must move to remain within existing thermal limits because of the uncertainties associated with these models (McCain & Colwell 2011). Rather, we were interested in identifying extirpation-prone species through vulnerability analysis at the local scale (Foden et al. 2013; Fortini & Schubert 2017).

Results

Bird Community Dynamics 1911–2016

In 1911 San Antonio had 201 bird species (105 forest specialists, 62 forest generalists, 34 open-area birds) and was 95% forested (Supporting Information). Forest declined to 48.6% after construction of the Cali to Buenaventura road from 1920 to 1940. In 1959, 33 forest birds

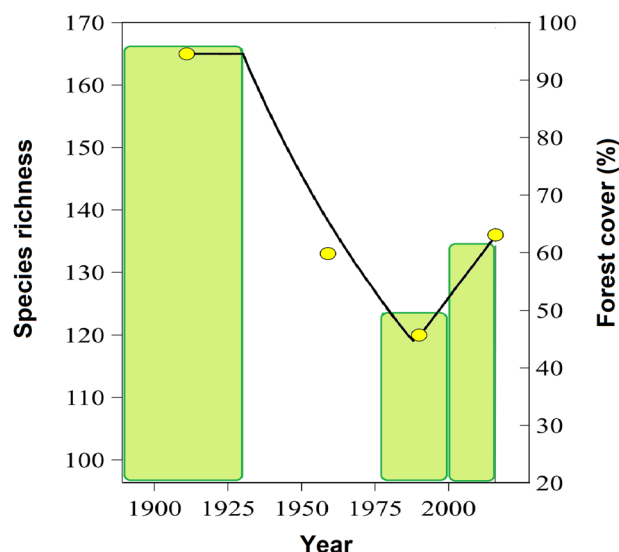


Figure 3. Trends in historic number of species in the San Antonio cloud forest (western Andes of Colombia) relative to forest cover (bars, forest cover for intervals with data; circles, bird surveys fitted to a relaxation formula for the decay in species richness at forest fragments [Halley et al. 2016]).

were extirpated (26 specialists, 7 generalists). Six species from open areas colonized. Forest cover remained stable through 1990, yet 14 more birds were extirpated (total 47 species or 28% of the historical forest community) and 37 birds decreased in abundance. There were 9 colonizations of forest birds and 4 in open areas.

Forest cover increased 26.1% after the late 1990s (gain of 1270 ha of naturally regenerated forest; current extent 6,065 ha or 57.6%; classification accuracy 98.1%). Recent surveys (2000–2016) showed no further extirpations. Instead, 17 species reestablished populations (Fig. 3 & Supporting Information). Ten were already missing by 1959, but surveys recorded them again in the early 2000s (e.g., Colombian Chachalaca [*Ortalis columbiana*] had a continuous presence since 2003 [Cornell Lab of Ornithology 2017]). Nine new forest birds colonized. Three were forest specialist birds within their elevational range, and the others were forest generalists. We recorded 4 new open-area species. From 1990 to 2016, 7 species declined and 24 species increased their number of populations; most species remained stable (Supporting Information).

Community Changes After 100 Years

Contemporary surveys showed 31 extirpated forest birds, 24 specialists, and 7 generalists, for a total of 19% of the historical avifauna, 23 of them lost since 1959 (Supporting Information). The richness-based species-exchange ratio between surveys ranged from 0.12 to

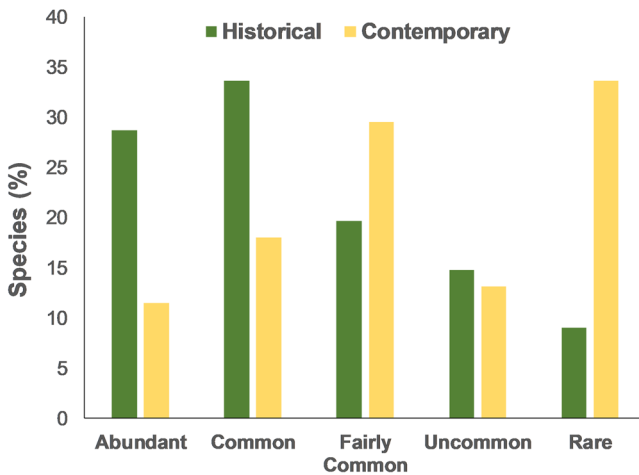


Figure 4. Changes in relative abundance categories for birds in the cloud forest of San Antonio, Colombia, in the historical (early to mid-20th century [1911–1959]) and contemporary (21st century [2007–2016]) periods.

0.19. Between the historical and contemporary bird community it was 0.24 (24% species exchange). The forest community became more functionally homogenous; the proportion of specialists to generalists declined from 63% to 43% ($Z = 3.60$, $p < 0.001$).

There was a shift from a preponderance of abundant and common species to a community dominated by uncommon and rare species ($X^2 = 35.34$, $p < 0.001$) (Fig. 4). Compared with historical levels, 43 species had lower relative abundances, 4 increased, and 105 were stable (Supporting Information).

We identified 17 functional groups formed by 3–19 species (Supporting Information). Eight of them had 50% or more of their species extirpated or declining in abundance. Large-canopy frugivores declined substantially, whereas half of all nectarivores declined in abundance. All 4 water-dependent birds were extirpated (Supporting Information).

Patterns of Landscape Change

We detected 3 core forest areas of >100 ha in the San Antonio region: Cerro de la Horqueta (227 ha), Km-18 (1041 ha), and Chicoral-Dapa (333 ha) (Fig. 2). The Cali-Buenaventura road divides the first 2 core areas, and we observed only minor difference in species composition that resulted from 4 species not being found in Cerro de la Horqueta and 1 species not being detected in Km-18. These 5 species (Supporting Information) were recorded recently in the core area of Chicoral-Dapa according to the eBird basic data set (2017) and a 2016 checklist (M. Gable, personal communication).

Seven extirpated species in the San Antonio region were present in the buffer zone of the Farallones de Cali National Natural Park. Four of these species were recorded at La Teresita (Supporting Information) and had been present since the mid-20th century (Gniadek 1973, unpublished data). At Monteguadua, we recorded 3 additional extirpated species and 1 that was absent from the core area of Cerro de la Horqueta (Supporting Information).

Patterns of Regional Change

Eighty-one percent of extirpated birds were peripheral species with source populations in adjacent biotic regions. The highest ratios of extirpated species concentrated in the Pacific lowlands, whereas stable species were widespread (Fig. 5). We attributed this difference to a <5 km deforestation gap. It was present in our 1977 map and remained a prevalent feature (confirmed by visual inspection of the area from 1984 to 2016 with the Timelapse of Google Earth Engine [<https://earthengine.google.com/timelapse/>]). This gap was in a critical connecting point for both the Pacific lowlands and Andean highlands, where the highest species richness of the historical avifauna occurred (Fig. 1). Our connectivity analysis showed this gap is the major barrier for dispersal between the 2 regions due to limited available pathways to species movement through forests.

Species Vulnerability to Climate Disruption

Of the 19 habitat specialists that have narrow elevational ranges, 10 (53%) declined; overall, 35% of species declined. These 19 include 4 species (Supporting Information) categorized as vulnerable on Colombia's Bird Red List (Renjifo et al. 2014). For the entire bird community, there was no effect of body mass or elevational range on population density ($F_{2,135} = 0.8$, $p = 0.44$) (Supporting Information), meaning that large-bodied and species with narrow vertical ranges were not less abundant.

Discussion

We revealed the impacts of land-use change over a century (1911–2016) on the dynamics of the bird community in the cloud forest of San Antonio. Species were lost as forest cover declined to 50% following the construction of a major road from 1920 to 1940. Forest cover remained stable up to 1990, but extirpations continued (Kattan et al. 1994). Given what is known about the timing and extent of extinction, loss of forest cover is likely the best explanation for the continued extirpations (Brooks et al. 1999; Ferraz et al. 2003; Halley et al. 2016). Forest cover recovered starting in the late 1990s, a general trend observed in the Colombian Andes (Sanchez-Cuervo et al.

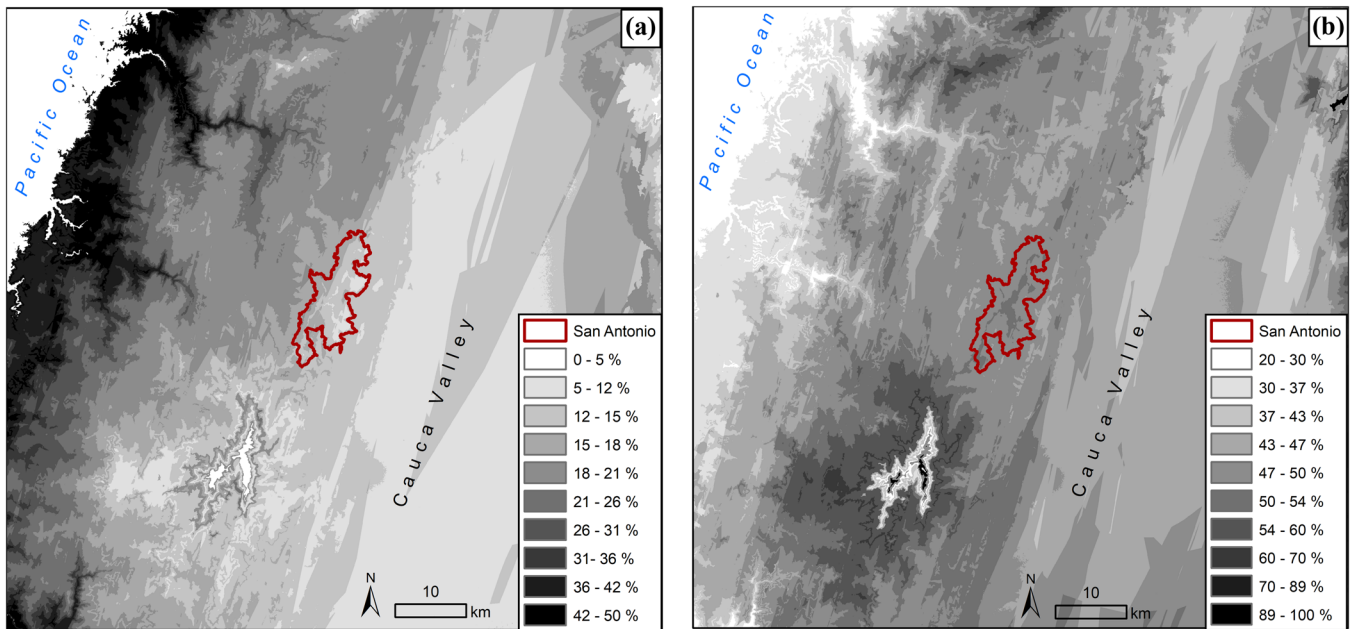


Figure 5. (a) Extirpated species concentrated in the Pacific lowlands as a percentage of expected species richness and (b) stable species without a detectable abundance change over time as a percentage of expected species richness.

2012). There were no further species losses and several species recolonized. More extirpations would surely have occurred had there been less forest remaining and it had been more extensively fragmented.

Other factors help explain species losses. The Toucan Barbet (*Semnornis ramphastinus*) was heavily traded by the 1950s (Lehmann 1957), and hunting affected species such as the Pale-vented Pigeon (*Patagioenas cayennensis*). But given the deforestation patterns in the region, land-use changes are the most parsimonious explanation for species extirpations and colonizations; other factors had added impacts (Brook et al. 2008). Could climate change have explained the loss of species up to 1990? Extirpated species were not the most vulnerable to climate disruption, and it would be surprising if species extirpations stopped or reversed thereafter.

Our results on species extirpations are conservative. Collecting efforts of the early 20th century yielded more species than later surveys, even though sampling methods have improved and survey effort increased. Thus, other extirpations may have gone unnoticed. Several species recolonized. Were they really extirpated? The evidence suggests so. Most species have been lost in other well-studied fragments in the central Andes (Renjifo 1999; Castaño-Villa & Patiño-Zabala 2008). Others are highly vocal and detectable when present, but have not been recorded since the mid-20th century (Supporting Information). However, some species may have survived in the agriculture-dominated mosaics between remnant forests. Yet claims of substantial biodiversity in these patches touted by those who stress

“countryside conservation” (e.g., Mendenhall et al. 2012) are hard to reconcile with the overwhelmingly dominant role of forest loss in driving species extirpations.

Our work sheds light on 3 important conservation topics that transcended our case study. First, our findings factor in the debate on whether local species losses are offset by colonizations, such that there might be no net biodiversity loss (Cardinale et al. 2018). Compared with the historical bird community in 1911, San Antonio lost 31 forest birds (24 specialists and 7 generalists). It gained only 18 forest birds (7 specialists and 11 generalists). Simply, there was a decline in species richness, and there were far fewer forest specialists as well. At least 14 non-forest species colonized due to the increase of clearings, but it is the change in forest birds that addresses the question at hand, not the overall species richness (Primack et al. 2018).

We also found that species have declined in abundance over time (Fig. 4). This trend may be an artifact of different sampling methods, but, again, our methods were conservative. We required changes in 2 classes of relative abundance as evidence of decline or increase. There were many more declines than increases. Moreover, the raw numbers of collected individuals also indicated the depletion in abundance for most of the forest community. For instance, Chapman (1917) secured 8 individuals of both the Golden-headed Quetzal (*Pharomachrus auriceps*) and Red-ruffed fruitcrow (*Pyroderus scutatus*). The former is now uncommon and the latter is extirpated. Other changes mirror well-known declines elsewhere. Our estimates are consistent with the

documented trend of the Canada Warbler (*Cardellina canadensis*), which has declined 66% in the last 50 years (Sauer et al. 2017). In our classification, this migrant went from abundant in Chapman's time (1911), to fairly common in 1990, to uncommon in our contemporary survey (2015–2016).

Second, we investigated whether regional habitat loss influences local species extirpations. This involves different processes at a range of geographical scales; we chose to study the spatial arrangement of the extirpated species ranges. Because San Antonio is a mid-elevation mountain ridge in the Andes, the loss of forest continuity with the adjacent regions (Andean highlands, Pacific and Cauca Valley lowlands) resulted in a differential loss of peripheral species. Several of these species are still present regionally in nearby localities of the Farallones de Cali National Park, and further explorations may find others (Palacio et al. 2017). Although populations in the periphery of their ranges may not be intrinsically vulnerable (Channell & Lomolino 2000), a decrease in connectivity limits the dispersal of species whose source populations are found in other regions or located at lower or higher elevations. Thus, peripheral species whose ranges only partially overlap with a particular region may be more prone to extirpation (Terborgh & Winter 1983; Nathan et al. 1996).

Third, even assuming no future loss of forest cover at San Antonio, species losses from climate disruption are likely and their causes complex (Pimm 2009). Rising temperatures will force species in our study area to higher elevations, as they have elsewhere in the Andes (Forero-Medina et al. 2011). To complicate matters, an analysis of recent trends for the region shows an increase in the number of dry days (Cardona-Guerrero et al. 2014). The diversion of water for urbanization (Kattan et al. 1994) has already contributed to the extirpation of water-dependent birds such as the Crested Ant-Tanager (*Habia cristata*), a bird found near streams, and others that depend on humid conditions such as the Fulvous-dotted Treerunner (*Margarornis stellatus*). Furthermore, there are projected precipitation changes across the tropics that may increase extirpation risks in mountain sites (McCain & Colwell 2011).

Our vulnerability analysis showed that most species that are intrinsically vulnerable to climate change, based on their ecological and biological traits, declined in abundance (Supporting Information). Although the numbers are too small for statistical significance, they suggest land-use changes have left the remaining bird species in a perilous state, rather than hardened it against future losses. For instance, many species with narrow elevational ranges are also forest specialists. Their abundances in the contemporary survey were below their historical abundances, and their populations were declining. We found no relationship between elevational range and population density, meaning that these past changes are

independent of future threats. Also, there were other forest birds that were not as sensitive to climatic disruptions, but contemporary survey results showed they are at immediate risk of extirpation because they are rare and decreasing. The overall effect is increasing the vulnerability of the community to new drivers of change.

The vulnerability of the cloud forest community in San Antonio was most apparent when in the analysis of functional groups. Eight out of 17 functional groups had 50% or more of their species extirpated or declining in abundance. Canopy association, large body size, and ecological specialization were the main traits shared. Large-bodied frugivores lost several species, yet they are critical to maintaining seed-dispersal processes (Palacio et al. 2016). More than 50% of nectarivores (hummingbirds and flower piercers) declined in abundance, and 2 were lost (Supporting Information). They are essential pollinators, and they are ecologically dominant in Andean mountain forests (Renjifo et al. 1997). Therefore, future species losses, if not avoided, may profoundly alter forest dynamics and capacity for provisioning of ecosystem services (Sekercioglu et al. 2004).

Our study revealed the impacts of one hundred years of land-use change. There were important losses that included extirpations, population declines, and increased vulnerability to future threats. But there were also important gains as the forest recovered, including recolonizations and population increases. Our results suggest that an effective way to conserve biodiversity during climate disruption will be to counter the past effects of landscape transformation by increasing the extent and connectivity of remaining habitat patches at local and landscape scales. These actions may give disappearing cloud forest lineages a second opportunity on Earth.

Acknowledgments

We thank J. Luna-Solarte, G. Ventolini, J. Restrepo, A. Muñoz, and J. Muñoz for field assistance and E. Carvajal and Corporación Autónoma Regional del Valle del Cauca (CVC) for logistical support. The Pontificia Universidad Javeriana Cali funded fieldwork.

Supporting Information

Supplementary methods and results (Appendix S1), historical bird avifauna (Appendix S2), species relative abundance trends (Appendix S3), and climate-change vulnerability assessment (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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