**Climate moderates composition of plant-pollinator networks**

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**Abstract**

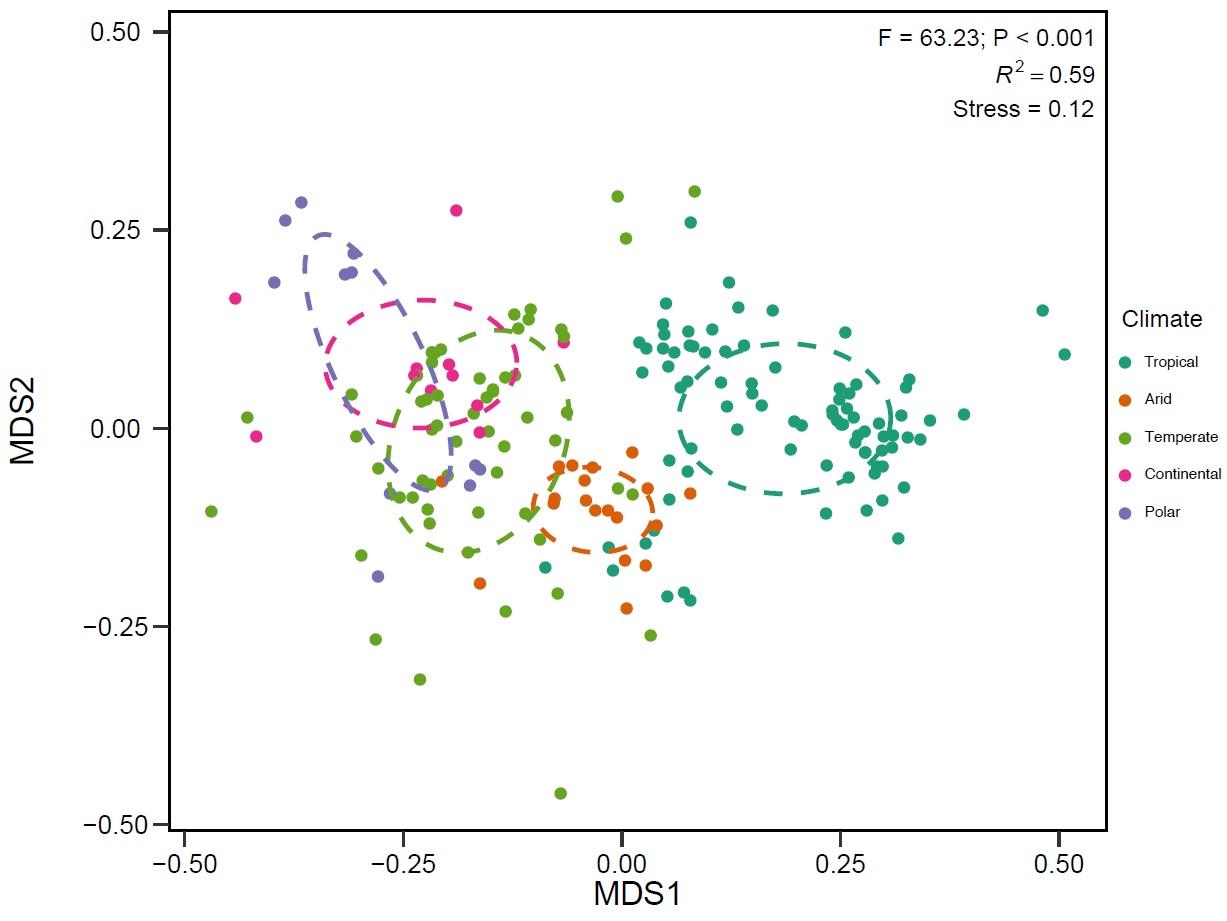
A major knowledge gap exists on how environmental factors drive composition of pollinator communities across large scales1,2. Climate is thought to have a strong influence on pollinator community composition because insects have limited ability to regulate body temperature and are thus more sensitive to temperature extremes3. However, there is very little evidence of how climate drives composition of plant-pollinator interactions at the global scale4. Here we analyse 184 plant-pollinator networks from all five major climate zones to show that climate drives the relative proportion of flower-visiting insects in pollination networks. Our global analysis reveals that ecological generalism5 of pollinator taxa varies across climate zones. Relative to other taxa, non-syrphid Diptera had the greatest proportion of links in polar climates, while bees and syrphid flies dominated networks in the continental zone. The effect of climate zone explained more variation in pollinator community composition than latitude, highlighting the ecological nuances that are overlooked in the latitudinal gradient debate6. Our analysis provides substantial advances in knowledge of how response diversity influences community composition at the global scale, and supports the need for greater research effort to understand the vulnerability of plant-pollinator interactions to global environmental change.

**Main**

Temperature has a strong influence on plant-pollinator interactions. The activity of flower visiting insects generally increases as ambient temperature rises, and warmer flowers may attract more pollinators7,8. Thermal tolerance varies across 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 have been recorded as the most common flower visitors in some arctic and alpine plant-pollinator networks9,10, as well as at sites with cooler temperatures in other climate zones11. Bees are most abundant and diverse in warm arid regions12, and are generally less active during winter and in cold, inclement weather. This response diversity among taxa provides buffering effects for ecosystem function and delivery of ecosystem services13,14. Yet evidence of how local response diversity scales up to general biogeographic patterns in plant-pollinator networks is lacking.

Historically, plant-pollinator network studies have largely been localised, descriptive and focused on documenting diversity and interactions15. The small number of studies that have identified effects of climate on plant-pollinator networks have been largely speculative, based on simulated data, or from local or regional systems16,17. Large-scale analyses investigating global patterns in plant-pollinator networks have focused on broader patterns in network metrics and species richness, with limited discussion of taxonomic identity or community composition18–20. Where biogeographical gradients were considered, the focus has traditionally been on testing the effects of latitude on network interactions21,22. However, latitude is a poor proxy for the environmental nuances that drive community-level interactions, and historical focus on the latitudinal gradient as a predictor has limited our understanding of global-scale patterns of ecosystem function6. Here we provide empirical evidence, for the first time, that climate zone moderates variation in the relative proportions of insect taxa in plant-pollinator networks.

We conducted an exhaustive search of peer-reviewed literature and research theses published online and collated 184 community networks linking flowering plants to insect pollinators or flower visitors (see Methods). Hereafter, we refer to these as plant-pollinator networks. At the global scale, we found that Köppen climate zone drives compositional dissimilarities between plant-pollinator interactions (PERMANOVA, F(4,179) = 63.23; *R2* = 0.59; *P* < 0.001; Figure 1). In particular, the composition of tropical and arid zone plant-pollinator networks are distinct from each other and from all other climate zones (SI: Table S1). The composition of temperate zone plant-pollinator networks is strongly dissimilar from polar zone networks, while networks in the continental climate zone are weakly dissimilar from those in temperate and polar climate zones. Dispersion of plant-pollinator interaction composition is similar across all climate zones (all pairwise Tukey’s HSD *P* > 0.05).

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**Figure 1.** NMDS ordination of plant-pollinator interaction composition in each climate zone.

One dipteran family (Syrphidae) and one hymenopteran family (Apidae) had over one-quarter (28%) of total links across all networks (Table 1). To explore taxonomic differences in pollinator generalism (i.e. absolute and proportional ecological generalism5) across climate zones, we used Bayesian generalised linear mixed effects models (see Methods) and grouped pollinator species by functional groupings that reflect key pollinator taxa: Syrphidae, non-syrphid Diptera, Bees, non-bee Hymenoptera, Lepidoptera, Coleoptera. We accounted for variation among networks by including an offset term in the absolute generalism model (log-transformed total number of plant-pollinator links within each network), and a random effect of “network” nested within “study” in both models, to account for the dependent data structure of multiple networks within studies. The interaction between ‘pollinator taxa : climate zone’ was the best predictor for pollinator generalism (Bayesian *R2*: 0.265, ΔWAIC: -592.62).

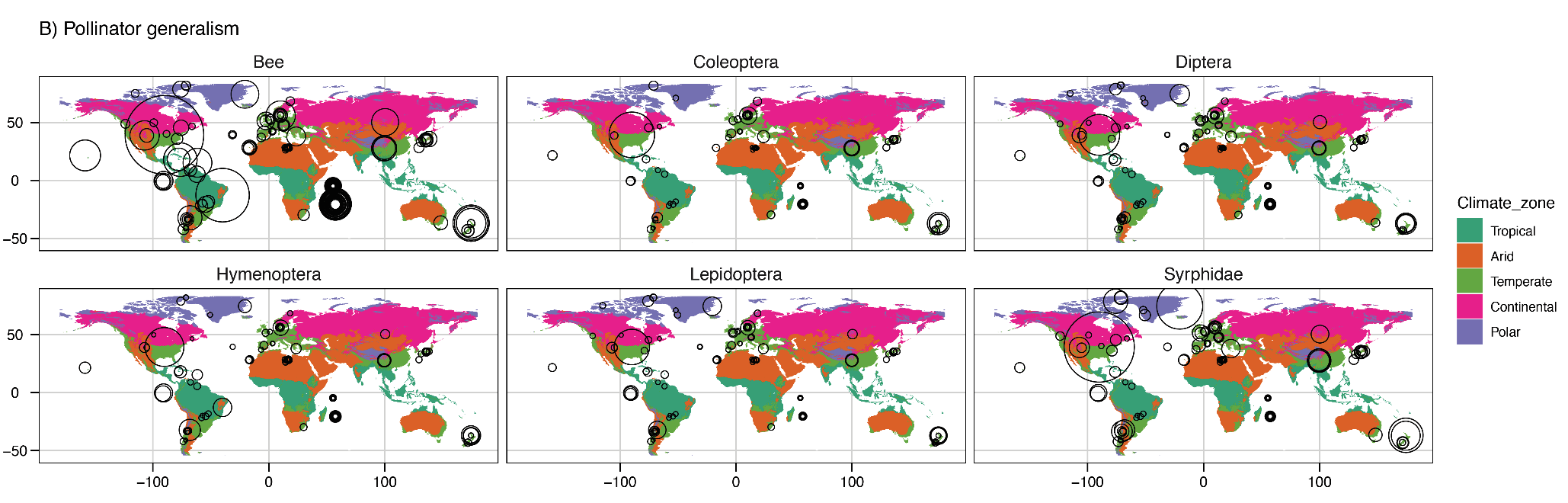
**Table 1: Top ten pollinator families with the greatest proportion of total links (n = 44,468) across all networks. See S1 Data for full list.**

|  |  |
| --- | --- |
| **Family** | **Proportion of total links** |
| Syrphidae | 0.142 |
| Apidae | 0.134 |
| Halictidae | 0.074 |
| Tachinidae | 0.045 |
| Andrenidae | 0.039 |
| Megachilidae | 0.037 |
| Muscidae | 0.037 |
| Bombyliidae | 0.022 |
| Crabronidae | 0.022 |
| Vespidae | 0.021 |

Relative to other pollinator taxa, bees had the greatest proportion of links in tropical, temperate and continental climate zones (Figure 2A). In the arid zone, non-bee Hymenoptera had similar levels of proportional generalism to bees. In the polar zone, non-syrphid Diptera had the highest level of proportional generalism (Figure 2A). Across all climate zones, except polar, we found that bees showed greater absolute generalism (i.e. visited more plant partners) compared with other pollinator taxa (Figure 2B). However, compared to other climate zones, bees visited more plant species in the tropical climate zone (Figure 3). Syrphidae had the highest proportion of total links across all networks, and recorded the highest number of plant partners in polar zones, but did not show the highest proportional generalism in any climate zone (Figure 2). We separated Syrphidae from other Diptera, because they are common and recognisable pollinators, were the most common fly visitors in our dataset, and because analysing all data at family level was not possible, due to the high number of zeros across most insect families. Therefore, this result is likely an artefact of our groupings, not an indication that Syrphidae are not important pollinators.

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**Figure 2.** A) Model-estimated proportion of network links (proportional generalism) and (B) species-level absolute generalism for each pollinator taxonomic group, in each climate zone. Dots are posterior mean estimates and error bars denote ± 95% credible intervals. Predictions of pollinator generalism are constrained to equal network size (100 plant-pollinator links).

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**Figure 3** Global map of absolute generalism for each pollinator taxonomic group within climate zones. Circles represent individual networks. Circle size is relative to the model estimates for pollinator generalism (number of plant partners) for each pollinator taxonomic group within each network.

There are multiple ways to measure generalisation (cf. specialisation) in plant-pollinator networks5,23. We focused on comparing absolute and proportional ecological generalism, which are quantitative representations of network linkages. Our results highlight how focusing only on actual numbers of links in network studies overlooks important community-level information about plant-pollinator communities. For example, Syrphidae had the highest number of plant partners in polar climates, and the greatest proportion of network links in continental climates (Figure 2). Similarly, bees visited the most plant species in tropical zones, but had the greatest proportion of network links in continental zones (higher than Syrphidae). Non-syrphid Diptera were recorded on fewer plant partners, in absolute terms, across all networks; but, relative to other taxa and other climate zones, they were the most dominant pollinator in polar zones (Figure 2). This shows that, for pollinators, actual number of plant species they are observed visiting is not necessarily indicative of their relative importance in the system.

Our results provide empirical evidence that non-syrphid flies are relatively more common as pollinators in polar zones, and bees are relatively more common as pollinators in continental and temperate climate zones. Our analysis is based on the most comprehensive set of insect pollinator networks collated thus far. Moreover, we separate insect pollinators into functional groupings to identify response diversity among taxa, whereas other studies have largely considered overall patterns for all pollinators, often grouping birds and insects together. We also focus on relative proportions of observed pollinator taxa, rather than comparing network structure or diversity metrics, which can be influenced by sampling effort or network size. We are confident that our results are not influenced by latitude, which has received much attention as a potential driver of plant-pollinator interactions6,21. We tested the effect of latitude on our data (see Methods), but both the proportion of network links and species-level generalism were better explained by the climate zone model than the latitude model (proportion of network links ΔWAIC: -47.71; species-level generalism ΔWAIC: -34.15). Furthermore, although previous work has discussed the influence of climate on plant-pollinator networks21, relationships were tested using temporal or annual temperature data. Yet climate is a multivariate space encompassing more than just temperature fluctuations. Köppen climate zone classifications are extremely useful for aggregating complex climate gradients and vegetation patterns into simple, ecologically meaningful categories24. As we show here, climate zone is a more useful predictor of insect community composition than proxy variables like latitude. More networks across other parts of the world are needed to test whether the sub-categories of the Köppen classifications identify more complex plant-pollinator interactions.

Climate change affects plant-pollinator networks through phenological mismatches, with potentially devastating effects on ecosystem function17. Understanding how composition of plant-pollinator networks varies across climate zones is a key first step to developing detailed analyses that identify how climate change affects species-level interactions at local and regional scales.

**Methods**

We collated 184 plant-pollinator networks from 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. Although it is likely we have missed some networks, we are confident our analysis is more comprehensive than previous global network analyses, because we cover all climate zones and sourced new networks that have not been included in previous studies. We only used insect pollinator networks that recorded multiple taxonomic orders. All networks were analysed as binary networks, to address differences in sampling methods and effort among networks. We identified the Köppen climate zone for each network based on the spatial coordinates provided with each dataset. All data, code and analyses are available at <https://github.com/JoseBSL/Geonet>.

We tested whether the composition of plant-pollinator interactions varied among climate zones by calculating pairwise Raup-Crick dissimilarity25 between networks using the *vegan* package (v.2.5-3)26. To account for varying network sizes, we computed the Raup-Crick dissimilarity using a null model, repeated for 999 iterations, to control for differing species’ richness among networks. Then, we assessed differences in the composition of plant-pollinator interactions among climate zones using a permutational analysis of variance (PERMANOVA)27. 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 Honest-Significant Difference (HSD) tests. We computed pairwise differences in the composition of plant-pollinator interactions between each climate zone using a pairwise PERMANOVA28. To account for multiple comparisons, *P*-values were adjusted using the false discovery rate (FDR) method29. Finally, we visualised differences in plant-pollinator interactions among networks in two-dimensional space with non-metric multidimensional scaling (NMDS) ordination.

To test whether climate zone influenced how pollinator taxonomic groups interacted within their networks, we focused on the following functional groupings: bees, non-bee Hymenoptera, Coleoptera, Lepidoptera, non-Syrphid Diptera, and Syrphidae. We separated bees from non-bee Hymenoptera, and syrphid flies (Syrphidae) from non-syrphid Diptera, because bees and syrphid flies are the most commonly-recorded pollinator taxa from their respective orders. We focus on two aspects of ecological generalism: proportional generalism and absolute generalism. Proportional generalism is the proportion of links to different plant species for each pollinator taxonomic group; we calculated this as the sum of unique links within each pollinator group, divided by the total sum of unique links within each network. We defined absolute generalism of a pollinator as the number of links between each pollinator species to different plant species within a network. To estimate the proportional generalism (i.e. relative proportion of links) and absolute generalism (i.e. number of links per species) for each pollinator group within each climate zone, we specified Bayesian generalised linear mixed effects models using the *brms* package (version 2.5.0)30. These models were fit 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 species links within each network. Fixed effects were “pollinator taxa” (categorical), “climate zone” (categorical) and the two-way “pollinator order” : “climate zone” interaction. To account for differences in network size in the species generalism model, we included an offset term of the log-transformed total number of plant-pollinator links within each network. 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. Pairwise differences between climates and pollinator group for either proportion of network links or pollinator species generalism were considered significant when the 95% highest density intervals did not overlap zero (see Supplementary Information, Table SX)31. We set weakly informative priors and manipulated Δ and maximum tree depth to reduce divergent transitions. We undertook posterior predictive checks visually using *bayesplot* (v1.6.0)32 and *Shinystan* (v.2.5.0)33. All data analyses were undertaken in R (v.3.5.1, R Core Team 2018).

**Author Contributions**

MES conceived the idea and led the study; LK, JB and JS collated datasets, wrote the code and conducted the analysis; all authors contributed to study design and manuscript preparation.

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**Data availability**

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

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