ECOGRAPHY

Research article

Citizen science data reveal altitudinal movement and seasonal ecosystem use by hummingbirds in the Andes Mountains

Cristina Rueda-Uribe ✉[1], **Leonel Herrera-Alsina**[1], **Lesley T. Lancaster**[1], **Isabella Capellini**[2], **Kara K. S. Layton**[1] and **Justin M. J. Travis**[1]

[1]School of Biological Sciences, University of Aberdeen, Aberdeen, UK
[2]School of Biological Sciences, Queen's University Belfast, Belfast, UK

Correspondence: Cristina Rueda-Uribe (cristinaruedauribe@gmail.com)

Ensuring connectivity is crucial to protect landscapes but it requires knowledge about how animals use ecosystems throughout the year. However, animal movements remain largely unknown in biodiversity hotspots, even for species that fulfill key ecological roles, as is the case of hummingbirds in the Andes. In the complex topography of mountain slopes, movement of these avian pollinators may occur either between habitat patches with asynchronous plant blooms or across ecosystems that are located within the same elevation bands or along altitudinal gradients. Here, we used two decades (2000–2020) of records from citizen science data and boosted regression trees to predict monthly distributions for 55 hummingbird species in the Andes. We identified shifts in altitudinal distribution between contiguous months and calculated changes in the proportion of predicted distributions occupied by ecosystem types. Our findings reveal substantial altitudinal movement and differences in the proportion of ecosystem types utilized throughout the year that had not been previously reported for several species. Yet the magnitude of altitudinal and ecosystem shifts varies between hummingbird clades, and in some cases changes in the proportion of ecosystem types within estimated distributions occurs with little variation in altitude. All ecosystems across the Andes show temporal changes in hummingbird occurrence, but these are higher in natural landscapes compared to croplands or urban areas. Finally, we used phylogenetic logistic regression to test whether altitudinal and ecosystem shifts affect population trends. We found that higher ecosystem seasonality is more strongly associated with decreasing populations in comparison to altitudinal shifts. Altogether, our study reveals complex patterns of movement in hummingbirds and highlights the importance of ecological connectivity across different ecosystem types. More generally, it demonstrates the opportunity of using citizen science data to increase understanding about species' seasonal occurrences, so that landscapes can be better managed to protect animal movement.

Keywords: boosted regression trees, eBird, ecological connectivity, species distribution models

Introduction

Effective conservation measures are limited by our understanding of the patterns and drivers of animal movement (Runge et al. 2014). Protecting landscapes for mobile species demands full annual cycle approaches that include several sites (Marra et al. 2015), critical movement bottlenecks (Berger et al. 2008) and resource patches along routes (Weber et al. 1999, Sheehy et al. 2011, Xu et al. 2020). In addition, knowledge about the drivers of movement helps identify possible current and future environmental factors that impede movement and thus threaten the persistence of natural populations (Singh and Milner-Gulland 2011). However, movement data are difficult to collect because of the effort needed for long-term monitoring of natural populations, the high costs of tracking studies in the field or laboratory methods for isotopic and genetic analyses. As a result, there is a sharp contrast among geographic regions, taxonomic groups and movement types that have been studied thus far (Holyoak et al. 2008, Boyle et al. 2017, Hsiung et al. 2018). There is an urgent need for more information on the patterns and drivers of animal movement for data-poor species and regions, particularly for biodiversity hotspots that are under threat or especially vulnerable to ongoing global change.

The Andes Mountains in South America are an increasingly threatened hotspot for biodiversity (Myers et al. 2000) but animal movement in these mountains remains understudied in comparison to temperate regions (Jahn et al. 2020). This mountain range is characterized by steep and complex environmental gradients that shelter high levels of species richness (Rahbek et al. 2019, Freeman et al. 2021, Sonne et al. 2022). Natural habitats in the Andes encompass a diversity of dry and wet ecosystems, ranging from 0 m a.s.l. in the lowlands to over 6000 m a.s.l. on mountaintops and including wetlands, shrubs, grasslands and forests (Young et al. 2007). However, natural ecosystems have been severely reduced since preindustrial times (Comer et al. 2022), mainly due to extensive agricultural development and human settlement (Etter et al. 2008, Jarvis et al. 2010, Correa-Ayram et al. 2020). Consequently, wildlife in the Andes is under pressure of habitat degradation and fragmentation (Brooks et al. 2002, Ocampo-Peñuela et al. 2022), which is further exacerbated by climate change (Malcolm et al. 2006).

Given the complexity of environmental gradients in the region, animal movement in the Andes is presumably widespread (Barçante et al. 2017, Jahn et al. 2020) and may respond to changes in weather, limitation or variation of food resources, and biotic interactions (Hsiung et al. 2018, Tsai et al. 2021). Temperature fluctuates with the seasons in subtropical and temperate regions of the Andes, whereas there are no marked seasonal temperature changes in the tropical Andes. However, rainfall in the tropics is seasonal and causes spatiotemporal fluctuations of food resources that may be followed by animals (Cotton 2007). In addition, temperature decreases with increasing altitude and the topographical complexity of mountain slopes results in a mosaic of climatic conditions at fine spatial scales: for example

between, and even within, adjacent valleys (Jiménez-Robles and De la Riva 2019). Altogether, this allows animals to exploit temporal peaks in available food while moving over relatively short distances, either between habitat patches with asynchronous resource peaks or across ecosystem types that shelter different species assemblages. In the rugged topography of the Andean mountains, distinct ecosystem types can be found within same-elevation bands (e.g. valleys with different precipitation regimes caused by orographic effects) or along elevation gradients.

Hummingbirds are specialized on a highly variable food resource and thus move to follow spatiotemporal variations in plant phenology (Levey and Stiles 1992). There is limited information on hummingbird movement along elevation gradients, although 119 of all extant hummingbird species have been reported to perform some type of altitudinal movement (Barçante et al. 2017). Here we refer to altitudinal movement as a broad term that includes altitudinal migration (usually defined as movement between breeding and non-breeding grounds at different elevations (Rappole 2013)), but is not exclusive of other seasonal habitat uses in addition to breeding. In temperate regions, both hummingbirds with latitudinal migration and those undertaking altitudinal movements move in accordance to local patterns of plant phenology (López-Segoviano et al. 2018), although hummingbird abundance and occurrence may also respond to other factors such as competition with conspecifics (Feldman and Mcgill 2014). In the tropics, there is also some evidence of hummingbird seasonal movement, with examples ranging from wet and dry forests in the lowlands (Stiles 1980, Arizmendi and Ornelas 1990, Cotton 2007, Abrahamczyk and Kessler 2010, Bustamante-Castillo et al. 2018) to high-Andean forests and paramo at high elevations (Gutiérrez Z. et al. 2004, Tinoco et al. 2009).

However, evidence of hummingbird movement has been obtained primarily from tracking changes in within-site abundances, leaving unanswered the question of where hummingbirds move to when occurrence or abundance decrease in a monitored location. Only a few studies have compared fluctuation in species occurrence and abundance across sites to infer movement between areas. In one example, monitoring in lowland forests in Costa Rica suggested that some hummingbirds move from mature forest to second growth forest and forest edges in response to differences in flowering phenology across these habitats (Stiles 1980). A second study indicated that lower abundance of hummingbirds in montane forests of southwestern Colombia corresponds with increased abundance at higher elevations in the paramo, although not for all species (Gutiérrez Z. et al. 2004).

Improving our knowledge about the movement patterns of hummingbirds is important for the conservation of their populations and ecological roles as pollinators. Of the 236 hummingbird species with available data at a global scale, 60% have declining populations and 10% are classified as threatened (Leimberger et al. 2022). Degraded matrices with little or no suitable habitat may be significant barriers to hummingbird movement (Hadley and Betts 2009, Volpe et al. 2014, Volpe et al. 2016) and result in lower abundance or absence

of hummingbirds in suitable habitat patches (Kormann et al. 2016). Importantly, isolation between populations causes reduced gene flow between populations of hummingbirds (Licona-Vera and Ornelas 2014) and pollinated plant species (Torres-Vanegas et al. 2019, Gamba and Muchhala 2022). Reduced movement of hummingbirds may therefore lead not only to population declines and lower genetic diversity in their populations but also reduce plant reproduction (Kormann et al. 2016), modify plant-pollinator networks (Chávez-González et al. 2020) and affect trait evolution between coadapted species (Medeiros et al. 2018). Although we do not know if altitudinal or ecosystem seasonality may put hummingbirds, and the plants they pollinate, at greater risk of extinction, there is a clear need for efficient tools that improve our understanding about their complex movements.

Increasingly popular citizen science databases offer an opportunity to investigate movement of populations in regions lacking movement ecology studies (Supp et al. 2021). Citizen science platforms harness millions of species occurrence records across the globe and have successfully been used to shed light on the distribution and movement of populations, particularly for birds (La Sorte et al. 2016, Heim et al. 2020, Johnston et al. 2020, Tsai et al. 2021, Freeman et al. 2022). eBird is a global database where citizen scientists report observations of birds (Sullivan et al. 2009) and has several advantages for studying seasonally shifting distribution patterns: 1) observations are organized in checklists, which enable species absences to be inferred, and 2) data are 'semistructured', meaning that observers may report information on sampling effort. By considering sampling effort, analytical tools may control for biases inherent in citizen science data (Callaghan et al. 2021). Finally, 3) data are readily available for many species over large geographic areas and time periods covering several decades, which would otherwise be difficult to sample.

In this study, we used two decades (2000–2020) of records from eBird to identify seasonal altitudinal movement and ecosystem use of hummingbird populations in the Andes Mountains. We limited our geographic scope to this mountain range because it is particularly rich in hummingbird clades (McGuire et al. 2014, Sonne et al. 2022) and this region is of special conservation interest due to its high number of threatened and range-restricted birds (Lees et al. 2022). Also, the Andes have steep environmental gradients that may enable hummingbirds to exploit peaks of flowering over relatively small distances yet these still remain understudied. We modelled monthly hummingbird distributions using boosted regression trees (BRT) and quantified changes in occurrence across and within elevations, and between ecosystem types, throughout the year. We expected to find evidence for altitudinal movement and seasonal ecosystem use by hummingbirds that has not been previously reported, for movement patterns for this group are still largely unknown. In addition, we predicted that movement across elevations is linked to the use of different ecosystem types throughout the year but some hummingbird species may occupy different ecosystems without changes in altitude, given the topographical complexity of the region. Furthermore, we investigated differences in hummingbird seasonality between ecosystems by testing if natural ecosystem types exhibited greater changes in hummingbird occurrence in comparison to transformed landscapes; and whether humidity, altitude or vegetation type are ecosystem characteristics that influence seasonality. We anticipated that greater changes in hummingbird occurrence would appear in natural ecosystems because urban areas and croplands may provide nectar continuously through bird feeders and ornamental plants (Ramírez-Burbano et al. 2022). Also, humidity, altitude and vegetation type should all affect patterns of plant flowering and in turn predict hummingbird seasonality in different ecosystems. Finally, we tested if there is a positive relationship between population trends and hummingbird altitudinal shifts or ecosystem type change by using phylogenetic regression analyses. We expected changes in altitude and ecosystem types to negatively influence population trends because habitat degradation and fragmentation in the region has most probably reduced ecological connectivity along elevation gradients or across ecosystems.

Material and methods

Species occurrence records

Species records were downloaded for all hummingbirds occurring in South America (Remsen et al. 2022) and in the Andes Mountains (with at least one eBird record in the region) from the eBird Basic Dataset (EBD) (Sullivan et al. 2009). Checklists from eBird's sampling event dataset (SED), which are sampling events carried out by observers, were downloaded for countries that overlap with the Andes Mountain Range (Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile and Argentina) between the years 2000 and 2020. Checklists were filtered to limit sampling effort (Supporting information). Species records of EBD were combined with the SED to obtain presence-absence data for species distribution models (Fig. 1), where an absence was inferred when a species was not detected in a checklist. We accounted for differences in sampling effort between months (Supporting information) by generating independent monthly models that included year and time of day as predictors. To minimize spatial aggregation of sampling effort, we subsampled checklists by dividing the Andes region into a grid of 10 km² hexagons and randomly selecting only one checklist per hexagon for each month of every year in our dataset to continue with downstream analyses. Hexagonal grids are an alternative to square lattices and provide less spatial distortion to subdivide large areas (Strimas-Mackey et al. 2020). After testing different hexagon areas, we chose 10 km² as a subsampling threshold that did not drastically decrease sample size (Supporting information).

Environmental covariates

For each location (checklist) in our subsampled dataset, we obtained information on elevation, ecosystem type and
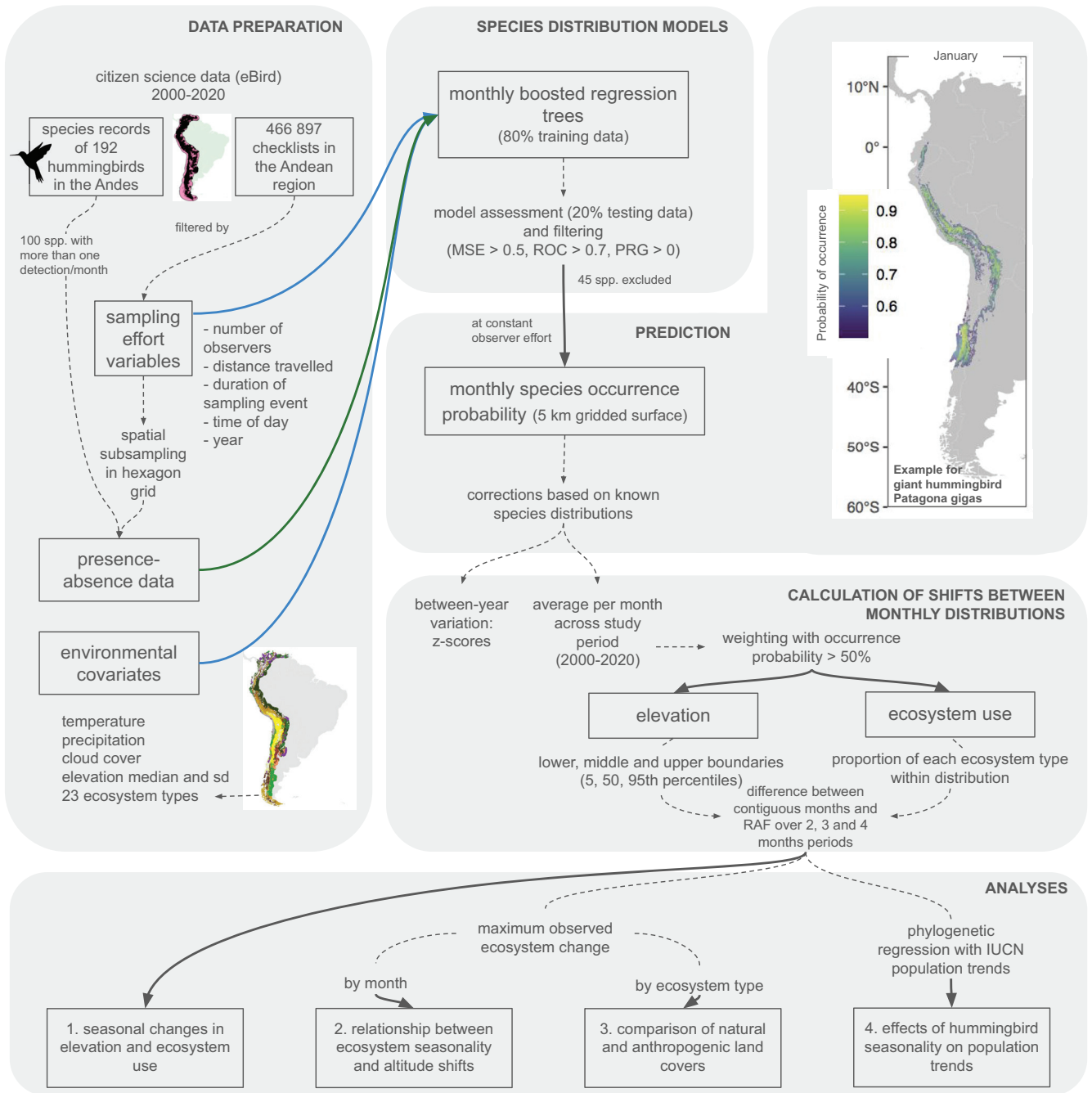
Figure 1. Summary of methods workflow used for this study, outlining steps taken for data preparation, species distribution models, prediction of distributions, calculation of shifts in elevation and used ecosystem types, and analyses to answer four main questions. Arrows with dashed lines show processes and solid lines indicate inputs. Blue lines show predictors and green line response variable of species distribution models. Abbreviations: MSE = mean square error, ROC = area under the receiver operating characteristic curve, PRG = precision-recall gain curve, IUCN = International Union for Conservation of Nature, RAF = rolling average functions.

climatic covariates. Elevation data were obtained from a ground elevation layer at 1 km resolution (Amatulli et al. 2018). We used 23 ecosystem types (Table 1) at a 300 m resolution by combining natural areas from the South America Ecosystems layer (The Nature Conservancy 2008, Supporting information) and transformed land covers from the Copernicus Climate Change Service (ESA CCI Land Cover 2019, see Supporting information for details). As climatic predictors, we used monthly means of total precipitation, air temperature 2 m above the surface, relative humidity at the surface and total atmospheric cloud cover, retrieved from the ERA5 monthly averaged data in the Copernicus Climate Data Store (0.25 × 0.25 grid, Hersbach et al. 2018) for our study period (2000–2020).

Table 1. Ecosystem categories used in our analyses, grouped from the South American ecosystems layer (The Nature Conservancy 2008) for natural ecosystems and transformed land covers from the Copernicus Climate Change Service (ESA CCI Land Cover 2019).

Type	Source	New assigned value	New ecosystem group
Natural ecosystems	South American Ecosystems (The Nature Conservancy 2008)	1	Lowland humid forest
		2	Lowland dry forest
		3	Lower montane humid forest
		4	Lower montane dry forest
		5	Montane humid forest
		6	Montane dry forest
		7	Upper montane humid forest
		8	Upper montane dry forest
		9	Montane saxicolous vegetation
		10	Upper montane saxicolous vegetation
		11	Lowland humid shrub and grassland
		12	Lowland dry shrub and grassland
		13	Lower montane humid shrub and grassland
		14	Lower montane dry shrub and grassland
		15	Montane humid shrub and grassland
		16	Montane dry shrub and grassland
		17	Upper montane humid shrub and grassland
		18	Upper montane dry shrub and grassland
		19	Coastal shrub and grassland
		20	Coastal swamp mangrove
		21	Barren
		0	NA (non-terrestrial)
Transformed land covers	Land cover classification gridded maps (ESA CCI Land Cover 2019)	22	Croplands
		23	Urban

Climatic covariates were assigned to checklists within each 0.25×0.25 cell, and elevation (1 km resolution) and ecosystem type (300 m resolution) were annotated to checklists using a 2.5 km radius. An area rather than a single point was preferred when assigning elevation and ecosystem type in order to account for uncertainty in how the geographic positions of checklists were recorded (Graham et al. 2008) and to capture abiotic conditions experienced by birds in the area. For ground elevation, we included median elevation and the standard deviation of elevation as a measure of terrain ruggedness, both calculated from the 2.5 km radius. For ecosystem types, we calculated the proportion of overlap of each ecosystem with the 2.5 km radius, weighted by the inverse distance of each pixel to the centre of the circle in order to avoid overestimation outside the sampling area.

Species distribution models

We used BRT to model monthly occurrence distributions for each hummingbird species (Fig. 1). BRT is an ensemble modeling tree approach, based on decision trees that split predictors to match response variable values. The boosting method builds a large number of tree models to iteratively improve predictive performance and drop uninformative predictors, an optimization method that reduces the loss function with each new tree (Elith et al. 2008). Predictive performance of BRT to model species distributions is high (Valavi et al. 2021), and BRT has been previously used to model weekly distribution of birds using eBird data (Fink et al. 2020). Monthly distributions for hummingbirds were modelled

separately across our study period (2000–2020), meaning each species had 12 models representing each month of the year, with the year checklists included as a predictor in the models. Months of the year were chosen as the temporal scale for our study because they do not make any a priori assumptions (i.e. no subdivision of previously defined breeding and non-breeding or dry and wet periods) and cover a time frame that is long enough to identify change but not too short as to confound analyses and decrease sample sizes. The response variable of the models was the binary occurrence for each species: presence (1) or absence (0) derived from spatially subsampled checklists. Predictor variables included proportion overlap with 23 ecosystem types (Table 1), four climatic variables, median elevation, standard deviation of elevation, four sampling effort variables, year and latitude (Supporting information). We used the package 'gbm' in R to fit and run BRT models (Greenwell et al. 2020).

Predictive model performance was assessed by comparing outputs generated with the optimal number of trees (determined through cross-validation) on independent test data (20% split). We calculated the mean square error (MSE), area under the receiver operating characteristic (ROC) and precision-recall gain (PRG) curves (Pearce and Ferrier 2000). We considered models with $MSE > 0.5$, $ROC < 0.7$ and negative PRG (Valavi et al. 2021, Osborne et al. 2022) to have low discriminatory ability, and thus species with these values in any given month were excluded from further analyses.

After model filtering, monthly probabilities of species occurrences were predicted on a 5 km gridded raster of the Andes region and checked for consistency with published

species records (Supporting information). Given that a constant observer effort is needed to generate prediction surfaces that account for variation between observers (Fink et al. 2020, Strimas-Mackey et al. 2020), we chose to standardize our predictions with a constant observer effort of one observer traveling 1 km during 60 min starting at 06:00. We then averaged monthly predicted occurrence probabilities across the years 2000–2020 because we were interested in intra-annual variation in distribution rather than changes between years, even if there may be inter-annual differences in species' occurrences due to extreme climatic events or phenomena caused by El Niño-Southern Oscillation (ENSO). Nevertheless, we assessed variation between years by calculating z-scores ((observed value − average)/standard deviation) for predicted occurrence probabilities of cells within estimated distributions for every year in the dataset.

Seasonal changes in elevation and ecosystem use

Estimated species distributions from BRT model predictions were used to quantify changes in elevation and ecosystem types between months of the year. For these calculations, we only considered predicted monthly species occurrences over 50% (i.e. greater than expected by chance), and included occurrence probabilities as weights. Changes in realized altitudinal bounds were estimated from the lower, middle and upper boundaries of monthly species distributions, as the 5th, 50th and 95th percentiles of elevation. To estimate changes in utilized ecosystems, we calculated the difference between contiguous months in the proportion of the predicted distribution occupied by each ecosystem type. For this, we counted the pixels (300 m resolution) in each ecosystem category and divided by the total number of pixels. In addition, we applied smoothing functions of rolling averages over 2, 3 and 4 month periods to calculations of change in elevation and ecosystem use to account for noise in our chosen monthly time period and evaluate findings over broader temporal scales. Finally, we checked if species had been previously reported to have altitudinal movement in Barçante et al. (2017) and complemented this information with species accounts published in Birds of the World (BOTW, birdsoftheworld.org, Billerman et al. 2022) and a literature search in academic research databases Scopus and Web of Science (Supporting information).

Relationship between ecosystem use and altitude shift

We fitted generalized additive models (GAM) to identify how changes in ecosystem type and altitude shifts are associated. The response variable was maximum change in ecosystem type by month and the fixed effect was the altitude shift at either the upper, median or lower bound. Models used cubic splines to smooth regressions, selecting smoothing parameters with restricted maximum likelihood. Species and the major hummingbird clades (McGuire et al. 2014) were included as random effects of intercept and slope. We used the R package 'mgcv' (Wood 2003) to fit models, generate model outputs and check residuals.

Comparisons of natural and anthropogenic land covers

We calculated maximum changes in the proportion of each ecosystem type within species' distributions to assess differences between ecosystems in the magnitude of change in hummingbird occurrence. Using linear mixed effects models, we tested whether ecosystems had greater maximum changes during the year if they were natural or anthropogenic land covers (urban and croplands) and, for natural ecosystems, if maximum changes in ecosystem type varied according to ecosystem variables of humidity regime (dry or humid), altitude category (coastal, lowland, lower montane, montane and upper montane) and vegetation type (swamp mangrove, shrubs and grassland, forest and saxicolous vegetation) (Table 1). Models included maximum changes in ecosystem type as the response variable (transformed by log10 to achieve normality) and species nested within clade as random effect. The first model included land cover transformation (natural or urban and croplands) as fixed effect and used a maximum likelihood ratio test to compare the model with the null. The second set of models only included natural ecosystems, and used humidity, altitude category and vegetation type as fixed effects. For these, we used the Bayesian (BIC) and Akaike (AIC) information criteria to compare all possible combinations of fixed effects and the null, and selected the highest-ranking model. We used the R packages 'lme4' to fit models (www.r-project.org, Bates et al. 2015), 'lmtest' (Zeileis and Hothorn 2002) for maximum likelihood ratio tests, 'DHARMa' (Hartig 2020) to check model assumptions and 'MuMIn' (Bartoń 2020) to calculate model selection criteria.

Effects of seasonality on population trends

We used phylogenetic logistic regression to test if altitudinal or ecosystem seasonality is related to population decline. For this, we assigned species with population trends (Supporting information), which are qualitative categories assigned by International Union for Conservation of Nature (IUCN) expert panels based on existing population data or indirect evidence (IUCN 2022). We did not use the global Red List categories from IUCN because none of the hummingbird species in our final set of models were threatened. We pruned the phylogeny in Leimberger et al. (2022) for the species in our data, using the R package 'ape' (www.r-project.org, Paradis and Schliep 2019). This phylogeny is a maximum clade credibility tree derived from 10 000 trees for Trochilidae in birdtree.org (Jetz et al. 2012) (Supporting information). Population trend was transformed into a binomial response variable: declining or not declining (increasing or stable). Species with unknown population trends were excluded from this analysis. Average altitudinal shift (at median bound) and average ecosystem type changes for each species were included as explanatory variables. Explanatory variables were first transformed by their square root to avoid skewed distributions and scaled around their mean before running the model. We ran the model with the 'logistic_IG10' method to

optimize the generalized estimating equations to a penalized likelihood using Firth's correction and calculated 95% confidence intervals (CI) with 1000 bootstrap replicates using the R package 'phylolm' (www.r-project.org, Ho and Ane 2014). We calculated the variance inflation factor (VIF) between fixed effects to check for collinearity.

Results

We processed 466 897 citizen science checklists between 2000 and 2020, for occurrences of 192 hummingbird species in the Andes Mountains. On average, checklists lasted 74 min (73 SD) and were carried out by 2 (1.9 SD) observers over 1.7 (1.3 SD) km (Supporting information). We excluded 92 species that had only one or no records during this time period for any given month of the year in either the 80 or 20% training and testing datasets, respectively, and therefore did not have enough data to run BRT models. After running monthly models on the remaining 100 species, 37 species were further excluded due to low predictive performance of models (MSE ≥ 0.5, ROC ≤ 0.7 and PRG < 0 for at least one month of the year). An additional eight species were removed because models failed to predict > 50% occurrence probability over the extent of their known distributions, for any month. The final set of models included in subsequent analyses (n = 660 models, 55 species) had an average MSE = 0.22 (0.05 SD), ROC = 0.95 (0.02 SD) and PRG = 0.91 (0.06 SD) (Supporting information). On average, median elevation and latitude were the model predictors with greater influence on occurrence across species (28% (24 SD) and 26% (20 SD), respectively). In contrast, sampling effort variables had lower predictive influence compared to elevation, latitude, terrain ruggedness (elevation SD) and climatic variables, with the duration of sampling event having the greatest influence within sampling effort variables (3% (1 SD). Year had low predictive influence across all species (0.4% (0.2 SD), Supporting information). Z-scores by species describing variation in probability of occurrence between years ranged between −0.91 and 0.94, albeit with a trend of positive z-scores during the second decade of the dataset (2010–2020) compared to negative z-score values in the first decade (2000–2010, Supporting information).

Predicted monthly distributions showed changes in altitude and ecosystem use for the studied hummingbird species of the Andes. Shifts in altitude between contiguous months of the year ranged from zero up to 2400 m in species' lower distribution bounds, 1043 m at middle bounds and 1000 m at upper bounds (Fig. 2A–B). Six species performed elevation shifts of over 1000 m (Table 2), two of which have no previous reports of altitudinal movement (Table 2, Supporting information). Maximum elevation changes at any distribution boundary (upper, middle or lower) by species had a median value of 434 (358 SD m (Fig. 2C). Changes in ecosystem type ranged from maximum values by species between 5 and 51% of predicted distributions (median = 13% (8% SD), Fig. 2D). Maximum changes in elevation and ecosystem

type calculated with rolling average functions (RAF) considering 2, 3 and 4 month periods produce qualitatively similar results (Supporting information).

Maximum changes in ecosystem types and altitude shifts at all distribution bounds (upper, middle and lower) had positive and significant relationships, although with different regression curves according to distribution bound (Fig. 2E, Supporting information). Changes in altitude for upper bounds had an approximately linear relationship with ecosystem type change (effective degrees of freedom − edf = 1) whereas for middle and lower bounds it was closer to a quadratic relationship (edf = 2.6 and 2.4, respectively). In addition, the deviance explained by the models was low (48–63% and adjusted R-square 0.43–0.59) and there was high variation among species and clades (in all models species and clade were significant smoothing terms for either slope or intercept, Supporting information). Positive relationships were also obtained when considering ecosystem change and altitude shifts in RAF over 2, 3 and 4 month time periods, albeit with some variation in edf values and with weaker effects of clades as a smoothing term on slopes and intercepts (Supporting information). Notably, hermits had steeper regression slopes than other hummingbird clades (Fig. 2E). Steeper regression slopes indicate greater changes in ecosystem type than expected from the observed altitude shift, whereas more shallow slopes show smaller changes in ecosystem type according to altitude shift. For example, the pale-bellied hermit *Phaethornis anthophilus* exhibits changes in the percentage of croplands and lowland humid forest within its distribution over 10% and up to 34% (within 3–6% and 6–10% considering RAF), respectively, yet in its mid-elevation the median change over the year is of 27 m (28–75 m in RAF), and the maximum altitudinal shift is 355 m (29–69 m in RAF) in September (Fig. 3A). In contrast, the giant hummingbird *Patagona gigas* increases its lower distribution altitude limit from 145 to 2545 m a.s.l. between February and March (equivalent to a change of 2400 m between contiguous months or within 681–1312 m in RAF), which coincides with an 11% increase (10–15% in RAF) of upper montane humid shrubs and grassland in its estimated range. In August, it reappears in lowland ecosystems with a decrease of 2007 m (603–1090 m in RAF) in the elevation of its lower distribution (Fig. 3B).

Linear mixed effects models showed that, across species, seasonality of occupied ecosystems varied between natural and anthropogenic ecosystems (croplands and urban land covers) and within natural ecosystems, according to humidity (Fig. 4). On average, the magnitude of ecosystem use change by hummingbirds was greater in natural ecosystems compared to anthropogenic land covers (Supporting information). Within natural ecosystems, humidity was the sole predictor of maximum changes in ecosystem type in the highest-ranking model (99% BIC and 52–82% AIC criteria weights depending on RAF used, Supporting information), with greater estimated coefficients in humid rather than in dry ecosystems (Supporting information).

Finally, the results of the phylogenetic logistic regression showed that seasonal ecosystem type changes were more
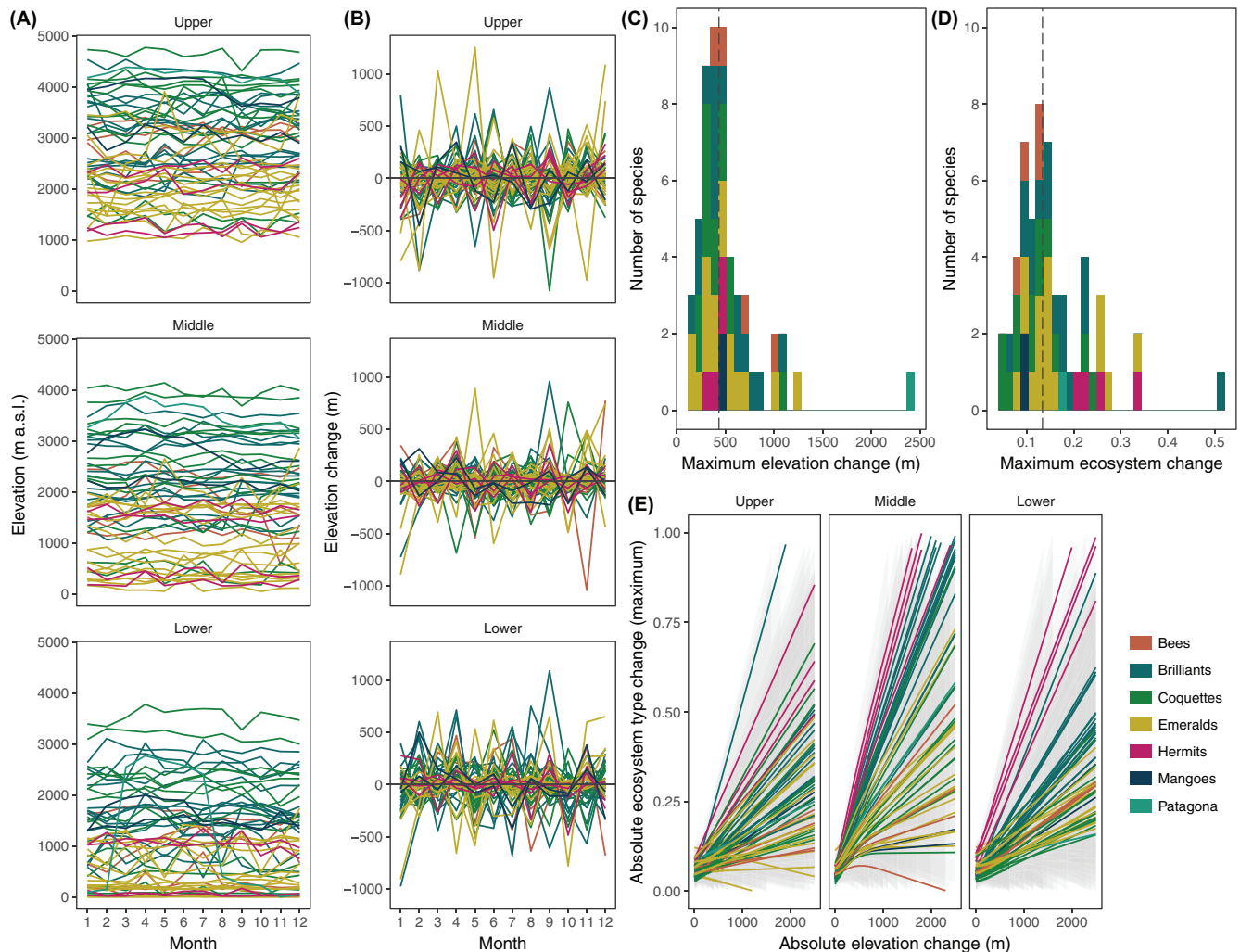
Figure 2. (A) Monthly elevation for the upper, middle and lower elevation distribution boundaries (percentiles 5, 50 and 95) estimated from occurrence probabilities using boosted regression tree models for 55 species of hummingbirds in the Andes Mountains of South America. (B) Change in elevation between months of the year for each species, excluding the giant hummingbird *Patagona gigas* as an outlier (with changes up to 2400 m a.s.l.) to ease visualization. (C) Number of hummingbird species according to maximum observed elevation (D) and maximum ecosystem type changes between months of the year. Vertical dashed lines show median values of maximum elevation change (434 (358 SD) m) and maximum ecosystem change (0.13 (0.08 SD)). See Supporting information for average values of elevation and ecosystem type change. (E) Predictions of generalized additive models (GAM) for relationship between change in elevation and change in ecosystem type calculated as proportion of predicted distribution and selecting maximum change by month. In GAM models, species and hummingbird clades were included as random effects of intercept and slope. Lines indicate separate species, with confidence intervals calculated as 1.96 times standard error. Colours in all panels represent main hummingbird clades. Supporting information for plots showing results with rolling average functions over 2, 3 and 4 month periods.

strongly predictive of IUCN declining status of species than were seasonal altitudinal shifts, including when results were calculated using RAF for 2, 3 and 4 month periods (Fig. 5, Supporting information). However, estimated 95% confidence intervals for both effects overlapped with zero, and 17 (31%) species had unknown population trends and thus were not included in this analysis.

Discussion

Our results show changes in elevation between predicted monthly distributions for 55 hummingbird species that

occur in the Andes, providing evidence for intra-annual shifts in altitudinal bounds and ecosystem use that has been previously understudied. Furthermore, we found that shifts in altitude and ecosystem use are associated, but there is high interspecific variation, and changes in the proportion of an ecosystem type within predicted distributions can also occur even with little or no altitudinal change. This suggests that some hummingbird species may move at fine spatial scales along mountain slopes and also within same-elevation bands, possibly exploiting different ecosystem types by travelling short distances. Notably, there was a difference in the magnitude of hummingbird seasonality between ecosystem types, with anthropogenic land covers exhibiting lower changes

Table 2. Species with altitudinal changes greater than 1000 m between contiguous months of the upper, median and lower distribution boundaries (percentiles 5, 50 and 95) estimated from occurrence probabilities using boosted regression tree models for 55 species of hummingbirds in the Andes Mountains of South America. Values in parentheses indicate change in elevation considering rolling average functions calculated for longer periods of time: 2, 3 and 4 months. The last column indicates if a species had been previously reported to have evidence of some type of altitudinal movement (according to Barçante et al. (2017), Birds of the World (BOTW) birdsoftheworld.org, Billerman et al. (2022) or a literature search in academic databases, see Supporting information).

Clade	Latin name	English name	Maximum elevation change (m)	Distribution bound of observed maximum elevation change	Previous evidence of altitudinal movement
Patagona	Patagona gigas	Giant hummingbird	2400 (681–1312)	Lower	Reported in various sources
Emeralds	Thaumasius taczanowskii	Spot-throated hummingbird	1253 (304–612)	Upper	No reports
Brilliants	Heliodoxa jacula	Green-crowned brilliant	1088 (382–639)	Lower	Barçante et al. (2017) as probable altitudinal migrant
Coquettes	Sappho sparganurus	Red-tailed comet	1077 (182–332)	Upper	Barçante et al. (2017) as probable altitudinal migrant and other sources report seasonal occurrence and movements
Bees	Myrtis fanny	Purple-collared woodstar	1043 (393–560)	Median	Suggestion of altitudinal movements in BOTW without citation
Emeralds	Chlorostilbon lucidus	Glittering-bellied emerald	1029 (330–569)	Upper	No reports

compared to natural ecosystems. In addition, the positive effect of ecosystem type change on decreasing population trends indicates that connectivity between ecosystems is essential for hummingbirds to feed on nectar throughout the year. The patterns to support these findings remained unchanged when repeating analyses over 2, 3 and 4 month time periods.

The approach of using citizen science data at a broad, continental scale revealed changes in altitude and ecosystem use between monthly distributions of Andean hummingbirds.
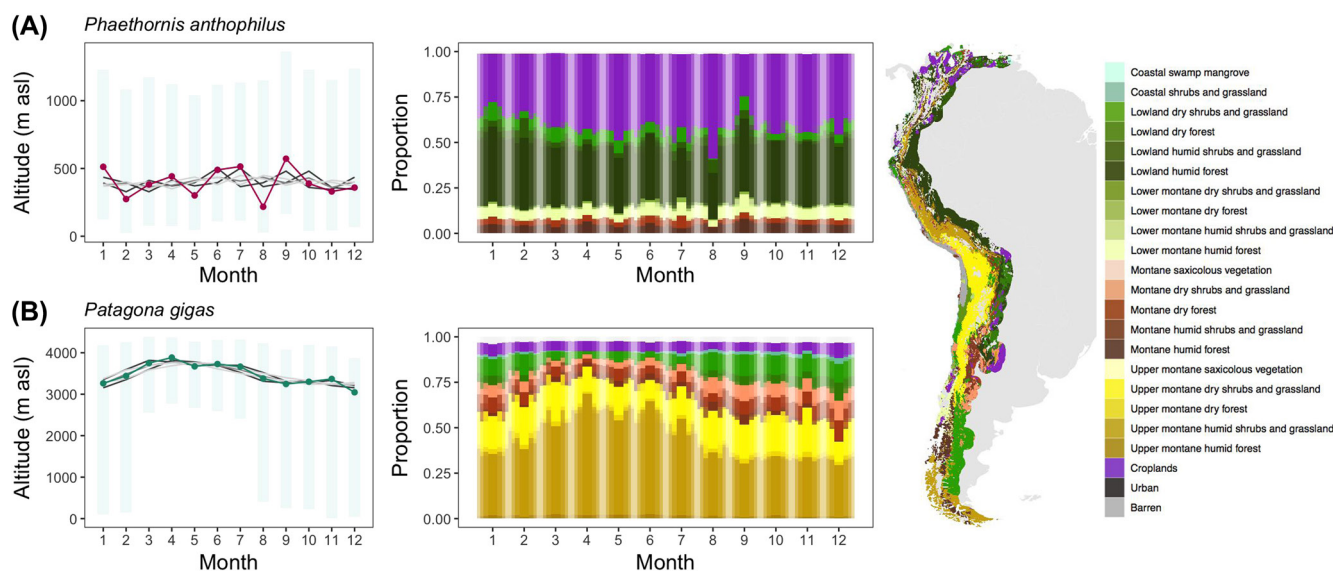

Figure 3. Altitude of lower, median and upper bounds and proportion of ecosystem type within monthly predicted distributions modelled with boosted regression trees for (A) the pale-bellied hermit *Phaethornis anthophilus* and (B) the giant hummingbird *Patagona gigas*. In panels indicating monthly altitude, light blue rectangle shows upper and lower bounds (5th and 95th percentiles, respectively) and dots represent median altitude (50th percentile). Grey lines indicate elevation calculated with rolling average functions (RAF) over 2, 3 and 4 month periods, with 2 months in a darker shade of grey, 3 months in an intermediate shade and 4 months in a lighter shade. Note that for 2 and 4 month periods, rolling averages may be calculated with a tilt towards the left or right, so both are shown. Coloured bars show the proportion of predicted distribution occupied by each South American ecosystem type (see Material and methods) as indicated in the legend on the right. Darker coloured bar centred around each month shows calculated monthly values, and outward bars get lighter to indicate changes in ecosystem type calculated with RAF over 2, 3 and 4 month periods, respectively. Ecosystems that had less than 1% representation in distribution are grouped into 'others' to aid visualization. See Supporting information for altitude and ecosystem type graphs for all studied Andean hummingbird species (55).
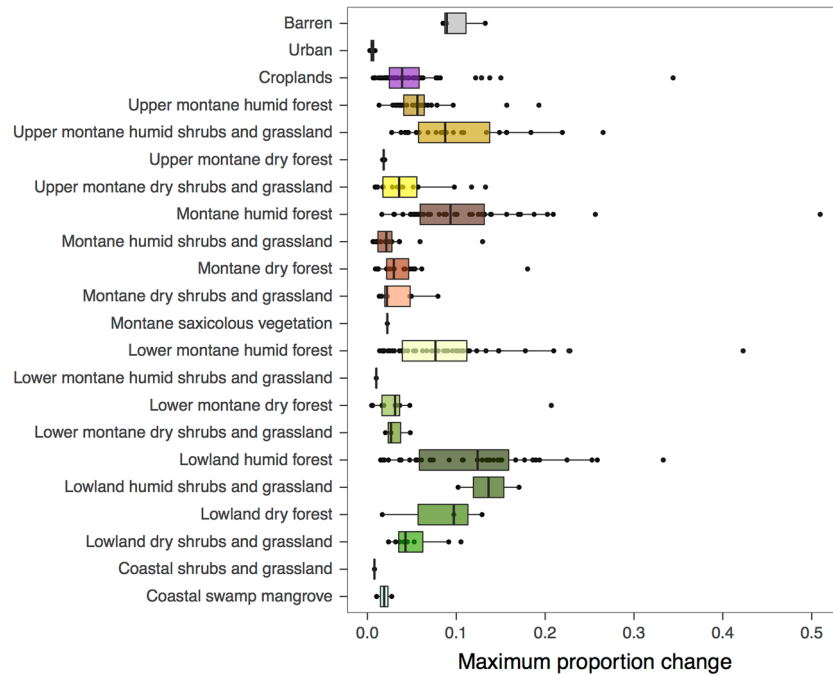
Figure 4. Maximum change in the proportion occupied by ecosystem type of predicted monthly distributions for 55 hummingbirds in the Andes Mountains. Change is calculated as the difference in the proportion of the predicted distribution occupied by each ecosystem type between contiguous months of the year. Monthly occurrence probabilities averaged across years of study period (2000–2020) to focus our comparisons on intra-annual variation. Species are represented by points, and boxplots summarize interspecific variation in ecosystem use change, with first and third quartiles at box hinges, median values with middle thick lines and 1.5 times interquartile range with box whiskers. See Supporting information for plots showing results with rolling average functions over 2, 3 and 4 month periods.

Such seasonal changes in distribution throughout the year have been under-reported for this group. Of the hummingbirds that we found to have altitudinal shifts greater than the median calculated in monthly periods (434 (358 SD) m), five species have no previous reports of altitudinal movement and another five only have suggestions of altitudinal movement in BOTW accounts but no cited sources for this information. In addition, two species with very large shifts in altitude (over 1000 m) had no published previous evidence on altitudinal movement (Supporting information).

However, we found that several species have marked altitudinal shifts in lower or upper bounds but not in median elevations, which may reflect variation in movement patterns among populations. Especially for species with large ranges, populations should exhibit local variation in response to differences in environmental factors such as climate, flower diversity and abundance, and inter- and intraspecific competition (Simmons et al. 2019). Landscape characteristics like matrix permeability and distances between habitat patches may also influence movement decisions (Gannon et al. 2021). For example, the giant hummingbird *P. gigas* has populations in coastal Chile with partial altitudinal and latitudinal migration to the highlands (Williamson and Witt 2021b), but there is no evidence for such large-scale movement for the subspecies *P. gigas peruviana* in the northern part of its range. Williamson and Witt (2021b) estimated that the maximum shift in elevation for *P. gigas* was 2830 m, whereas our methods resulted in a maximum change of 2400 m, showing a

rough difference between the two approaches that may be a consequence of how upper limits are defined, type of records that are used and, most importantly, the focus on single subspecies or populations. However, this comparison also suggests that our methods were successful in calculating similar magnitudes of change in elevation. Extreme shifts were captured by a monthly temporal scale, but the magnitude of change inevitably decreased by repeating calculations over broader time periods (in the case of *P. gigas*, to 1312, 892 and 681 m depending if 2, 3 or 4 month time periods are used, respectively). However, we note that also considering results over longer time periods has the benefit of smoothing error produced by monthly models, and that the choice of a single temporal scale is arbitrary but necessary to capture intra-annual variation.

In addition, species like the giant hummingbird and the green-backed firecrown *Sephanoides sephaniodes* inhabit temperate regions of the Andes and therefore also have populations that move latitudinally (Supporting information). Only these two species of the 55 we analysed have previous reports of latitudinal migration (Supporting information) and maximum changes in latitude between months were not high (average at median latitude = 2.36° (1.57 SD), northern limit = 1.76° (1.45 SD), southern limit = 2.94° (2.28 SD)); yet we found that shifts in latitude increase as species have a more southern range (Supporting information). As is the case with altitudinal movement, austral bird migration in South America is also understudied (Jahn et al. 2020).
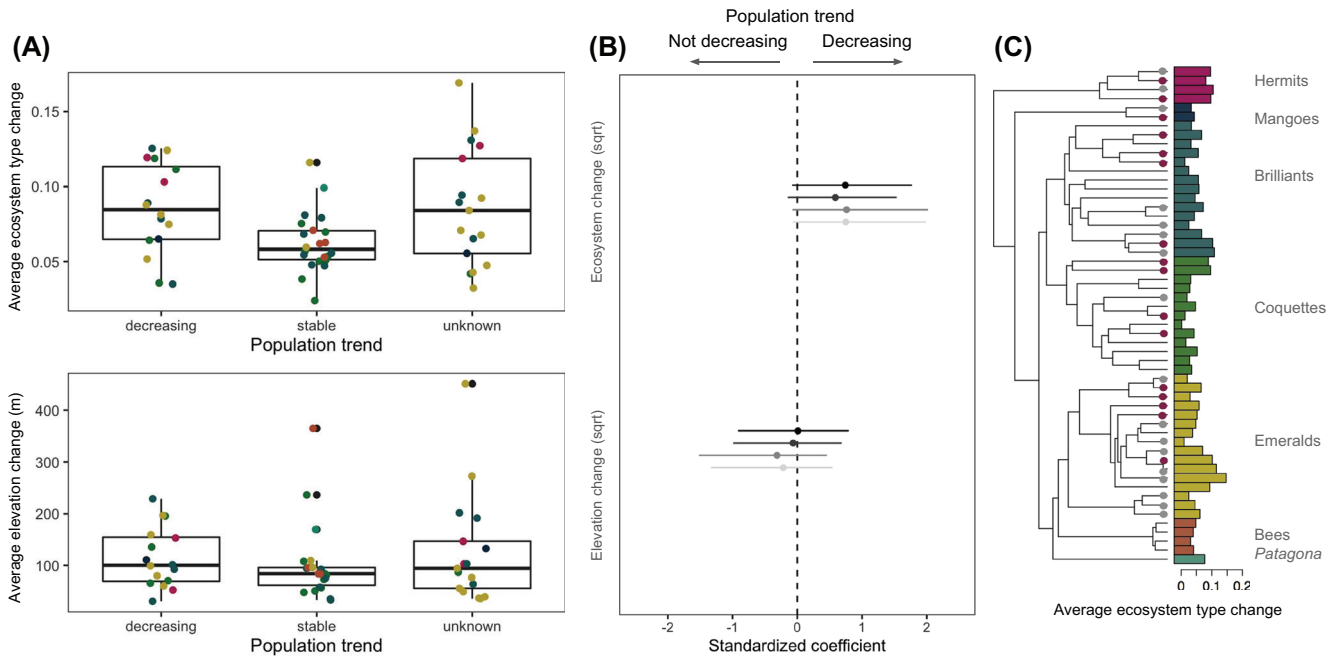
Figure 5. (A) Average change in median elevation (50th percentile of distribution) and average ecosystem use change (calculated as the proportion of predicted distribution) according to population trend for 55 Andean hummingbird species. Points represent each species and are coloured with the major hummingbird clades, boxplots show median values with the middle thick line, first and third quartiles with box hinges and 1.5 of the interquartile range with box whiskers. Supporting information for values calculated with rolling average functions (RAF) over 2, 3 and 4 month periods. (B) Effects of elevation and ecosystem type change on population trend estimated with phylogenetic regression, for 38 hummingbird species with reported population trends (17 species with unknown population trends were excluded from this analysis). Positive values indicate a positive relationship with decreasing population trends while negative values indicate population trends that are not decreasing (stable). Points show estimated coefficients and horizontal lines indicate the 95% confidence interval calculated with 1000 bootstrap replicates. Values are transformed by the square root and centred around the mean. Black colours indicate estimates from values calculated over monthly periods, and shades of grey get lighter to show results using RAF over 2, 3 and 4 month periods, respectively. (C) Phylogenetic tree of 55 Andean hummingbird species used in this analysis (refer to text for methods and Supporting information for phylogenetic tree). Red dots at tree tips show species with decreasing population trends, while grey dots show species with unknown population trends. Bar length represents the proportion of absolute maximum ecosystem type change and bars are coloured according to major hummingbird clades.

Further complexity can be revealed by tracking individuals, since populations may be partially migratory and movement propensities may be context-dependent and driven by intrinsic factors such as sex, dominance and social rank, age and body size (Hsiung et al. 2018). Technological advances in tracking devices can help reveal fine-grained movements for larger hummingbird species (Williamson and Witt 2021a), and complementary methods that will also be useful to study species with smaller body sizes include isotope analyses (Hobson et al. 2003, Hardesty and Fraser 2010), population genetics (Benham and Witt 2016), mark-recapture (Ovaskainen et al. 2008) and long-term monitoring. In addition, future research focused on single populations will benefit from testing the interactions between the biotic and abiotic factors that more strongly influence occurrence probability and drive movement patterns.

Optimal movement decisions at the individual or population level should involve the energetic trade-off between the gain from food and the costs of flight, searching and settling in a suitable habitat patch, and interacting with possible competitors or predators. Also, matching bill length and shape with floral morphology determines feeding efficiency (Rico-Guevara et al. 2021) and ecological specialization (Maglianesi et al. 2014), so movements to ecosystems where vegetation types are morphologically different (Tovilla-Sierra et al. 2019) may be limited. For instance, the sword-billed hummingbird *Ensifera ensifera* has an exceptionally long bill that matches the long-tubed corollas of *Passiflora* flowers (Lindberg and Olesen 2001). In a monitoring study in southwestern Colombia, peaks in seasonal abundance of the sword-billed hummingbird matched blooms of *Passiflora* and *Fuchsia* flowers, but low abundance did not coincide with the presence of the species at other elevations (Gutiérrez Z. et al. 2004). This suggests that the sword-billed hummingbird could move within the same altitudinal band rather than along elevation gradients, which coincides with our findings that this species has small changes in altitude (average of 84 m or 18–24 with RAF change at median elevation bound) but shifts in ecosystem use over the observed median (maximum 16 or 4–10% with RAF of predicted distributions, Supporting information).

Our study shows that hummingbirds may exploit different ecosystem types without performing shifts in altitude,

and the relationship between ecosystem seasonality and changes in elevation varies between species and clades. Hermits in particular have greater change in ecosystem type than expected from observed altitudinal shifts in comparison to other hummingbirds. Seasonal changes in hermit abundance had been previously described in lowland forests of Costa Rica (Stiles 1980). However, hermits are considered to be forest-dependent (Hadley et al. 2018) and have high specialization to plant partners due to their long, curved bills (Maglianesi et al. 2014). High specialization may limit switching to different ecosystem types where plant species assemblages differ. Yet morphological specialization does not necessarily result in ecological specialization, and bill length seems to be weakly correlated to resource specialization in hummingbirds (Dalsgaard et al. 2021). Also, trait-matching between bill and corolla is not a requisite for nectar feeding (e.g. nectar robbery, Maruyama et al. 2015). In fact, there are contrasting examples of resource specialization in hermits, and specialization may be largely context-dependent (reviewed by Leimberger et al. 2022). In hermits, movement is most likely limited altitudinally by factors such as interspecific competition (i.e. the presence of other species filling similar ecological niches according to elevation band, Freeman et al. 2022), or movement may also be obstructed by unsuitable habitat between habitat patches. Past tracking studies have found hermits are sensitive to habitat fragmentation and avoid forest gaps or agricultural matrices (Hadley and Betts 2009, Volpe et al. 2014). There is also evidence that corridors are needed for the movement of hermits between patches (Kormann et al. 2016), but such connectivity requirements must be extended to other hummingbird clades and revisited in light of seasonal movements across ecosystem types.

Moreover, available resources within patches also play a role in determining movement. For example, food resources in human-disturbed areas may increase connectivity (Ramírez-Burbano et al. 2022), but transformed landscapes do not favour all species equally (Puga-Caballero et al. 2020) and new plant-pollinator interactions emerge (Marín-Gómez et al. 2022). Our analyses showed that hummingbird seasonality was lower in transformed landscapes compared to natural ecosystems. One possible explanation is that nectar availability and abundance in transformed landscapes is less variable during the year because bird feeders are not seasonal, and exotic plants in human settlements are not adapted to the same phenological patterns as native vegetation, which may result in hummingbirds not having to follow flowering pulses. Alternatively, transformed landscapes may favour less specialized hummingbirds (Maruyama et al. 2019) that can benefit from asynchronous flowering across plant species in single sites and not require movement to visit other areas with distinct nectar phenology. A third option is that some hummingbirds move between different vegetation patches within urban areas, a possibility that to the best of our knowledge has no published evidence yet but may occur, particularly in the cities that cover very large areas, which is the case of most capitals in South America.

For natural environments, we found that humid ecosystems on average exhibit greater seasonality in hummingbird occurrence compared to dry ecosystems. Arid environments have marked flowering pulses that shape temporal patterns of hummingbird-plant interactions (Souza et al. 2018, Chávez-González et al. 2020), but our results also support a few studies that have found changes in flower abundance between the rainy and dry seasons in humid ecosystems cause fluctuations in hummingbird occurrence (Cotton 2007, Abrahamczyk and Kessler 2010). In contrast, altitude categories and vegetation type were predictors that were not informative for the highest-ranking model. Overall, these findings suggest that changes in hummingbird occurrence are generalized across natural ecosystems in the Andes, highlighting the need for further studies on phenological patterns, particularly in humid ecosystems.

Finally, we found that seasonal changes in ecosystem use are more strongly related to decreasing population trends than altitudinal shifts. Therefore, species that require movement across ecosystems to exploit seasonal floral resources may be affected by reduced connectivity. As suitable habitat patches are more distant from one another and matrix permeability is decreased, hummingbird movement is obstructed (Gannon et al. 2021). Yet hummingbirds with altitudinal movement may have higher resilience to fragmented habitats (Leimberger et al. 2022) or simply move over shorter distances, since in the rugged topography of the Andes elevation may change drastically within the scale of hundreds of metres or less. In contrast, because of landscape homogenization in the region, different ecosystem types may be isolated over increasingly larger areas, and management plans usually do not prioritize connectivity between different ecosystem types. However, 31% of the species we analysed here had 'unknown' population trends, and we recognize that population trends for species without standardised monitoring schemes may be based on indirect evidence or anecdotal information (Cazalis et al. 2022, Lees et al. 2022). Monitoring is needed to obtain better information on population sizes and changes through time, and quantitative analyses on indirect factors that affect population fluctuations (such as land cover change, Santini et al. 2019) can be used to infer population trends.

In conclusion, the data available in citizen science databases are useful to detect broad movement patterns at the population level that, combined with local movement ecology studies on populations and individuals, are urgently needed for conservation and management efforts. We found that the movement of Andean hummingbirds along elevation gradients and across ecosystems is a widespread phenomenon, yet the approach of using citizen science data excluded several species that are not frequently observed and therefore do not have enough detections by citizen scientists to run species distribution models. In particular, species that are rare, range-restricted and threatened were removed from our analysis because they lacked data. Also, our methods were focused on detecting continental-scale patterns across species, but in the mountains of the Andes movement between finer-scale ecosystem categories may occur over very short distances (a few metres). In addition, our study focused on

detecting intra-annual variation rather than changes across years. Although our assessment of z-scores for variation in occurrence probability does not reveal any year to be a considerable outlier for any species, results show an overall upward trend that may reflect the greater detection capacities of citizen scientists and an increasing number of checklists contributed to eBird in more recent years. However, future research could detect change in species' occurrences driven primarily by climatic events such as El Niño and La Niña, but should be investigated at finer spatial scales, since the effects of ENSO oscillations are heterogeneous over regions of the Andes. Altogether, our findings suggest that a better understanding of animal movement and its incorporation in conservation strategies will benefit from the growing popularity of citizen science databases across different taxonomic groups. Further studies focused on single populations are relevant, and directing efforts towards areas or species of special conservation interest through local initiatives is also necessary.

Author contributions

Cristina Rueda-Uribe: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Leonel Herrera-Alsina**: Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Writing – review and editing (equal). **Lesley T. Lancaster**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Isabella Capellini**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Kara K. S. Layton**: Investigation (supporting); Methodology (supporting); Supervision (equal); Writing – review and editing (equal). **Justin M. J. Travis**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (lead); Validation (equal); Visualization (supporting); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.06735.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.w3r2280xs (Rueda-Uribe et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Abrahamczyk, S. and Kessler, M. 2010. Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. – J. Ornithol. 151: 615–625.

Amatulli, G., Domisch, S., Tuanmu, M. N., Parmentier, B., Ranipeta, A., Malczyk, J. and Jetz, W. 2018. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. – Sci. Data 5: 180040.

Arizmendi, M. del C. and Ornelas, J. F. 1990. Hummingbirds and their floral resources in a tropical dry forest in Mexico. – Biotropica 22: 172–180.

Barçante, L., Vale, M. M. and Alves, M. A. S. 2017. Altitudinal migration by birds: a review of the literature and a comprehensive list of species. – J. Field Ornithol. 88: 321–335.

Bartoń, K. 2020. Mumin: multi-model inference. – R package ver. 1.43.17, https://CRAN.R-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Benham, P. M. and Witt, C. C. 2016. The dual role of Andean topography in primary divergence: functional and neutral variation among populations of the hummingbird, *Metallura tyrianthina*. – BMC Evol. Biol. 16: 22.

Berger, J., Young, J. K. and Berger, K. M. 2008. Protecting migration corridors: challenges and optimism for Mongolian saiga. – PLoS Biol. 6: e165.

Billerman, S. M., Keeney, B. K., Rodewald, P. G. and Schulenberg, T. S. 2022. Birds of the world. – https://birdsoftheworld.org/bow/home.

Boyle, W. A. 2017. Altitudinal bird migration in North America. – Auk 134: 443–465.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. and Hilton-Taylor, C. 2002. Habitat loss and extinction in the hotspots of biodiversity. – Conserv. Biol. 16: 909–923.

Bustamante-Castillo, M., Hernández-Baños, B. E. and Arizmendi, M. del C. 2018. Hummingbird diversity and assemblage composition in a disturbed tropical dry forest of Guatemala. – Trop. Conserv. Sci. 11: doi:10.1177/1940082918793303.

Callaghan, C. T., Poore, A. G. B., Hofmann, M., Roberts, C. J. and Pereira, H. M. 2021. Large-bodied birds are over-represented in unstructured citizen science data. – Sci. Rep. 11: 19073.

Cazalis, V. et al. 2022. Bridging the research-implementation gap in IUCN Red List assessments. – Trends Ecol. Evol 37: 359–370.

Chávez-González, E., Vizentin-Bugoni, J., Vázquez, D. P., MacGregor-Fors, I., Dáttilo, W. and Ortiz-Pulido, R. 2020. Drivers of the structure of plant–hummingbird interaction networks at multiple temporal scales. – Oecologia 193: 913–924.

Comer, P. J. et al. 2022. Conserving ecosystem diversity in the tropical Andes. – Remote Sens. 14: 2847.

Correa Ayram, C. A., Etter, A., Díaz-Timoté, J., Rodríguez Buriticá, S. R., Ramírez, W. and Corzo, G. 2020. Spatiotemporal evaluation of the human footprint in Colombia: four decades of anthropic impact in highly biodiverse ecosystems. – Ecol. Indic. 117: 106630.

Cotton, P. A. 2007. Seasonal resource tracking by Amazonian hummingbirds. – Ibis 149: 135–142.

Dalsgaard, B. et al. 2021. The influence of biogeographical and evolutionary histories on morphological trait-matching and resource specialization in mutualistic hummingbird–plant networks. – Funct. Ecol. 35: 1120–1133.

Elith, J., Leathwick, J. R. and Hastie, T. 2008. A working guide to boosted regression trees. – J. Anim. Ecol. 77: 802–813.

ESA CCI Land Cover, 2019. Land cover classification gridded maps from 1992 to present derived from satellite observations. – https://doi.org/10.24381/cds.006f2c9a.

Etter, A., McAlpine, C. and Possingham, H. 2008. Historical patterns and drivers of landscape change in Colombia since 1500: a regionalized spatial approach. – Ann. Assoc. Am. Geogr. 98: 2–23.

Feldman, R. E. and Mcgill, B. J. 2014. How important is nectar in shaping spatial variation in the abundance of temperate breeding hummingbirds? – J. Biogeogr. 41: 489–500.

Fink, D., Auer, T., Johnston, A., Ruiz-Gutierrez, V., Hochachka, W. M. and Kelling, S. 2020. Modeling avian full annual cycle distribution and population trends with citizen science data. – Ecol. Appl. 30: e02056.

Freeman, B. G., Song, Y., Feeley, K. J. and Zhu, K. 2021. Montane species track rising temperatures better in the tropics than in the temperate zone. – Ecol. Lett. 24: 1697–1708.

Freeman, B. G., Strimas-Mackey, M. and Miller, E. T. 2022. Interspecific competition limits bird species' ranges in tropical mountains. – Science 377: 416–420.

Gamba, D. and Muchhala, N. 2022. Pollinator type strongly impacts gene flow within and among plant populations for six Neotropical species. – Ecology: e3845.

Gannon, D. G., Hadley, A. S. and Frey, S. J. K. 2021. Pairing automated mark-recapture and social network models to explore the effects of landscape configuration on hummingbird foraging patterns. – Biol. Lett. 17: 20210188.

Graham, C. H., Elith, J., Hijmans, R. J., Guisan, A., Townsend Peterson, A., Loiselle, B. A. and The Nceas Predicting Species Distributions Working Group. 2008. The influence of spatial errors in species occurrence data used in distribution models. – J. Appl. Ecol. 45: 239–247.

Greenwell, B., Boehmke, B. and Cunningham, J. 2020. gbm: generalized Boosted Regression Models. – R package ver. 2.1.8, https://CRAN.R-project.org/package=gbm.

Gutiérrez Z., A., Rojas-Nossa, S. V. and Stiles, F. G. 2004. Dinámica anual de la interacción colibrí-flor en ecosistemas altoandinos. – Ornitol. Neotrop. 15: 205–213.

Hadley, A. S. and Betts, M. G. 2009. Tropical deforestation alters hummingbird movement patterns. – Biol. Lett. 5: 207–210.

Hadley, A. S., Frey, S. J. K., Robinson, W. D. and Betts, M. G. 2018. Forest fragmentation and loss reduce richness, availabil-

ity, and specialization in tropical hummingbird communities. – Biotropica 50: 74–83.

Hardesty, J. L. and Fraser, K. C. 2010. Using deuterium to examine altitudinal migration by Andean birds. – J. Field Ornithol. 81: 83–91.

Hartig, F. 2020. Dharma: residual diagnostics for hierarchical (multi-level / mixed) regression models. – R package ver. 0.3.3.0, https://CRAN.R-project.org/package=DHARMa.

Heim, W., Heim, R. J., Beermann, I., Burkovskiy, O. A., Gerasimov, Y., Ktitorov, P., Ozaki, K., Panov, I., Sander, M. M., Sjöberg, S., Smirenski, S. M., Thomas, A., Tøttrup, A. P., Tiunov, I. M., Willemoes, M., Hölzel, N., Thorup, K. and Kamp, J. 2020. Using geolocator tracking data and ringing archives to validate citizen-science based seasonal predictions of bird distribution in a data-poor region. – Global Ecol. Conserv. 24: e01215.

Hersbach, H., et al. 2018. ERA5 hourly data on single levels from 1979 to present. Copernicus climate change service (C3S). – Climate Data Store (CDS), https://doi.org/10.24381/cds.adbb2d47.

Hobson, K. A., Wassenaar, L. I., Milá, B., Lovette, I., Dingle, C. and Smith, T. B. 2003. Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. – Oecologia 136: 302–308.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. and Spiegel, O. 2008. Trends and missing parts in the study of movement ecology. – Proc. Natl Acad. Sci. USA 105: 19060–19065.

Hsiung, A. C., Boyle, W. A., Cooper, R. J. and Chandler, R. B. 2018. Altitudinal migration: ecological drivers, knowledge gaps, and conservation implications. – Biol. Rev. 93: 2049–2070.

IUCN. 2022. – The IUCN red list of threatened species, ver. 2022–1. – https://www.iucnredlist.org.

Jahn, A. E., Cueto, V. R., Fontana, C. S., Guaraldo, A. C., Levey, D. J., Marra, P. P. and Ryder, T. B. 2020. Bird migration within the Neotropics. – Auk 137: 1–23.

Jarvis, A., Touval, J. L., Schmitz, M. C., Sotomayor, L. and Hyman, G. G. 2010. Assessment of threats to ecosystems in South America. – J. Nat. Conserv. 18: 180–188.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. and Mooers, A. O. 2012. The global diversity of birds in space and time. – Nature 491: 444–448.

Jiménez-Robles, O. and De la Riva, I. 2019. Lizards in the mist: thermal niches constrained by habitat and microclimates in the Andes of southern Bolivia. – J. Biogeogr. 46: 1676–1686.

Johnston, A., Auer, T., Fink, D., Strimas-Mackey, M., Iliff, M., Rosenberg, K. V., Brown, S., Lanctot, R., Rodewald, A. D. and Kelling, S. 2020. Comparing abundance distributions and range maps in spatial conservation planning for migratory species. – Ecol. Appl. 30: e02058.

Kormann, U., Scherber, C., Tscharntke, T., Klein, N., Larbig, M., Valente, J. J., Hadley, A. S. and Betts, M. G. 2016. Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. – Proc. R. Soc. B 283: 20152347.

La Sorte, F. A., Fink, D., Hochachka, W. M. and Kelling, S. 2016. Convergence of broad-scale migration strategies in terrestrial birds. – Proc. R. Soc. B 283: 20152588.

Lees, A. C., Haskell, L., Allinson, T., Bezeng, S. B., Burfield, I. J., Renjifo, L. M., Rosenberg, K. V., Viswanathan, A. and Butchart, S. H. M. 2022. State of the world's birds. – Annu. Rev. Environ. Resour. 47: 231–260.

Leimberger, K. G., Dalsgaard, B., Tobias, J. A., Wolf, C. and Betts, M. G. 2022. The evolution, ecology, and conservation of hum-

mingbirds and their interactions with flowering plants. – Biol. Rev. 97: 923–959.

Levey, D. J. and Stiles, F. G. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. – Am. Nat. 140: 447–476.

Licona-Vera, Y. and Ornelas, J. F. 2014. Genetic, ecological and morphological divergence between populations of the endangered Mexican sheartail hummingbird (*Doricha eliza*). – PLoS One 9: e101870.

Lindberg, A. B. and Olesen, J. M. 2001. The fragility of extreme specialization: *Passiflora mixta* and its pollinating hummingbird *Ensifera ensifera*. – J. Trop. Ecol. 17: 323–329.

López-Segoviano, G., Arenas-Navarro, M., Vega, E. and Arizmendi, M. D. C. 2018. Hummingbird migration and flowering synchrony in the temperate forests of northwestern Mexico. – PeerJ 2018: e5131.

Maglianesi, A., Blüthgen, N., Böhning-Gaese, K. and Schleuning, M. 2014. Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. – Ecology 95: 3325–3334.

Malcolm, J. R., Liu, C., Neilson, R. P., Hansen, L. and Hannah, L. E. E. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. – Conserv. Biol. 20: 538–548.

Marín-Gómez, O. H., Rodríguez Flores, C. R. and Arizmendi, M. 2022. Assessing ecological interactions in urban areas using citizen science data: insights from hummingbird–plant meta-networks in a tropical megacity. – Urban For. Urban Greening 74: 127658.

Maruyama, P. K., Vizentin-Bugoni, J., Dalsgaard, B., Sazima, I. and Sazima, M. 2015. Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure. – Oecologia 178: 783–793.

Maruyama, P. K., Bonizário, C., Marcon, A. P., D'Angelo, G., da Silva, M. M., da Silva Neto, E. N., Oliveira, P. E., Sazima, I., Sazima, M., Vizentin-Bugoni, J., dos Anjos, L., Rui, A. M. and Marçal Júnior, O. 2019. Plant-hummingbird interaction networks in urban areas: generalization and the importance of trees with specialized flowers as a nectar resource for pollinator conservation. – Biol. Conserv. 230: 187–194.

Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E. and Tonra, C. M. 2015. A call for full annual cycle research in animal ecology. – Biol. Lett. 11: 20150552.

McGuire, J. A., Witt, C. C., Remsen Jr, J. V., Corl, A., Rabosky, D. L., Altshuler, D. L. and Dudley, R. 2014. Molecular phylogenetics and the diversification of hummingbirds. – Curr. Biol. 24: 910–916.

Medeiros, L. P., Garcia, G., Thompson, J. N. and Guimarães, P. R. 2018. The geographic mosaic of coevolution in mutualistic networks. – Proc. Natl Acad. Sci. USA 115: 12017–12022.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. – Nature 403: 853–858.

Ocampo-Peñuela, N., Suárez-Castro, A. F., Díaz-Timoté, J. J., Gómez-Valencia, B., Olaya-Rodríguez, M. H., Sánchez-Clavijo, L. M. and Correa-Ayram, C. A. 2022. Increased exposure of Colombian birds to rapidly expanding human footprint. – Environ. Res. Lett. 17: 114050.

Osborne, O. G., Fell, H. G., Atkins, H., van Tol, J., Phillips, D., Herrera-Alsina, L., Mynard, P., Bocedi, G., Gubry-Rangin, C., Lancaster, L. T., Creer, S., Nangoy, M., Fahri, F., Lupiyaningdyah, P., Sudiana, I. M., Juliandi, B., Travis, J. M. J., Papadopulos, A. S. T. and Algar, A. C. 2022. Fauxcurrence: simulat-

ing multi-species occurrences for null models in species distribution modelling and biogeography. – Ecography 7: 1–7.

Ovaskainen, O., Rekola, H., Meyke, E. and Arjas, E. 2008. Bayesian methods for analyzing movements in heterogeneous landscapes from mark-recapture data. – Ecology 89: 542–554.

Paradis, E. and Schliep, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in {R}. – Bioinformatics 35: 526–528.

Pearce, J. and Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. – Ecol. Modell. 133: 225–245.

Puga-Caballero, A., Arizmendi, M. D. C. and Sánchez-González, L. A. 2020. Phylogenetic and phenotypic filtering in hummingbirds from urban environments in central Mexico. – Evol. Ecol. 34: 525–541.

Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B., Holt, B. G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R. J. and Fjeldså, J. 2019. Humboldt's enigma: what causes global patterns of mountain biodiversity? – Science 365: 1108–1113.

Ramírez-Burbano, M. B., Amorim, F. W., Torres-González, A. M., Sonne, J. and Maruyama, P. K. 2022. Nectar provision attracts hummingbirds and connects interaction networks across habitats. – Ibis 164: 88–101.

Rappole, J. H. 2013. The avian migrant: the biology of bird migration. – Columbia Univ. Press.

Remsen, J. V.., Areta, J., Bonaccorso, E., Claramunt, S., Del-Rio, G., Jaramillo, A., Lane, D. F., Robbins, M. B., Stiles, F. G. and Zimmer, K. J. 2022. A classification of the bird species of South America. – http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm.

Rico-Guevara, A., Hurme, K. J., Elting, R. and Russell, A. L. 2021. Bene"fit" assessment in pollination coevolution: mechanistic perspectives on hummingbird bill–flower matching. – Integr. Comp. Biol. 61: 681–695.

Rueda-Uribe, S., Herrera-Alsina, L., Lancaster, L. T., Capellini, I., Layton, K. K. S. and Travis, J. M. J. 2023. Data from: Citizen science data reveal altitudinal movement and seasonal ecosystem use by hummingbirds in the Andes Mountains. – Dryad Digital Repository, https://doi.org/10.5061/dryad.w3r2280xs.

Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G. and Fuller, R. A. 2014. Conserving mobile species. – Front. Ecol. Environ. 12: 395–402.

Santini, L., Butchart, S. H. M., Rondinini, C., Benítez-López, A., Hilbers, J. P., Schipper, A. M., Cengic, M., Tobias, J. A. and Huijbregts, M. A. J. 2019. Applying habitat and population-density models to land-cover time series to inform IUCN Red List assessments. – Conserv. Biol. 33: 1084–1093.

Sheehy, J., Taylor, C. M. and Norris, D. R. 2011. The importance of stopover habitat for developing effective conservation strategies for migratory animals. – J. Ornithol. 152: 161–168.

Simmons, B. I. et al. 2019. Abundance drives broad patterns of generalisation in plant–hummingbird pollination networks. – Oikos 128: 1287–1295.

Singh, N. J. and Milner-Gulland, E. J. 2011. Conserving a moving target: planning protection for a migratory species as its distribution changes. – J. Appl. Ecol. 48: 35–46.

Sonne, J., Dalsgaard, B., Borregaard, M. K., Kennedy, J., Fjeldså, J. and Rahbek, C. 2022. Biodiversity cradles and museums segregating within hotspots of endemism. – Proc. R. Soc. B 289: 20221102.

Souza, C. S., Maruyama, P. K., Aoki, C., Sigrist, M. R., Raizer, J., Gross, C. L. and de Araujo, A. C. 2018. Temporal variation in

plant–pollinator networks from seasonal tropical environments: higher specialization when resources are scarce. – J. Ecol. 106: 2409–2420.

Stiles, F. G. 1980. The annual cycle in a tropical wet forest hummingbird community. – Ibis 122: 322–343.

Strimas-Mackey, M., Hochachka, W. M., Ruiz-Gutierrez, V., Robinson, O. J., Miller, E. T., Auer, T., Kelling, S., Fink, D. and Johnston, A. 2020. Best practices for using eBird data. – Cornell Laboratory of Ornithology.

Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D. and Kelling, S. 2009. eBird: a citizen-based bird observation network in the biological sciences. – Biol. Conserv. 142: 2282–2292.

Supp, S. R., Bohrer, G., Fieberg, J. and La Sorte, F. A. 2021. Estimating the movements of terrestrial animal populations using broad-scale occurrence data. – Mov. Ecol. 9: 1–19.

The Nature Conservancy. 2008. South America ecosystems, 3rd edn. – USGS.

Tinoco, B. A., Astudillo, P. X., Latta, S. C. and Graham, C. H. 2009. Distribution, ecology and conservation of an endangered Andean hummingbird: the violet-throated metaltail (*Metallura baroni*). – Bird Conserv. Int. 19: 63–76.

Torres-Vanegas, F., Hadley, A. S., Kormann, U. G., Jones, F. A., Betts, M. G. and Wagner, H. H. 2019. The landscape genetic signature of pollination by trapliners: evidence from the tropical herb, *Heliconia tortuosa*. – Front. Genet. 10: https://doi.org/10.3389/fgene.2019.01206.

Tovilla-Sierra, R. D., Herrera-Alsina, L., Bribiesca, R. and Arita, H. T. 2019. The spatial analysis of biological interactions: morphological variation responding to the co-occurrence of competitors and resources. – J. Avian Biol. 50: 1–12.

Tsai, P. Y., Ko, C. J., Chia, S. Y., Lu, Y. J. and Tuanmu, M. N. 2021. New insights into the patterns and drivers of avian altitudinal migration from a growing crowdsourcing data source. – Ecography 44: 75–86.

Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J. J. and Elith, J. 2021. Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. – Ecol. Monogr. 92: e01486.

Volpe, N. L., Hadley, A. S., Robinson, W. D. and Betts, M. G. 2014. Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species. – Ecol. Appl. 24: 2122–2131.

Volpe, N. L., Robinson, W. D., Frey, S. J. K., Hadley, A. S. and Betts, M. G. 2016. Tropical forest fragmentation limits movements, but not occurrence of a generalist pollinator species. – PLoS One 11: 1–13.

Weber, T. P., Houston, A. I. and Ens, B. J. 1999. Consequences of habitat loss at migratory stopover sites: a theoretical investigation. – J. Avian Biol. 30: 416–426.

Williamson, J. L. and Witt, C. C. 2021a. A lightweight backpack harness for tracking hummingbirds. – J. Avian Biol. 52: 1–9.

Williamson, J. L. and Witt, C. C. 2021b. Elevational niche-shift migration: why the degree of elevational change matters for the ecology, evolution, and physiology of migratory birds. – Ornithology 138: 1–26.

Wood, S. N. 2003. Thin-plate regression splines. – J. R. Stat. Soc. Ser. B 65: 95–114.

Xu, Y., Si, Y., Takekawa, J., Liu, Q., Prins, H. H. T., Yin, S., Prosser, D. J., Gong, P. and de Boer, W. F. 2020. A network approach to prioritize conservation efforts for migratory birds. – Conserv. Biol. 34: 416–426.

Young, K. R., León, B., Jørgensen, P. M. and Ulloa, C. U. 2007. Tropical and subtropical landscapes of the Andes. – In: Veblen, T. T., Young, K. R. and Orme, A. R. (eds), The physical geography of South America. Oxford University Press, pp. 200–216.

Zeileis, A. and Hothorn, T. 2002. Diagnostic checking in regression relationships. – R News 2: 7–10.