



# Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community

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**Montane species worldwide are shifting upslope in response to recent temperature increases. These upslope shifts are predicted to lead to mountaintop extirpations of species that live only near mountain summits, but empirical examples of populations that have disappeared are sparse. We show that recent warming constitutes an “escalator to extinction” for birds on a remote Peruvian mountain—high-elevation species have declined in both range size and abundance, and several previously common mountaintop residents have disappeared from the local community. Our findings support projections that warming will likely drive widespread extirpations and extinctions of high-elevation taxa in the tropical Andes. Such climate change-driven mountaintop extirpations may be more likely in the tropics, where temperature seems to exert a stronger control on species’ range limits than in the temperate zone. In contrast, we show that lowland bird species at our study site are expanding in range size as they shift their upper limits upslope and may thus benefit from climate change.**

biotic attrition | global warming | mountaintop extinction | range shift | tropical mountain

Climate change is causing many montane species to shift their distributions upslope to track their optimal climate (1–3). Summit-dwelling species lack higher-elevation habitats to receive them and are widely predicted to decline or disappear altogether as upslope shifts drive an “escalator to extinction” (4–6). Indeed, mountaintop extinctions are a primary mechanism underlying the broader projection that climate change alone will lead to extinctions on the order of ~10% of all eukaryotic species on Earth by 2100 (7, 8). Mountaintop extinctions may be more likely in the tropics, where the nearly flat latitudinal gradient in temperature means that tropical montane taxa are unlikely to persist by shifting to higher latitudes, an option that is more available to taxa in the temperate zone where the latitudinal temperature gradient is much steeper (9). In light of these predictions, conservation biologists and global change researchers have substantial interest in documenting the impact of recent warming on the distributions of high-elevation species. If projections of widespread mountaintop extinctions are valid, we expect to uncover empirical examples of mountaintop populations that have been extirpated associated with recent climate change. However, despite a large literature reporting the geographic responses of species to recent climate change, there are surprisingly few examples of recent mountaintop extirpations plausibly driven by climate change (10).

Models that predict mountaintop extinctions to be pervasive assume that temperature is the primary factor that controls range limits of montane species. The observation that species are generally shifting toward historically cooler environments associated with recent temperature increases is strong evidence that temperature is indeed a generally important factor limiting species’ distributions, although biotic interactions can also influence range limits (11). Crucially, however, observed range shifts for temperate zone species typically lag far behind those predicted by recent warming (1). In contrast, observed shifts among tropical species roughly match those predicted by climate shifts (12). These observations suggest the hypothesis that

current mean temperatures (or perhaps factors tightly correlated with temperature) are a dominant driver of most tropical species’ elevational range limits, while additional factors set range limits of temperate zone species. If so, recent temperature increases may be more likely to cause mountaintop extirpations in tropical populations than in temperate zone ones. While populations of high-elevation tropical species are already threatened due to introduced diseases (13–15) and habitat destruction (16), extirpations of tropical mountaintop populations driven primarily by climate change have yet to be documented.

We tested the prediction that populations of high-elevation tropical species are threatened by climate change by examining how birds on a remote Peruvian mountain have shifted their elevational distributions in response to recent temperature increases. We compared the results of a modern survey conducted in 2017 with data from a historic survey conducted in 1985 by J.W.F. and colleagues from the Field Museum. This historic survey was specifically designed to document elevational limits of bird species along a ~8-km river-to-ridgetop transect in the Cerro de Pantiacolla (470 m at the Palatoa River to 1,415 m at the ridge summit) (Fig. 1). This dataset provided the opportunity to test the idea of mountaintop extirpations, because the historic survey documented 16 species of birds that were restricted to the ridgetop (i.e., found only above 1,300 m). Our resurvey, conducted in 2017, covered the same ground at the same time of year and matched the methods of the historic survey (*Methods* and *SI Appendix, Table S1*). The Pantiacolla Transect remains uninhabited by humans and consists of primary evergreen forest. While no anthropogenic land use changes have occurred between

## Significance

Global warming is predicted to constitute an “escalator to extinction” for species that live on mountains. This is because species are generally moving to higher elevations as temperatures warm, and species that live only near mountaintops may run out of room. However, there is little evidence that high-elevation populations are disappearing as predicted. Here, we show that recent warming does indeed act as an escalator to extinction for birds that live on a remote Peruvian mountain. High-elevation species have shrunk in range size and declined in abundance, and several previously common species have disappeared. We suggest that high-elevation species in the tropics are particularly vulnerable to climate change.

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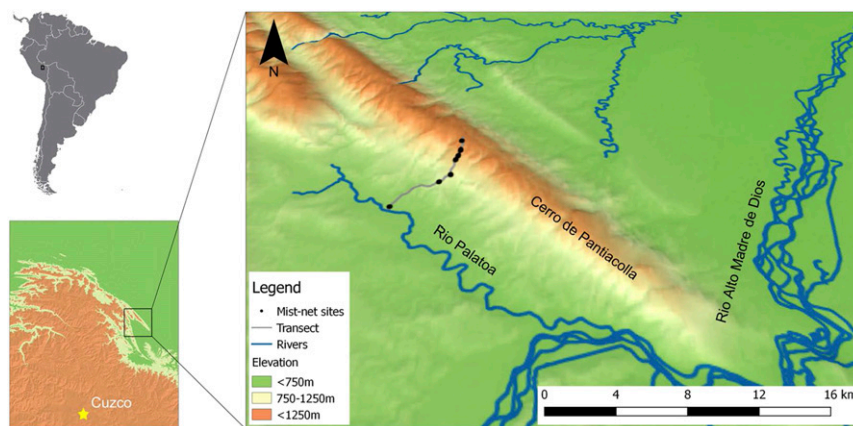
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**Fig. 1.** The Cerro de Pantiacolla rises out of the Amazonian lowlands in southeastern Peru, with elevations from 470 m at the Rio Palatua to 1,415 m at the ridgetop. We measured elevational distributions of bird species along the Pantiacolla Transect (gray line; circles mark mist-net sampling sites) in 1985 and again in 2017. There has been no land use change along the Pantiacolla Transect, which remains covered with primary forest. However, mean annual temperatures have risen by  $\sim 0.42$  °C since 1985.

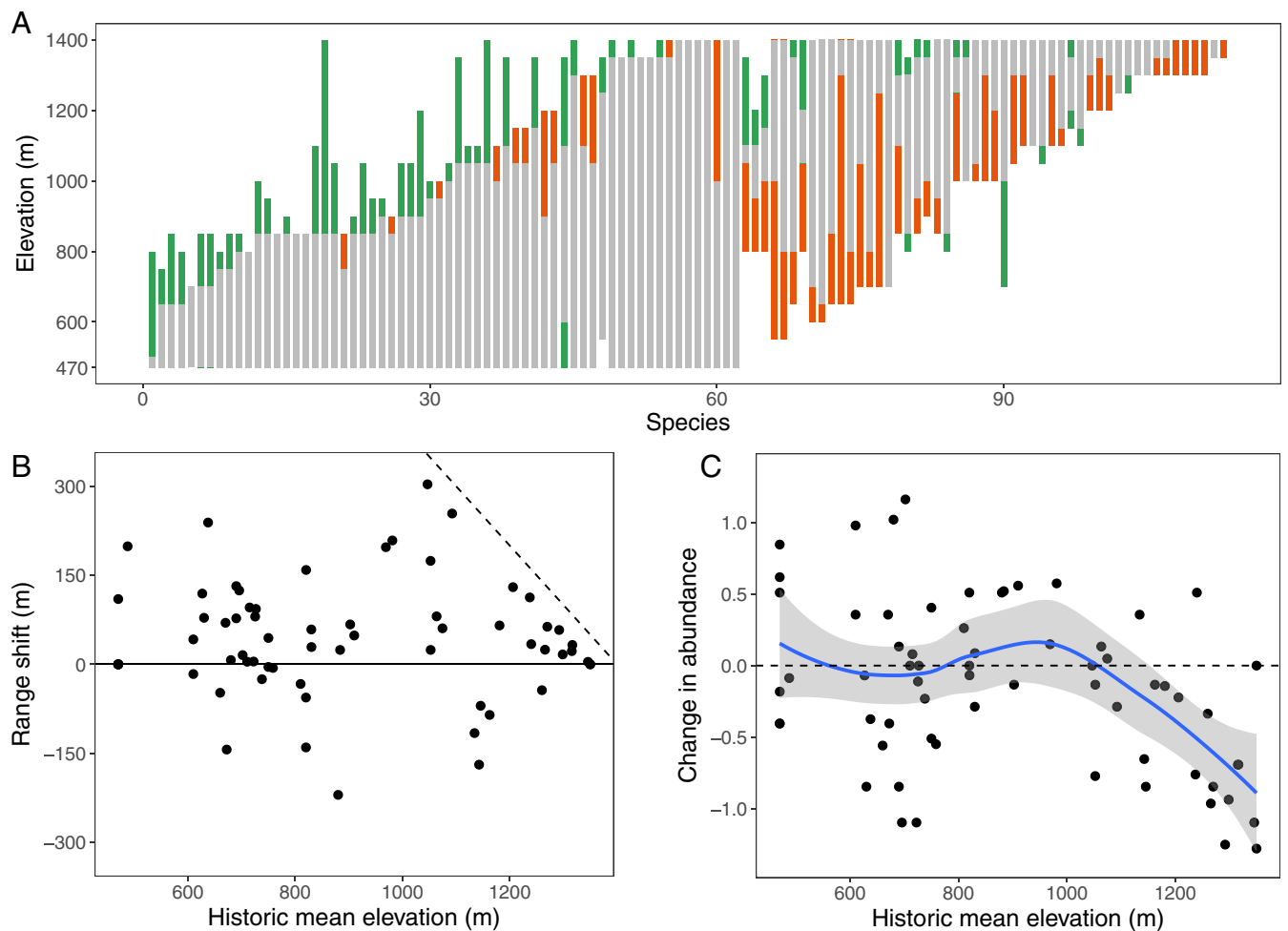
historic and modern surveys, annual mean temperatures have increased in the intervening three decades by  $\sim 0.42$  °C (*Methods*). In this region of southeastern Peru, mean annual temperature declines by  $\sim 0.55$  °C per 100-m increase in elevation (17). Thus, populations would have to shift upslope by  $\sim 75$  m to experience temperature ranges in 2017 comparable with what they experienced in 1985. Based on this expectation, we predicted that, among high-elevation species found along the Pantiacolla Transect, upslope shifts would result in (i) narrower elevational distributions, (ii) a decline in available area, (iii) concomitant declines in overall abundance, and (iv) the extirpation of at least some species that were previously found only on the ridgetop. We view the Pantiacolla Transect—a narrow trail between a valley bottom and the top of a local ridge—as providing a miniature, real-world model of the same processes that are likely occurring on a larger geographical and elevational scale in the tropical Andes and potentially elsewhere on tropical mountains worldwide.

Bird species on the Pantiacolla Transect have responded to recent climate change as predicted and have shifted upslope both in mean elevation and at low and high elevational limits. Mean elevations for commonly mist-netted species shifted significantly upslope by  $40 \pm 98$  m (mean  $\pm$  SD;  $n = 65$  species;  $t_{64} = 3.32$ ,  $P = 0.002$ ; 43 species shifted upslope vs. 15 downslope vs. 7 with no change) (Fig. 2A; raw data are in [Datasets S1 and S2](#)). Most commonly observed species shifted upslope at their lower-elevation limits ( $117 \pm 170$  m;  $n = 48$  species;  $t_{47} = 4.78$ ,  $P < 0.001$ ; 32 species shifted upslope vs. 8 downslope and 8 with no change). These species also shifted upslope at their upper-elevation limits ( $68 \pm 152$  m;  $n = 68$  species;  $t_{67} = 3.67$ ,  $P < 0.001$ ; 47 species shifted upslope vs. 13 downslope and 8 with no change) (Fig. 2B and [Dataset S3](#)). Functional traits associated with greater dispersal may explain why some species undergo large shifts at their leading range margins while others do not (18, 19). However, we found that variation in upper-limit expansions was not explained by diet, body mass, or foraging strata ([SI Appendix, Table S2](#)), perhaps because dispersal limitation is negligible along steep elevational gradients, such as the Pantiacolla Transect.

Upslope shifts have had negative consequences for the distribution and abundance of high-elevation species. First, the low-elevation limit of mountaintop species (those historically found up to the ridgetop) has generally shifted upslope. As a consequence, the portion of the elevational gradient inhabited by these mountaintop species has shrunk by an average of 110 m

(change in elevational extent;  $t_{33} = -3.85$ ,  $P < 0.001$ ) (Fig. 3). Second, because the Cerro de Pantiacolla is roughly shaped like a pyramid, with less area within elevational bands at higher elevations, upslope shifts are squeezing high-elevation populations into a smaller total area of land ( $t_{33} = -4.01$ ,  $P < 0.001$ ) ([SI Appendix, Figs. S1 and S2](#)). Third, while most high-elevation species do still persist on the Pantiacolla Transect, nearly all species with historic mean elevations above 1,200 m have declined in abundance (Fig. 2C). Fourth, despite thorough ridgetop sampling, we failed to detect 8 species of the 16 ridgetop specialists ([SI Appendix, Table S3](#)). Five of these species were repeatedly detected during the historic survey (one to eight individuals mist netted and detected on 3–6 d) ([SI Appendix, Table S3](#)) and thus, may represent populations that have been extirpated.

These are plausible instances of mountaintop extirpations driven solely by climate change in tropical mountains. Given the importance of this finding, it is vital to evaluate whether “missing” ridgetop species represent extirpations vs. the alternative explanation: that such taxa were present but not detected on the ridgetop during the modern survey. Multiple lines of evidence suggest that several species have indeed disappeared from the Pantiacolla Transect. First, most tropical birds are highly sedentary (20, 21), making it unlikely that these species were absent during the modern survey but present at other times of year. Second, seven of the eight missing species are easily detected by voice ([SI Appendix, Table S3](#)) but were detected neither in the field during the modern survey nor in an exhaustive examination of dawn choruses from autonomous recording units placed on the ridgetop during the modern survey ([SI Appendix](#)). Third, we expect some rare species to be found on only one survey due to chance alone, but ridgetop species were disproportionately likely to have been found on the historic survey but not detected in the modern survey ([SI Appendix, Fig. S3](#)). For example, there were six species captured three or more times in mist nets during the historic survey but not captured at all in the modern survey, and all six were ridgetop or high-elevation taxa. Similarly, while three ridgetop species were found only on the modern survey, all three were detected only once. In comparison, eight ridgetop species were recorded only on the historic survey, five of which were repeatedly detected ([SI Appendix, Table S3](#)). Fourth, for the five missing species that were captured in mist nets during the historic survey, we fit single-season occupancy models to estimate occupancy probability for the two time periods by treating time period as a group-level effect (historic, modern). This analysis



**Fig. 2.** Elevational shifts in bird species' distributions and abundances on the Cerro de Pantiacolla between 1985 and 2017. (A) Shifts at lower- and upper-elevational limits for observations of all 108 common forest species showing range expansions (green), contractions (orange), and elevations where species were found during both historic (1985) and modern (2017) surveys (gray). The five ridgetop species that were repeatedly detected in 1985 but not found in 2017 are shown as entirely orange bars. (B) Shifts in mean elevation for the 65 most common species captured in mist nets compared with the zero no change line. Lower-elevation species have more space available to shift upslope than do higher-elevation species; the dashed line denotes where possible upward shifts are bounded by the ridgetop. (C) Change in abundance for the same 65 commonly mist-netted species as a function of mean elevation on the historic survey. Positive values represent increases in abundance, and negative values represent decreases in abundance; the trend line shows the fit from a generalized additive model, with the 95% confidence interval shaded in gray.

gives us the occupancy probability of a species for the ridgetop sites during the modern mist-netting survey while correcting for species-specific mean values of detection probability from historic mist-net surveys (*SI Appendix*, Tables S4 and S5). We found strong evidence that four of these missing species are unlikely to persist atop the Pantiacolla Transect—for these four species, estimates of occupancy probability for the historic time period were  $\psi = 0.14\text{--}0.30$ , while estimates for the modern time period were close to  $\psi = 0.0$  (*SI Appendix*, Table S5). Taken together, our evidence indicates that high-elevation taxa have become disproportionately rare and that mountaintop extirpations have occurred atop the Pantiacolla Transect between 1985 and 2017. It is important to note that populations of the species that are putatively extirpated along the Pantiacolla Transect persist on larger and higher mountain massifs elsewhere in the Andes.

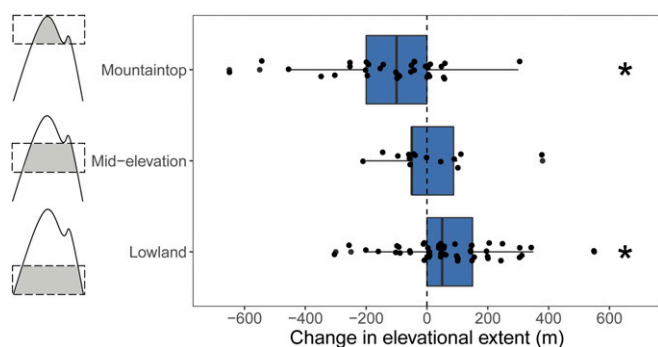
High-elevation birds on the Cerro de Pantiacolla are indeed riding an escalator to extinction. Several high-elevation species seem to have disappeared, and those that persist have generally shifted upslope and now inhabit smaller distributions with lower abundances. Thus, persisting high-elevation species are more vulnerable to extirpation today than they were just three decades

ago. For example, the russet-crowned warbler (*Myiothlypis coronata*), an understory insectivore, was the most commonly mist-netted species near the ridgetop in 1985 (*Dataset S2*). This species still occurs on the Pantiacolla Transect, but it has shifted its lower limit much closer to the top of the ridge—from 1,300 to 1,380 m—and has an estimated population decline of 72%.

The “escalator” is also affecting species below the ridgetop. Midelevation species are shifting upslope by similar amounts at both low- and high-elevation limits, leading to no net change in their elevational extent ( $t_{13} = 0.056$ ,  $P = 0.96$ ) (Fig. 3) or available area ( $t_{13} = -0.060$ ,  $P = 0.95$ ) (*SI Appendix*, Fig. S1). Consequently, today's midelevation species are likely to be tomorrow's mountaintop species, growing ever more vulnerable to extirpation as climate warming continues.

In contrast to high-elevation species, low-elevation species on the Pantiacolla Transect seem to be benefitting from temperature increases. The upper elevational limits of species found at the lowest elevations (i.e., at the Palatoa River) during the historic survey have shifted upward even as these species continue to exist at the bottom of the transect. As a consequence, lowland species have increased in elevational distribution by an average





**Fig. 3.** Change in range size along the Pantiacolla Transect for lowland, midelevation, and mountaintop species. These three categories are defined based on the location of historical range limits. Lowland species were historically found at the river, midelevation species had both low and high historic range limits along the transect, and mountaintop species were historically found at the ridgetop. Asterisks show categories where mean change in elevational extent is significantly different from zero.

of 71 m (change in elevational extent;  $t_{51} = 3.36$ ,  $P = 0.002$ ) (Fig. 3) and also increased in available area ( $t_{51} = 3.33$ ,  $P = 0.002$ ) (*SI Appendix*, Fig. S1). These results suggest that lowland Amazonian bird species may be able to tolerate temperature increases, at least where intact primary forest persists. Thus, the escalator to extinction metaphor does not apply to the lowland species that we studied. Instead, for most species occurring along the base of the Pantiacolla, warming temperatures provide conditions that promote range expansion. Additional research investigating how climate change is impacting tropical species living in low-elevation forests, particularly near sea level, is urgently needed to assess whether warming temperatures threaten lowland tropical biodiversity.

Rapid upslope shifts in birds on the Pantiacolla Transect at rates similar to expectations from observed temperature increases are consistent with the few available reports from other tropical localities [e.g., birds (12, 22), insects (23), reptiles and amphibians (24), and plants (25, 26)]. Taken together, these findings are consistent with the hypothesis that temperature is the dominant driver of tropical species' elevational distributions (12). In contrast, recent studies show that temperate zone species are generally undergoing only modest upslope shifts that “lag” far behind expectations given observed warming (12), consistent with the idea that the relationship between elevational range limits and annual mean temperature is weaker for temperate zone taxa. We speculate that a tighter link between mean temperature and species' elevational limits in the tropics may explain why there are so few compelling temperate zone examples of mountaintop extirpations (10). In this regard, it is perhaps noteworthy that nearly all studies documenting geographic responses to recent climate change have been conducted in the temperate zone (2, 27).

Tropical species may be more responsive to warming temperatures, because limited seasonal temperature variation in the tropics allows tropical species to evolve greater thermal physiological specialization (28, 29) (ref. 30 has an alternative explanation). Such thermal specialization is likely to be strongest for tropical ectotherms (31); indeed, tropical montane birds (which are endotherms) show little physiological specialization to temperature (32, 33). Because tropical montane birds are rapidly shifting upslope yet do not seem to be physiologically specialized to particular temperatures, we speculate that warming temperatures control tropical birds' elevational range limits only indirectly, perhaps via interactions with physiologically specialized ectotherms that are important prey or vectors of diseases. In comparison, temperate zone residents must survive cold winters

and hot summers, preventing adaptation to narrow temperature regimes. Greater temperature seasonality at high latitudes also offers the opportunity for organisms to respond to temperature increases by shifting their activity patterns in time (phenological shifts) rather than in space (34).

With Andean birds as the harbinger, our results support models that project widespread mountaintop extinctions in tropical taxa as Earth's climate warms (4, 35). In the timespan of just one and a half human generations, warming of less than 0.5 °C has set in motion an escalator to extinction for Andean birds. The magnitude of warming is forecast to greatly increase in the coming decades. Earth is expected to warm 2.6 °C to 4.8 °C by 2100 in the “business as usual” scenario (36), which could cause tropical species to shift upslope by 500–900 m. Tropical mountains harbor more species than any other terrestrial environment on Earth (37), and minimizing the negative impacts of large upslope shifts on high-elevation tropical species will require concerted effort. In a climate change context, current clearing of montane forests not only causes habitat loss that immediately reduces populations of species that depend on those forests, but also limits the capacity of lower-elevation species to shift upslope in the future. Thus, preserving and restoring forested wildlife corridors along tropical elevational gradients are more crucial than ever (38). Wildlife corridors were originally conceived to permit movement of individual animals over short timescales. In the climate change era, we now understand that protected elevational corridors are essential for facilitating upslope movement of populations and avoiding extirpations over much longer timescales.

## Methods

**Study Site and Survey Methodologies.** The Cerro de Pantiacolla is an outlying ridge that runs northwest to southeast through the Amazonian lowlands on the north side of the Alto Madre de Dios River in southeastern Peru (Fig. 1). Both historic (1985) and modern (2017) surveys studied the avifauna along a ~8-km transect trail that ascends from the Palatoa River at 470 m to the ridgetop at 1,415 m (Fig. 1; *SI Appendix*, Table S1 shows coordinates). Vegetation changes markedly along this river-to-ridgetop transect from *Guadua* bamboo along the Palatoa River and hilly terra firme forest in the lowlands to dense palm-dominated forest with stunted moss-laden trees on the ridgetop. Bird communities also change with elevation along the Pantiacolla Transect. Species richness declines threefold between ridge and river, and species turnover is nearly complete between the start and end of the transect: of the 500+ bird species found to date along the Pantiacolla Transect, fewer than 25 are found at all elevations (*Dataset S4*).

In 1985, J.W.F. led a Field Museum (Chicago, IL) expedition to determine species' elevational limits along the Pantiacolla Transect. The historic survey documented species' elevational limits by (i) conducting mist-net surveys at seven elevations (typically 20–25 12 × 3-m mist nets open for 5–10 d per site) (*SI Appendix*, Table S1), (ii) recording ad libitum observational data of the elevations where species were detected along the transect to determine elevational limits (rounded to the nearest 50-m interval), and (iii) using shotguns to collect specimens. J.W.F. and colleagues used a barometric altimeter to determine elevation. This historic survey comprised 31 field days, of which 10 were spent at the ridgetop (>1,300 m).

In October 2016, J.W.F. and original team member David Willard relocated their 1985 base camp alongside the Palatoa River by (i) comparing the camp's location on a topographic map from 1985 (generated using side-scanning radar) with modern topographic maps from Google Earth (generated from satellites) and (ii) motoring upriver on the Palatoa until the view of distant ridges to the northwest matched that of photographs taken from the 1985 base camp. Because no trace of the 1985 transect trail remained, J.W.F. helped cut a new trail from the riverside base camp up to the ridgetop in 2016. The modern transect trail ended at the same ridgetop as the historic trail (a local high point of the Cerro de Pantiacolla).

In August and September 2017, B.G.F. and M.N.S. led an expedition to determine species' modern elevational limits along the Pantiacolla Transect. This modern survey attempted to replicate the survey effort of the historic survey and was conducted blind with respect to the results of the historic survey. The modern survey documented species' elevational limits by (i) conducting mist-net surveys at the same seven elevations surveyed by the historic survey (the modern survey matched mist-netting effort at each site

in number of nets deployed but mist netted for fewer days—typically 3 d per site), (ii) recording ad libitum observational data of the elevations where species were detected along the transect to determine elevational limits, and (iii) deploying SWIFT units (autonomous recording units from the Cornell Lab of Ornithology) to passively record soundscapes every 50 vertical m of elevation for an average of 12 d per site. We measured elevation during the modern survey using the barometric altimeter on a Garmin 60CSx GPS (calibrated at the river at 470 m) supplemented with a digital elevation model from the Shuttle Radar Topography Mission (39). The modern survey was shorter than the historic survey (22 vs. 31 d), but effort was similar at the ridgetop (>1,300 m; 9 d in modern survey vs. 10 d in historic survey).

In 1985, the Palatua was a wilderness river, and the Pantiacolla Transect was covered entirely in primary forest. There is now a small community of ~100 people (“Palatua”) along the river ~5 km south of our river base camp, and the site of the 1985 expeditions’ river base camp is now a small community-run ecotourism lodge. However, with the exception of the small (<1-ha) lodge clearing, the entire transect remains covered entirely in primary forest, and community members seldom visit these mountain slopes. Large birds, such as curassows and guans, were common along the transect trail, indicating that hunting pressure is minimal. While the Pantiacolla Transect remains swathed in primary forest, average mean temperatures have increased in southeastern Peru in the intervening decades. There are no long-term weather stations from the Pantiacolla Ridge area to directly quantify the magnitude of local warming since 1985. We, therefore, used data from the Climatic Research Unit global climate models to estimate warming for the  $1 \times 1$  grid cell that includes the Pantiacolla Transect (40), following the methodology of previous studies (25, 41). Specifically, we estimated the magnitude of temperature change at our site between historic and modern surveys by calculating the change in average temperature for 5-y windows preceding the historic and modern surveys (1980–1984 vs. 2011–2015; data were unavailable for 2016).

**Calculating Warming-Associated Range Shifts.** We calculated shifts in species’ mean elevations using data from mist-net surveys for commonly mist-netted species with at least three captured individuals in both historic and modern surveys ( $n = 65$ ). This method requires similar samples from historic and modern surveys (22). Because historic mist-net surveys were longer (5–10 vs. ~3 d) than modern mist-net surveys, we analyzed birds captured over comparable survey durations, typically the first 3 d of historic sampling vs. the 3 d of modern sampling. This resulted in similar-sized datasets (1,019 captures of resident species in the historic survey from seven sites arrayed along the Pantiacolla Transect vs. 966 captured individuals of resident species in the modern survey from the same seven sites) (*SI Appendix, Table S1*). Numbers of individuals captured at each site were similar but not (usually) identical between historic and modern surveys (*SI Appendix, Table S1*). To account for sampling differences between surveys, we randomly sampled the mist-netting data to make the number of captured individuals per site equal between historic and modern surveys. We then calculated mean range shifts for each species based on 1,000 iterations of this randomization procedure and used a  $t$  test to quantify whether range shifts from mist-net data were significantly different from zero.

Next, we calculated shifts at species’ lower and upper elevational limits using observational data for 108 common species. The historic dataset reported species’ elevational limits rounded to the nearest 50 m, and we, therefore, rounded species’ modern limits to the nearest 50 m before calculating changes in elevational limits. We did not calculate shifts for species with historic and modern range limits that coincided with the boundaries of the survey, because these limits likely reflect geographical constraints rather than true range limits. We used  $t$  tests to test whether changes in species’ lower- ( $n = 48$ ) and upper-elevation ( $n = 68$ ) limits were significantly different from zero.

**Investigating Variation in Range Shifts.** Studies that quantify warming-associated range shifts invariably show great interspecific variation in the magnitude (and direction) of shifts. Invasion theory predicts that range expansions at species’ leading range margins should be larger for ecological generalists and good dispersers (18). To test these ideas, we used univariate linear models to investigate whether three traits linked to generalism and dispersal—mass, diet, and foraging height—predicted observed variation of range shifts. We compiled data on mass using our field data (mean mass of mist-netted birds) and a standard reference volume (42), and we described foraging height and diet using data from a global bird trait database (43). Large-bodied birds and species with flexible diets (omnivores) are predicted to be generalists, while canopy birds (vs. understory or terrestrial taxa) and

species that consume ephemeral resources (fruit or nectar) are typically thought to have greater dispersal ability.

**Quantifying Changes in Species’ Range Sizes.** Species’ range sizes may shrink, expand, or remain stable as a consequence of shifts at elevational range limits. We first investigated changes in vertical range size (elevational extent). In the simplest case where all species shift upslope at both warm and cool range limits, lowland and midelevation species will maintain stable elevational extents, while high-elevation species will shrink in elevational extent, because they are constrained by the physical mountaintop. This expectation has two important implications for biodiversity. First, lowland environments may decline in species richness as today’s lowland species become tomorrow’s midelevation species and are not replaced. This idea is termed lowland biotic attrition (9). An alternate perspective is that lowland species inhabit “truncated” realized niches and can persist in hotter environments that do not (yet) actually exist (44). Second, high-elevation species may shrink in elevational extent, presumably leading to declines in population size even for high-elevation species that persist. To investigate these ideas, we categorized species as (i) lowland (if their historic warm limit was the river at 470 m;  $n = 52$ ), (ii) midelevation (if their historic warm limit was above the river and their historic cool limit was below the ridgetop;  $n = 14$ ), and (iii) mountaintop (if their historic cool limit was the ridgetop at 1,400 m;  $n = 39$ ). We used  $t$  tests to test whether changes in elevational extent were significantly different from zero for each category of elevational zone after correcting for multiple testing.

We also tested how elevational range shifts have influenced the available area within species’ elevational distributions (45). We investigated how available area is related to elevation along the Pantiacolla Transect by plotting the hypsometric curve (with area binned into 50-m bands of elevation) for a polygon centered on the Pantiacolla Transect and extending ~1 km to the north and south using the Shuttle Radar Topography Mission 1 Arc-Second Global digital elevation model (30-m resolution; available from the US Geological Survey (USGS) Earth Explorer at <https://earthexplorer.usgs.gov>) and the “raster” package (46). Next, we calculated the available area within species’ historic elevational extents, the available area within species’ modern extents, and the change in area that resulted from warming-associated upslope shifts (all units in meters squared). We then used  $t$  tests to test whether changes in available area were significantly different from zero for each category of elevational zone after correcting for multiple testing and additionally calculated the correlation between changes in elevational extent and changes in available area.

**Quantifying Changes in Species Abundances.** Extirpations occur when the last individual in a population dies, but this extreme scenario is preceded by declines in population size. We used the number of individuals captured in historic and modern surveys as an index of abundance to test whether high-elevation species have disproportionately decreased in abundance as predicted by the escalator to extinction model. We calculated the change in abundance for commonly mist-netted species as follows. We first took the number of individuals captured in the modern survey divided by the number of individuals captured in the historic survey. We then took the log of this value as our metric of change in abundance and used this as our response variable in ordinary least squares linear regression, nonlinear regression, and generalized additive models using the “mgcv” package (47), and evaluated model fit using Akaike information criterion (*SI Appendix, Table S6*).

**Investigating Possible Mountaintop Extirpations.** Eight species of birds found only at the ridgetop in the historic survey were not detected during the modern survey. These species may have disappeared between the time of the historic survey and the modern survey. Alternatively, these missing species could have been present on the ridgetop during the modern survey but not detected. We evaluated these competing explanations by (i) listening to the autonomous recording units placed on the ridgetop during the modern survey in an attempt to detect missing species that are known to be vocally conspicuous when present and (ii) converting capture histories of mist-netted birds into detection–nondetection data, using these to fit single-season occupancy models to estimate occupancy probability for the two time periods by treating each as a group-level effect (historic, modern). This analysis gives us the estimated probability that species occurred at the ridgetop sites during the modern survey while correcting for species-specific mean values of detection probability using mist nets (*SI Appendix* as detailed methods).

**Species Turnover Between Historic and Modern Surveys.** The avifauna of southeastern Peru is extraordinarily diverse (48), with many species found at

low density that are easily overlooked even by surveys of relatively long duration. Moreover, the historical survey had greater effort (31 vs. 22 field days; the increased effort of the historical survey was primarily at low elevations and midelevations). Thus, for both biological and nonbiological reasons, we do not expect the modern survey to detect all species detected by the historic survey. Indeed, the historic survey recorded 71 resident species that were not recorded on the modern survey (while the modern survey recorded 52 resident species not recorded on the historic survey) (Dataset S4). The null expectation is that species detected by the historic survey but missed during the modern survey should be a random mix of lowland, midelevation, and mountaintop species, while if climate change has caused upslope shifts, such taxa will disproportionately be high-elevation species.

We conducted two analyses to test these alternatives. First, we analyzed the elevational distribution of six species that were commonly mist netted in 1985 (three or more individuals mist netted) but were not mist netted in 2017 ("missing mist-netted" species). Second, we considered the 344 diurnal forest species for which the historic survey defined elevational limits and calculated the proportion of these species that we failed to detect in the modern survey ("missing observed" species) across the elevational gradient.

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