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Climate, habitat, and socioeconomic gradients shape divergent occupancy and co-occurence patterns between two hummingbirds in western North America

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Climate and land-use change are reshaping species distributions and biotic interactions, yet assessments of these processes across broad spatial extents remain limited. Using 2023 eBird records from spring and early summer on the breeding grounds, combined with high-resolution environmental predictors, we modelled occupancy of Anna's hummingbird (*Calypte anna*), an increasing and range-expanding species, and rufous hummingbird (*Selasphorus rufus*), a declining species, across 1.1 million km^2 of western North America. Single-species occupancy models revealed similar detectability patterns and affinities for coniferous and shrub habitats with low canopies (≤15 m), but marked divergence in climatic preferences and responses to human-modified landscapes. Rufous hummingbird was associated with colder climates, low urban cover (< 25%), and low-to-moderate cropland, whereas Anna's was associated with warmer conditions and showed greater affinity for urban environments. Multispecies occupancy models showed that co-occurrence was highest in areas with low-to-moderate urbanisation and high Gross Domestic Product (GDP), consistent with the 'Luxury Effect' hypothesis. However, co-occurrence declined sharply in highly urbanised, high-GDP areas. Anna's occupancy increased steadily with GDP across the urban–rural gradient, whereas rufous responded positively to GDP only where urbanisation was low. We hypothesize that this divergence could reflect differential environmental filtering rather than direct competition: the resident Anna's hummingbird may be better able to exploit year-round anthropogenic resources, use simplified urban vegetation, and establish breeding territories earlier, whereas the migratory rufous hummingbird may remain more dependent on structurally complex semi-natural habitats and on the seasonal availability of suitable resources along its migration route and within its breeding range. Overall, climate, habitat, and socioeconomic gradients jointly shaped occupancy and co-occurrence patterns in these contrasting species.

Keywords Occupancy models, Citizen science, Supplementary feeding, eBird, Urban ecology, Luxury effect

Ecological novelty, defined as the emergence of environmental conditions and species assemblages without historical precedent, is increasingly widespread as human activities rapidly transform the planet[1,2]. Climate change, urbanisation, and other anthropogenic factors are driving species into new areas, creating novel biotic interactions (e.g.[3,4]). Rising temperatures shift phenology and species distributions, generating new zones of overlap[5,6], while urban expansion can create new resource-rich, subsidised habitats that disrupt natural processes[7,8]. These changes can promote biotic homogenization[9,10], increase competition, and may displace less adaptable species[11]. Yet, detecting such dynamics across broad spatial extents remains challenging, especially

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when interactions are subtle or shaped by complex environmental and behavioural factors. In this context, citizen-science data have become invaluable for tracking range shifts, species interactions, and habitat use at unprecedented resolutions[12,13], although applications explicitly focused on species interactions across broad extents remain limited. Coupled with advanced remote sensing and modern geospatial analytics, these data provide a powerful means to probe species coexistence in a rapidly changing world. As climate change reshapes ecosystems, fully harnessing citizen science data will be essential for anticipating and mitigating biodiversity loss at species distribution scales. Anna's (*Calypte anna*) and rufous (*Selasphorus rufus*) hummingbirds provide a compelling system for examining emerging interspecific interactions as the two species have only recently come into broad sympatry across parts of western North America[14–16]. Historically, Anna's hummingbird was largely confined to coastal California and the Baja California Peninsula (Mexico), where it was predominantly resident, undertaking only short-distance seasonal movements as a partial facultative migrant[17]. By contrast, rufous hummingbird (*Selasphorus rufus*) is a long-distance migrant between Mexico and the temperate forests of northwestern North America. During the twentieth century, Anna's hummingbird expanded markedly northward and eastward into human-modified environments[14–16]. Its breeding range now extends into British Columbia, with non-breeding records as far north as Alaska and year-round populations now established across much of the Pacific Northwest and coastal southwestern Canada, where it increasingly overlaps with rufous hummingbird[18–20]. The two species appear to use similar habitats and food resources, including bird feeders[20–24] and may forage in close proximity. Nevertheless, they are exhibiting contrasting population trends: Anna's hummingbird is increasing in abundance and range, whereas rufous hummingbird is undergoing marked declines[14,25].

The mechanisms underlying these contrasting population trends remain poorly understood but are likely linked to differences in how the two species respond to anthropogenic habitat and climate change. Outside its native range, Anna's hummingbird expansion has been linked to a combination of milder winters, increasing urbanisation, and the widespread use of bird feeders that provide reliable food year-round, potentially promoting more resident behaviour[16,18,19,26]. In contrast, rufous hummingbird declines have been linked to habitat loss across breeding, migratory and wintering areas[15,25,27]. Demographic analyses further suggest that population growth in Anna's hummingbird is driven by high recruitment and adult survival, whereas rufous hummingbird declines are associated with low juvenile survival and recruitment, particularly in human-modified landscapes[15]. Together, these findings suggest that anthropogenic habitat modification, and potentially climate, play a critical role in shaping demographic outcomes, especially during vulnerable life stages. How these processes might translate into differences in habitat selection in areas of overlap on the breeding grounds, particularly along gradients of socioeconomic context, remains poorly understood. Given that anthropogenic resources such as feeders and ornamental vegetation are unevenly distributed across human-dominated landscapes, particularly within urban environments, we expected that patterns of co-occurrence between the two species would vary across urban contexts where resource availability may differ.

To address these gaps, we integrated citizen science data with spatially explicit occupancy models to evaluate habitat selection and co-occurrence in a recently emerged zone of overlap between Anna's and rufous hummingbirds across the north-western U.S. and western Canada. Our approach aims at combining the broad coverage of community-contributed data with the inferential power of occupancy modelling to disentangle patterns of species presence from variation in detection. By incorporating remote-sensing variables, we aimed to capture fine-scale environmental heterogeneity, such as vegetation structure and urban extent, that is often overlooked in biodiversity studies conducted across broad spatial extents. In addition, we explicitly tested whether patterns of species occupancy follow the Luxury Effect hypothesis, the tendency for biodiversity to be concentrated in economically affluent areas due to greater resource availability, such as feeders, gardens, and exotic ornamentals[28]. To our knowledge, this is the first study to integrate citizen-science records, fine-scale remote-sensing climate and habitat metrics, and spatially explicit occupancy models that account for detectability to evaluate species distributions and co-occurrence across the Pacific Northwest. Specifically, we (i) modelled habitat selection for each species, accounting for detectability and spatial structure, to assess climatic and habitat influences across western North America and predict species-specific occupancy patterns; (ii) evaluated co-occurrence within an urban–rural extent, where anthropogenic resources are expected to be most available; and (iii) examined whether occupancy patterns within this extent are associated with socioeconomic conditions.

Methods

Study area

The study was conducted across an extensive region of western North America, encompassing the province of British Columbia (BC, Canada) and the states of Washington and Oregon (United States). The study area spans approximately 1.1 million km^2, between latitudes 42°N and 60°N (Fig. 1). It covers a wide range of elevations, from sea level along the Pacific coast to over 3000 m in the Coast Mountains, Cascade Range, and northern interior ranges. The region includes diverse ecoregions such as the Pacific Maritime, Boreal Cordillera, and Montane Cordillera, supporting a mosaic of habitats including temperate coastal rainforests, interior coniferous and mixed forests, alpine meadows, shrublands, agricultural lands, and urban areas[29]. Mean winter temperatures range from + 4 °C in coastal areas to −18 °C in the northern interior, while summer temperatures typically range from 15 °C to 22 °C, depending on latitude and elevation[30,31]. Annual precipitation is highest in the coastal zone, up to 3000 mm in windward mountain areas and temperate rainforests, and significantly lower in interior valleys, where it typically ranges from 250 to 600 mm, shaped by local topography and rain shadow effects[32]. Urban areas occupy approximately 1–3% of the region, mainly concentrated in low-elevation zones such as the Puget Sound region in Washington and the Lower Mainland of British Columbia.

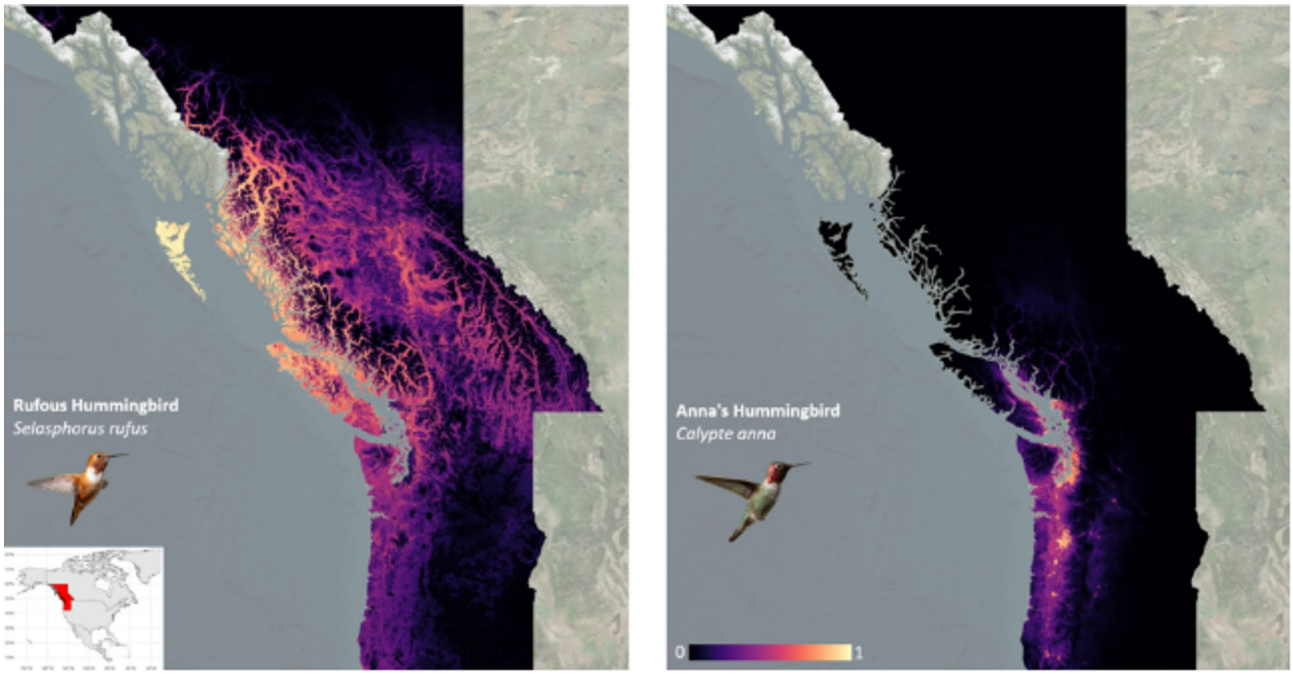


Fig. 1. Predicted single-season single-species occupancy probabilities (0 = low predicted occupancy probability, 1 = high predicted occupancy probability) for rufous (*Selasphorus rufus*; (**a**) and Anna's (*Calypte anna;* (**b**) hummingbirds across western North America, derived from spatially explicit occupancy models accounting for imperfect detection and fitted to 2023 eBird data. The maps depict 2023 predicted distributions within the study area (outlined in red in the inset). The figure was created using QGIS version 3.44 (https://qgis.org/) with the Bing Maps Satellite Imagery as a basemap (included with QGIS 3.44 software). Rufous and Anna's hummingbird photographs by Jonathan Eisen, used under CC BY open access license.

Hummingbird data

We obtained hummingbird data from eBird, a global citizen science platform managed by the Cornell Lab of Ornithology[33]. Due to the substantial computational demands of modelling detection, occupancy, and co-occurrence across the large geographic extent of the study area, we restricted the analysis to 2023, the most recent complete year available at the time of analysis. Our objective was not to quantify temporal trends or range shifts, but rather to examine spatial variation in occupancy and co-occurrence along climatic, habitat, and socioeconomic gradients during a recent breeding season. The broad spatial patterns observed in the 2023 records were consistent with those documented in multi-year regional bird atlases and established range maps, suggesting that the single-year dataset was broadly representative of the known distributions of both species[34,35]. Within the year, we restricted observations to species-specific spring and early summer periods; March 1st to June 30th for Anna's hummingbird and May 1st to June 30th for rufous hummingbird[34]. These windows were intended to capture the interval during which individuals of each species were using their breeding landscapes while recognising that detections may represent a combination of active breeders, pre-breeding individuals and immediate post-breeding or post-territorial movements. Because the timing of breeding and seasonal movements varies across the study region, these windows were treated as seasonal bounds for analysis to identify habitat associations rather than exact periods of overlap or breeding activity. Data were processed following the eBird "*Best Practices for Using eBird Data*"[36] and extracted using the R package "*auk*"[37], which allows efficient filtering of the eBird Basic Dataset (EBD) and associated Sampling Event Data (SED). We analysed complete eBird checklists (all species reported) from stationary or travelling protocols no longer than 2 km, submitted by ≤ 10 observers. To reduce spatial clustering, we randomly retained one repeatedly sampled site unit per approximately 2-km grid cell and retained all valid survey occasions from that site during the study period[36]. We retained sites with ≥ 2 repeat visits and included both detections and non-detections of the focal species. The 2 km limit was chosen to align with the spatial scale relevant to breeding distributions and foraging behaviour[38,39], while minimising noise from fine-scale variability that does not reflect true habitat selection at the population level. Detection data were defined as detections of the target species, while absences were inferred from complete checklists where the species was not observed. The datasets were then zero-filled using the *auk_zerofill* function to produce structured presence–absence data suitable for occupancy analysis. Additional pre-processing steps included the removal of duplicate group checklists, conversion of ambiguous counts (e.g., "X") to NA, and standardisation of effort variables such as duration, distance, and time of day. After filtering, the final dataset included 2380 presences and 12695 absences for rufous hummingbird, and 1643 presences and 4385 absences for Anna's (Figure S1).

Climatic, environmental and socioeconomic data

To characterise the environmental conditions associated with each presence–absence location, we extracted a suite of climatic, topographic, land cover, and socioeconomic variables using circular buffers with a 2 km radius around each location. Data extraction and processing were conducted in Google Earth Engine[40], using the native spatial resolution of each input dataset. Predictor values were summarised within buffers and subsequently exported as a stacked dataset for analysis.

Climatic variables were obtained from WorldClim v2[41] and included Bio10 (mean temperature of the warmest quarter) and Bio16 (precipitation of the wettest quarter), over the period 1970–2000 at a spatial resolution of 30 arc-seconds (~ 1 km). These long-term climate normals were used instead of short-term weather conditions to better represent medium-term climatic patterns that shape vegetation structure and composition, which in turn are likely to influence breeding habitat suitability[6]. Topographic variables included elevation (m), slope (°), and aspect (categorical variable with four classes), all of which were derived within Google Earth Engine (GEE) using the high-resolution (30 m) Copernicus GLO-30 Digital Elevation Model (DEM;[42]). Habitat composition was quantified using the 2020 North American Land Cover dataset (Landsat, 30 m resolution), which includes 19 unique classes (11 of which were present in our study area) available in GEE ("USGS/NLCD_RELEASES/2020_REL/NALCMS"). Habitat variables were expressed as the percentage cover of each land-cover class within each buffer (Table S1). To represent vertical habitat structure, we also included the mean and standard deviation of canopy height model (CHM) estimates from NASA's GEDI (Global Ecosystem Dynamics Investigation) mission, following Tolan et al.[43]. Socioeconomic patterns were assessed using a gridded global dataset of Gross Domestic Product (GDP) at purchasing power parity (PPP) for the year 2020[44], originally provided at 30 arc-second resolution (~ 1 km at the equator). This dataset does not represent directly observed fine-scale socioeconomic measurements, but rather a spatially downscaled estimate derived from national GDP per capita (PPP), subnational disaggregation procedures, and gridded population data. All predictors were summarised within the same 2 km buffers using zonal statistics. Continuous variables (e.g., topography, climate, and canopy height) were averaged across raster cells to represent mean environmental conditions within the buffer, while land-cover variables were expressed as proportional cover. GDP values were similarly averaged within buffers and interpreted as an indicator of the average economic intensity of the surrounding landscape rather than total GDP within the buffer area.

Statistical analysis

Analyses were conducted in two steps according to two different spatial extents. First, we quantified environmental and climatic associations for each species separately (i.e., rufous alone and Anna's alone) across western North America. This step aimed to identify the key climatic and land-cover variables associated with occupancy, while explicitly accounting for imperfect detection. To this end, we fitted single-season occupancy models[45] using the R package "unmarked"[46] in R (version 4.3.2). We evaluated the main occupancy-model assumptions, and no substantial violations were detected; diagnostics and their interpretation are provided in Section S1. Given the large number of candidate predictors (Table S1), we used a structured variable-selection procedure (e.g.[47,48]), since the main drivers of occupancy for these species are still unknown. Each detection covariate (with continuous variables tested in both linear and quadratic form) was first evaluated univariately against an intercept-only model, in which both detection probability (p) and occupancy probability (ψ) were estimated with intercept terms only (i.e., $p(\sim 1)$, $\psi(\sim 1)$). Detection covariates were retained only if they reduced AIC (Akaike Information Criterion) by ≥ 2 relative to the intercept-only model[49,50]. The retained detection covariates (Table S2 and S3) were then combined into an additive best-supported detection model. Holding this detection structure fixed (e.g.[48,51]), occupancy covariates (habitat, vegetation structure/composition, and climate; tested in both linear and quadratic form) were then screened univariately using the same $\Delta AIC \geq 2$ criterion, with the detection model as the reference. Supported occupancy variables were then combined into an additive global model and ranked by AIC for all possible model combinations via the *dredge* function ("MuMIn" R package;[52]; Table S4 and S5). To evaluate model fit and assess potential overdispersion, we used a parametric bootstrap approach with the *parboot* function in the "unmarked" R package[46]. We generated 1,000 bootstrap datasets under the fitted model and calculated the sum of squared errors (SSE) as the fit statistic. The dispersion parameter ($\hat{c}$, or c-hat;[53]) was then computed as the ratio of the observed SSE to the mean SSE from the simulated datasets. A $\hat{c}$ value approximating 1.0 indicates adequate model fit, meaning the model explains the observed variability well. Values much greater than 1.0 suggest overdispersion, more variability in the data than the model accounts for, while values well below 1.0 indicate underdispersion. For both species, $\hat{c}$ computed for the most-parameterised single species, single season occupancy models indicated adequate fit (rufous = 1.03, Anna's = 1.06), so no overdispersion adjustment using the quasi-likelihood counterpart (QAICc;[49]) was required. Finally, we included latitude and longitude as covariates in all models to capture broad-scale spatial patterns in variable associations, given the extensive north–south gradient of the study area (42°N to 60°N). Latitude and longitude were included as independent additive effects (i.e., no interaction term), and polynomial terms were fitted separately for each variable. Preliminary model comparisons (based on AIC) indicated that a cubic polynomial term provided the best-supported structure for both latitude and longitude in the rufous hummingbird models, whereas a quadratic polynomial was supported for both variables in the Anna's hummingbird models. Predictors were evaluated for potential multicollinearity using both Pearson's r with a threshold of 0.6 and Variance Inflation Factor (VIF) with a threshold of 5. Elevation was correlated ($r = 0.63$) with Bio10 and the first was excluded as it held less explanatory power. No evidence of spatial autocorrelation was detected (Figure S2).

In the second step, after parameterising the single-species occupancy models with the most supported detection and environmental covariates, we evaluated whether patterns of occurrence and co-occurrence varied across the urban–rural extent, where the two species feed in close proximity at shared resources and where interactions have been observed[14,25]. For this analysis, we restricted the dataset to sites containing ≥ 10% urban

or cropland land cover (N = 2542 sites) and to the shared seasonal window (1 May–30 June 2023) to maximize spatiotemporal overlap between species. We assessed occurrence and co-occurrence patterns using a multispecies (two-species), single-season occupancy model following Rota et al.[54], implemented with the *occuMulti* function in the "unmarked" R package[46]. The model estimated species-specific detection probabilities and three natural parameters: two first-order parameters describing species-specific occupancy components and one second-order parameter describing pairwise association between species. For the two-species model, we denote these natural parameters as f_{Rufous}, f_{Anna}, and $f_{\text{Rufous:Anna}}$, with the latter representing pairwise association. These parameters determine four mutually exclusive latent occupancy-state probabilities: ψ_{10} (rufous only), ψ_{01} (Anna only), ψ_{11} (both species present), and ψ_{00} (neither species present). The resulting state probabilities were used to derive marginal occupancy probabilities, describing occupancy of each species regardless of the presence of the other, and conditional occupancy probabilities, describing occupancy given the presence or absence of the other species. Marginal occupancy probabilities were derived as $\psi_{\text{Rufous}}=\psi_{10}+\psi_{11}$ and $\psi_{\text{Anna}}=\psi_{01}+\psi_{11}$.

Following Evans and Mortelliti[55], detection probabilities for each species (p_{Rufous}, p_{Anna}) were modelled using the same covariates, identified in the best-supported single-species models (Tables S4 & S5). First-order natural parameters (f_{Rufous}, f_{Anna}) and the pairwise association between the two species ($f_{\text{Rufous:Anna}}$) were modelled using the key covariates (scaled: centred at zero and scaled to unit variance) identified in the single-species analyses, including: (i) climate (Bio10, Bio16), (ii) vegetation structure (CHM and CHM2), (iii) a simplified index for woody vegetation cover (sum of temperate or sub-polar needleleaf forest, temperate or sub-polar broadleaf deciduous forest, mixed forest, temperate or sub-polar shrubland forest and shrub habitats), (iv) cropland cover, (v) urban cover, and (vi) log-transformed GDP.

For this analysis, we developed a structured set of candidate multispecies occupancy models to evaluate whether environmental and socioeconomic drivers influenced species-specific occupancy, the pairwise association between the species, or both (Table 1). The candidate set began with an intercept-only model in which the first-order natural parameters, pairwise association parameter, and detection probabilities were held constant across sites, followed by a detection-only model in which occupancy and pairwise association remained constant while detection varied with survey covariates. A first group of models evaluated the effects of environmental conditions on species-specific occupancy component by including vegetation structure (CHM and CHM^2), woody cover, cropland cover, urban cover, temperature and precipitation. For the pairwise association component, we compared a constant association with a model in which association varied with temperature. These models tested whether broad habitat structure and climate gradients predicted spatial variation in species-specific occupancy and pairwise association. A second group of models evaluated socioeconomic effects by adding GDP to the species-specific occupancy component and/or modelling the pairwise association as a function of GDP.

p Rufous	*p* Anna	*f* Rufous, *f* Anna	*f* Rufous:Anna	AIC	ΔAIC	k
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10 + GDP	GDP × Urban	21820.9	0	35
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10 + GDP	GDP	21832.1	11.2	33
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10 + GDP	GDP × Cropland	21834.7	13.8	35
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10 + GDP	*f*(.)	21859.1	38.2	32
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10	GDP × Urban	21897.4	76.5	33
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10	GDP × Cropland	21925.9	105.0	33
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10	GDP	21927.2	106.3	31
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10	*f*(.)	21935.9	115.0	30
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10	Bio10	21936.5	115.6	31
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	CHM^2 + Woody veg.^{2} + Cropland + Urban + Bio10 + Bio16	*f*(.)	21939.9	119.0	32
Time^2 + Effort(duration)^2 + eBird protocol	Time^2 + Effort(duration)^2 + N. of observers^2	*f*(.)	*f*(.)	22539.3	718.4	16
p(.)	p(.)	*f*(.)	*f*(.)	22863.7	1042.8	5

Table 1. Set of candidate multispecies occupancy and detection models for rufous and Anna's hummingbirds within urban and cropland areas. Models were ranked using Akaike's Information Criterion (AIC). ΔAIC represents the difference from the top-ranked model and k is the number of estimated parameters. Detection (*p*) and state-process covariates (*f*) were selected based on broad-extent, single-species occupancy analyses identifying the most influential predictors of detectability and site use. Quadratic terms (^{2}) indicate potential nonlinear responses and always include the corrispondent linear term. The best-supported model (first row) included both habitat structure, climate and socioeconomic gradients (GDP) in the species-specific occupancy components, with the effect of GDP on pairwise association varying across the urbanisation gradient through a GDP × Urban interaction. For additional details see "Methods" and "Results".

GDP was incorporated as a socioeconomic predictor influencing species-specific occupancy and/or the pairwise association parameter ($f_{\text{Rufous:Anna}}$). To test whether socioeconomic conditions modify habitat relationships in line with the Luxury Effect hypothesis, we included interaction terms between GDP and land-cover variables, specifically GDP × Urban and GDP × Cropland, in the pairwise association occupancy component. Under the Luxury Effect hypothesis, wealthier neighbourhoods tend to support higher species richness because they often contain more extensive and better maintained green spaces including gardens, ornamental vegetation, and supplementary resources such as feeders; therefore, we expected the positive influence of GDP on occupancy and co-occurrence to be strongest under low-to-moderate levels of urbanisation, and weaker in rural (high natural vegetation regardless of wealth) or densely urbanised environments (limited vegetation regardless of wealth).

Results

Detection and occupancy patterns of hummingbirds across western North America

Single-species, single-season occupancy models indicated that detection (p) covariates influenced detection probabilities for both rufous and Anna's hummingbirds. Detection was highest during the morning and around midday, although the peak occurred earlier for rufous hummingbirds, at approximately 07:00–09:00 than for Anna's hummingbirds, at approximately 11:00–13:00, and both subsequently declined later in the day (Figures S3 and S4). Stationary eBird protocols were more effective at detecting rufous hummingbird than travelling ones (Table S4 & S5). In contrast, p_{Anna} showed a weak quadratic relationship with the number of observers (Table S5). The single-species single-season occupancy models also revealed both similarities and key differences in how environmental factors influence the occupancy probability (ψ) of rufous and Anna's hummingbirds. Overall, the two species exhibited broadly comparable habitat associations, although the form and strength of these relationships differed. Temperate or sub-polar needleleaf forests were related quadratically to ψ_{Rufous}, with a peak at approximately 25% cover within the 2-km-radius buffer surrounding each site, whereas the relationship was generally positive and linear for ψ_{Anna} (Figures S3 & S4). Temperate or sub-polar shrubland showed a quadratic relationship for both species with higher tolerance for Anna's (peaking at ~ 50% cover) than for rufous (peaking at ~ 25%). The Canopy Height Model (CHM) revealed partially overlapping but distinct associations with vegetation height: Anna's hummingbird occupancy peaked at relatively low-to-intermediate canopy heights (approximately 10m), whereas rufous hummingbird occupancy was highest in somewhat taller vegetation (approximately 14m). Slope influenced the two species differently, with rufous hummingbird exhibiting higher ψ_{Rufous} in steeper, cooler montane areas, while ψ_{Anna} was more frequently associated with flatter and warmer valley bottoms. ψ_{Rufous} was associated weakly with urban areas (up to ~ 25% cover), while Anna's hummingbird showed a strong positive association, with ψ_{Anna} remaining high even above 75% urban cover. Cropland cover was retained in the best-supported rufous hummingbird models and showed a nonlinear relationship, with occupancy highest at intermediate-to-high cover of approximately 60–70%. Cropland was not retained in the best-supported Anna's hummingbird models. Climatically, rufous hummingbird exhibited a quadratic relationship with temperature (Bio10), preferring moderate values (around 17–18 °C), whereas Anna's showed a strong positive association with temperature (Bio10) and a negative association with precipitation (Bio16; Figures S3 & S4).

Hummingbird co-occurrence in relation to socioeconomic gradients

Across the urban–rural subset of the eBird dataset, both species were detected at the same site in 14.4% of locations (366 of 2542 sites), indicating relatively limited observed spatial overlap in our study region. At these co-detected sites, the two species were recorded during the same survey occasion on 1063 of 4123 valid occasions (25.8%). Across all candidate models, the best-supported two-species occupancy model included vegetation structure (CHM and CHM2), woody vegetation cover, cropland extent, temperature (Bio10), and GDP, with a strong GDP × urban cover interaction in the pairwise association term (Table 1 & S6). The pairwise association parameter $f_{\text{Rufous:Anna}}$ was positive, indicating that the two hummingbird species tended to co-occur more often than expected under statistical independence (Table S6). However, the strength of this association varied markedly along the socioeconomic and urbanisation gradients.At low-to-medium urbanisation, increased GDP was associated with stronger pairwise association ($f_{\text{Rufous:Anna}}$), whereas at high urbanisation, higher GDP sharply reduced $f_{\text{Rufous:Anna}}$ (Fig. 2 and 3). Correspondigly, predicted co-occurence probability declined in affluent, highly urbanised areas. Species-specific state responses also showed distinct patterns between the two species. The first-order rufous component (f_{Rufous}) increased with woody vegetation cover and cropland and exhibited a nonlinear peak at intermediate canopy heights. Warmer temperatures (Bio10) reduced rufous occupancy, and GDP had only weak positive effects. The first-order Anna's component (f_{Anna}) increased with GDP (strongest predictor) and cropland but declined with higher temperatures, and peaked at intermediate woody vegetation cover and canopy height. Detection probabilities for both species were strongly influenced by survey conditions. p_{Rufous} and p_{Anna} increased with longer survey duration, declined after 10:00 local time, and differed across observer numbers and eBird protocols (Table S6).

Discussion

Rapid environmental change is altering not only species distributions but also patterns of spatial overlap among species. Our results showed that occupancy and co-occurrence in Anna's and rufous hummingbirds were jointly structured by climatic, habitat, and socioeconomic gradients. In particular, the influence of wealth depended strongly on urbanisation, with affluent landscapes associated with higher predicted co-occurrence only where urban cover remained low to moderate. In highly urbanised landscapes, increasing Gross Domestic Product

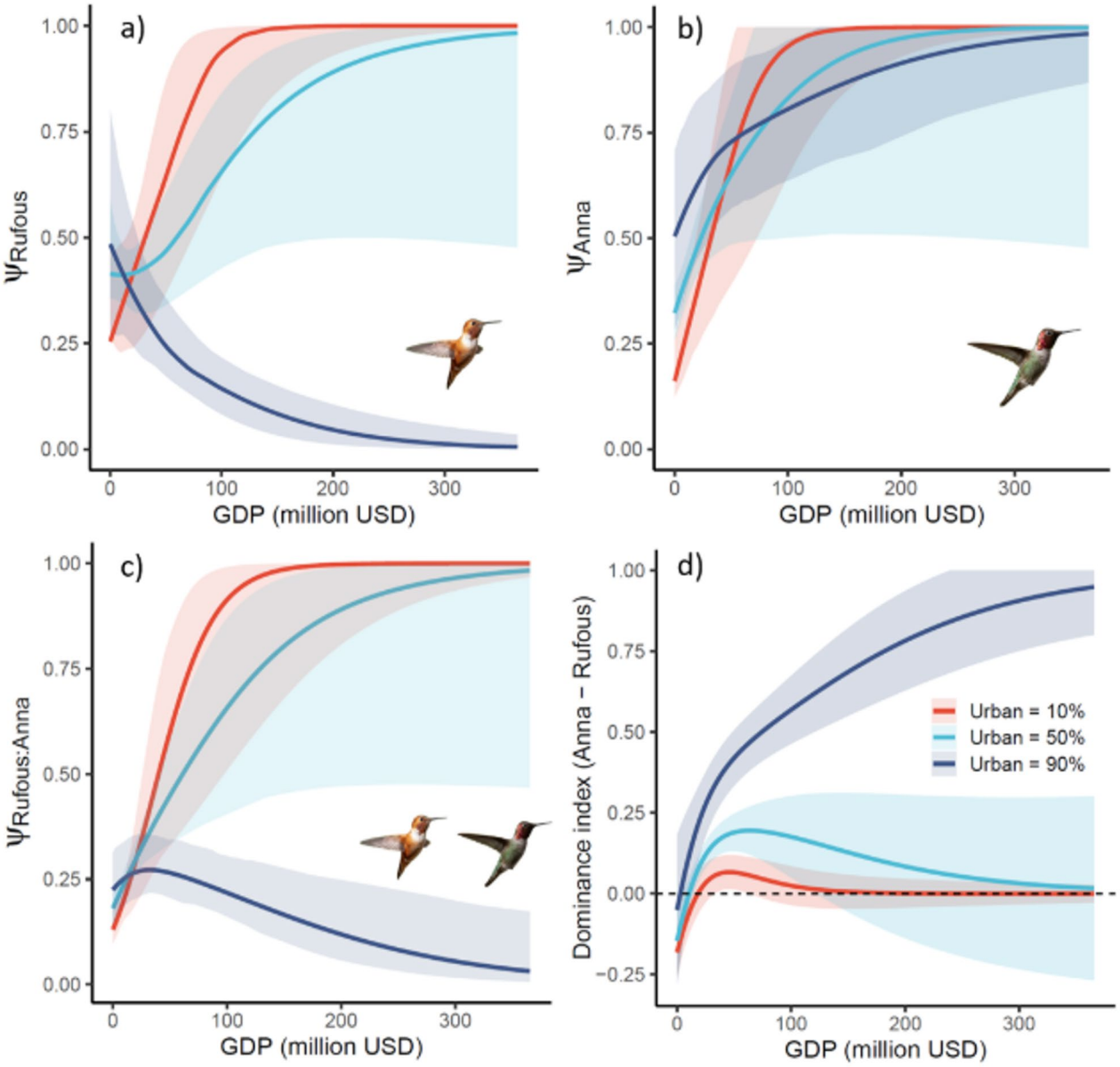


Fig. 2. Predictions from the best-supported two-species occupancy model, from which four latent occupancy-state probabilities were derived: ψ_{10} (Rufous only), ψ_{01} (Anna only), ψ_{11} (both present), and ψ_{00} (neither), while accounting for imperfect detection. (**a**) Marginal rufous occupancy ($\psi_{10} + \psi_{11}$) rises with GDP in low-urban areas but declines with GDP in medium and highly urbanised areas. (**b**) Marginal Anna occupancy ($\psi_{01} + \psi_{11}$) increases steadily with GDP across all urbanisation levels. (**c**) Co-occurence probability (ψ_{11}) is highest in low-urban areas and decreases with GDP under high urbanisation. (**d**) Relative occupancy index (here termed the Dominance Index), calculated as (ψAnna – ψRufous)/(ψAnna + ψRufous), where values > 0 indicate relatively higher occupancy by Anna's hummingbird and values < 0 indicate relatively higher occupancy by rufous hummingbird; the index increases sharply with both GDP and urbanisation. Rufous and Anna's hummingbird photographs by Jonathan Eisen, used under CC BY open access license.

(GDP) favoured Anna's hummingbird and was associated with declining rufous hummingbird occupancy and reduced predicted co-occurrence.

The two species exhibited broadly similar habitat associations across western North America, differing mainly in their relationships with canopy height and the proportional cover of needleleaf forest and shrubland. These results are in line with the limited information available on the nesting and foraging ecology of both species, which use secondary-succession forests, deciduous or evergreen forests depending on latitude, and shrubby habitats, typically nesting on branches of shrubs and trees[20,23]. This ecological similarity may help explain the positive baseline association observed across parts of their shared range. Nevertheless, their climatic and anthropogenic associations diverged. These contrasting associations are consistent with their broad breeding distributions. Rufous hummingbird occupies colder, mesic, and more forested montane and interior habitats

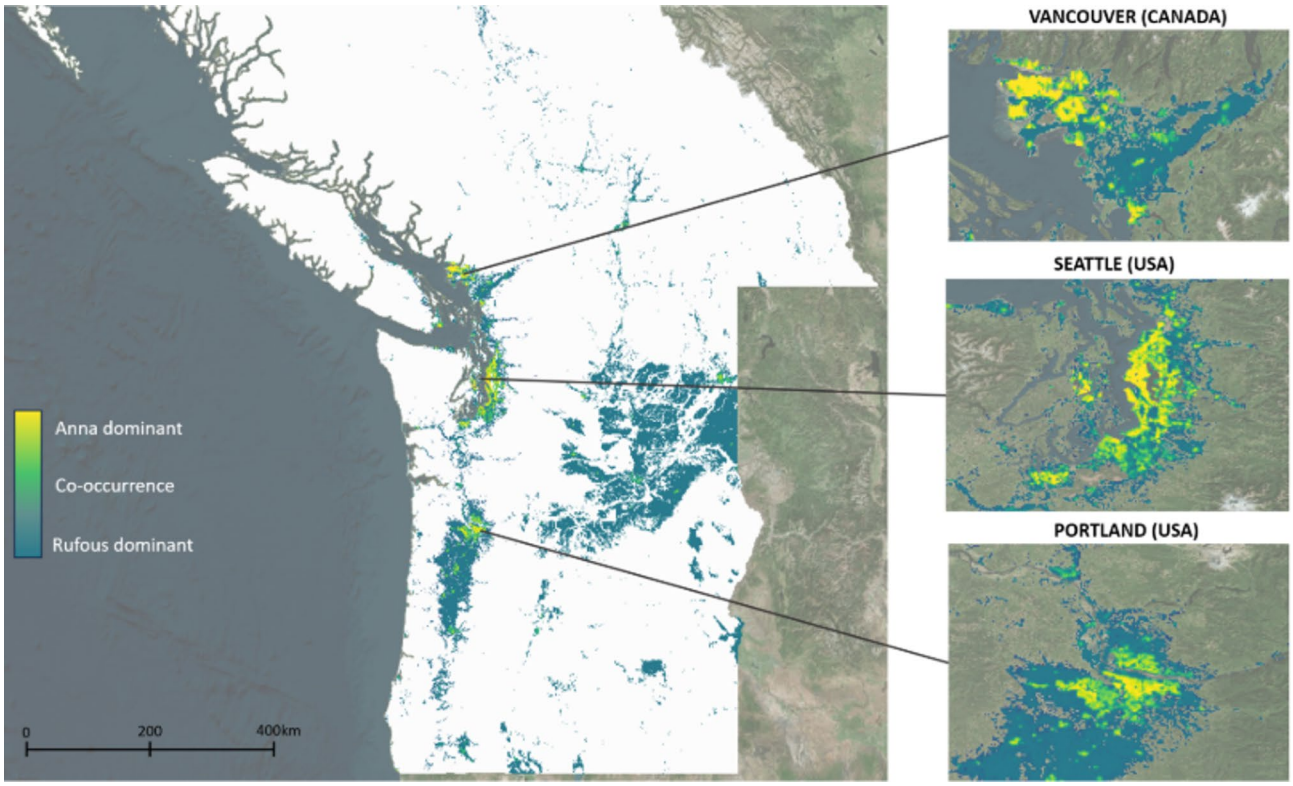


Fig. 3. Spatial predictions of the relative occupancy index (here defined as the Dominance Index) between Anna's and rufous hummingbirds across urban and cropland areas in the study region, based on the best supported model (Table S6). The index, calculated as $(\psi_{Anna} - \psi_{Rufous})/(\psi_{Anna} + \psi_{Rufous})$, represents the relative difference in predicted marginal occupancy between the two species from the two-species occupancy model, ranging from − 1 (higher predicted occupancy for rufous hummingbird) to + 1 (higher predicted occupancy for Anna's hummingbird). Values near zero indicate similar predicted occupancy probabilities for the two species. Yellow tones denote areas where predicted occupancy is higher for Anna's hummingbird, blue tones indicate areas where predicted occupancy is higher for rufous hummingbird, and green tones indicate similar predicted occupancy between the two species. The right panels show enlarged views of three major metropolitan regions: Vancouver (Canada), Seattle (USA), and Portland (USA), highlighting areas of relatively higher predicted occupancy for Anna's hummingbird in highly urbanised zones and relatively higher predicted occupancy for rufous hummingbird in surrounding agricultural and semi-natural areas. The figure was created using QGIS version 3.44 with Bing Maps Satellite Imagery as the basemap.

extending to approximately 60°N, while tolerating only low to moderate levels of urbanisation. In contrast, Anna's hummingbird is primarily associated with milder coastal and lowland environments, rarely exceeding 51°N inland, and persists even in highly urbanised landscapes, consistent with patterns reported by Fink et al.[35].

The socioeconomic patterns observed along the urban–rural gradient are consistent with the Luxury Effect hypothesis[28]. GDP was positively associated with occupancy of both species, although much more strongly for Anna's hummingbird, whereas increasing urban cover reduced rufous hummingbird occupancy but had little direct effect on Anna's. The GDP × urban-cover interaction further indicated that the effect of wealth on pairwise association depended on the degree of urbanisation. Wealthier areas may provide more extensive green spaces, nectar-rich vegetation, and supplementary feeding, thereby increasing resource availability for hummingbirds[7,8,56–58]. Anna's hummingbird appears particularly responsive to these subsidies. Alexandre et al.[16] showed that feeder use was associated with rapid morphological change, including longer, more tapered bills and increased bill pointedness in males, traits consistent with enhanced nectar exploitation. By contrast, the weaker GDP effect and negative association with urban cover suggest that rufous hummingbird may tolerate moderately modified landscapes but become less likely to occur as urbanisation intensifies. This interpretation is consistent with English et al.[15], who found that rufous hummingbird responded negatively to high human population density, whereas moderate cropland cover was associated with improved survival.

One possible explanation for this contrasting response is that the benefits of wealth depend on the degree of urbanisation. A closely analogous pattern was reported for South African bird communities, where species richness increased with income at low levels of urban cover but declined with income in highly urbanised landscapes[59]. In highly urbanised landscapes in our study area, resources associated with wealth may be embedded within simplified vegetation dominated by ornamental shrubs, lawns, and scattered small trees. Such environments may provide Anna's hummingbird with year-round food and potential nesting sites, whereas rufous hummingbird may continue to use feeders but encounter less of the structurally complex, shrubby, or

coniferous habitats with which their occupancy was associated. Thus, the benefits of wealth-related resource provisioning may depend on the retention of suitable vegetation and habitat structure.

More broadly, these processes may also help explain the recent expansion of Anna's hummingbird. This expansion appears closely linked to anthropogenic resource provisioning, especially the availability of year-round food sources, and to the buffering effects of urban microclimates (e.g., the urban heat island effect), which may reduce exposure to cold extremes during the nonbreeding period[18]. The contribution of broader climatic changes to the expansion of Anna's range remains less clear. Although global warming may increase climatic suitability further north and higher in elevation[60–62], improved climatic suitability alone may not be sufficient to support colonisation and persistence ([19]; but see[18]). Range expansion may occur most successfully where favourable climatic conditions coincide with feeders, nectar-rich urban vegetation and suitable nesting vegetation ([19]; but see[18]).

Life-history and behavioural differences may further reinforce the contrasting responses of the two species at high levels of urbanisation. Anna's hummingbird is resident, can exploit predictable anthropogenic food resources throughout the year, and generally begins breeding earlier, whereas rufous hummingbird undertakes a long-distance migration and initiates breeding later. In parts of the overlap zone, Anna's hummingbird may therefore establish territories and begin nesting before rufous hummingbird arrives, creating a possible phenological priority effect through earlier access to food and nesting sites. Residency may also expose Anna's hummingbird to more persistent urban selective pressures, as individuals experience feeders, ornamental vegetation, and urban microclimates throughout the year. By contrast, rufous hummingbird encounters different environments across breeding, migration, and wintering areas, potentially generating more variable or conflicting selective pressures. The feeder-associated morphological changes reported by Alexandre et al.[16] provide evidence of a rapid phenotypic response to anthropogenic resources in Anna's hummingbirds, possibly reflecting heritable adaptation, developmental effects, or phenotypic plasticity. Comparable evidence is lacking for rufous hummingbird, as it is unknown whether they exhibit similar, weaker, or fundamentally different phenotypic responses to urban resource provisioning.

Our results should be interpreted as evidence of spatial association and co-occurrence rather than direct competition given that our multispecies occupancy models identify where species overlap but cannot distinguish competitive interactions from shared or contrasting responses to habitat, climate, and other environmental gradients[54]. Thus, the reduced co-occurrence predicted at high levels of urbanisation could result from environmental filtering, competitive interactions, phenological priority effects, or a combination of these processes. However, the widespread co-occurrence of the two species across urban and rural landscapes does not support a simple competitive relationship. Although rufous hummingbirds are more frequently reported to dominate Anna's hummingbirds during interactions at feeders, the reverse has also been observed in some locations or contexts[63], suggesting that competitive dominance is not consistently asymmetric. Comparative studies of arrival timing, territory establishment, behaviour, survival, and reproductive performance across urbanisation gradients are needed to determine whether earlier establishment by Anna's hummingbird contributes to reduced co-occurrence in highly urbanised landscapes. Urban environments may also differ in levels of human disturbance and exposure to pets and other anthropogenic hazards. Records of hummingbirds admitted to wildlife rehabilitation centres from urban areas indicate that both species frequently encounter anthropogenic hazards[64], although direct comparisons of their tolerance to urbanisation and other human-related pressures are currently lacking. Both species are also highly territorial. [63]. Overall, available observations do not support a consistent dominance hierarchy and highlight the need for experimental studies of interspecific behaviour across urbanisation gradients.

Two aspects of the study design should be considered when interpreting our results. First, the seasonal windows were selected to capture the use of breeding landscapes rather than to restrict the analysis to confirmed breeding individuals. Consequently, some records may have involved pre-breeding or early post-breeding individuals, and the results should be interpreted as broad spatial co-occurrence during spring and early summer rather than as evidence of direct interactions between confirmed breeders. Second, because the analysis was restricted to a single year, we could not assess whether the strength of the estimated relationships varied among years. Multi-year analyses would therefore be valuable for evaluating the temporal stability of the observed co-occurrence patterns.

Within these limitations, our results and existing evidence are more consistent with habitat change or loss than with direct competition as a major explanation for rufous hummingbird decline. Loss of early-seral, open, and shrubby habitats, which provide key nesting and foraging environments for rufous hummingbirds, has been strongly linked to population declines across the core coastal range of the species[27]. High human population density has been associated with reduced survival[15], and datasets from western Washington indicate declines in urban detection, including at feeders[63]. Breeding Bird Survey data further indicate an average annual decline of approximately 2.3% between 1966 and 2015[65]. As a long-distance migrant, rufous hummingbird may also be affected by habitat and resource changes across multiple stages of the annual cycle, including possible mismatches between migration timing and peak resource availability[66]. Although aggressive interactions with Anna's hummingbird occur at feeders[63,67], evidence that they generate population-level competition is lacking.

Our results suggest that management of public and private urban green spaces should not rely on feeder provisioning alone. Parks, gardens, and other green spaces could retain or establish structurally diverse native vegetation, including flowering shrubs, early-seral patches, open areas, and scattered trees of intermediate height, while maintaining connections with surrounding semi-natural habitats. Measures to reduce hazards from free-ranging cats and window collision may provide additional benefits. Because we measured occupancy rather than reproductive performance, these recommendations should be treated as testable management hypotheses and evaluated through monitoring of nest-site use, reproductive success, and juvenile survival. More broadly, our findings show that human-associated resources may promote co-occurence under moderate urbanisation

but increasingly favour Anna's hummingbird as urbanisation intensifies, highlighting the need to consider food availability, vegetation structure, life history, and socioeconomic context together in urban hummingbird conservation.

Data availability

All data and code are available on Figshare at https://figshare.com/s/b3fd7eb3b3687b1e199a

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Author contributions

Conceptualization: SW, KM, DS; Methodology: DS, SW, KM; Investigation: DS, TK, SW, KM; Data analysis and presentation: DS, SW, TK, KM; Writing – original draft: DS, SW, KM; Writing – review and editing: DS, SW, KM, TK. Funding acquisition: SW.

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Declarations

Competing interests

The authors declare no conflicts of interest.

Ethical approval

No ethical approval was required for this study as it was based exclusively on the analysis of existing citizen science data and did not involve direct interaction with animals or humans.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-026-68184-4.

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