





# Climate mediates roles of pollinator species in plant–pollinator networks

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## Abstract

**Aim:** Understanding how climate conditions influence plant–pollinator interactions at the global scale is crucial to understand how pollinator communities and ecosystem function respond to environmental change. Here, we investigate whether climate drives differences in network roles of the main insect pollinator orders: Diptera, Coleoptera, Lepidoptera and Hymenoptera.

**Location:** Global.

**Time period:** 1968–2020.

**Major taxa studied:** Diptera, Coleoptera, Lepidoptera and Hymenoptera.

**Methods:** We collated plant–pollinator networks from 26 countries and territories across the five main Köppen–Geiger climate zones. In total, we compiled data from 101 networks that included >1500 plant species from 167 families and >2800 pollinator species from 163 families. We assessed differences in the composition of plant–pollinator interactions among climate zones using a permutational ANOVA. We calculated standard network metrics for pollinator taxonomic groups and used Bayesian generalized mixed models to test whether climate zone influenced the proportion of pollinator network links and the level of pollinator generalism.

**Results:** We found that climate is a strong driver of compositional dissimilarities between plant–pollinator interactions. Relative to other taxa, bees and flies made up the greatest proportion of network links across climate zones. When network size was accounted for, bees were the most generalist pollinator group in the tropics, whereas non-bee Hymenoptera were the most generalist in arid zones, and syrphid flies were the most generalist in polar networks.

**Main conclusions:** We provide empirical evidence at the global scale that climate strongly influences the roles of different pollinator taxa within networks. Importantly, non-bee taxa, particularly flies, play central network roles across most climate zones, despite often being overlooked in pollination research and conservation. Our results identify the need for greater understanding of how global environmental change affects plant–pollinator interactions.

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## KEYWORD

Plant-pollinator, network ecology, climate zone, insect pollinators, pollination ecology, ecosystem function

## 1 | INTRODUCTION

Animal pollinators are critical to ecological function in terrestrial ecosystems, and insect taxa, particularly Lepidoptera, Hymenoptera, Coleoptera and Diptera, are the most diverse and abundant groups of known pollinators (Ollerton, 2017). Insect pollinators are sensitive to climate conditions, and knowledge of how climate influences plant–pollinator interactions at the global scale is crucial to understand how pollinator communities and pollination function might respond to environmental change. Insects can respond quickly to changing environmental conditions, including seasonality, weather conditions and resource availability, yet most research on these effects has focused on physiological or population processes and range shifts of conservation-relevant or economically relevant species (Halsch et al., 2021; Janes et al., 2014; Stange & Ayres, 2010). More recently, researchers have focused on community-level effects of environmental change on ecosystem function, particularly plant–pollinator interactions and networks (Byers, 2017; Forrest, 2015; Hegland et al., 2009). Climate patterns can influence plant–pollinator interactions by affecting global distributions of plants that provide floral resources to animals (Rech et al., 2016), by altering plant phenology or floral resource quality and quantity, or by affecting pollinator foraging patterns and sensory signals (Lawson & Rands, 2019; Park & Mazer, 2019). However, thermal tolerance varies across insect taxonomic groups, meaning that climatic conditions are likely to influence the composition of insect pollinator communities across space and time. For example, dipterans are generally thought to be more cold tolerant than other flying insects and are often recorded as the most common flower visitors in high-elevation or high-latitude plant–pollinator networks (Elberling & Olesen, 1999; Inouye & Pyke, 1988; McCabe et al., 2019; Tiusanen et al., 2016) and at sites with cooler temperatures in other climate zones (González et al., 2009). In contrast, bees are most abundant and diverse in dry, warm subtropical and mediterranean regions (Ollerton, 2017) and, with a few exceptions (e.g., *Bombus* spp.), are generally less active than other insect taxa during winter and in cold, inclement weather (Goodwin et al., 2021). This diversity of environmental responses among taxa provides buffering effects for ecosystem function and delivery of ecosystem services (Bartomeus et al., 2013; Rader et al., 2013). Understanding species responses to environmental conditions at broader scales can inform how plant–pollinator interaction networks are affected by global environmental change.

Historically, plant–pollinator network studies have mostly been localized, descriptive and largely focused on documenting diversity and interactions (Knight et al., 2018). Hence, there is a need for greater understanding of geographical trends in plant–pollinator interactions (Mayer et al., 2011), particularly how climate drives the composition of interactions across large spatial scales (Petanidou

et al., 2018). The small number of studies that have identified effects of climate on plant–pollinator networks have been based on simulated data or focus on local or regional systems (Hegland et al., 2009; Memmott et al., 2007). Broad-scale analyses investigating global patterns in plant–pollinator networks have generally focused on network-level metrics and general patterns in species richness, with limited discussion of taxonomic identity or species network roles (Olesen & Jordano, 2002; Traveset et al., 2016; Trøjelsgaard & Olesen, 2013). Where biogeographical gradients are considered, the focus has traditionally been on testing the effects of latitude on network structure (Ollerton & Cranmer, 2002; Schleuning et al., 2012). However, latitude might be inadequate for encompassing the environmental nuances that drive community-level interactions, and the historical focus on latitude has limited our understanding of global-scale patterns of ecological interactions that influence ecosystem function, such as pollination (Moles & Ollerton, 2016).

Here, we address an overlooked aspect of the plant–pollinator network discourse by focusing on the relative community roles of key taxonomic groups. Specifically, we ask whether the network roles of different pollinator taxa vary between climate zones. We predict that dipterans will have more important network roles in colder climates, whereas bees will have important network roles in warmer climates. We address this by assessing the proportion of network links (i.e., plant species visited by a pollinator) and the level of pollination generalism for different pollinator groups among different climate zones. We use Köppen–Geiger climate zones, which represent biome distributions and combine complex climate gradients and vegetation patterns into simple, ecologically meaningful categories (Beck et al., 2018). Our aim is to increase understanding of how climate influences the relative proportion of different pollinator taxa available in a community and to guide future research into how the network roles of different pollinator taxa can change in response to environmental conditions.

## 2 | METHODS

To build our dataset we conducted a comprehensive search of peer-reviewed literature and research theses and collated community network datasets that linked flowering plants to insect pollinators or flower visitors (hereafter, plant–pollinator networks). We searched for plant–pollinator networks that met all the following criteria: (1) observations of insect pollinator taxa visiting flowering plant taxa; (2) community-level data collection (i.e., networks that focused only on one closely related group of plants or pollinators were excluded); and (3) data were collected from natural or semi-natural systems. We collated 101 plant–pollinator networks that met our criteria (Supporting Information Table S1) from multiple sources: the Web of

Life ecological networks database (<http://www.web-of-life.es/>); an exhaustive search of published journal articles, data repositories and theses; and by directly contacting researchers of plant–pollinator network studies. Within our collated data, a total of 21 networks included vertebrate species [from three bird orders (Apodiformes, Passeriformes and Psittaciformes) and the reptile order Squamata]. Although vertebrates were not the focus of our study, we retained networks containing plant–vertebrate interactions, but we did not analyse vertebrate interactions directly because the focus of our study was to compare insect pollinator groups. Furthermore, vertebrate pollinators comprised 4% of interactions in those 21 networks and 0.97% of interactions across all 101 networks. We used the *taxize* package (v.0.9.99; Chamberlain & Szöcs, 2013) to identify both plant and insect families and orders from the datasets. In our dataset, not all networks were weighted (included the frequency of interactions); therefore, we converted weighted networks to binary because these data were sufficient for our analyses. We identified the main Köppen–Geiger climate zone (tropical, arid, temperate, continental or polar) for each network based on the spatial coordinates provided with each dataset using the *kgc* package (v.1.0.0.2; Bryant et al., 2017).

We assessed differences in the composition of plant–pollinator interactions among climate zones using a permutational analysis of variance (PERMANOVA) (Anderson, 2001). Initially, we counted the number of interactions between pollinator families and plant families in each network to make comparisons across regions that vary widely in their plant and animal taxa. We then calculated the Bray–Curtis dissimilarity index between interactions within networks using the *vegan* package (v.2.5-3; Oksanen, 2015). Data were  $\log_{10}$ -transformed before calculating the interaction dissimilarity to lessen the weighting of abundant interactions (Anderson et al., 2006). We evaluated dispersion of network dissimilarity values among climate zones with a permutational test of multivariate homogeneity of group dispersion (PERMDISP) and post-hoc pairwise Tukey's honestly significant difference (HSD) tests. We computed pairwise differences in the composition of plant–pollinator interactions between each climate zone using a pairwise PERMANOVA (Kandlikar et al., 2018). To account for multiple comparisons, *p*-values were adjusted using the false-discovery rate (FDR) method (Benjamini & Hochberg, 1995). We visualized differences in plant–pollinator interactions among networks in two-dimensional space using non-metric multidimensional scaling (NMDS) ordination. NMDS ordination is a visual tool that illustrates similarities and differences between data categories in a two-dimensional space. Here, we used it to visualize the similarity or difference between each set of networks, grouped by climate zone, in terms of the community composition of plant–pollinator interactions.

We tested whether climate zone influenced: (1) the proportion of pollinator network links; and (2) the level of pollinator generalism. We focused on the taxonomic groupings bees, non-bee Hymenoptera, Coleoptera, Lepidoptera, non-syrphid Diptera and Syrphidae, because they represent the four most diverse and abundant insect pollinator orders world-wide (Ollerton, 2017). Analyses at the family level were not feasible owing to a high number of singletons, but we

separated syrphid flies and bees from their respective taxonomic orders (Diptera and Hymenoptera) because adults of these species are predominantly nectar feeders and are important and recognizable pollinators across most terrestrial systems (Ollerton, 2017; Ssymank et al., 2008).

We focused on two measures of network roles for the different insect pollinator orders: (1) proportion of links (i.e., the proportion of total links in each network for each pollinator taxonomic group), which we calculated as the sum of unique links within each pollinator group divided by the total sum of unique links within each network; and (2) normalized pollinator generalism at the species level (i.e., the total number of links between each pollinator species and different plant species within a network, also called node degree). To account for differences in network size in the species generalism model, we included an offset of  $\log_{10}$ (network size). By including an offset, normalized generalism can be considered as the rate per unit network size. To estimate the proportion of links and species generalism for each pollinator group within each climate zone, we specified Bayesian generalized linear mixed-effects models using the *brms* package (v.2.15.0; Bürkner, 2017). These models were fitted with beta and negative binomial distributions, respectively. In each model, the response variable was the proportion of links for each pollinator taxonomic group or the number of plant partners for each pollinator species within each network. Fixed effects were “pollinator taxa” (categorical), in interaction with “climate zone” (categorical). In both models, we included a random effect of “network” nested within “study” to account for the dependent data structure of multiple networks within studies. Finally, to assess whether plant richness of networks differed between climate zones, we modelled plant richness as a function of climate zone. We fitted this model with a Poisson distribution and included “study” as a random effect. We compared the explanatory power of climate zone with latitude by refitting these models with absolute latitude (northern and southern latitudes were both positive) instead of climate zone as the predictor variable, in interaction with pollinator group. Latitude was scaled and centred ( $\mu = 0$ ,  $SD = 1$ ) before analyses. We then compared these models using leave-one-out cross-validation (Vehtari et al., 2017).

We determined whether pairwise differences in the proportion of network links and normalized generalism between climate zones and pollinator groups were significant when 95% highest density intervals did not overlap zero (Kruschke, 2014). We set weakly informative priors and manipulated  $\Delta$  and maximum tree depth to reduce divergent transitions. We undertook posterior predictive checks visually using *bayesplot* (v.1.8.0; Gabry & Mahr, 2017). All data analyses were undertaken in R (v.4.1.0; R Core Team, 2013). All R script and analyses are available at [<https://github.com/JoseBSL/Geonet>].

### 3 | RESULTS

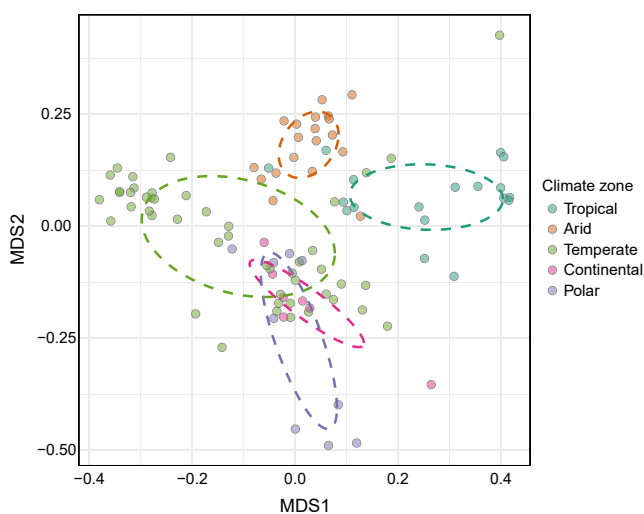
We collated a total of 101 unique networks (Supporting Information Table S1), including a total of >1500 plant species (167 families and 45 orders) and 2800 pollinator species (163 families) from the four

main insect pollinator orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera). These insect orders made up 91% of all plant-pollinator interactions across our networks.

Network data was sourced from 26 countries or territories spanning all five Köppen-Geiger climate zones: 18 networks from the tropical zone, 19 arid, 48 temperate, 7 continental and 9 polar. At the global scale, we found that climate is a strong driver of compositional dissimilarities between plant-pollinator interactions (PERMANOVA,  $F_{4,96} = 4.7$ ;  $R^2 = 0.16$ ;  $p < .001$ ; Figure 1). The composition of plant-pollinator interactions was statistically different ( $p < .05$ ) between all climate zone pairs (Supporting Information Table S2). In particular, the composition of interactions in tropical zone networks was distinct from all other climate zones along the first multidimensional scaling (MDS) axis, whereas the other climate zones were separated along the second MDS axis (Figure 1; Supporting Information Table S2). Dispersion of plant-pollinator interaction composition was similar across all climate zones (all pairwise Tukey's HSD  $p > .05$ ), except between arid and temperate zones ( $p < .001$ ) and between temperate and continental zones ( $p = .01$ ).

Relative to other taxa, bees and flies made up the greatest proportion of links in all networks across all climate zones, whereas lepidopterans, coleopterans and non-bee hymenopterans contributed <24% of links overall ( $R^2 = 0.43$ ; Figures 2 and 3a). Interactions in networks from the tropical climate zone were dominated by bees and non-syrphid Diptera. Arid zones were dominated by Hymenoptera (bees and non-bees) and non-syrphid Diptera. Temperate networks were dominated by bees, and continental and polar zone networks were dominated by bees and Diptera (Syrphidae and non-syrphids).

We found high levels of variation in pollinator generalism among taxa and climate zones ( $R^2 = 0.23$ ; Figures 2 and 3b), although networks did not differ in plant richness between climate zones (Supporting Information Figure S1). Within insect groups,



**FIGURE 1** NMDS ordination of plant-pollinator interaction composition in each climate zone. Each point represents the composition of interactions in a single plant-pollinator network. Dashed circles represent the 95% confidence ellipses for each climate zone mean (i.e., the group centroid). Stress = 0.14.

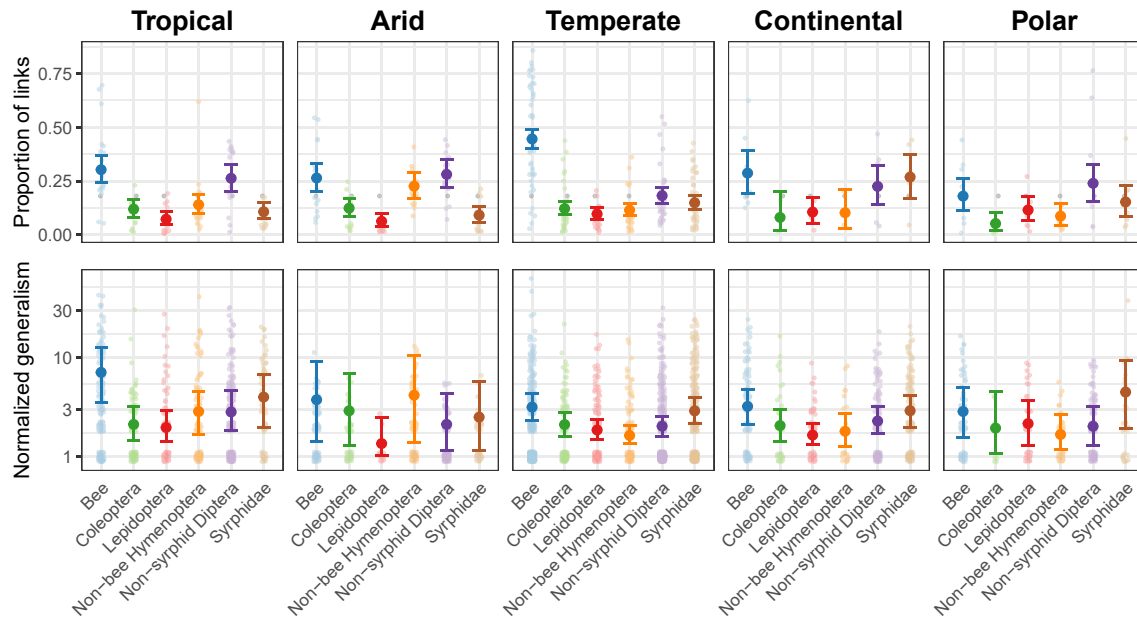
most pollinator species had relatively few plant partners, particularly in temperate and continental networks (Figure 2). Bee species, on average, visited the most plant species in tropical climate zones (Figures 2 and 3), whereas non-bee Hymenoptera had the highest number of plant partners in arid climate zones, and syrphid flies visited the most plant species in polar networks (Figure 2).

## 4 | DISCUSSION

We provide empirical evidence at the global scale that climate strongly influences the roles that different pollinator groups play in networks. Relative to other insect taxa, bees and flies made up the greatest proportion of links in all networks across all climate zones, whereas lepidopterans, coleopterans and non-bee hymenopterans contributed few links in most networks and were consistently less generalized than other pollinator species. The only exception was non-bee Hymenoptera from networks in the arid zone, which had more plant partners compared with other climate zones, suggesting that they play an important role in networks within this climate zone. Our results also support individual reports (Cirtwill et al., 2018; Tiusanen et al., 2016) that flies are the most frequent pollinators (relative to other insect taxa) in polar zone plant-pollinator networks. Bees are generally considered the most important pollinators globally, but knowledge of other pollinators is limited (Ollerton, 2017; Wardhaugh, 2015). We show that non-bee taxa often play central roles in plant-pollinator networks, especially in continental and polar climate zones, which should stimulate greater research effort into understanding the relative importance of non-bee pollinator taxa across a representative range of ecosystems globally (Willcox et al., 2017).

Our results show that pollinator species generalism in plant-pollinator networks varies between climate zones. For example, non-syrphid Diptera had the greatest proportion of network links in polar zone networks, but most of these species had relatively few plant partners. In contrast, Syrphidae had a much lower proportion of links in polar networks relative to other taxa but were more generalized, having a greater number of plant partners when network size was accounted for. Relative to other climate zones, bees had the highest number of plant partners in tropical zone networks and were also more generalist in these networks relative to all other pollinator taxa (Figure 2). Two-thirds of the networks we analysed included *Apis mellifera*, a bee species recognized as invasive in most of its introduced range (Supporting Information Figure S2). An additional area for further research is to use similar analytical approaches to understand how network roles of invasive species (both plants and pollinators) compare in different climate zones (Parra-Tabla & Arceo-Gómez, 2021; Santos et al., 2012).

These differences among taxa contribute further insight into discussion over whether specialization in interaction networks is higher, equal or lower in tropical regions compared with other regions (Ollerton, 2012; Ollerton & Cranmer, 2002; Schleuning et al., 2012; Vizentin-Bugoni et al., 2018). Studies of other



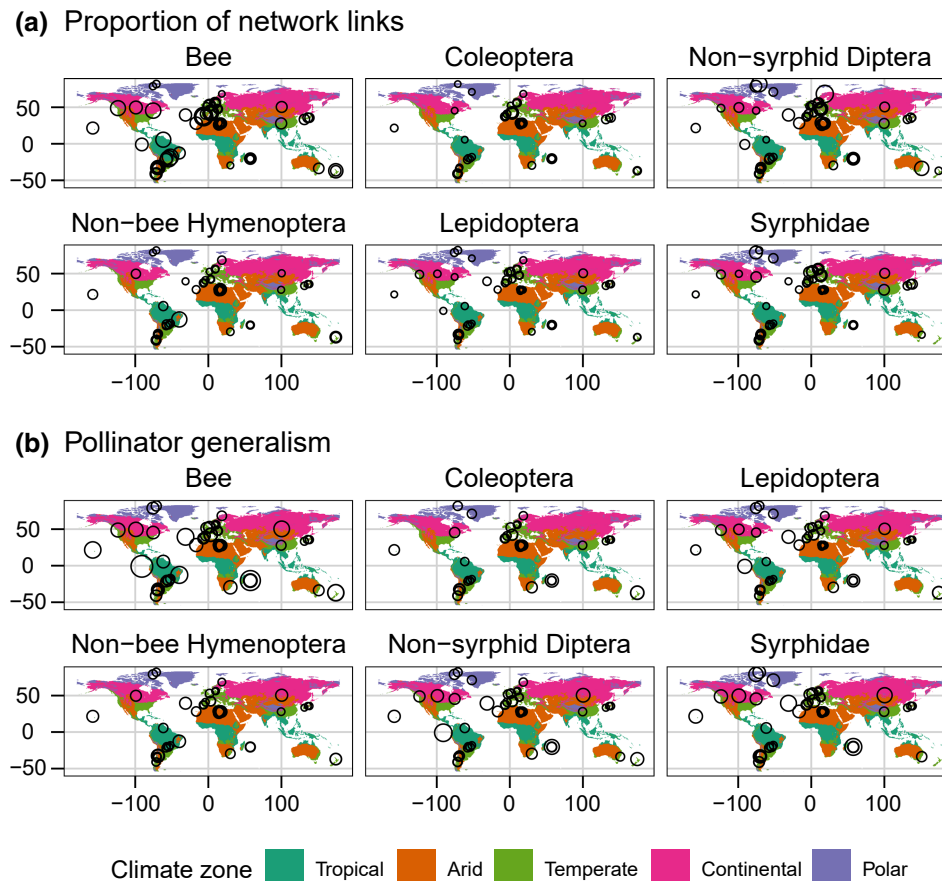
**FIGURE 2** Proportion of links within networks and normalised generalism (standardised by containing estimates to equal network size) for each pollinator taxonomic group, in each climate zone. Solid dots are posterior mean estimates and error bars denote  $\pm 95\%$  credible intervals. Raw data are jittered and plotted behind the model estimates. The y-axis for pollinator generalism is plotted on the log-10 scale to improve interpretability.

functional groups, such as dung beetles (Frank et al., 2018) and parasitoids (Galiana et al., 2019), have found the reverse for generalism for networks, which tends to be lower in the tropics, and different tropical regions might exhibit different generalism patterns (Dugger et al., 2019). Our supplementary analysis comparing the predictive effect of climate zone versus latitude showed that latitude is unlikely to be a key explanatory factor for the differences we found here (Supporting Information Figure S3; Table S3). Although all climate zones support different combinations of interacting plants and pollinators, plant–pollinator networks in tropical and arid zones might support more distinct sets of interactions relative to other climate zones. Plant richness per se is also unlikely to be driving this pattern, because we found no difference in plant richness within networks among climate zones (Supporting Information Figure S1). The relative importance of plants versus pollinators in terms of network structure might also shift from tropical to temperate climates (Sakai et al., 2016). Hence, focusing on specific taxa (e.g., bees only) in pollination studies might result in strong biases about community-level interactions. The variation between taxa network roles among different climate zones could also be reflective of the multiple functional roles that pollinators play in ecosystems; for example, many pollinating flies and wasps are also predators or parasites, and pollinating moths and butterflies are also herbivores (Saunders et al., 2016). An important area for future research is to integrate knowledge of the trade-offs and synergies between species interactions that affect plant reproduction in a given community (pollination, herbivory, predation and parasitism) with traditional plant–pollinator network matrices. For example, we are familiar with specialized examples of plant–insect interactions that shift between positive and negative (e.g.,

nursery pollination systems; Dufaÿ & Anstett, 2003), but knowledge of community-level effects of shifting interactions between plant and insect species over time is limited.

Many ecological network metrics are highly correlated or redundant. To avoid “metric hacking”, we focused on two simple metrics that were most relevant to our study aim and combined network analysis with other statistical methods appropriate to answer our question. Our focal metrics (species generalism and proportion of links) represent dietary breadth and are particularly relevant to identifying functional roles of pollinators (Coux et al., 2016; Tylianakis et al., 2010). Previous work on seed dispersal networks has shown that the network role (degree) of a species is linked to the length of fruiting phenology (González-Castro et al., 2012). It is possible that our results reflect a similar relationship between the proportion of links for each pollinator group and the length of flowering seasons across different climate zones, and this relationship could be examined further with more detailed phenological data across different climate zones. There is also scope for future research to investigate how climate influences other network attributes. For example, exploration of the link between network metrics, such as modularity, and ecosystem function and services is an emerging area of research, with potential to inform conservation and land management outcomes (Saunders & Rader, 2019).

Our finding that climate zone is a strong driver of species network roles provides valuable information about how environmental conditions influence community-level interactions. Although previous work has discussed the influence of climate on plant–pollinator networks (Schleuning et al., 2012), these relationships have mostly been tested using temporal or annual temperature data. Yet climate is a multivariate space encompassing more than temperature



**FIGURE 3** Global maps showing the proportion of links and normalised generalism (standardised by containing estimates to equal network size) for each pollinator taxonomic group within climate zones. Circles represent individual networks. Circle size is relative to the actual proportion of links (a) and the model estimated normalised generalism (b) for each pollinator group within each network.

fluctuations. Köppen–Geiger climate zone classifications are extremely useful for aggregating complex climate gradients and vegetation patterns into simple, ecologically meaningful categories (Beck et al., 2018). We used these broad climate zone classifications here to initiate further exploration of how the multivariate climate space influences network structure and the functional roles of pollinator insect species. We now require additional networks across underrepresented regions of the world to test whether the subcategories of the Köppen–Geiger classifications can better predict more complex environmental variation in plant–pollinator community interactions.

#### AUTHOR CONTRIBUTIONS

Manu E. Saunders conceived the idea and led the study; Liam K. Kendall and Jamie R. Stavert conducted the data analyses; all authors collated datasets and contributed to study design and manuscript development.

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#### CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

All data, code and analyses are available at: <https://github.com/JoseBSL/Geonet>.

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## REFERENCES

- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46.
- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9, 683–693.
- Bartomeus, I., Park, M. G., Gibbs, J., Danforth, B. N., Lakso, A. N., & Winfree, R. (2013). Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecology Letters*, 16, 1331–1338.
- Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, E. F. (2018). Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data*, 5, 180214.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57, 289–300.
- Bryant, C., Wheeler, N. R., Rubel, F. & French, R. H. (2017). kgc: Koeppen-Geiger Climatic Zones.
- Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80, 1–28.
- Byers, D. L. (2017). Studying plant-pollinator interactions in a changing climate: A review of approaches. *Applications in Plant Sciences*, 5, 1700012.
- Chamberlain, S. A., & Szöcs, E. (2013). Taxize: Taxonomic search and retrieval in R. *F1000Research*, 2, 191.
- Cirtwill, A. R., Roslin, T., Rasmussen, C., Olesen, J. M., & Stouffer, D. B. (2018). Between-year changes in community composition shape species' roles in an Arctic plant-pollinator network. *Oikos*, 127, 1163–1176.
- Coux, C., Rader, R., Bartomeus, I., & Tylanakis, J. M. (2016). Linking species functional roles to their network roles. *Ecology Letters*, 19, 762–770.
- Dufaÿ, M., & Anstett, M.-C. (2003). Conflicts between plants and pollinators that reproduce within inflorescences: Evolutionary variations on a theme. *Oikos*, 100, 3–14.
- Dugger, P. J., Blendinger, P. G., Böhning-Gaese, K., Chama, L., Correia, M., Dehling, D. M., Emer, C., Farwig, N., Fricke, E. C., Galetti, M., García, D., Grass, I., Heleno, R., Jacomassa, F. A. F., Moraes, S., Moran, C., Muñoz, M. C., Neuschulz, E. L., Nowak, L., ... Schleuning, M. (2019). Seed-dispersal networks are more specialized in the Neotropics than in the Afrotropics. *Global Ecology and Biogeography*, 28, 248–261.
- Elberling, H., & Olesen, J. M. (1999). The structure of a high latitude plant-flower visitor system: The dominance of flies. *Ecography*, 22, 314–323.
- Forrest, J. R. K. (2015). Plant-pollinator interactions and phenological change: What can we learn about climate impacts from experiments and observations? *Oikos*, 124, 4–13.
- Frank, K., Krell, F.-T., Slade, E. M., Raine, E. H., Chiew, L. Y., Schmitt, T., Vairappan, C. S., Walter, P., & Blüthgen, N. (2018). Global dung webs: High trophic generalism of dung beetles along the latitudinal diversity gradient. *Ecology Letters*, 21, 1229–1236.
- Gabry, J., & Mahr, T. (2017). *Bayesplot: Plotting for Bayesian models*. R Package Version, 1.
- Galiana, N., Hawkins, B. A., & Montoya, J. M. (2019). The geographical variation of network structure is scale dependent: Understanding the biotic specialization of host-parasitoid networks. *Ecography*, 42, 1175–1187.
- González, A. M. M., Dalsgaard, B., Ollerton, J., Timmermann, A., Olesen, J. M., Andersen, L., & Tossas, A. G. (2009). Effects of climate on pollination networks in the West Indies. *Journal of Tropical Ecology*, 25, 493–506.
- González-Castro, A., Yang, S., Nogales, M., & Carlo, T. A. (2012). What determines the temporal changes of species degree and strength in an oceanic Island plant-disperser network? *PLoS One*, 7(7), e41385. <https://doi.org/10.1371/journal.pone.0041385>
- Goodwin, E. K., Rader, R., Encinas-Viso, F., & Saunders, M. E. (2021). Weather conditions affect the visitation frequency, richness and detectability of insect flower visitors in the Australian alpine zone. *Environmental Entomology*, 50, 348–358.
- Halsch, C. A., Shapiro, A. M., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Forister, M. L. (2021). Insects and recent climate change. *PNAS*, 118, e2002543117.
- Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters*, 12, 184–195.
- Inouye, D. W., & Pyke, G. H. (1988). Pollination biology in the Snowy Mountains of Australia: Comparisons with montane Colorado, USA. *Australian Journal of Ecology*, 13, 191–205.
- Janes, J. K., Li, Y., Keeling, C. I., Yuen, M. M. S., Boone, C. K., Cooke, J. E. K., Bohlmann, J., Huber, D. P. W., Murray, B. W., Coltman, D. W., & Sperling, F. A. H. (2014). How the mountain pine beetle (*Dendroctonus ponderosae*) breached the Canadian Rocky Mountains. *Molecular Biology and Evolution*, 31, 1803–1815.
- Kandlikar, G. S., Gold, Z. J., Cowen, M. C., Meyer, R. S., Freise, A. C., Kraft, N. J. B., Moberg-Parker, J., Sprague, J., Kushner, D. J., & Curd, E. E. (2018). Ranacapa: An R package and shiny web app to explore environmental DNA data with exploratory statistics and interactive visualizations. *F1000Research*, 7, 1734. <https://doi.org/10.12688/f1000research.16680.1>
- Knight, T. M., Ashman, T.-L., Bennett, J. M., Burns, J. H., Passonneau, S., & Steets, J. A. (2018). Reflections on, and visions for, the changing field of pollination ecology. *Ecology Letters*, 21, 1282–1295.
- Kruschke, J. (2014). *Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan*. Academic Press.
- Lawson, D. A., & Rands, S. A. (2019). The effects of rainfall on plant-pollinator interactions. *Arthropod-Plant Interactions*, 13, 561–569.
- Mayer, C., Adler, L., Armbruster, S. W., Dafni, A., Eardley, C., Huang, S.-Q., Kevan, P. G., Ollerton, J., Packer, L., Ssymank, A., Stout, J. C., & Potts, S. G. (2011). Pollination ecology in the 21st century: Key questions for future research. *Journal of Pollination Ecology*, 3, 8–23.
- McCabe, L. M., Colella, E., Chesshire, P., Smith, D., & Cobb, N. S. (2019). The transition from bee-to-fly dominated communities with increasing elevation and greater forest canopy cover. *PLoS One*, 14, e0217198.
- Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, 10, 710–717.
- Moles, A. T., & Ollerton, J. (2016). Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea? *Biotropica*, 48, 141–145.
- Oksanen, J. (2015). *Multivariate analysis of ecological communities in R: Vegan Tutorial*. 43.
- Olesen, J. M., & Jordano, P. (2002). Geographic patterns in plant-pollinator mutualistic networks. *Ecology*, 83(9), 2416–2424.
- Ollerton, J. (2012). Biogeography: Are tropical species less specialised? *Current Biology*, 22, R914–R915.
- Ollerton, J. (2017). Pollinator diversity: Distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics*, 48, 353–376.
- Ollerton, J., & Cranmer, L. (2002). Latitudinal trends in plant-pollinator interactions: Are tropical plants more specialised? *Oikos*, 98, 340–350.
- Park, I. W., & Mazer, S. J. (2019). Climate affects the rate at which species successively flower: Capturing an emergent property of regional floras. *Global Ecology and Biogeography*, 28, 1078–1092.
- Parra-Tabla, V., & Arceo-Gómez, G. (2021). Impacts of plant invasions in native plant-pollinator networks. *New Phytologist*, 230, 2117–2128.
- Petanidou, T., Kallimanis, A. S., Lazarina, M., Tschoulin, T., Devalez, J., Stefanaki, A., Hanlidou, E., Vujčić, A., Kaloveloni, A., & Sgardelis, S. P. (2018). Climate drives plant-pollinator interactions even along small-scale climate gradients: The case of the Aegean. *Plant Biology*, 20(Suppl 1), 176–183.

- R Core Team. (2013). *R foundation for statistical computing*. Author.
- Rader, R., Reilly, J., Bartomeus, I., & Winfree, R. (2013). Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Biology*, *19*, 3103–3110.
- Rech, A. R., Dalsgaard, B., Sandel, B., Sonne, J., Svenning, J.-C., Holmes, N., & Ollerton, J. (2016). The macroecology of animal versus wind pollination: Ecological factors are more important than historical climate stability. *Plant Ecology & Diversity*, *9*, 253–262.
- Sakai, S., Metelmann, S., Toquenaga, Y., & Telschow, A. (2016). Geographical variation in the heterogeneity of mutualistic networks. *Royal Society Open Science*, *3*, 150630.
- Santos, G. M. M., Aguiar, C. M. L., Genini, J., Martins, C. F., Zanella, F. C. V., & Mello, M. A. R. (2012). Invasive Africanized honeybees change the structure of native pollination networks in Brazil. *Biological Invasions*, *14*, 2369–2378.
- Saunders, M. E., Peisley, R. K., Rader, R., & Luck, G. W. (2016). Pollinators, pests, and predators: Recognizing ecological trade-offs in agroecosystems. *Ambio*, *45*, 4–14.
- Saunders, M. E., & Rader, R. (2019). Network modularity influences plant reproduction in a mosaic tropical agroecosystem. *Proceedings of the Royal Society B*, *286*, 20190296.
- Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G. K. S., Bazarian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D. M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C. N., Kreft, H., Morris, R. J., ... Blüthgen, N. (2012). Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology*, *22*, 1925–1931.
- Ssymank, A., Kearns, C. A., Pape, T., & Thompson, F. C. (2008). Pollinating flies (Diptera): A major contribution to plant diversity and agricultural production. *Biodiversity*, *9*, 86–89.
- Tiusanen, M., Hebert, P. D. N., Schmidt, N. M., & Roslin, T. (2016). One fly to rule them all—muscid flies are the key pollinators in the Arctic. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20161271.
- Traveset, A., Tur, C., Trøjelsgaard, K., Heleno, R., Castro-Urgal, R., & Olesen, J. M. (2016). Global patterns of mainland and insular pollination networks. *Global Ecology and Biogeography*, *25*, 880–890.
- Trøjelsgaard, K., & Olesen, J. M. (2013). Macroecology of pollination networks. *Global Ecology and Biogeography*, *22*, 149–162.
- Tylianakis, J. M., Lalibertè, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, *143*, 2270–2279.
- Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, *27*, 1413–1432. <https://doi.org/10.1007/s1122-016-9696-4>
- Vizentin-Bugoni, J., Maruyama, P. K., de Souza, C. S., Ollerton, J., Rech, A. R., & Sazima, M. (2018). Plant-pollinator networks in the tropics: A review. In W. Dáttilo & V. Rico-Gray (Eds.), *Ecological networks in the tropics: An integrative overview of species interactions from some of the Most species-rich habitats on earth* (pp. 73–91). Springer International Publishing.
- Wardhaugh, C. W. (2015). How many species of arthropods visit flowers? *Arthropod-Plant Interactions*, *9*, 547–565.
- Willcox, B. K., Aizen, M. A., Cunningham, S. A., Mayfield, M. M., & Rader, R. (2017). Deconstructing pollinator community effectiveness. *Current Opinion in Insect Science*, *21*, 98–104.
- Stange, E. E., & Ayres, M. P. (2010). Climate Change Impacts: Insects. In: *Encyclopedia of Life Sciences (ELS)*. John Wiley & Sons, Ltd: Chichester.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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