

A pilot analysis shows that climatic conditions and resource availability along tropical and temperate gradients of the Americas impact the co-occurrence pattern of nectarivorous species

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Abstract

Aim

While biodiversity trends and patterns are shaped by both biotic interactions and abiotic factors, biodiversity may vary in space and time when responding to environmental conditions across clines. However, we lack the knowledge of how biotic and abiotic factors determine species co-occurrence to influence community assemblage that can impact biodiversity trends and patterns across scales.

Location

The Americas

Methods

We downloaded a sample of species occurrence data from the Global Biodiversity Information Facility (GBIF) and environmental variables that are hypothesized to influence the association between hawk moths and hummingbirds' co-occurrence across gradients. We then used the generalized additive models to understand how variations in environmental conditions across gradients will influence the co-occurrence between species.

Results

We found that the peak of species abundance and richness of both families was highest at the equator along latitude, while species abundance and richness increased with longitude. Increased colder temperatures, drier conditions, and low resource availability simultaneously reduced the occurrence of both hummingbirds and hawk moths across clines. In contrast, warmer annual temperature and reduced seasonality concurrently increased the occurrence of both hummingbirds and hawk moth species. Interestingly, we found that hummingbird abundance and species richness persisted with increasing elevation when compared to hawk moths.

Main Conclusion

Our results suggest that hummingbirds and hawk moths co-occur more along the tropics and in certain areas of the temperate regions of the Americas that have suitable environmental

conditions. We also found a pattern that suggests the possibility of niche partitioning between hummingbirds and hawk moths with increasing elevations, indicating hummingbirds with higher abundance and richness at higher elevations compared to hawk moths. We hypothesize that hummingbirds have traits that offer them certain advantages to occupy higher elevations, necessitating the need for future studies to use a multi-scale approach (e.g., integrating occurrences records and traits) when assessing biodiversity trends and patterns, and how these trends and patterns are shaped by both biotic interactions and abiotic factors are essential for the successful implementation of regional conservation programs of species.

Keywords: Biodiversity, coexistence, the Americas, Hawk moths, Hummingbirds

Introduction

Biodiversity trends and patterns are shaped by both biotic interactions and abiotic factors (Thomas, 2010; Alofs et al., 2014; Cadotte & Tucker, 2017; Cohen & Satterfield, 2020; Schofield et al., 2023). Because of these biotic interactions and abiotic factors, biodiversity trends and patterns may shift and vary through space (Mammola et al., 2024) and time (Thomas, 2010; Daru et al., 2018) as species and their interactions respond to changing environmental conditions differently (Cadotte & Tucker, 2017). For instance, studies have shown that climate change, land use change, and ecological factors all affect biodiversity at different magnitudes and directions (Sequeira et al. 2018). For example, abiotic factors can individually or jointly determine the migration time for multiple species which influences community assemblage across scales (Bell et al. 2013). However, our understanding of the specific abiotic determining species' associations, or co-occurrence, across scales and the resulting implications on biodiversity trends and patterns is limited (Thomas et al., 2004; Foley et al., 2005; Zhao et al., 2021). Worryingly, this gap in knowledge hinders our ability to understand the key processes contributing to species co-occurrence and dictate community assembly and the changes in biodiversity trends and patterns that might be impacting conservation efforts under the current global change (Cohen & Satterfield, 2020). Studies have continued to show the impact of anthropogenic-driven environmental change and ecosystem degradation on biodiversity loss (Díaz et al., 2019; Burns et al., 2021; Gudex-Cross et al., 2022; Ombugadu et al., 2023). Without the proper knowledge of how complex associations between species niches and environmental heterogeneity across scales drive biodiversity trends and patterns (Mirochnitchenko et al., 2021; Diamond et al., 2023), we might arrive at biased conclusions about the status of biodiversity under the current changing environments (Bar-Massada, 2015).

Recently, studies attempting to develop biodiversity conservation actions have shown that assessing for between-site interspecies occurrence can help us understand whether there is a trade-off (i.e., negative relationships) between species co-occurring (Mirochnitchenko et al., 2021). For instance, there is evidence to suggest that co-migrant species sharing habitats or resources are imposing constraints on individual and/or population-levels, which can impact their fitness, success, and phenology (review in Cohen & Satterfield, 2020). However, other studies

have shown that occurrence of other species can restore focal species' abundances (i.e., positive relationships), which can help buffer declining biodiversity across spatiotemporal scales due to anthropogenic climatic threats (Zhao et al., 2021). Importantly, species occupying the same habitats can act as facilitators and not as inhibitors of each other, depending on the habitat-specific scenario influencing their interactions (Peres-Neto, 2004). Relying on this evidence, we can expect that species co-occurrences can significantly be impacted by the ability of species to biologically interact within an environment (Basile et al., 2021; Mirochnitchenko et al., 2021; Schofield et al., 2023; Mammola et al., 2024). Species co-occurrence may be due to (1) suitability of habitats to allow different species to interact in an environment (Kiernan, 2014; Chandler et al., 2022), (2) the extent to which species can overlap when interacting in an environment, depending on the suitability of environmental conditions (Peres-Neto, 2004; Sblendorio et al., 2024), and (3) the number of individuals of species that can be established within a habitat when co-occurring, depending on the habitat's occupancy carrying capacity (Peres-Neto, 2004; Kiernan, 2014). Indeed, the measuring of species co-occurrence (i.e., the biotic interactions of species) can be as important as measuring the importance of abiotic (environmental) factors when assessing species distribution to understand biodiversity patterns, the effect of individual and population tradeoffs among co-occurring species can shape the community composition and structure of species, which can have monumental effects on conservation and management planning (Webb et al., 2010). Thus, there is the need for more studies that will assess the mechanisms through which environments could affect co-occurring species at the population and community levels.

Interspecies co-occurrence (i.e., coexistence) can be present along geographic gradients across different ecosystems or clines (Ficetola et al., 2021), with studies suggesting that the ability of interspecies to coexist can be significantly determined ecological processes (Losos, 2000; Ohlberger et al., 2008; Zhang et al., 2022). For example, studies have shown that environmental pressure can result in character displacement in species which permits coexistence among species with morphological differences (Adams and Rohlf, 2000). Perhaps, species with different morphology and physiology can mask or interact with the effects of biotic interactions at a broad-scale because of species-habitat or environmental specificities (Peres-Neto, 2004). Thus, understanding how changes in environmental conditions can impact interspecies interactions is necessary to better predict how biodiversity is responding to anthropogenic climate change (Zhang et al., 2022). Because interspecies interactions at a large biogeographical scale can shape ecological communities and biodiversity at large (Alofs et al., 2014; Davis et al., 2018). Since ecological theory predicts that species' co-occurrence patterns due to environmental gradients can either be positive or negative (Kass et al., 2020). Indeed, our understanding of the extent to which interspecific interaction patterns, such as species' co-occurrence vary across environmental gradients is limited. Therefore, it is important for more studies that evaluate interspecific interactions by assessing patterns of species co-occurrence across environmental gradients.

Pollination systems across different environmental gradients provide opportunities to assess co-occurrence between taxa across biogeographic scales (García-Callejas et al. 2018). For instance, although hummingbirds usually help to transport mites to new areas, this usually leads to competition for resources (i.e., nectar) between these two species (Colwell, 1995). It is hypothesized that interspecies competition for resources will lead to interspecies interactions that would negatively influence biodiversity along gradients (García-Callejas et al. 2018). However, if we assume that ecologically similar sympatric species are to avoid or minimize niche overlap by utilising different resources while co-occurring along gradients, we should expect reduced interspecific competition that would support greater biodiversity along gradients (Chesson 2000; Manlick et al. 2020). Further, minimised interspecific competition in heterogeneous environments promotes species co-occurrence due to the availability of more partitionable niches in heterogeneous habitats or environments (Manlick et al. 2020). In order to assess how abiotic factors may influence species co-occurrence, we turned to the pollination systems of hummingbirds (family Trochilidae) and hawkmoths (family Sphingidae). Both families have convergent characteristics that allow them to interact. They are highly specialised nectar feeders and pollinators as adults, with remarkably similar functional forms, an overlapping morphology in body size (Janzen 1984; Schumann, 1999) and wingspan (Johnsgard, 1997; Kitching and Cadiou, 2000), and a similar flight behaviour of hovering when feeding (Carpenter, 1979). Furthermore, there is a considerable overlap in the flowers from which hawk moths (Sphingidae) and hummingbirds (Trochilidae) as pollinators feed (Carpenter, 1979) with species in both families preferring high sugar and high volume nectar and flowers with long corolla (Willmer, 2011). Despite them having these seemingly trait similarities, they are key differences between the species. These include life history (independent herbivorous larval stage with metamorphosis vs. dependent juvenile stage), morphology (ectothermic and passive respiration vs. endothermic and active respiration), and behavior (nocturnal/crepuscular vs. diurnal for hawk moths and hummingbirds respectively). These differences also bleed into differences in partner flower morphology and phenology, i.e., pollination syndromes, as moth-pollinated plants are typically white, bloom at night, thin corolla, and produce a lot of scent while bird-pollinated plants are colored typically red or purple, bloom in the day, have a wide corolla, and are without much scent (Faegri and van der Pijl, 1979; Willmer, 2011). Due to the complex patterns of converging and diverging of traits between hawk moths and hummingbirds, they provide us with an excellent system to examine interspecies co-occurrence at large geographic scales (Buckley et al., 2021; Grady et al., 2019). Thus, we seek to understand a broad scale of geographic and climatic correlations between the co-occurring of hawk-moths and hummingbirds to provide insights into the patterns of diversity between species that can support maximum biodiversity in response to climate change. Specifically, we ask: (i) To what degree would the convergent features and ecologies of hawk moths and hummingbirds give them the advantage to co-occur? i.e., can endotherms and ectotherms positively co-occur along gradients? (ii) Is there species-specific dominance along geographical gradients? Can we observe a clear niche

partitioning between endotherms (hummingbirds) and ectotherms (hawk moths) along gradients with environmental and climatic heterogeneity? We believe that answering these questions will enable us to clearly demonstrate the causative factors that determine species distributions to support biodiversity in the era of climate change to provide insights into the driving forces of biodiversity trends across environments.

Methods

Species data collection and cleaning

For occurrence data of hawk moths and hummingbirds, we turned to Global Biodiversity Information Facility, a.k.a. GBIF. We downloaded our data from GBIF because it hosts the largest global biodiversity occurrence records of species by compiling the occurrence records of species from various sources (e.g., from the museum and citizen science records), as explained in (Heberling et al., 2021). In total, there are nearly twenty million records of hummingbirds and only approximately two million records of hawkmoths on GBIF. This discrepancy is further amplified by the fact that hawk moths are found all across the world and hummingbirds are mostly restricted to the Americas. Reducing the geographical coverage to just spaces of potential co-occurrence between hawk moths and hummingbirds, i.e., the Americas, there are still nearly twenty million records of hummingbirds but just under 350,000 records of hawkmoths on GBIF (accessed between October – November 2023; GBIF, 2023). Therefore, to alleviate the effect of sample bias, we downloaded the first twenty thousand (20,000) records of hummingbird and hawk moth occurrence from the GBIF database using the *rgbif* package in R (Chamberlain et al., 2022). The first twenty thousand records ensure enough spatial variation of both families to cover the vast majority of their ranges in the Americas. Our downloaded spatial occurrence of hummingbirds and hawk moths (accessed on 30 October 2023; GBIF, 2023) from the GBIF (www.gbif.org) had a total of 40,000 records for both families.

To avoid data with possible errors, we cleaned our species occurrence data using the *scrubr* package in R (Chamberlain, 2020) by removing records with imprecise and invalid coordinates (zero coordinates, integers, records in oceans), duplicates, and records with uncertainty over 5 km. After cleaning our record data using the mentioned criteria, our final cleaned database had 28,600 geospatial occurrence records, with 18,496 records of hummingbirds and 10,104 records of hawk moths (Fig. S1). Because we wanted to evaluate factors influencing the co-occurrence of hummingbirds and hawk moths, and hummingbirds are only found within North and South America, we only considered occurrence records from these two continents for each species.

Environmental data

In this study, we only considered the environmental variables that are suggested to be influential in the occurrence of our study species, as summarized in (Table 1). Thus, considering only the environmental variables that significantly impact the biology of our study species, we selected; annual mean temperature, mean diurnal range, temperature seasonality, mean temperature of the warmest quarter, mean temperature of the coldest quarter, precipitation of wettest quarter, precipitation of the driest quarter, elevation, and net primary productivity (NPP). We wanted to

understand how these environmental variables will associate with hawk moth's and hummingbirds' co-occurrence across North and South America. We used the *Raster* package in R (Hijmans and Etten, 2012) to extract environmental variables for each population of species all the selected climatic variables and elevation from the Worldclim2.1 database (<http://www.worldclim.org>; accessed on 30 September 30 2023), and Net Primary Productivity (NPP) from the CHELSA v2.1 (<https://chelsa-climate.org/>; accessed on September 30 2023). For our measure of NPP, we used the calculated total plant biomass minus the carbon lost to respiration measured in $\text{gC m}^{-2} \text{yr}^{-1}$ from Earth's land surface areas, as computed in CHELSA v2.1 (<https://chelsa-climate.org/>; accessed on September 30 2023). All environmental variables were extracted and projected at a fine resolution within a 2.5 arc minute resolution grid (1×1 km).

Table 1. Details on climatic variables included for subsequent analyses to evaluate factors impacting hawk moth and hummingbirds' co-occurrence. All climatic variables included because of their reported biological relevance to occurrence of these species across geographic gradients.

S/N	Term	Term definition	Reference
1	BIO1	Annual Mean Temperature	Krüger et al. (1982); Sublett et al. (2019); Schofield et al. (2023)
2	BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	Kingsolver et al. (2015); Briga and Verhulst (2015)
3	BIO4	Temperature Seasonality (standard deviation $\times 100$)	Graham et al. (2016); Schofield et al. (2023)
4	BIO10	Mean Temperature of Warmest Quarter	Sublett et al. (2019); Schofield et al. (2023)
5	BIO16	Precipitation of Wettest Quarter	Graham et al. (2016); Schofield et al. (2023)
6	BIO17	Precipitation of Driest Quarter	Graham et al. (2016); Schofield et al. (2023)
7	Elevation	Elevation (meters above sea level)	Camargo et al. (2016); Graham et al. (2016); Sublett et al. (2019)
8	NPP	Net Primary Productivity ($\text{gC m}^{-2} \text{yr}^{-1}$)	Camargo et al. (2016); Graham et al. (2016); Sublett et al. (2019)

Principal component analysis

To establish the hypothesized association between environmental variables and these families, we did a principal component analysis (PCA) with the climatic variables predicted to influence the biology of hawk moths and/or hummingbirds using the *prcomp* function in *R*. By doing a PCA, we are able to apply a linear transformation to a set of n features to output a set of n orthogonal principal components that are uncorrelated climatic variables to explain the percentage of the total variance in the environmental variables. The environmental data was centered and scaled to avoid biasing the PCA due to differences in magnitude and scale between each environmental value across the locations where these species occurred. The first to fourth PC scores combined explained 92.75% of the total variance (Table 2). We extracted the scores of PC1 to PC4, which we used to evaluate the impact of climate conditions on hawk moth and hummingbirds species' co-occurrence across gradients.

Statistical analysis

To understand how variations in environmental conditions across gradients will influence the co-occurrence between hawk moth and hummingbird species, we used the generalized additive models (GAMs) with a smoothing approach (Wood et al., 2016). We used the GAMs because of the expected non-linear relationship between species with environmental variables (Batáry et al. 2018) across gradients, which can differentially influence the co-occurrence of species across gradients (Fig. S1). Because we were evaluating species co-occurrence at a coarse (family) level, we fitted all our GAMs using the *mgcv* package in *R* (Wood, 2016) with species richness or species abundance as response variable and different predictor variable of interest as smooth term, with a penalized cubic regression spline with 10 knots. Since environmental variability across different gradients is key to our species occurring in places, we fitted all our models without including any random variable to allow us to appropriately assess the influence of species' co-occurrence to environmental or gradient variability. To ensure that we can adequately compare our model outputs when visualizing our results, each model was fit using the same approach described above (i.e., response variable \sim family + s(predictor variable, k=10)). Because of the observed differences in the distribution of species across the two continents in our data as obtained from GBIF, we statistically tested the effect of possible sampling differences in the occurrence data across the North and South America continents. In testing this, we fitted models with the natural log-transformed species richness or species abundance as the response variable and the location of collection (i.e latitude vs longitude) as the predictor variable of interest as smooth term, with a penalized cubic regression spline with 10 knots, while including the continent term as the random variable, which we found qualitatively and quantitatively similar results between the two continents (Fig. S2). The natural log-transformed species richness or species abundance was used to normalise our data. All data visualizations and analyses were performed using the *R* programming language version 4.3.0 (www.r-project.org).

Results

The occurrence records of hummingbirds were higher than the number of hawk moths by ~ 10,200 records, with a slight remarkable difference for the number of hummingbirds (261 species) and hawk moths (215 species) present in our data, fewer than the known number of species of each family in the Americas. Relying on the occurrence records in our study, species' co-occurrence between hummingbirds and hawk moth species showed a non-linear relationship with latitude, with high species abundance and richness being supported only along the equator (Fig. 1a & 1b). However, we found that species' co-occurrence showed a linear relationship with longitude, with hummingbirds and hawk moth species abundance and richness both increasing along longitudinal gradients (Fig. 1c & 1d). The implication of these results would suggest that there is a significant variation in co-occurrence patterns of hummingbirds and hawk moth species across geographic gradients, such as latitude and longitude.

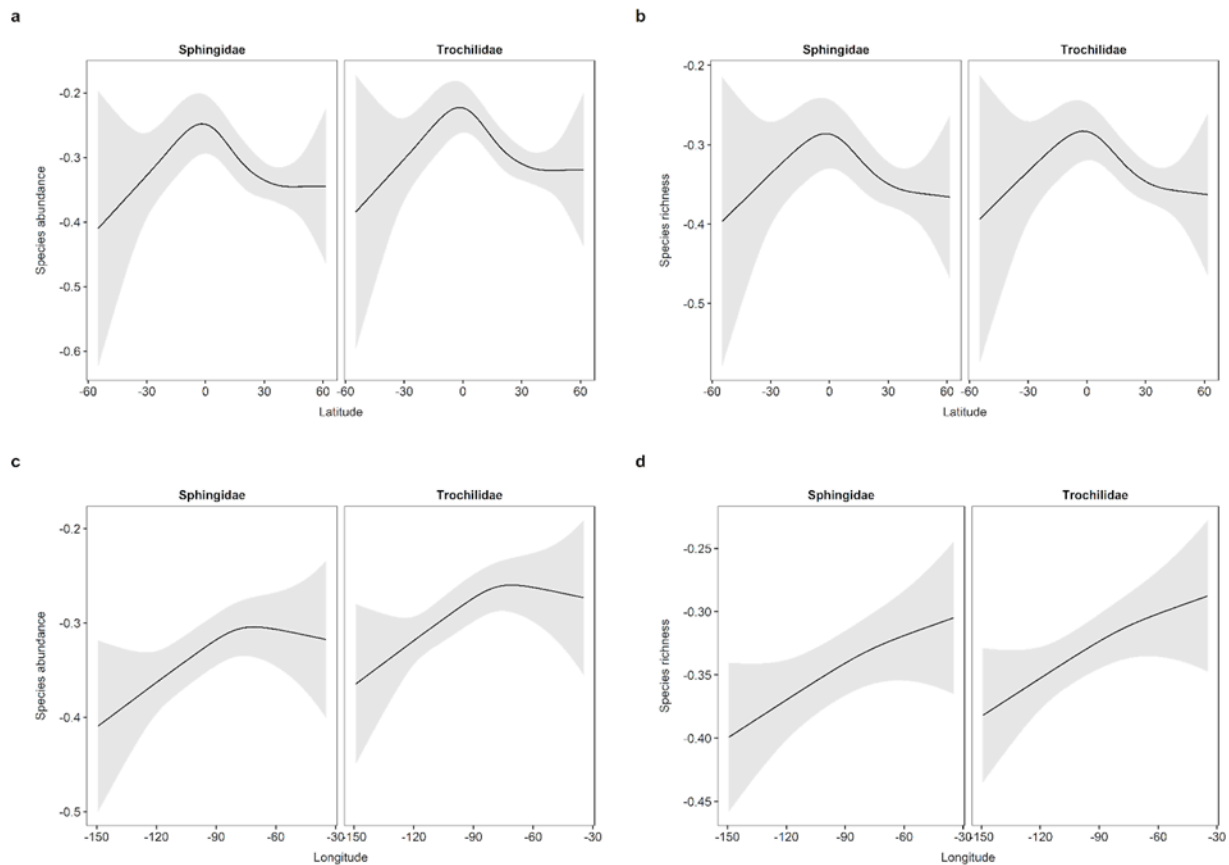


Figure 1. Results of our analysis for biodiversity patterns of hummingbirds and hawk moth families across gradients for: (a) species abundance along latitude, (b) species richness along latitude, (c) species abundance along longitude, and (d) species richness along longitude. The y-axis is represented as the magnitude changes of biodiversity patterns across latitudes and longitudes, with a soothing effect of the family-level. Grey-coloured lines and ribbons represent the predicted values \pm 1 SE of estimates of GAMs.

On the selected environmental conditions influencing species' co-occurrence (Fig. S2), we found that Principal component (PC) 1 loaded on increased seasonality temperature (BIO4), reduced mean temperature of coldest quarter (BIO11), precipitation of wettest quarter (BIO16), and resource availability (i.e., net primary productivity), while PC2 loaded on reduced annual mean temperature (BIO1) and mean temperature of the warmest quarter. However, PC3 loaded on increased seasonality temperature (BIO4) and reduced precipitation of driest quarter (BIO17) at high elevation, while PC4 loaded on increased mean diurnal range (BIO2) at high elevation (Table 2), with each of these PC loadings contributing to the patterns of species occurrence observed (Fig. 2).

PC1-PC4 explained 92.7% of the variance of environmental conditions influencing species' co-occurrence (Fig. S3). There was a strong linear relationship between the species co-occurrence of hummingbirds and hawk moths with PC1, PC2, and PC4 (Table 2). We found that PC1 negatively affects the abundance and richness of hummingbirds and hawk moth species (Fig. 3a), suggesting that the concurrent effect of increased seasonality and extreme environmental conditions, such as reduced mean temperature, precipitation, and resources as loaded in PC1 might be negatively impacting the manner and way species' are co-occurring (Fig. 2a). However, we found that PC2 and PC4 positively impacted the abundance and richness of hummingbirds and hawk moth species (Fig. 3b), demonstrating that low annual temperature with reduced seasonality as loaded in PC2 and low annual temperature at increased elevation as loaded in PC4 might support increased species co-occurrence (Fig. 2b). We found that PC3 showed no significant impact on the co-occurrence between hummingbirds and hawk moth species (Fig. 3c). However, we found species' co-occurrences to be even between the North and South American continents, with no significant variations in the distribution patterns between hummingbirds and hawk moth species distribution across South and North America (Fig. S4), which could be based on the almost similar spatial species occurrence records used in this study (Fig. S1).

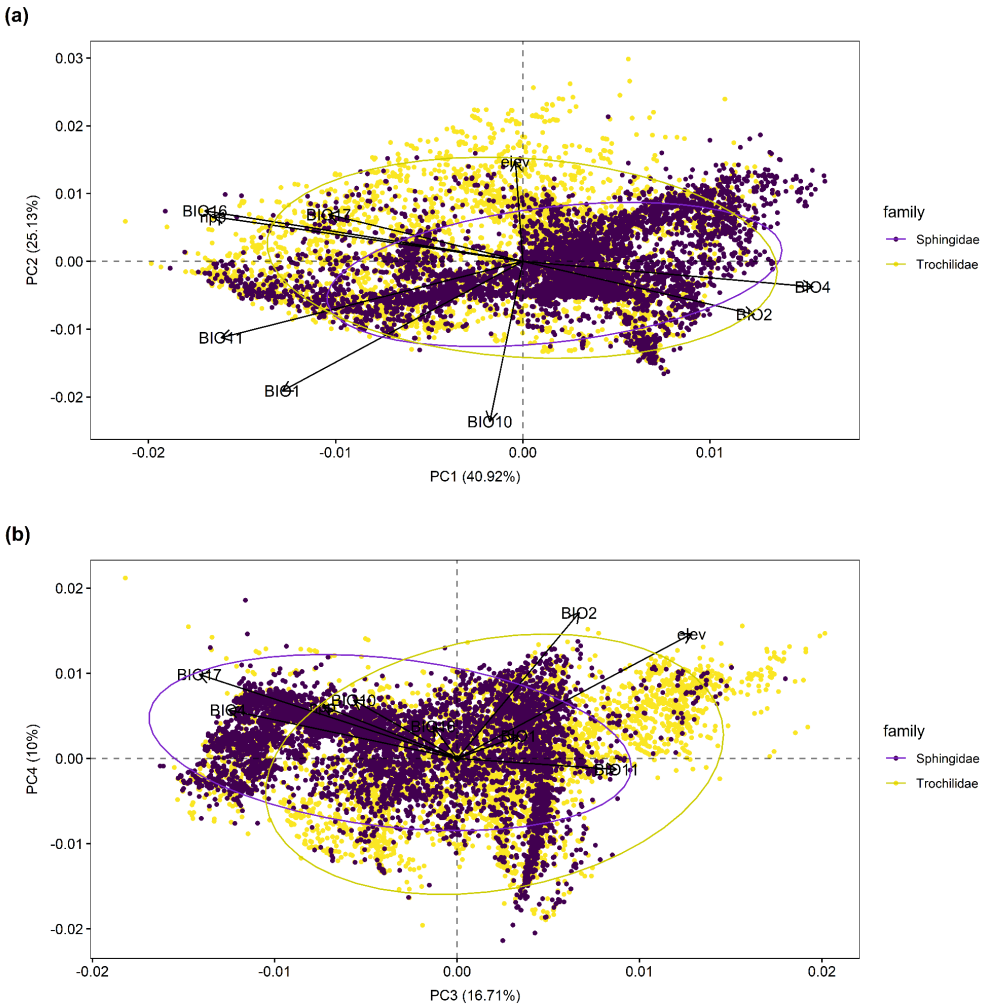


Figure 2. Principal components (PCs) scatter plots showing the relationships between PC loadings and hummingbird and hawk moth species co-occurrence along clines

Table 2 Principal Component loadings from the PCA of climatic conditions that are relevant to the biology of hummingbirds and hawk moth species. Principal components with eigenvalues greater or almost 1 were retained for further analysis to understand the influence of climatic conditions on biodiversity patterns. Principal components loadings at ≥ 0.40 are given in bold to show the loading direction for each component.

Factors	PC1	PC2	PC3	PC4
BIO1	-0.3326	-0.4945	0.1238	0.0973
BIO2	0.3201	-0.2025	0.2451	0.6269
BIO4	0.4011	-0.0973	-0.4605	0.2090
BIO10	-0.0456	-0.6122	-0.2081	0.2508
BIO11	-0.4173	-0.2915	0.3203	-0.0469
BIO16	-0.4400	0.1930	-0.0483	0.1386
BIO17	-0.2686	0.1790	-0.5184	0.3615

Elevation	0.0103	0.3827	0.4713	0.5364
Net Primary Productivity	-0.4286	0.1710	-0.2704	0.2254
Eigenvalue	1.9190	1.5040	1.2262	0.9486
Percentage variance	40.92	66.05	82.76	92.75

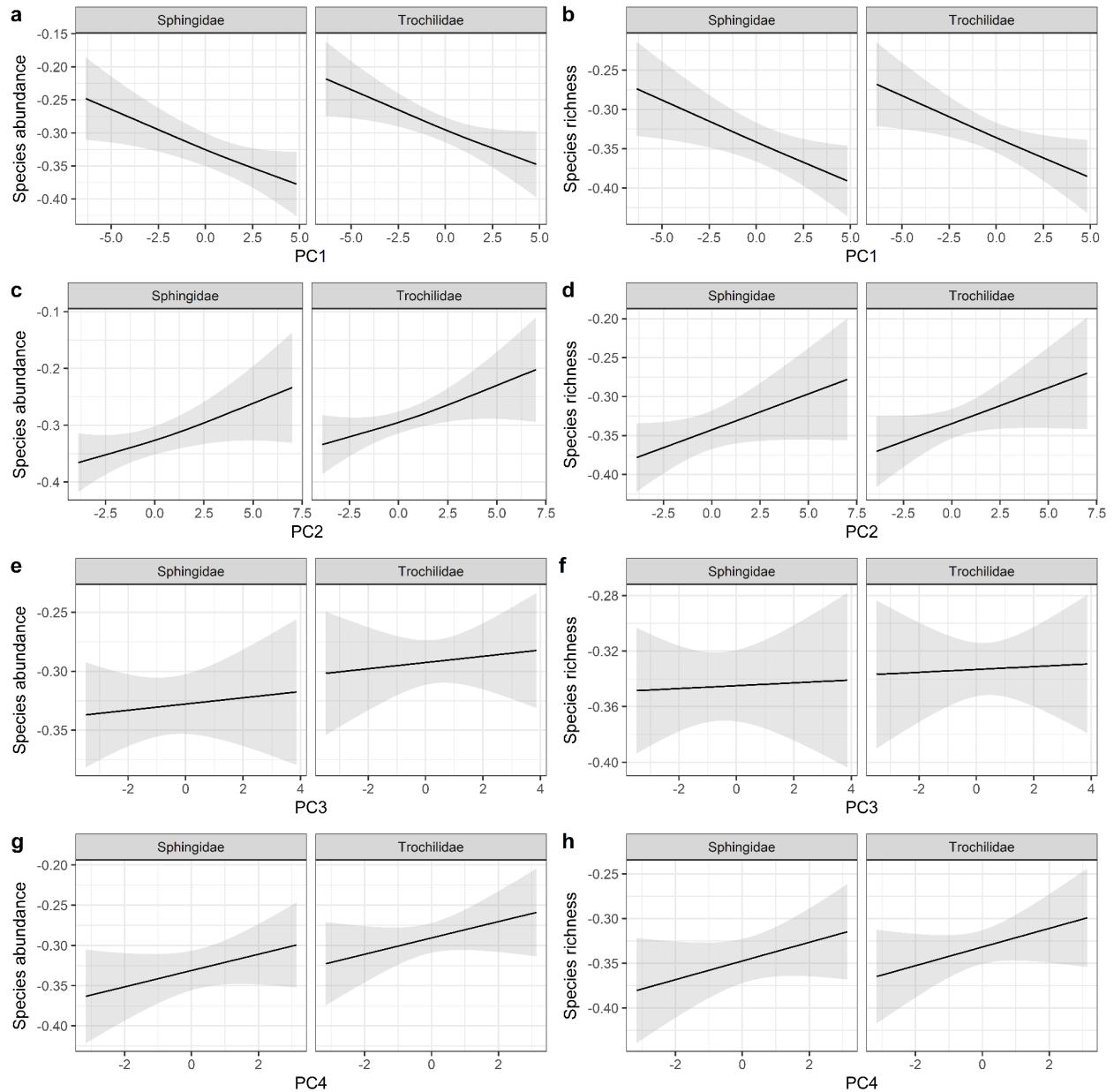


Figure 3. The relationships between occurrence of hummingbirds and hawk moths and prevailing environmental conditions along clines, as summarized in PCs: (a) species abundance with PC1, (b) species richness with PC1, (c) species abundance with PC2, (d) species richness with PC2, (e) species abundance with PC3, (f) species richness with PC3, (g) species abundance with PC4, (h) species richness with PC4. The y-axis is represented as the magnitude changes of biodiversity

patterns as impacted by environmental conditions along clines, with a soothing effect of the family-level. Grey-coloured lines and ribbons represent the predicted values ± 1 SE of estimates of GAMs.

Discussion

In this study, we investigated broad-scale geographical patterns of species richness of two key, convergent, yet phylogenetically distant, pollinator families: hawk moths (family Sphingidae) and hummingbirds (family Trochilidae). Our primary objective was to evaluate the driving factors influencing species co-occurrence in North and South America, which is needed to provide insights into biodiversity conservation in a changing environment. We found a non-linear pattern of species co-occurrence with latitudes, with the peak of species abundance and richness of hummingbirds and hawk moths only occurring at the equator. However, there was a linear pattern of species co-occurrence with longitude, with hummingbirds and hawk moth species abundance and richness increasing along longitude. Furthermore, our study demonstrated that increased seasonality with unfavourable environmental conditions (e.g., colder temperature, drier conditions, and low resources) negatively influenced how hummingbirds and hawk moths species co-occurred while low annual temperature with reduced seasonality at high elevation supports increased hummingbirds and hawk moths species co-occurrence. Although we found that hummingbirds and hawk moths co-occurred in most parts of the area in our study, we also found that hummingbirds' abundance and richness when compared to the abundance and richness of hawk moths increased at higher elevations, indicating that hummingbirds might be having a certain advantage over hawk moths, and this enables them to occupy higher elevations.

The influence of biotic interactions on species' co-occurrence have been suggested to revolve around the presence of species that are facilitators, competitors, or predators occupying the same geographic area to significantly influence the presence of other species (Jackson et al., 2001). In this study, we found positive interspecies interactions between hummingbirds and hawk moths across both latitude and longitude, with hummingbirds' and hawk moths' abundance and richness being almost similar across both gradients. The pattern of species co-occurrence between hummingbirds and hawk moths in our study was not surprising because of the consistent positive interspecies relationships between hummingbirds and insect-like organisms, with hummingbirds in the relationship mostly serving as facilitators of these smaller organisms rather than their inhibitors (Colwell, 1995). For example, there is evidence to suggest that hummingbirds do enhance the dispersion of mites to certain habitats or niches (Colwell, 1995). Perhaps the consistent positive interspecies correlations between hummingbirds and hawk moths along geographic gradients might be determined by their ability to biologically interact or by metrics not measured in our study, such as species-specific-habitat relationships across gradients (Peres-Neto et al., 2001). We did not measure species-specific-habitat relationships because we only considered co-occurrence between hummingbirds and hawk moths at the family level. Considering that there are instances where species-habitat relationships can be more important

than species associations across clear gradients (Mammola et al., 2024), we suggest that future studies account for species-specific relationships with habitat characteristics and environmental filters for us to adequately understand the magnitude and directions of specific processes driving species co-occurrence (Peres-Neto, 2004).

The pattern in which species co-occur in time and space is not only a function of the ability of species to biologically associate but can also be significantly determined by environmental filters (Jackson et al., 2001; Peres-Neto et al., 2001; Blois et al., 2014; Mammola et al., 2024), such as prevailing environmental conditions and resource availability across gradients (e.g., Ferger et al., 2014; Beck et al., 2016;). In this study, we accounted for the effect of family in our models that seek to evaluate how environmental conditions will shape species co-occurrence to provide insights into the inconsistencies and difficulty of evaluating how biotic interactions and environmental conditions can interact with each other to affect species co-occurrence on a large spatial scale. As expected, we found a strong effect of environmental filters (i.e., environmental conditions across gradients) to determine the pattern of species co-occurrence and coexistence between hummingbirds and hawk moths. Specifically, the concurrent effect of increased seasonality, colder temperatures, drier conditions, and low resources reduce hummingbirds and hawk moth species' abundance and richness. Further, we found that low temperatures across the year with reduced seasonality did increase hummingbirds' and hawk moths' abundance and richness. Our findings agree with previous findings that found extreme environmental conditions, such as low colder temperature can negatively impact the patterns of species community assemblage (Bishop et al., 2016), and co-occurrence and coexistence because environmental conditions can serve as promoting or limiting factors enabling species to aggregate or segregate which can impact species' abundance and richness (Blois et al., 2014). For example, stressful environmental conditions were found to increase competition for resources among three species of birds, leading to negative interactions between these birds, with their abundance and richness reducing (Zhang et al., 2022), suggesting that biotic interactions among species are influenced by environmental heterogeneity that can determine species co-occurrence (Bar-Massada and Belmaker, 2017). Therefore, we believe that studies that will model to account for traits, taxonomic differences at the family, genera, or species levels to evaluate for interspecies associations based on co-occurrence and environmental data across temporal and spatial scales are needed to provide a comprehensive understanding of the ability of species to co-occur and the mechanisms that of biodiversity maintenance in a changing environment (Blois et al., 2013).

While there is an overall broad-scale of co-occurrence between these two families as shown in our earlier results, we also found interesting nuances in their cooccurrence. Specifically, we found that while both families increased in abundance and richness with increasing elevations, hummingbird populations were found to be more persistent at much higher elevations. Perhaps, multiple factors, like physiological, behavioural, or species-specific habitat characteristics. Based

on physiology, some species have been found to show a physiological comparative advantage when compared to others (Bujan et al., 2020). Birds are less susceptible than insects to the lower atmospheric due to their ability to maximize the intake of oxygen (Berger, 1974; Laguë, 2017). Hummingbirds such as *Colibri coruscus* have been shown to minimally adjust their oxygen consumption at higher altitudes (Berger, 1974). On the other hand, insects, due to their tracheal respiratory system of spiracles on their exoskeletons, are more susceptible to low oxygen since oxygen assimilation occurs via diffusion (Dorsett, 1962). Adult insects like *Manduca sexta* are smaller when reared under hypoxic conditions (Harrison et al., 2010). This physiological advantage may further compound the substantial differences in thermoregulation as hummingbirds are largely endothermic and hawk moths are largely ectothermic (although the considerable overlap in size does make the distinction less binary). A smaller organism has greater difficulty maintaining heat, especially for a crepuscular and nocturnal organism. Higher elevation habitats are less likely to retain heat from solar radiation during the day and as such may limit hawk moths' potential exploitation of the system. Indeed, behavioral and physiological traits may interact to allow hummingbirds to thrive at higher elevations over hawk moths.

Our work using the first 20,000 occurrence records of hummingbirds and hawk moth species each, demonstrated how continuous environmental changes, like temperature, precipitation and resource availability are important predictors of the geographic variation in hummingbirds and hawk moth species co-occurrence patterns. We must acknowledge the fact that this is a pilot study and therefore lacks the substantial analysis required to come to any definitive conclusions about these two families and the way they co-occur and partition along environmental variables. Given the potential consequences of spatial sampling biases using the full dataset, we were constrained to use a small fraction of the GBIF occurrence records to allow us properly interpret our model outputs and the implications for the conservation of these species of pollination importance across large geographic areas. Though we feel our subsample was geographically broad enough and had enough records to be largely representative of the full sample records of both families, we acknowledge the possibility that further sampling bias may have crept into our analysis. Furthermore, we must acknowledge that there is a larger spatial sampling bias in the GBIF data. Sources of this data are human derived, either through field sampling or citizen science. As such, there is a tendency for the occurrence records to be associated with human populations; one can see that much of the occurrence data tends to be associated with urban agglomerations (Fig. S1). Such spatial autocorrelation would contribute significantly to the high levels of co-occurrence we see between the two families. Despite these limitations, we still believe that our results reveal key and interesting facts about how environmental gradients influence the co-occurrence and potential interactions of these two convergent families. Although we used a small fraction of the GBIF occurrence records available for each species at the time of the study, we suspect that this methodology is broadly applicable to assess the co-occurrence patterns across different taxa exhibiting similar spatial trends and patterns in their habitat associations along relatively same geographic gradients. Indeed, multi-scale studies

assessing biodiversity trends and patterns, and how these observed trends and patterns are shaped by both biotic interactions and abiotic factors are essential for the successful implementation of conservation of species.

Conclusion

In sum, we found that the positive interactions that influenced the ability of hummingbirds and hawk moths to co-occur across gradients may have been impacted by habitat heterogeneity (suitability) and/or environmental heterogeneity. While increased environmental stress levels, such as colder temperatures, drier conditions, and low resources negatively impacted the interspecific interactions between hummingbirds and hawk moths, optimal temperature across the year and short seasonality increased the ability of hummingbirds and hawk moths to overlap in their occurrence across gradients, which supports species to co-occurrence. Interestingly, our study provides a new insight that these species might be experiencing niche partitioning at high elevations that might be influenced by species habitat-specific filtering, with the hummingbirds and not hawk moths occupying higher elevations. Indeed, relying on the co-occurrence data and the environmental data in our study, we suggest that the interspecific interactions between hummingbirds and hawk moths to support biodiversity maintenance across gradients might be limited to only certain elevational gradients, with niche partitioning between these species being possible at higher elevations. However, for a more in depth understanding of the specific mechanisms driving the niche partitioning between hummingbirds and hawk moths at higher elevations, we recommend that future studies will need to use a more robust non-biased occurrence records of species, combined their functional traits, phylogenetic diversity, and the environmental data of species habitat-specifics for us understand the advantages hummingbirds have over hawk moth when occupying higher elevations. This is because the occurrence records used in our study is not a holistic reflection of the total number of species of both hawk moths and hummingbirds distribution in the Americas. Finally, because of the highly biased occurrence records between the two families, we suggest the need for an aggressive citizen science approach in collecting the occurrence records of species with presence across large areas, to address these biases and inconsistencies in the records of species given less attention.

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Supplementary materials

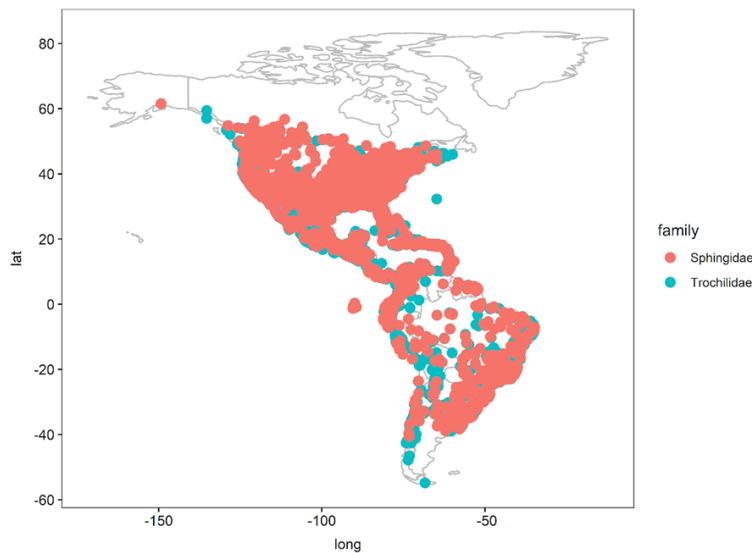


Figure S1. The distributional patterns between hummingbirds and hawk moth species continents in our study, with coloured points representing hummingbirds and hawk moth families.

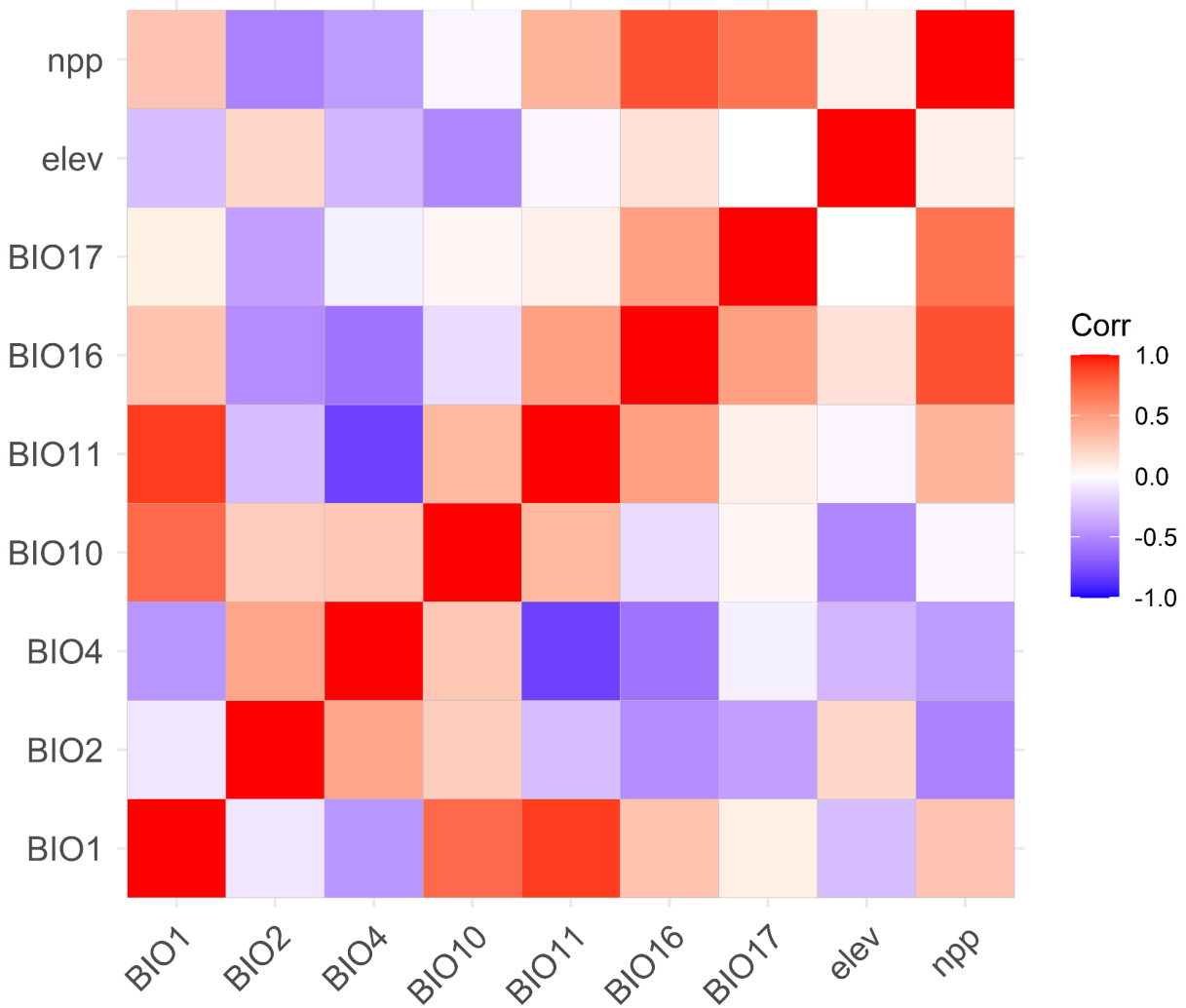


Figure S2. Correlation plot of selected environmental variables that impact the biology of hummingbirds and hawk moth species continents in our study, with coloured squares representing the strength and direction of correlation between variables.

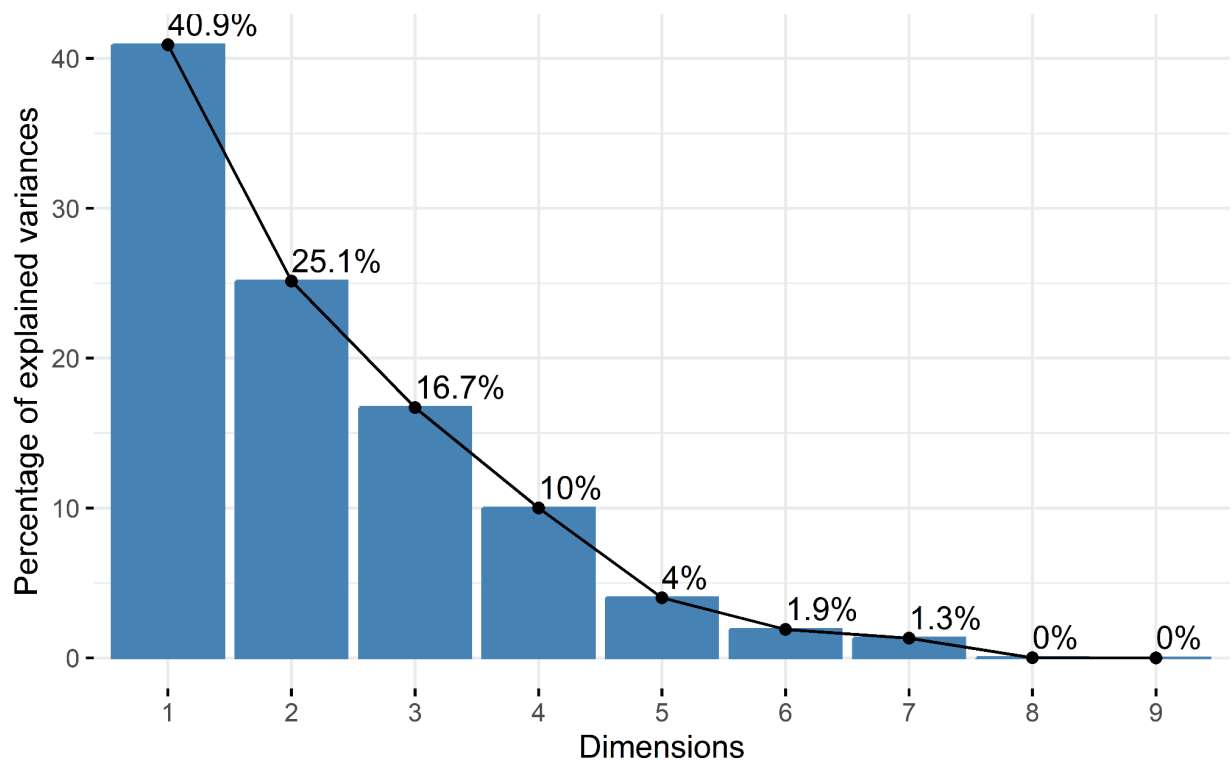


Fig. S3: Principal component (PC) loading for environmental variables influencing species' associations between hummingbirds and hawk moths.

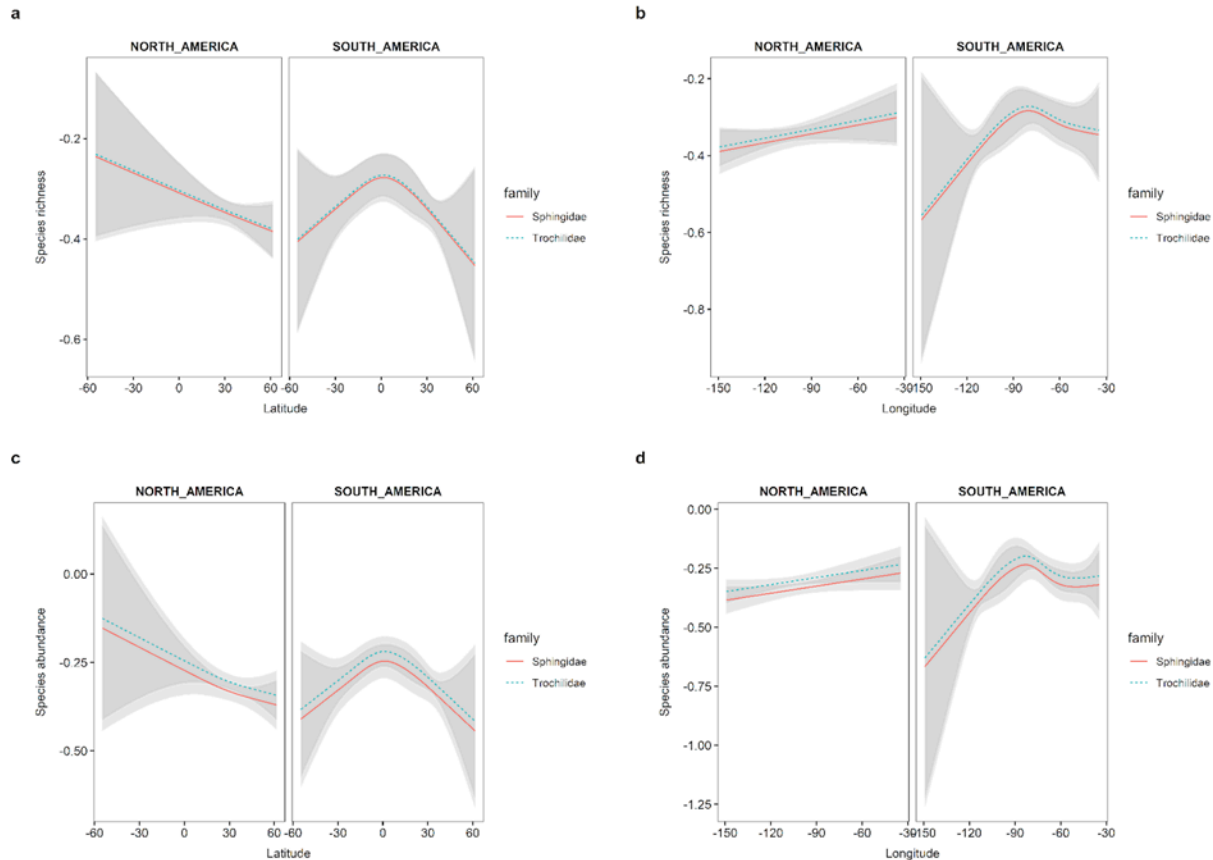


Figure S4: Continental differences in biodiversity patterns between hummingbirds and hawk moth families across gradients: (a-b) species richness with continents across gradients, and (c) species abundance with continents across gradients. The y-axis is represented as the magnitude changes of biodiversity patterns across latitudes and longitudes, with a soothing effect of the family-level.

Author contribution: **Gideon Gywa Deme:** Conceptualization; data curation; formal analysis; investigation and questions; methodology; software; validation; visualization; writing of first draft, review and editing. **Abdel H. Halloway:** Conceptualization; investigation; methodology; Supervision; validation, review and editing. **Malann Yoila David:** investigation and questions; methodology; validation. **Christopher J. Whelan:** Supervision, review, and editing. **Joel S. Brown:** Conceptualization and supervision

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