Opposing Patterns of Altitude-Driven Pollinator Turnover in the Tropical and Temperate Americas

Agnes S. Dellinger,[1,2,*] Ashley M. Hamilton,[3] Carolyn A. Wessinger,[3] and Stacey D. Smith[2]

1. Department of Botany and Biodiversity Research, University of Vienna, Austria; 2. Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309; 3. Department of Biological Sciences, University of South Carolina, Columbia, South Carolina 29208

Submitted September 6, 2022; Accepted January 27, 2023; Electronically published July 12, 2023

Online enhancements: supplemental PDF.

ABSTRACT: Abiotic factors (e.g., temperature, precipitation) vary markedly along elevational gradients and differentially affect major groups of pollinators. Ectothermic bees, for example, are impeded in visiting flowers by cold and rainy conditions common at high elevations, while endothermic hummingbirds may continue foraging under such conditions. Despite the possibly far-reaching effects of the abiotic environment on plant-pollinator interactions, we know little about how these factors play out at broad ecogeographic scales. We address this knowledge gap by investigating how pollination systems vary across elevations in 26 plant clades from the Americas. Specifically, we explore Cruden's 1972 hypothesis that the harsh montane environment drives a turnover from insect to vertebrate pollination at higher elevations. We compared the elevational distribution and bioclimatic attributes for a total of 2,232 flowering plants and found that Cruden's hypothesis holds only in the tropics. Above 30°N and below 30°S, plants pollinated by vertebrates (mostly hummingbirds) tend to occur at lower elevations than those pollinated by insects. We hypothesize that this latitudinal transition is due to the distribution of moist, forested habitats favored by vertebrate pollinators, which are common at high elevations in the tropics but not in the temperate Americas.

Keywords: altitudinal gradient, hummingbird habitats, pollinator shift, precipitation.

Introduction

Biotic interactions are among the most prominent factors limiting, promoting, and structuring organismal diversity on Earth (Schemske et al. 2009; Wessinger et al. 2019; Sinnott-Armstrong et al. 2021). For plant-pollinator interactions, associations are unevenly distributed across space owing to variation in pollinator availability and importance in different regions and ecosystems (Ollerton 2017; Dellinger et al. 2021; Orr et al. 2021). Ecogeographical variation in plant-pollinator relationships emerges across broad latitudinal and altitudinal gradients as major groups of pollinating animals vary in their distributions (e.g., Classen et al. 2015; Dellinger et al. 2021; McCabe and Cobb 2021). For example, bats, rodents, and passerine birds are important pollinators, particularly in tropical regions (Ratto et al. 2018), while insects and hummingbirds act as pollinators across latitudes in the Americas. Similarly, diverse insect pollinator assemblages (i.e., bees, beetles, wasps, butterflies), common at low to middle elevations, are narrowed to bumblebee-dominated and, particularly, fly-dominated systems in many high-elevation communities (Arroyo et al. 1982; Warren et al. 1988; Primack and Inouye 1993; Lefevbre et al. 2018; Adedoja et al. 2020; McCabe and Cobb 2021). Although these patterns suggest a critical role of climatic factors in structuring plant-pollinator associations, we currently lack broadscale ecogeographic assessments of the distribution of pollination modes.

Major turnovers in pollinator groups across latitudinal and altitudinal gradients may reflect differences in the pollinators' tolerance of extrinsic abiotic climatic stressors (Ollerton 2017; Lefevbre et al. 2018). For example, cool and wet weather generally restricts the activity of ectothermic animals like many bees and other small insects (McCallum et al. 2013; Classen et al. 2015; Cozien et al. 2019), while large endothermic animals often continue to forage through moderate to heavy rain (hummingbirds, sunbirds; Sun et al. 2017; Lawson and Rands 2019). In Cruden's (1972) groundbreaking article, he used this observation to hypothesize that vertebrate-pollinated (particularly bird-pollinated) plants will be more abundant in cool and rainy montane habitats, as birds will be more reliable pollinators than bees under these climatic conditions. His empirical studies of pollinator communities along four elevational transects in the Mexican Sierra Madre mountains supported this hypothesis (Cruden

* Corresponding author; email: agnes.dellinger@univie.ac.at.

American Naturalist, volume 202, number 2, August 2023. Published by The University of Chicago Press for The American Society of Naturalists. https://doi.org/10.1086/725017

1972). The environment-induced differences in activity between ecto- and endothermic pollinators observed by Cruden have critical evolutionary implications (Arroyo et al. 1982; Krömer et al. 2006; Dellinger et al. 2021). Specifically, if cold and rainy conditions that are prevalent in mountains consistently reduce bee, but not bird, pollinator activity, we may expect to find repeated evolutionary pollinator shifts in plant lineages that occur across elevational gradients.

While Cruden's hypothesis of insect-vertebrate pollinator turnover across elevational (and thus climatic) gradients has been widely accepted, some reports indicate that this pattern does not hold across latitudes. In temperate regions, insects are often the dominant pollinators in high-elevation ecosystems (McCallum et al. 2013; Woodard 2017; McCabe and Cobb 2021), a pattern that may relate to the ability of many pollinator species, such as bumblebees and syrphid flies, to regulate their body temperature (Heinrich 1974; Oyen and Dillon 2018). Hummingbirds, by contrast, are more important pollinators in more mesic, lower-elevation temperate areas (Grant and Grant 1968; Hamilton and Wessinger 2022), so-called hummingbird habitats (Stebbins 1989). Whether more mesic habitats represent environments of increased hummingbird pollinator importance more broadly remains to be investigated.

Plant clades featuring evolutionary shifts in pollinators (e.g., between bee and hummingbird pollination; Thomson and Wilson 2008) and occurring across ecogeographic gradients represent ideal systems to test whether there is a strong link between abiotic environment and pollination strategy. If certain abiotic environmental conditions do indeed favor pollination by vertebrates over insects (i.e., through a significant reduction of bee pollinator efficiency; Thomson and Wilson 2008), we would expect to see vertebrate pollination associated with these conditions repeatedly across different plant lineages. To our knowledge, however, no attempts have been made to systematically test whether pollination strategies of clades that have colonized montane environments and shifted pollinators follow Cruden's altitude-/climate-driven bee-hummingbird pollinator turnover, and the potential bioclimatic thresholds linked to such turnovers have not been identified.

Here, we address these research gaps by investigating ecogeographic patterns of pollination systems across 2,232 plant taxa from 26 clades, serving as evolutionary replicates, across the entire Americas. We chose to focus on the Americas because, in contrast to other continents, vertebrate pollinators are represented across latitudes by hummingbirds there (Cronk and Ojeda 2008), allowing for a broadscale test of Cruden's (1972) altitude-/climate-driven pollinator turnover hypothesis. In addition to testing for associations between elevation and pollination systems, we consider how environmental factors (temperature, precipitation, cloud cover) and biome type relate to pollination mode and whether moist, shady habitats do indeed represent hummingbird habitats. Together, these analyses provide the hitherto broadest assessment of ecogeographic factors underlying the distribution of pollination strategies in the Americas.

Methods

Selection of Study Clades and Scoring Pollination Mode

For selecting study clades, we employed the following criteria: clades that (1) encompass both bee pollination and hummingbird pollination in order to span insects and vertebrates, (2) have molecular phylogenetic information available, and (3) occur across elevational gradients in the Americas. We note that, in targeting clades with evolutionary pollinator transitions that may be associated with elevation, our criteria exclude clades with narrow elevational ranges and clades with invariant pollination strategies, which could be informative about community-level questions (see "Discussion"). We also required that at least some members of the clade have empirical studies of pollination, allowing for system-specific predictions of pollination mode in the remaining taxa. For the latter, we relied on literature from experts in each system to classify the taxa (see literature cited in table S1). To find clades meeting these requirements, we began with the lists of Tripp and Manos (2008) and Abrahamczyk and Renner (2015), and we supplemented the dataset with other well-studied groups (e.g., Bromeliaceae, Loranthaceae, Merianieae) using keyword searches in Google Scholar (i.e., clade name + pollinat*). This resulted in an initial list of 2,563 taxa across 26 groups.

In summarizing the pollination literature for these taxa, we scored the principal pollinator for each species as one of five categories: bee, other insect, hummingbird, mixed hummingbird and insect, and other vertebrates (e.g., bats, other birds; table S1). These categories allow us to capture some of the diversity of systems within insect and vertebrate pollination and align with commonly used functional groupings of pollinators in Neotropical systems (Fenster et al. 2004). In total, we were able to score 27.6% of the taxa for empirical pollinator observations. For the remainder, we follow trait-based (pollination syndrome) scoring from the literature (table S1).

GBIF Occurrence Data and Environmental Variables

The following steps were performed in the programming environment R (R Development Core Team 2021). We screened the initial plant taxon list (n = 2,563) using

Taxonstand (Cayuela et al. 2021) to correct spelling mistakes and synonyms. Next, we submitted the list to the Global Biodiversity Information Facility (GBIF) to search for occurrence data for each taxon (rgbif; Chamberlain et al. 2021). We applied strict filtering using the function occ_issues, filtering out records with continent-country mismatch, country-coordinate mismatch, continent classification derived from coordinates, invalid continents or coordinates, zero coordinates, coordinates out of range, presumed swapped coordinates, invalid geodetic datum, fuzzy taxon matches, and nonmetric, nonnumeric, or unlikely elevation (leaving 732,047 records). Next, we filtered data using CoordinateCleaner (Zizka et al. 2019), removing records located in country centroids, the sea, or around GBIF headquarters; duplicates; and records with equal longitude and latitude (leaving 548,251 records). We then removed records outside of the Americas and calculated median elevation, median latitude, and median longitude for each taxon, leaving 1,807 taxa. Taking the median per taxon further minimizes bias due to potential single erroneous occurrence points.

Through this data extraction process, 29% of the taxa (756) were removed because of a lack of elevation information. To retain more species in the final dataset, we repeated the GBIF query for these 756 species, filtering for coordinate-related issues as above but not removing records lacking elevation information (8,913 records). For each of these records, we extracted an elevation value from a global 30-arc-second elevation raster (raster; Amatulli et al. 2018; Hijmans 2021) and again calculated median elevation, latitude, and longitude per taxon. To verify compatibility of both datasets, we use the same process to extract elevation information for the 1,807 that already had elevation data and found that the reported and extracted elevations produced a high positive correlation ($R^2 = 0.97$).

We ran an additional manual screening of the taxon list to identify misspelled taxon names or synonyms that had not been corrected by Taxonstand and downloaded additional data as specified above. Finally, since some rare taxa may have gotten lost by the strict filtering settings, we ran a last GBIF query for the remaining taxa with more relaxed filtering settings (filtering only through CoordinateCleaner, adding five taxa). This left us with a final dataset of 2,232 taxa across 26 study groups (table S1; fig. S1), with a median number of 22 occurrence points per taxon (range: 1–8,238). Of these, 68 taxa were represented by a single occurrence record, distributed evenly across pollination strategies (with 35 insect pollinated and 33 vertebrate pollinated).

To evaluate the associations between pollination modes and climate, we downloaded layers for mean annual temperature (bio1) and precipitation (bio12) from the WorldClim dataset at 30-arc-second resolution (Hijmans 2017). In addition, we downloaded data on mean annual cloud cover (https://www.earthenv.org/cloud), since high cloud cover strongly impacts flight activity of poikilothermic insects but not of birds (Cruden 1972). Next, for each pruned occurrence record, we extracted the respective precipitation, temperature, and cloud cover value and calculated the median per taxon. The final dataset is available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.bcc2fqzfg; Dellinger et al. 2023).

Ecogeographic Modeling

To summarize distribution patterns in our dataset, we plotted occurrence data on a map of the Americas (maptools; Bivand and Lewin-Koh 2021). We used Whittaker biomes (plotbiomes; Whittaker 1975; Ricklefs 2008; Stefan and Levin 2021) to assess whether vertebrate- or insect-pollinated species in our sample consistently associate with different major ecogeographic areas. We used χ^2 statistics to test for differences in biome occupation. To visualize the relative contribution of different biomes to χ^2 statistics, we plotted standardized residuals using correlation plots (corrplot; Wei and Simko 2021). Standardized residuals higher than ± 2 indicate a strong contribution of the respective biome (fig. 1).

We used generalized linear mixed effects models (GLMMs; lme4; Bates et al. 2015) to test whether associations between pollination mode and elevation or climate depend on latitude. Since elevation was strongly positively correlated with precipitation and temperature (fig. S2), we included only elevation, latitude, and cloud cover in our model. Furthermore, we merged the five pollinator groups into a binary response variable (insect vs. vertebrate) for two reasons. First, visualizing our data showed strikingly similar patterns among species classified as bee or other insect pollinated and among species classified as hummingbird, mixed hummingbird and insect, or other vertebrate pollinated (figs. S3, S4). Second, species initially classified as other vertebrate pollinated were restricted to the tropics, which would bias model estimation at higher latitudes. We used spline correlograms (Bjornstad 2022) to rule out issues related to spatial autocorrelation both in our raw data and in our fitted models (see below). We then constructed binomial GLMMs (logit link), testing for an interaction of elevation, cloud cover, and latitude. We included the respective study clades as a random effect variable, testing models with random intercepts and with random slopes (e.g., elevation | taxonomic group) and intercepts. Since initial models did not converge, we scaled and centered the numeric predictor variables and optimized models using bobyqa (Bates et al. 2014) across 200,000 iterations. For selecting the best-fit model, we ran stepwise model simplification

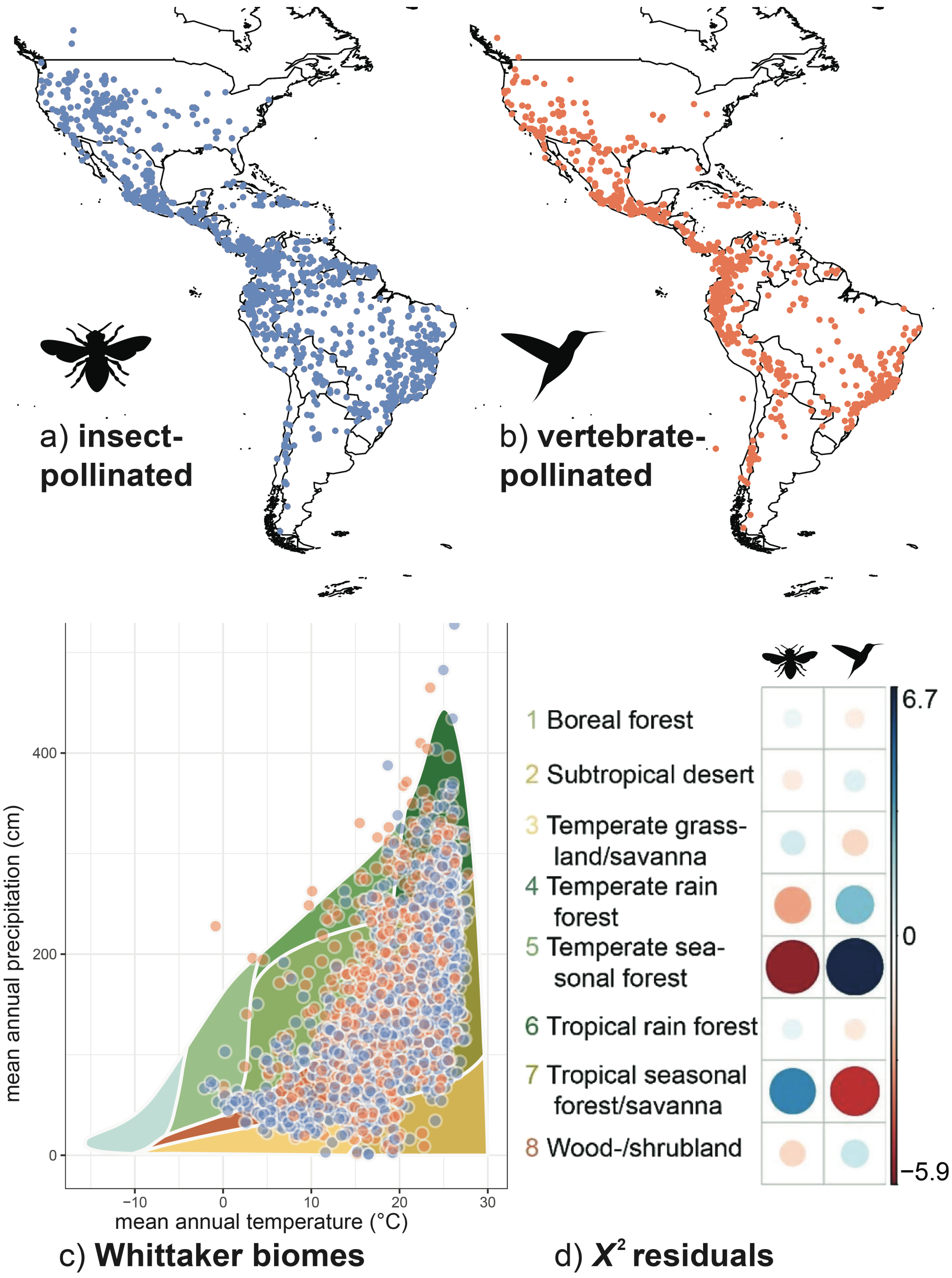


Figure 1: Geographical and biome distribution of insect- and vertebrate-pollinated species included in our dataset. *a*, *b*, Insect-pollinated species ($n = 1{,}262$; *a*) and vertebrate-pollinated species ($n = 970$; *b*) across the Americas; each point represents the median occurrence of each species. *c*, Vertebrate-pollinated species in our dataset were primarily found under intermediate mean annual temperature (10°C–20°C) and mean annual precipitation (e.g., in temperate seasonal forests), while insect-pollinated species also occurred under cooler and drier (e.g., in temperate grasslands, shrublands) and warmer (e.g., in tropical seasonal forests) conditions. *d*, Contribution of biomes (absolute standardized residuals) to total χ^2. Positive values (blue) indicate a positive relationship, and negative values (red) indicate a negative relationship. The size of the circle indicates the strength of the relationship.

(drop1) to identify the most parsimonious model and used χ^2 and ANOVA to check whether the simplified model led to a significant reduction in the residual sum of squares. We also compared model fit using Akaike information criterion (AIC; table S4). To validate the final model, we visually checked Pearson residuals, predicted versus original values, and the receiver operating characteristic curve (pROC; Robin et al. 2011; fig. S5). We visualized fixed and random effects using sjPlot (Lüdecke 2021; fig. S6), effects (Fox and Weisberg 2018), and ggplot2 (Wickham 2016). We back transformed model coefficients before plotting using custom settings in sjPlot (plot_model function; Lüdecke 2021).

Next, to assess the robustness of our results regarding the relationships between pollination, elevation, and latitude, we ran four additional sets of analyses. First, to assess potential bias arising from uneven sampling across study groups and pollination strategies, we randomly subsampled our dataset to 25% 100 times, reran model selection, refitted the best-fit models, and summarized model coefficients (tables S5, S6). Second, to assess potential bias from using pollination syndromes in the literature to classify taxa, we reran the model selection with only the 616 species from 23 clades (258 insect pollinated and 358 vertebrate pollinated) that had empirically documented pollinators (table S7; figs. S7, S8). Third, to check whether middomain effects (i.e., artificial peaks in species richness owing to geometric constraints when reducing distribution data to median values; Colwell et al. 2016) bias our results, we randomly resampled the pruned occurrence data to one occurrence point per species 100 times, refitted the best-fit model, and summarized results through boxplots (fig. S9). Finally, to test the effect of grouping plants with mixed hummingbird and insect pollination with vertebrate-pollinated plants (see above) to produce a binary response variable, we repeated the analyses comparing insect (n = 1,263) or vertebrate (n = 845) pollination versus mixed hummingbird and insect (n = 124) pollination in turn (table S8; fig. S10).

As our results showed marked differences in elevational patterns between (sub)tropical and temperate zones, we split the original dataset into widely circumscribed (including subtropics) tropics (30°S to 30°N; tropics are defined as ±23.46°), temperate north (above 30°N), and temperate south (below 30°S). For each partition, we used the approach outlined above to determine the best-fit model and estimate the effects of mean annual temperature, precipitation, and cloud cover on pollination mode.

While we accounted for some phylogenetic structure in our GLMMs by specifying the study groups as random effects, we additionally ran phylogenetic GLMMs for more accurate assessment of phylogenetic nonindependence of data points. To this end, we downloaded the angiosperm-wide phylogeny provided by Zanne et al. (2014) and Smith and Brown (2018) through Jin and Hong (2019; V.PhyloMaker) and pruned it to the species included in our sample. Approximately 41% of our study species (932) were covered by this phylogeny, with even sampling across the distribution range and pollination strategies (472 insect-pollinated species, 460 vertebrate-pollinated species; fig. S4; table S2). On this subset, we built binary phylogenetic GLMMs including elevation, latitude, and cloud cover under a Brownian motion model of trait evolution (binaryPGLMM function in ape; Paradis and Schliep 2019). We refrained from Bayesian fitting to avoid phylogenetic variance getting trapped around zero (a common problem in binomial GLMMs; Paradis and Schliep 2019). Since cloud cover did not show significant effects, we reduced the model to include only an interaction between elevation and latitude (table S9).

Results

Contrasting Patterns of Pollinator Turnover across Latitudes

Our analysis of pollination modes across the final set of 2,232 taxa belonging to 26 clades from 22 families showed marked variation in associations with elevation across latitudes. Considering the five pollination categories (bee, n = 1,141; insect, n = 122; hummingbird, n = 758; mixed hummingbird and insect, n = 124; other vertebrate, n = 87), we found that species with hummingbird, mixed, or other vertebrate pollination become more abundant at higher elevations in the tropics (above ~1,500 m) but not in temperate mountains (figs. S3, S4). Instead, in temperate regions, in our study clades, vertebrate pollination dominates at lower elevations (below 1,000 m in the Southern Hemisphere, below 1,300 m in the Northern Hemisphere). The species pollinated by bees and other insects show a contrasting pattern; they are most abundant at lower elevations in the tropics (below 1,000 m) and at higher elevations in the temperate zone (~1,000–2,000 m). These results suggest that Cruden's (1972) hypothesis of a turnover of insect and vertebrate pollination at high elevations holds only for tropical lineages.

We further explored this contrast using GLMMs, and given the similarity of the curves for plants pollinated by insects (bee and other insects) and the similarity of the curves for plants pollinated by vertebrates (hummingbird, mixed hummingbird and insect, and other vertebrate; fig. S3), we grouped the bee-pollinated and generalized insect-pollinated species into one insect category and the remaining partly or fully vertebrate-pollinated species into one vertebrate category. Using insect pollination as the reference level, we found that both elevation and latitude, but not cloud cover, had strong and significant effects on vertebrate pollination (estimate = −0.03, likelihood ratio = 21.4, $Z = -4.679$, $P < .001$, area under the receiver operating characteristic curve [AUC] = 0.806; tables 1, S4; figs. 2, S5). We recovered the same model in our sensitivity analyses when randomly selecting 25% of the data (96 of 100 replicates showed $P < .01$ effects of elevation × latitude; tables S5, S6), when resampling the dataset to include one randomly picked occurrence point per species (all 100 runs showed $P < .01$ effects of elevation × latitude; fig. S9), and when accounting for phylogenetic relatedness (table S9; fig. S11). Moreover, reducing the dataset to only taxa with empirical observations ($n = 616$) resulted in a best-fit model with the same significant interaction between latitude and elevation as the full model (estimate = −0.03, likelilhood ratio = 14.42, $Z = -3.703$, $P < .001$, AUC = 0.82; table S7). In this subset, the pattern of vertebrate-pollinated species occurring at higher elevations than insect-pollinated species in the tropics is well supported (fig. S7), but elevational differences between the two pollination modes are not clear in the temperate zones (note the wide confidence intervals for the slopes; figs. S7, S8).

We also examined whether these patterns of pollination mode varying with latitude and elevation were apparent in the 26 individual clades (used as random effects in our GLMM). Indeed, 25 of the 26 clades show the pattern of having a higher probability of vertebrate pollination at high elevations in the tropics and at low elevations at higher latitudes (note the crossing red and purple lines in fig. S6). A notable exception is found in the tropical Centropogonids (Campanulaceae), where insect-pollinated species (genus *Lysipomia*) commonly occur on tropical mountain summits (Páramo) above vertebrate-pollinated relatives.

Finally, we returned to consider the mixed hummingbird and insect category and whether it indeed more closely follows the pattern recovered for vertebrate-pollinated plants, as suggested by visual inspection (fig. S3). We repeated the GLMM analyses, first contrasting only the insect versus mixed taxa, and even with vertebrate pollination represented only in the mixed taxa, we recovered the same effects of elevation and latitude (estimate = −0.037, likelihood ratio = 21.8, $Z = -4.614$, $P < .001$; AUC = 0.845; removing the elevation × latitude interaction increases the AIC from 701 to 721; table S8; see also fig. S10*a*, S10*b*). By contrast, models with elevation are not among the top models when we compare mixed- versus vertebrate-pollinated taxa (table S8), and we observe no differences across elevation (best-fit model including latitude only: estimate = −0.987, likelihood ratio = 7.22, $Z = -2.337$, $P < .001$; fig. S10*c*). Together, these analyses support the observation that the species with mixed hummingbird and insect pollination more closely track the patterns of the vertebrate-pollinated taxa and thus that lineages that transition to high-elevation habitats in the tropics may benefit from some, if not exclusive, vertebrate pollination.

Cloud Cover and Moist Conditions Predict Vertebrate Pollination across Latitudes

Given that Cruden's (1972) hypothesis was based on associations of pollinator activity with climatic conditions,

Table 1: Best-fit generalized linear mixed effects models on the effect of elevation, latitude, and bioclimatic variables on pollination mode

	Estimate	SE	Z	P
Full model:				
Intercept	−.05157	.29089	−.177	.859
Elevation	**.86595**	**.19050**	**4.546**	**<.001**
Abs(latitude)	−.00498	.00624	−.798	.425
Elevation × abs(latitude)	**−.02729**	**.00583**	**−4.679**	**<.001**
Tropics:				
Intercept	.94678	.33336	2.840	.00451
Cloud cover	**.31511**	**.06725**	**4.685**	**<.001**
Temperate north:				
Intercept	−.9452	.4313	−2.192	.02841
Precipitation	**.5996**	**.2051**	**2.923**	**<.01**
Cloud cover	**−13.084**	**.2418**	**−5.412**	**<.001**
Temperate south:				
Intercept	.1035	.7781	.133	.8942
Precipitation	**14.595**	**.6877**	**2.122**	**.0338**

Note: Models for the full dataset and the tropics included random slopes and intercepts with elevation and temperature, respectively, for the study clades; see table S4 for details on model selection. Insect pollination was used as reference level, and significant factors are shown in bold. Abs = absolute.

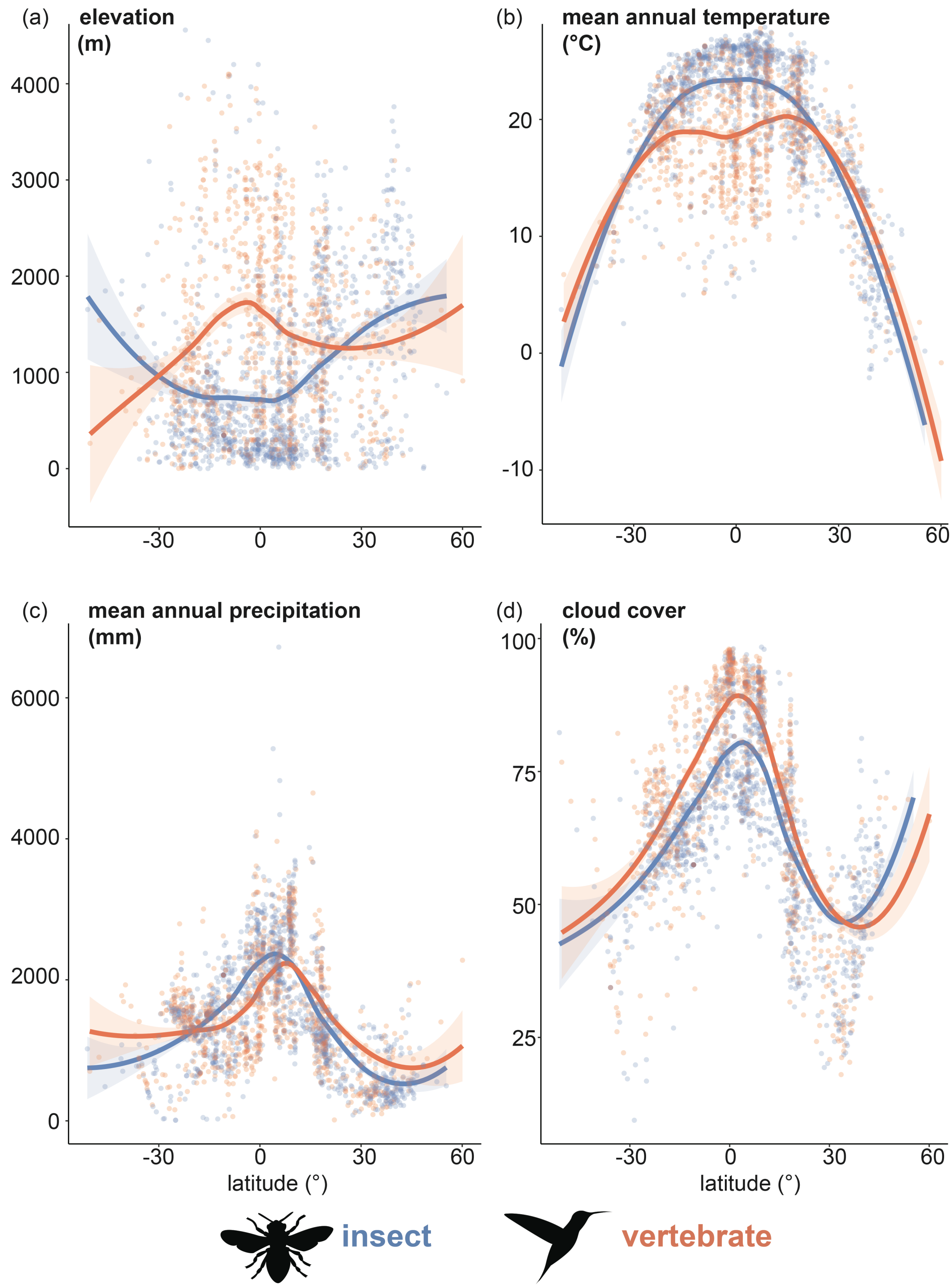


Figure 2: Relationship between pollination mode, elevation, and different bioclimatic variables across latitudes. *a*, Marked differentiation in the distribution of insect- and vertebrate-pollinated species across latitudes, with vertebrate-pollinated species occurring at higher elevations than insect-pollinated species in the tropics but not in temperate regions. *b*, Vertebrate-pollinated species associate with lower mean annual temperatures in tropical regions than insect-pollinated species but with slightly warmer conditions in temperate zones. *c*, Variable relationships among pollination strategies and mean annual precipitation, with bee-pollinated species in our dataset occurring under slightly wetter conditions than vertebrate-pollinated species around the equator. *d*, Vertebrate-pollinated species occur in areas with higher cloud cover than bee-pollinated species in the temperate south and the tropics.

we next examined possible environmental drivers of pollinator turnover, focusing on mean annual temperature, precipitation, and cloud cover (fig. 2*b*–2*d*). To avoid confounding effects owing to varying patterns across latitudes (fig. 2*a*), we split the dataset into tropical (grossly defined as ±30°, hence including subtropics) and temperate zones (north and south). Temperature was not significant in any of the models for either data partition and was never retained as a fixed effect in the best-fit models (tables 1, S4). However, precipitation emerged as a significant predictor in both the tropics and the southern temperate regions, with vertebrate pollination associated with higher precipitation. We also recovered an association of high cloud cover with vertebrate pollination in the tropics and the northern temperate zone (table 1; figs. 3, S12).

In addition, since climatic factors are associated with particular biomes (Whittaker 1975), we tested whether insect and vertebrate pollination also show an association with biome. We found that, indeed, insect- and vertebrate-pollinated species differ significantly in biome occupation ($\chi^2 = 149.81$, df $= 7$, $P < .001$; table S3; fig. 1*c*, 1*d*). While both pollination strategies were found in each biome (except tundra), vertebrate-pollinated species were significantly more common in temperate seasonal forests

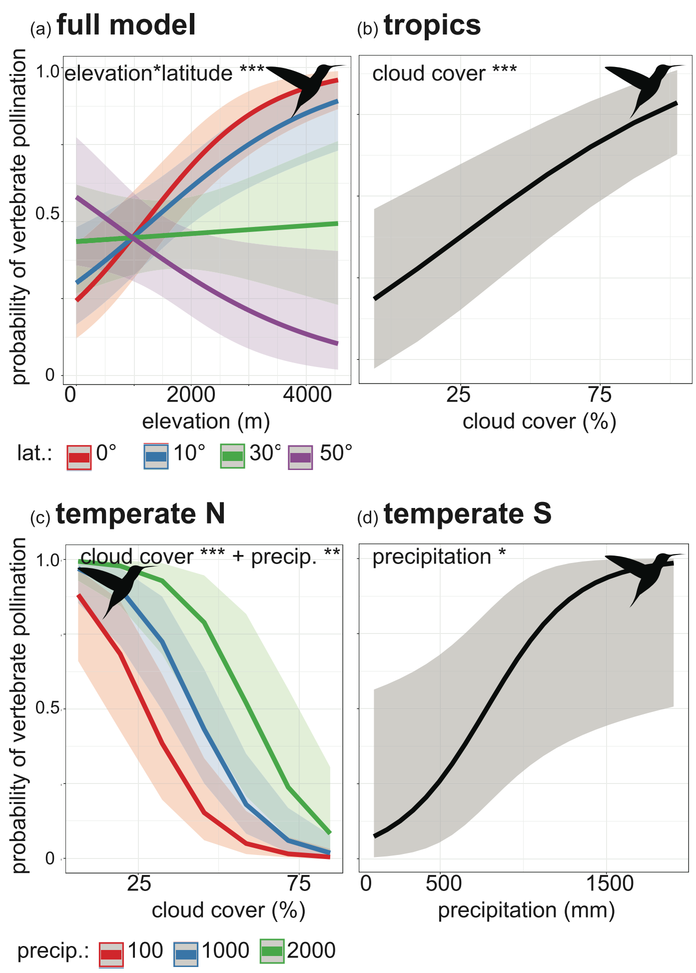


Figure 3: Results of the best-fit generalized linear mixed effects models (GLMMs) investigating the effects of different bioclimatic variables across latitudes. *a*, Probability of vertebrate pollination increases significantly across elevation in the tropics (0°, ±10° latitude), while it gradually decreases toward higher latitudes (±30°, ±50°). *b*, Probability of vertebrate pollination increases significantly with increased cloud cover in the tropics (i.e., montane cloud forests; $n = 1{,}917$). *c*, In the temperate zones of the Northern Hemisphere, the probability of vertebrate pollination decreased significantly with increasing cloud cover but less so when precipitation was high ($n = 265$). *d*, In the temperate zones of the Southern Hemisphere, the probability of vertebrate pollination increased with increasing precipitation ($n = 50$). Insect pollination was used as reference level in the binomial GLMMs (and is hence not depicted), and 95% confidence intervals are given. $^{*}P < .05$; $^{**}P < .01$; $^{***}P < .001$.

and temperate rainforests, where temperature and precipitation are intermediate (e.g., 10°C–20°C; fig. 1; table S3). Insect-pollinated species occurred significantly more often under warmer conditions in tropical seasonal forests/savannas and under both cooler conditions and drier conditions in wood-/shrublands, boreal forests, and temperate grasslands (fig. 1; table S3).

Discussion

Altitude-Driven Pollinator Turnover across the Americas

Cruden (1972) hypothesized that bird pollination is advantageous for flowering plants occurring in the often cold and rainy high-elevation habitats. Our study found that this hypothesis holds in the (sub)tropics (i.e., between ~30°N and ~30°S) but not in temperate regions, where insects are important pollinators also at high elevations. Although our dataset is largely composed of bee- and hummingbird-pollinated species (51% and 34%, respectively), the overall pattern holds for other types of pollinators (figs. S3, S4). Temperature is tightly correlated with elevation (figs. 2*a*, 2*b*, S2) and decreases at higher elevations globally, a phenomenon known as the elevational air temperature gradient (Blüthgen 1980). Not surprisingly, temperature was a poor predictor of the importance of vertebrate versus insect pollination across latitudes. Indeed, insect pollinators as a group are not restricted from high elevations simply because of thermal constraints due to smaller body size and physiology, since bumblebees can forage in near-freezing temperatures (Bruggemann 1958; Oyen and Dillon 2018) and thus are effective high-elevation pollinators (McCallum et al. 2013; Woodard 2017). Similarly, flies use sun basking to elevate their body temperature and are important high-elevation pollinators in many ecosystems (González et al. 2009; McCabe and Cobbs 2021; Pelayo et al. 2021).

We found that indicators of mesic versus arid conditions (mean annual precipitation and cloud cover) were predictors of the importance of vertebrates versus insects, even across latitudes (table 1). Consistent with the notion that cloudy and rainy weather deters insect pollinators (Cruden 1972; Kearns 1992; Michener 2000), we found that vertebrate pollination was positively associated with higher precipitation in temperate zones (fig. 3*c*, 3*d*) and with higher cloud cover in both the tropics and the temperate north (fig. 3*b*, 3*c*). Birds, in particular, are able to forage in wet weather (Lawson and Rands 2019), although bats may have reduced foraging capabilities in rain (Voigt et al. 2011). This strong relationship between pollination mode and precipitation has been recovered in previous smaller-scale studies, where precipitation was negatively correlated with insect pollination but positively correlated with vertebrate pollination (Cruden 1972; Devoto et al. 2005; Dalsgaard et al. 2009; González et al. 2009; Chalcoff et al. 2012). In accordance with this, our biome analysis suggested that vertebrate pollination is important in cool mesic and wet forests (e.g., cloud forests), while insect pollination is important in dry forests and savannas (fig. 1*c*, 1*d*). Insect pollination in moist biomes appears constrained to warmer conditions (fig. 1*c*). Together, these results suggest that—across latitudes—shady, moist, forested ecosystems are key habitats for endothermic vertebrate pollinators (hummingbird habitats; Stebbins 1989).

Evolutionary History, Pollinator Niche Saturation, and Seasonality

The associations between pollinator importance and elevation must be considered in light of the evolutionary history and ecological context of the tropics versus temperate regions. Tropical montane cloud forests feature abundant hummingbird habitats, as evidenced by notable radiations of several hummingbird lineages in tropical mountains (McGuire et al. 2014). By contrast, hummingbirds have not diversified extensively in tropical lowlands and have only recently (5 million years ago) diversified in temperate zones, resulting in ~300 hummingbird species in the tropics and only about 20 in temperate zones (McGuire et al. 2014; Abrahamczyk and Renner 2015). This pattern may suggest that the strong relationship between tropical mountains and vertebrate pollination is largely driven by the evolutionary radiation of hummingbirds in the cloud forest environment. Even if true, this conclusion would underscore how certain environmental conditions—the abundant hummingbird habitats in tropical cloud forests—favor a particular pollinator group and result in repeated evolutionary pollinator shifts across plant clades that have colonized this environment (Thomson and Wilson 2008; Lagomarsino et al. 2016; Dellinger et al. 2021; Hamilton and Wessinger 2022).

A similar case can be made for the importance of bumblebee pollination at high elevation in temperate regions. The temperate mountains included in our study (mostly southern Andes, Rocky Mountains) feature habitats that are suitable for species-rich bumblebee pollinator communities, including dry, cool, sparse forests or open grassland (Rundel 1994; McCabe and Cobbs 2021). Bumblebees appear to successfully occupy the available pollination niche space in these habitats (Pyke et al. 2011). By contrast, the tropical mountains included here are mostly wet, and comparatively few large, cold-adapted bee species (e.g., from the genera *Bombus*, *Centris*, *Eufriesia*) reach the montane cloud forest or Páramo zones (Roubik 1989; Gonzalez and Engel 2004; Perillo et al. 2021). The abundance and diversity of cold-adapted bees in tropical mountains may be further limited by competition for pollination niche space with abundant vertebrate pollinators (Temeles et al. 2016). Such competitive interactions, along with differences in abiotic tolerances, have been suggested as structuring the distribution of moth and hummingbird pollination (Cruden 1976) and should be considered for a full description of the drivers of broadscale patterns of plant-pollinator interactions.

Finally, latitudinal differences in seasonality likely contribute to the dominance of vertebrate pollinators in tropical, but not temperate, mountains. While tropical forests do present some seasonal variation, floral nectar resources are generally available year-round, and hummingbirds may track resources through small-scale (altitudinal) migration (Abrahamczyk et al. 2011; Maglianesi et al. 2015). By contrast, temperate zones are characterized by marked seasonal variation in nectar resources because of constrained flowering periods that are defined by snow melt at high elevations and summer drought at lower elevations (Inouye and Wielgolaski 2013). During their short summer breeding seasons, the long-distance migratory, temperate hummingbirds require nectar resources to be abundant and near to nesting sites in trees (Grant and Grant 1968; Stebbins 1989; McKinney et al. 2012). Truncated flowering periods and limited nesting sites at high elevations (above the treeline) possibly limit hummingbird-pollinated plants to lower elevations in temperate zones.

Parallel Trends Outside the Americas

While we focused on the ecogeographic patterns in the Americas because of the many temperate and tropical plant clades with bee-bird pollinator shifts, the broader findings may extend to other parts of the world. For example, pollination activities by insects, but not birds, are reduced during rainy and cloudy days in a lowland evergreen forest in South China (Sun et al. 2017), underscoring that continued flower visitation during rain is not a singularity of hummingbirds. Moreover, vertebrate pollination has increased importance during the rainy season in tropical African mountains (i.e., Janeček et al. 2015; Klomberg et al. 2022). Seasonality seems equally relevant in explaining flowering of (generalist) nectar-feeding bird-adapted plants in temperate Asia and Australia (Ford et al. 1979; Funamoto 2019) and rodent-pollinated plants in South Africa (Wiens 1983). In both cases, vertebrate-adapted plants tend to flower primarily during rainy and cool winter months (Chen et al. 2019), underscoring the increased importance of vertebrate pollination under wet conditions.

Patterns of pollinator turnover across elevations are less clear (Abrahamczyk 2019), but this is due in large part to a paucity of studies. For example, pollinator interaction networks from Mount Cameroon (5.7°N) suggest continued importance of insect pollinators across elevation (i.e., butterflies [Mertens et al. 2021], bees [Klomberg et al. 2022]), while another study from Mount Kilimanjaro (3°S) shows a decline with elevation (bees; Classen et al. 2015). Importantly, bumblebees are absent from sub-Saharan Africa and Australia, potentially freeing niche space at high elevations (e.g., for other bees, moths, beetles; Adedoja et al. 2020), while they are important pollinators in the Oriental region (i.e., India, tropical China, Southeast Asia; Corlett 2004) and mountains of temperate East Asia (Funamoto 2019; Paudel et al. 2019). Furthermore, studies of specific plant genera—some in plant clades that otherwise feature abundant insect pollination (i.e., Melastomataceae; Dellinger et al. 2022)—suggest a turnover from insect to vertebrate pollination with increasing elevation in African and Asian tropical mountains (i.e., *Mucuna*; Kobayashi et al. 2021). Similar to our study, the pattern may potentially be reversed outside of the tropics—for example, in temperate Himalayan *Rhododendron*, bird-pollinated species reportedly occur in moist montane forests, while bumblebee-pollinated species are found in the higher elevation Alpine zone (Basnett et al. 2019).

Conclusions and Future Directions

Building on decades of comparative pollination studies across North, Central, and South America, we uncovered consistent patterns showing that both Cruden (1972) and Stebbins (1989) were right. In the tropics, where vertebrate pollinators are most diverse, they serve as the most important high-elevation pollinators in our study clades, providing service in the rainy conditions that deter insect pollinators (Cruden 1972). However, in temperate regions, vertebrate pollination is more common at low to intermediate elevations, where those moist conditions are more common (e.g., wooded ravines; Stebbins 1989), leaving insects (especially large-bodied bees and flies) as the more important pollinators in dry montane habitats. These patterns highlight the importance of pollinator physiology as driving the turnover in plant-pollinator interactions along climatic gradients (Arroyo et al. 1982; Warren et al. 1988; Lefevbre et al. 2018; McCabe and Cobb 2021).

This study also points to several fruitful areas for future studies that seek to understand ecogeographic variation in pollination systems. First, we categorized species by the major pollinator to capture broad differences in the distribution of vertebrate and insect pollination. However, these relationships are naturally continuous (with each pollinator species varying in importance and across space and time; Mayfield et al. 2001). Delving into this continuous variation, while not possible at the scale of thousands of species, would give greater insight into the climatic thresholds where turnovers in pollination systems occur. Our analyses of the species with mixed hummingbird and insect pollination hint at this more complex dynamic, as they actually peak at a higher elevation than primarily bird-pollinated species (fig. S3). This result is consistent with the idea that a more generalized system provides a successful "backup" strategy in the harshest environments (Dellinger et al. 2019; Bergamo et al. 2021). Examining the degree of generalization (or specialization) would be a welcome complement to our study and, depending on the thermal tolerance of different pollinator species, may present relationships with temperature that did not emerge from our study at the level of entire functional groups. Furthermore, evolutionary pollinator shifts can clearly occur without species moving to a new/different abiotic environment (Hamilton and Wessinger 2022), exemplified by several clades featuring repeated pollinator shifts also in lowland rainforest environments (e.g., *Costus*; Vargas et al. 2020; Kay and Grossenbacher 2022). In parallel, plant clades may retain the same functional pollinator group even across ecogeographic gradients or be restricted to narrow elevational ranges (these were hence excluded from our study, since they did not meet our selection criteria). Including such clades and detailed pollinator and trait data in future studies would allow tackling intriguing questions, such as what variables (i.e., competition for/among pollinators, phenological mismatch, coflowering, flower developmental constraints) may drive or hinder evolutionary pollinator shifts in addition to or irrespective of the abiotic environment. Using community-level data would further allow for more complete tests of Cruden's hypotheses and explore whether, even at large biogeographic scales, the relative abundance of insect- and vertebrate-pollinated plants changes in correlation with climatic factors.

Finally, although our sampling is largely based on clades with hummingbird and bee pollination spanning wide elevational ranges, we predict that the broad associations between wet forests and vertebrate pollination will hold beyond our study clades from American mountains. Support for this hypothesis comes from, for example, the intriguing absence of hummingbird-pollinated plants in the Patagonian steppe (but high abundance in temperate, southern forests; Armesto et al. 1996; Devoto et al. 2005) and singular observations of vertebrate pollination in otherwise insect-pollinated lineages in mountains/wet seasons in the Paleotropics (Janeček et al. 2015; Funamoto 2019). Conducting studies similar to ours at a global scale or including community-level data will be necessary, however, to begin to partition the relative importance of abiotic and biotic factors in driving pollinator shifts and structuring broadscale distribution patterns of plant-pollinator interactions.

Acknowledgments

We thank the labs of Stacey Smith and Erin Manzitto-Tripp for inspiring discussions on this topic and helpful feedback on the project. We particularly thank Miranda Sinnott-Armstrong for support with and recommendations for data analyses. We further thank Andreas Berger for sharing data on pollination in Rubiaceae with us and Ana María Bedoya for support with the Spanish abstract. This work was supported by Austrian Science Fund grant T-1186 to A.S.D., National Science Foundation (NSF) grant DEB-2052904 to C.A.W., and NSF grant 1553114 to S.D.S.

Statement of Authorship

All authors conceived the study; A.S.D. and A.M.H. compiled the species datasets; A.S.D. ran the analyses and drafted the manuscript; A.M.H., C.A.W., and S.D.S. contributed to improving and revising the manuscript.

Data and Code Availability

All data analyzed in the manuscript and exemplary R code for analyses have been deposited in Dryad Digital Repository (https://doi.org/10.5061/dryad.bcc2fqzfg; Dellinger et al. 2023).

Literature Cited

Abrahamczyk, S. 2019. Comparison of the ecology and evolution of plants with a generalist bird pollination system between continents and islands worldwide. Biological Reviews 94:1658–1671.

Abrahamczyk, S., J. Kluge, Y. Gareca, S. Reichle, and M. Kessler. 2011. The influence of climatic seasonality on the diversity of different tropical pollinator groups. PLoS ONE 6:e27115.

Abrahamczyk, S., and S. S. Renner. 2015. The temporal build-up of hummingbird/plant mutualisms in North America and temperate South America. BMC Evolutionary Biology 15:104.

Adedoja, O., T. Kehinde, and M. J. Samways. 2020. Asynchrony among insect pollinator groups and flowering plants with elevation. Scientific Reports 10:13268.

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

Armesto, J. J., C. Smith-Ramírez, and C. Sabag. 1996. The importance of plant-bird mutualisms in the temperate rainforest of southern South America. Pages 248–265 *in* R. G. Lawford, P. B. Alaback, and E. Fuentes, eds. High-latitude rainforests and associated ecosystems of the west coast of the Americas. Springer, New York.

Arroyo, M. T. K., R. Primack, and J. Armesto. 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. American Journal of Botany 69:82–97.

Basnett, S., R. Ganesan, and S. M. Devy. 2019. Floral traits determine pollinator visitation in *Rhododendron* species across an elevation gradient in the Sikkim Himalaya. Alpine Botany 129:81–94.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bates, D., K. M. Mullen, J. C. Nash, and R. Varadhan. 2014. minqa: derivative-free optimization algorithms by quadratic approximation. R package version 1.2.4. https://CRAN.R-project.org/package=minqa.

Bergamo, P. J., N. S. Streher, V. Zambon, M. Wolowski, and M. Sazima. 2021. Pollination generalization and reproductive assurance by selfing in a tropical montane ecosystem. Naturwissenschaften 108:50.

Bivand, R., and N. Lewin-Koh. 2021. maptools: tools for handling spatial objects. R package version 1.1-1. https://CRAN.R-project.org/package=maptools.

Bjornstad, O. N. 2022. ncf: spatial covariance functions. R package version 1.3-2. https://CRAN.R-project.org/package=ncf.

Blüthgen, J. 1980. Allgemeine Klimageographie. de Gruyter, Berlin.

Bruggemann, P. F. 1958. Insects and environments of the high arctic. Proceedings of the 10th International Congress of Entomology 1:695–702.

Cayuela, L., I. Macarro, A. Stein, and J. Oksanen. 2021. Taxonstand: taxonomic standardization of plant species names. R package version 2.4. https://CRAN.R-project.org/package=Taxonstand.

Chalcoff, V. R., M. A. Aizen, and C. Ezcurra. 2012. Erosion of a pollination mutualism along an environmental gradient in a south Andean treelet, *Embothrium coccineum* (Proteaceae). Oikos 121:471–480.

Chamberlain, S., V. Barve, D. Mcglinn, D. Oldoni, P. Desmet, L. Geffert, and K. Ram. 2021. rgbif: interface to the Global Biodiversity Information Facility API. R package version 3.5.2. https://CRAN.R-project.org/package=rgbif.

Chen, K.-H., J.-Y. Lu, and C.-N. Wang. 2019. Effective pollination of *Aeschynanthus acuminatus* (Gesneriaceae) by generalist passerines, in sunbird-absent East Asia. Scientific Reports 9:17552.

Classen, A., M. K. Peters, W. J. Kindeketa, T. Appelhans, C. D. Eardley, M. W. Gikungu, A. Hemp, T. Nauss, and I. Steffan-Dewenter. 2015. Temperature versus resource constraints: which factors determine bee diversity on Mount Kilimanjaro, Tanzania? Global Ecology and Biogeography 24:642–652.

Colwell, R. K., N. J. Gotelli, L. A. Ashton, J. Beck, G. Brehm, T. M. Fayle, K. Fiedler, et al. 2016. Midpoint attractors and species richness: modelling the interaction between environmental drivers and geometric constraints. Ecology Letters 19:1009–1022.

Corlett, R. T. 2004. Flower visitors and pollination in the Oriental (Indomalayan) region. Biological Review 79:497–532.

Cozien, R. J., T. van der Niet, S. D. Johnson, and S. L. Steenhuisen. 2019. Saurian surprise. Ecology 100:1–4.

Cronk, Q., and I. Ojeda. 2008. Bird-pollinated flowers in an evolutionary and molecular context. Journal of Experimental Botany 59:715–727.

Cruden, R. W. 1972. Pollinators in high elevation ecosystems: relative effectiveness of birds and bees. Science 176:1439–1440.

Cruden, R. W., S. Kinsman, R. E. Stockhouse II, and Y. B. Linhart. 1976. Pollination, fecundity, and the distribution of moth-flowered plants. Biotropica 8:204–210.

Dalsgaard, B., A. M. Martín González, J. M. Olesen, J. Ollerton, A. Timmermann, L. H. Andersen, and A. G. Tossas. 2009. Plant-hummingbird interactions in the West Indies: floral specialization gradients associated with environment and hummingbird size. Oecologia 159:757–766.

Dellinger, A. S., A. M. Hamilton, C. A. Wessinger, and S. Smith. 2023. Data from: Opposing patterns of altitude-driven pollinator turnover in the tropical and temperate Americas. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.bcc2fqzfg.

Dellinger, A. S., C. Kopper, K. Kagerl, and J. Schönenberger. 2022. Pollination in Melastomataceae: a family-wide update on the little we know and the much that remains to be discovered. Pages 585–608 *in* R. Goldenberg, F. A. Michelangeli, and F. Almeda, eds. Systematics, evolution, and ecology of Melastomataceae. Springer, Cham, Switzerland.

Dellinger, A. S., R. Pérez-Barrales, F. A. Michelangeli, D. S. Penneys, D. M. Fernández-Fernández, and J. Schönenberger. 2021. Low bee visitation rates explain pollinator shifts to vertebrates in tropical mountains. New Phytologist 231:864–877.

Dellinger, A. S., L. M. Scheer, S. Artuso, D.-M. Fernández-Fernández, F. Sornoza, D. S. Penneys, R. Tenhaken, S. Dötterl, and J. Schönenberger. 2019. Bimodal pollination systems in Andean Melastomataceae involving birds, bats and rodents. American Naturalist 194:104–116.

Devoto, M., D. Medan, and N. H. Montaldo. 2005. Patterns of interaction between plants and pollinators along an environmental gradient. Oikos 109:461–472.

Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution, and Systematics 35:375–403.

Ford, H. A., D. C. Paton, and N. Forde. 1979. Birds as pollinators of Australian plants. New Zealand Journal of Botany 17:509–519.

Fox, J., and S. Weisberg. 2018. Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. Journal of Statistical Software 87:1–27.

Funamoto, D. 2019. Plant-pollinator interactions in East Asia: a review. Journal of Pollination Ecology 25:46–68.

González, A. M. M., B. Dalsgaard, J. Ollerton, A. Timmermann, J. M. Olesen, L. Andersen, and A. G. Tossas. 2009. Effects of climate on pollination networks in the West Indies. Journal of Tropical Ecology 25:493–506.

Gonzalez, V. H., and M. S. Engel. 2004. The tropical Andean bee fauna (Insecta: Hymenoptera: Apoidea), with examples from Colombia. Entomologische Abhandlungen 62:65–75.

Grant, K. A., and V. Grant. 1968. Hummingbirds and their flowers. Columbia University Press, New York.

Hamilton, A. M., and C. A. Wessinger. 2022. Adaptation to lower latitudes and lower elevations precedes the evolution of hummingbird pollination in western North American *Penstemon*. American Journal of Botany 109:1047–1055.

Heinrich, B. 1974. Thermoregulation in endothermic insects. Science 185:747–756.

Hijmans, R. J. 2017. WorldClim 2: new 1 km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

———. 2021. raster: geographic data analysis and modeling. R package version 3.4-10. https://CRAN.R-project.org/package=raster.

Inouye, D. W., and F. E. Wielgolaski. 2013. Phenology at high altitudes. Pages 249–272 *in* M. Schwartz, ed. Phenology: an integrative environmental science. Springer, Dordrecht.

Janeček, Š., M. Bartoš, and K. Y. Njabo. 2015. Convergent evolution of sunbird pollination systems of *Impatiens* species in tropical

Africa and hummingbird systems of the New World. Biological Journal of the Linnean Society 115:127–133.

Jin, Y., and Q. Hong. 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. Ecography 42:1353–1359.

Kay, K. M., and D. L. Grossenbacher. 2022. Evolutionary convergence on hummingbird pollination in Neotropical *Costus* provides insight into the causes of pollinator shifts. New Phytologist 236:1572–1583.

Kearns, C. A. 1992. Anthophilous fly distribution across an elevational gradient. American Midland Naturalist 127:172–182.

Klomberg, Y., R. Tropek, J. E. J. Mertens, I. N. Kobe, J. Hodeček, J. Raška, N. T. Fominka, D. Souto-Vilarós, P. Janecková, and S. Janeček. 2022. Spatiotemporal variation in the role of floral traits in shaping tropical plant-pollinator interactions. Ecology Letters 25:839–850.

Kobayashi, S., S. Panha, T. Seesamut, N. Nantarat, N. Likhitrakarn, T. Denda, and M. Izawa. 2021. First record of non-flying mammalian contributors to pollination in a tropical montane forest in Asia. Ecology and Evolution 11:17604–17608.

Krömer, T., M. Kessler, and S. K. Herzog. 2006. Distribution and flowering ecology of bromeliads along two climatically contrasting elevational transects in the Bolivian Andes. Biotropica 38:183–195.

Lagomarsino, L. P., F. L. Condamine, A. Antonelli, A. Mulch, and C. C. Davis. 2016. The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). New Phytologist 210:1430–1442.

Lawson, D. A., and S. A. Rands. 2019. The effects of rainfall on plant-pollinator interactions. Arthropod-Plant Interactions 13:561–569.

Lefevbre, V., C. Villemant, C. Fontaine, and C. Daugeron. 2018. Altitudinal, temporal and trophic partitioning of flower-visitors in Alpine communities. Scientific Reports 8:4706.

Lüdecke, D. 2021. sjPlot: data visualization for statistics in social science. R package version 2.8.9. https://CRAN.R-project.org/package=sjPlot.

Maglianesi, M. A., N. Blüthgen, K. Böhning-Gaese, and M. Schleuning. 2015. Functional structure and specialization in three tropical plant-hummingbird interaction networks across an elevational gradient in Costa Rica. Ecography 38:1119–1128.

Mayfield, M. M., N. M. Waser, and M. V. Price. 2001. Exploring the "most effective pollinator principle" with complex flowers: bumblebees and *Ipomopsis aggregata*. Annals of Botany 88:591–596.

McCabe, L. M., and N. S. Cobb. 2021. From bees to flies: global shifts in pollinator community along elevational gradients. Frontiers in Ecology and Evolution 8:626124.

McCallum, K. P., F. O. McDougall, and R. S. Seymour. 2013. A review of the energetics of pollination biology. Journal of Comparative Physiology B 183:867–876.

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

McKinney, A. M., P. J. CaraDonna, D. W. Inouye, B. Barr, C. D. Bertelsen, and N. M. Waser. 2012. Asynchronous changes in phenology of migrating broad-tailed hummingbirds and their early-season nectar resources. Ecology 93:1987–1993.

Mertens, J. E. J., L. Brisson, S. Janeček, Y. Klomberg, V. Maicher, S. Sáfián, S. Delabye, et al. 2021. Elevational and seasonal patterns of butterflies and hawkmoths in plant-pollinator networks in tropical rainforests of Mount Cameroon. Scientific Reports 11:9710.

Michener, C. D. 2000. The bees of the world. John Hopkins University Press, Baltimore.

Ollerton, J. 2017. Pollinator diversity: distribution, ecological function, and conservation. Annual Review of Ecology, Evolution, and Systematics 48:353–376.

Orr, M. C., A. C. Hughes, D. Chesters, J. Pichering, C.-D. Zhu, and J. S. Ascher. 2021. Global patterns and drivers of bee distribution. Current Biology 31:451–458.

Oyen, K. J., and M. E. Dillon. 2018. Critical thermal limits of bumblebees (*Bombus impatiens*) are marked by stereotypical behaviors and are unchanged by acclimation, age or feeding status. Journal of Experimental Biology 221:jeb165589.

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

Paudel, B. R., A. Kessler, M. Shrestha, J. L. Zhao, and Q. J. Li. 2019. Geographic isolation, pollination syndromes, and pollinator generalization in Himalayan *Roscoea* spp. (Zingiberaceae). Ecosphere 10:e02943.

Pelayo, R. C., L. D. Llambi, L. E. Gámez, Y. C. Barrios, L. A. Ramírez, J. E. Torres, and F. Cuesta. 2021. Plant phenology dynamics and pollination networks in summits of the high tropical Andes: a baseline for monitoring climate change impacts. Frontiers in Ecology and Evolution 9:679045.

Perillo, L. N., F. S. de Castro, R. Solar, and F. de Siqueira Neves. 2021. Disentangling the effects of latitudinal and elevational gradients on bee, wasp and ant diversity in an ancient Neotropical mountain range. Journal of Biogeography 48:1564–1578.

Primack, R., and D. Inouye. 1993. Factors affecting pollinator visitation rates: a biogeographical comparison. Current Science 63:257–261.

Pyke, G. H., D. W. Inouye, and J. D. Thomson. 2011. Activity and abundance of bumble bees near Crested Butte, Colorado: diel, seasonal, and elevation effects. Ecological Entomology 36:511–521.

Ratto, F., B. I. Simmons, R. Spake, V. Zamora-Gutierrez, M. A. MacDonald, J. C. Merriman, C. J. Tremlett, G. M. Poppy, K. S.-H. Peh, and L. V. Dicks. 2018. Global importance of vertebrate pollinators for plant reproductive success: a meta-analysis. Frontiers in Ecology and the Environment 16:82–90.

R Development Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ricklefs, R. E. 2008. The biome concept. Pages 87–112 *in* R. E. Ricklefs, ed. The economy of nature. W. H. Freeman, New York.

Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J. C. Sanchez, and M. Müller. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics 12:77.

Roubik, D. 1989. Ecology and natural history of tropical bees. Cambridge Tropical Biology Series. Cambridge University Press, Cambridge.

Rundel, P. W. 1994. Tropical alpine climates. Pages 21–44 *in* W. P. Rundel, A. P. Smith, and F. C. Meinzer, eds. Tropical alpine environments: plant form and function. Cambridge University Press, Cambridge.

Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review of Ecology, Evolution, and Systematics 40:245–269.

Sinnott-Armstrong, M. A., M. J. Donoghue, and W. Jetz. 2021. Dispersers and environment drive global variation in fruit colour syndromes. Ecology Letters 24:1387–1399.

Smith, S. A., and J. W. Brown. 2018. Constructing a broadly inclusive seed plant phylogeny. American Journal of Botany 105:302–314.

Stebbins, L. G. 1989. Adaptive shifts toward hummingbird pollination. Pages 39–60 *in* J. H. Beck and Y. B. Linhart, eds. The evolutionary ecology of plants. CRC, Boca Raton, FL.

Stefan, V., and S. Levin. 2021. plotbiomes: plot Whittaker biomes with ggplot2. R package version 0.0.0.9001. https://valentinitnelav.github.io/plotbiomes/.

Sun, S. G., Z. H. Huang, Z. B. Chen, and S. Q. Huang. 2017. Nectar properties and the role of sunbirds as pollinators of the golden-flowered tea (*Camellia petelotii*). American Journal of Botany 104:468–476.

Temeles, E. J., J. T. Newman, J. H. Newman, S. Y. Cho, A. R. Mazzotta, and W. J. Kress. 2016. Pollinator competition as a driver of floral divergence: an experimental test. PLoS ONE 11:e0146431.

Thomson, J. D., and P. Wilson. 2008. Explaining evolutionary shifts between bee and hummingbird pollination: convergence, divergence, and directionality. International Journal of Plant Science 169:23–38.

Tripp, E. A., and P. S. Manos. 2008. Is floral specialization and evolutionary dead-end? pollination system transitions in *Ruellia* (Acanthaceae). Evolution 62:1712–1737.

Vargas, O. M., B. Goldston, D. L. Grossenbacher, and K. M. Kay. 2020. Patterns of speciation are similar across mountainous and lowland regions for a Neotropical plant radiation (Costaceae: *Costus*). Evolution 74:2644–2661.

Voigt, C. C., K. Schneeberger, S. L. Voigt-Heucke, and D. Lewanzik. 2011. Rain increases the energy cost of bat flight. Biology Letters 7:793–795. https://doi.org/10.1098/rsbl.2011.0313.

Warren, S. D., K. T. Harper, and G. M. Booth. 1988. Elevational distribution of insect pollinators. American Midland Naturalist 120:325–330.

Wei, T., and V. Simko. 2021. corrplot: visualization of a correlation matrix. R package version 0.90. https://CRAN.R-project.org/package=corrplot.

Wessinger, C. A., M. D. Rausher, and L. C. Hileman. 2019. Adaptation to hummingbird pollination is associated with reduced diversification in *Penstemon*. Evolution Letters 3:521–533.

Whittaker, R. H. 1975. Communities and ecosystems. 2nd ed. MacMillan, New York.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer, New York.

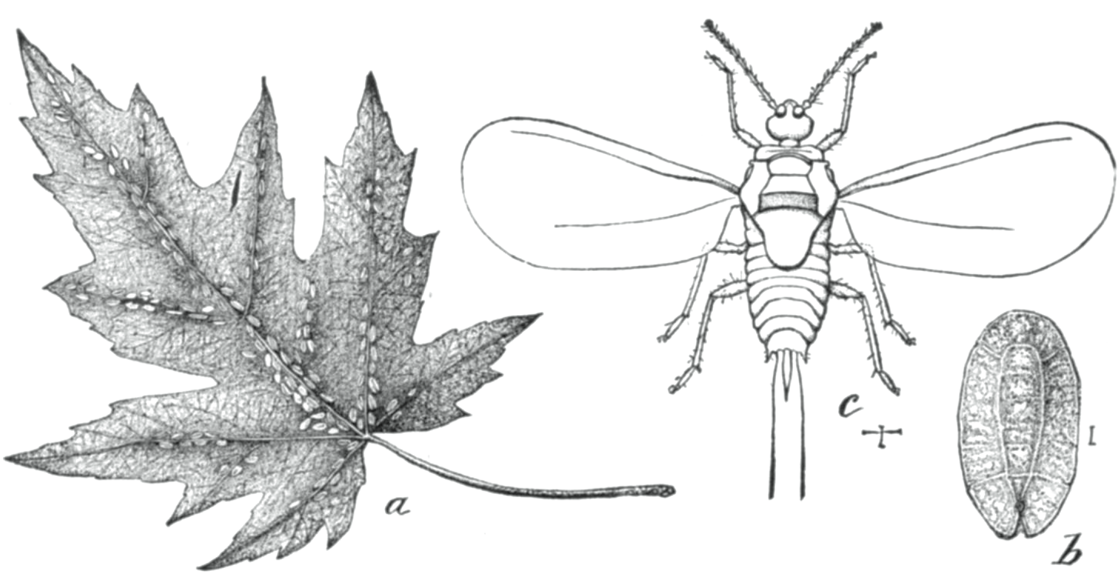
Wiens, D., J. P. Rourke, B. B. Casper, E. A. Rickart, T. R. Lapine, and C. J. Peterson. 1983. Non-flying mammal pollination of southern, African *Proteas*: a non-coevolved system. Annals of the Missouri Botanical Garden 70:1–31.

Woodard, S. H. 2017. Bumble bee ecophysiology: integrating the changing environment and the organism. Current Opinion in Insect Science 22:101–108.

Zanne, A. E., D. C. Tank, W. K. Cornwell, J. M. Eastman, S. A. Smith, R. G. FitzJohn, D. J. McGlinn, et al. 2014. Three keys to the radiation of angiosperms into freezing environments. Nature 506:89–92.

Zizka, A., D. Silvestro, T. Andermann, J. Azevedo, C. Duarte Ritter, D. Edler, H. Farooq, et al. 2019. CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases. Methods in Ecology and Evolution 10:744–751.

Associate Editor: Vincent M. Eckhart
Editor: Daniel I. Bolnick



"The reports of the special agents comprise those of Mr. Hubbard on the rust of the orange, Professor Packard's on the causes of destruction of the evergreen trees of Northern New England and New York; Mr. Webster's on the insects affecting fall wheat; Mr. Smith's on those affecting the hop and cranberry; and Mr. Bruner's on the Rocky mountain locust, etc., in Nebraska." From the review of Riley's *Entomological Report for 1884* (*The American Naturalist*, 1885, 19:607).