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RESEARCH

Assessing the relationship between latitude and plant-pollinator network specialization

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Background: Research investigating the relationship between latitude and network specialization plant-pollinator networks present conflicting results. While some studies indicate a positive link between latitude and network specialization, particularly in tropical regions, others suggest contradictory trends, with specialization declining towards lower latitudes. These studies underscore the intricate nature of ecological specialization in plant-pollinator networks and the need for further studies in this field to gain a more nuanced understanding of the underlying mechanisms driving these patterns. In this study, we explore the relationship between plant-pollinator network specialization and latitude using a global dataset comprising 93 plant-pollinator networks.
Results: Our analysis revealed a significant relationship with latitude mostly in the Southern Hemisphere, particularly concerning metrics such as connectance and nestedness. However, notably, we found no association with H2, a metric immune to the size, shape, or sampling effects of the network and considered highly suitable for measuring network specialization in both Hemispheres.
Conclusions: The absence of latitudinal trends in network specialization (H2) in both Hemispheres in this study imply that the mutual attraction between plants and pollinators remains relatively stable across various latitudes. Our comparison with prior research highlights the diversity of conclusions regarding how latitude influences plant-pollinator networks. While our results are consistent with certain studies, indicating no direct impact of latitude on network specialization, discrepancies persist.

Keywords: bipartite metrics, latitudinal effects, network specialization, plant-pollinator networks

Introduction

Plant-pollinator interactions play a fundamental role in ecosystem functioning as they facilitate plant reproduction and provide food sources for animals (Blüthgen and Klein 2011; Fontaine et al. 2006; Vizentin-Bugoni et al. 2018). Approximately 88% of angiosperms rely on animals for pollination, while in tropical regions (Ollerton et al. 2011), up to 90% of tree species are dependent on animal interactions for their life cycles, including flower pollination and seed dispersal (Fenner 2000). Insect pollination is predominant, accounting for about 82% of angiosperms, followed by vertebrates at 6%, with wind pollination being less common (Ollerton et al. 2011). Furthermore, one-third of angiosperms fail to produce seeds in the absence of pollinators, and among those that do, 80% of seed production relies on pollinators (Rodger et al. 2021).

There is a growing concern regarding the potential collapse of plant-pollinator networks due to human activities (Lever et al. 2014; Potts et al. 2010; Potts et al. 2016). Various factors, including climate change (Hegland et al. 2009; Rahimi and Jung 2024), land use modifications (Ollerton et al. 2014; Rahimi and Jung 2023), reduced floral diversity, and the proliferation of harmful pathogens and pesticides (Goulson et al. 2015), have been identified as drivers altering plant-pollinator network topology, defined as the species-level pattern of plant-pollinator interactions observed over time (Biella et al. 2017). The degree of specialization within these networks has been highlighted as a factor influencing their susceptibility to anthropogenic pressures (Bond 1994; Carstensen et al. 2018; Dorado et al. 2011; Weiner et al. 2014), Consequently, regions harboring a high number of specialized species within their plant-pollinator networks may be particularly vulnerable to human disturbances compared to other global regions.

The notion that biotic interactions are more pronounced in tropical regions forms the basis of our understanding of global ecological patterns (Brown 2014; Schemske et al. 2009; Wiens 2011). It has been proposed that species-rich tropical communities exhibit higher levels of specialization compared to temperate regions (Jocque et al. 2010). While some investigations into plant-pollinator networks have observed an increase in biotic specialization towards the tropics (Schleuning et al. 2012), others have failed to identify such latitudinal trends after accounting for sampling biases (Ollerton and Cranmer 2002) or variations in plant diversity (Novotny et al. 2006). Thus, the direction of the latitudinal specialization gradient remains a topic of contention. For instance, in a study examining the number of pollinators and flowering plants across different regions, Ollerton and Cranmer (2002) discovered a positive correlation between geographic latitude and the number of pollinators per flower. However, they concluded that plant specialization in lower latitudes is influenced by sampling effort and did not find a clear relationship between latitude and specialization.

In a separate investigation, Olesen and Jordano (2002) analyzed 29 pollinating plant networks across various latitudes and observed a decrease in network connectance (defined as the realized proportion of possible links) with decreasing latitude. Additionally, Ollerton et al. (2006) conducted a study examining plant-pollinator networks in diverse geographical regions, revealing a higher ratio of specialized plants interacting with bees, butterflies, beetles, and fig wasps in tropical forests compared to other latitudes. In their study, plant species were categorized as specialized if 85% of their visitations were attributed to a specific pollinator group (bee, butterfly, fly, bird, and beetle).

Through an assessment of 54 pollination networks on a global scale, Dalsgaard et al. (2013) discovered that modularity (the tendency of a network to form distinct clusters) increases with decreasing latitude. Similarly, Pauw and Stanway (2015) examined 59 plant-pollinator networks worldwide, revealing that network specialization rises with increasing latitude in the Southern Hemisphere but not in the Northern Hemisphere. However, in contrast to expectations, Schleuning et al. (2016) observed a decrease in the degree of specialization in plant-pollinator networks towards lower latitudes across 282 networks. Meanwhile, Liu et al. (2021) investigated the robustness of 79 pollination networks worldwide against species removal scenarios relative to latitude. They found a latitudinal trend only in the robustness of phylogenetic diversity under the specialist first-removal scenario, which increased toward lower latitudes on the mainland but decreased on islands.

Research investigating the correlation between latitude and ecological specialization within pollination networks presents conflicting results. While some studies indicate a positive link between latitude and specialization, particularly in tropical regions, others suggest contradictory trends, with specialization declining towards lower latitudes. These disparities likely stem from variations in research methodologies, geographical coverage, and ecological variables. Overall, these studies underscore the intricate nature of ecological specialization in pollination networks the necessity for a more nuanced comprehension of the underlying mechanisms driving these patterns. In this study, we explore the relationship between plant-pollinator network specialization and latitude using a global dataset comprising 120 plant-pollinator networks. Our findings are then compared with previous studies, offering new insights that contribute to the existing body of knowledge in this field.

Materials and Methods

Database description

Plant-pollinator networks can be categorized into two distinct types: binary and quantitative, depending on the nature of their connections. Binary networks simply denote the presence or absence of interactions between plants and pollinators, whereas quantitative or weighted networks provide information on the quantity and strength of these interactions. This study utilizes weighted networks, as outlined in Table 1. The research involves collecting and analyzing plant-pollinator networks sourced from platforms like https://www.web-of-life.es/ comprising a total of 120 networks, representing the maximum number of qualitative networks available on this website. The latitudinal range of these plant-pollinator networks spans from −41 to 75 degrees. This dataset facilitates the examination of global-scale patterns and dynamics in plant-pollinator interactions, as depicted in Figure 1. The data used in this study include only weighted networks. In these networks, we removed data on reptiles and birds, and we kept only insects as pollinators. Therefore, out of the 120 networks collected, 93 were applicable for use in this study.

Bipartite metrics for assessing dataset

We employed the "networklevel" function from the bipartite package (Dormann et al. 2008) within the Rv4.3

Table 1 The number of binary and quantitative networks in this study

	Quantitative
Number of networks	93
Mean number of species	48.5
Mean number of pollinators	34.4
Mean number of plants	20.2
North Hemisphere	17
South Hemisphere	76

Fig. 1 Geographic locations of quantitative plant-pollinator networks examined in this study.

Table 2 Network-level and group-level bipartite metrics and their definition

Metric	Definition
Connectance	The realized proportion of possible links.
Nestedness	Nestedness temperature of the matrix (0 means cold, i.e. high nestedness, 100 means hot, i.e. chaos).
NODF	Nestedness measure based on overlap and decreasing fill. High values indicate nestedness.
Interaction strength asymmetry	The asymmetry in the interaction strength of two interacting species. Negative values indicate that the plants exert a stronger effect on pollinators.
Specialization asymmetry	Asymmetry (higher vs. lower trophic level) of specialization. Negative values show a higher specialization of the lower trophic level.
Linkage density	Marginal totals-weighted diversity of interactions per species (quantitative).
H2	H2 is a measure of specialization. H2 is between 0 and 1, with 1 indicating maximum specialization.
Web asymmetry	The balance between numbers in the two levels: positive values indicate higher trophic level species, negative more lower-trophic level species.
Links per species	Mean number of links per species (qualitative): sum of links divided by number of species.
Robustness HL	Measure of the robustness of of the system to the loss of higher level (e.g., pollinator).
Robustness LL	Measure of the robustness of the system to the loss of lower level (e.g., plants).

software to assess various attributes of the studied networks. Within this framework, we computed 11 distinct metrics for each network obtained from every network (Table 2). These network metrics encompass the entire network, while additional group-level metrics furnish values for both higher and lower trophic tiers (Blüthgen et al. 2007).

Statistical relationship between latitude and network specialization

Within our dataset, all networks had geographic coordinates, facilitating an exploration of the potential correlation between latitude and network specialization. To determine the relationship between latitude (in North and South Hemispheres) and bipartite metrics, we utilized Spearman's rank correlation in R software.

Results

Dataset characteristics

Table 3 presents the average values of bipartite metrics for the networks under study, offering insights into their structural characteristics and ecological dynamics. The observed low connectance value of 0.24 indicates that the networks have relatively few realized links compared to all possible interactions, suggesting an incomplete utilization of potential connections among species. Additionally, a web asymmetry metric of 0.26 reveals an uneven distribution of species across trophic levels, with a greater abundance of pollinators than plants. With an average of 1.5 links per species, it's evident that species tend to engage in multiple interactions within these networks. The notable nestedness value of 20.1 indicates a structured organization in the networks, with specialist-specialist interactions being more prevalent, particularly in pollination networks. This observation is further supported by the NODF (nestedness measure based on overlap and decreasing fill) value of 36.1, affirming a significant level of nestedness. Despite slight asymmetries in interaction strength and specialization, as indicated by values of 0.04 and −0.03 respectively, the networks demonstrate a moderate level of specialization, with an H2 value of 0.46. Furthermore, both robustness metrics suggest high robustness in interaction patterns between species of pollinators and plants, with values of 0.68 and 0.53 respectively.

Latitude and network specialization

Table 4 presents correlations between bipartite metrics of quantitative networks and latitude, providing insights into how ecological dynamics correlate with geographical location across the Northern and Southern Hemispheres. The study analyzed 93 networks to explore these relationships comprehensively. In the Northern Hemisphere, several significant correlations were observed: connectance showed a positive correlation of 0.34 ($p = 0.17$), while web asymmetry and Links per species displayed weaker positive correlations of 0.15 ($p = 0.54$) and −0.12 ($p = 0.63$), respectively. Strong positive correlations were found for nestedness (0.32, $p = 0.20$), NODF (0.38, $p = 0.12$), interaction strength asymmetry (0.39, $p = 0.12$), and robustness lower level or plants (−0.39, $p = 0.12$). Conversely, the Southern Hemisphere exhibited significant negative correlations for connectance (−0.63, $p < 0.01$), web asymmetry (−0.44, $p < 0.01$), links per species (−0.47, $p < 0.01$), nestedness (0.53, $p < 0.01$), NODF (0.31, $p < 0.01$), and robustness higher level or pollinators (−0.54, $p < 0.01$). Notably, specialization asymmetry showed a significant negative correlation of −0.47 ($p = 0.05$) in the North Hemisphere and −0.10 ($p = 0.39$) in the South Hemisphere.

Table 3 The average value of bipartite metrics for the networks under study

Bipartite metrics	Mean values
Connectance	0.24
Web asymmetry	0.26
Links per species	1.5
Nestedness	20.1
NODF	36.1
Interaction strength asymmetry	0.04
Specialization asymmetry	−0.03
Linkage density	4
H2	0.46
Robustness HL	0.68
Robustness LL	0.53

Abbreviations are seen in Table 2.

Discussion

Our investigation into the relationship between latitude and the analyzed networks revealed notable correlations predominantly in the Southern Hemisphere, specifically concerning metrics like connectance, nestedness, and robustness concerning pollinators. The inverse correlation identified between connectance (r = −0.63) and latitude in the Southern Hemisphere indicates that as latitude increases, there tends to be a reduced realized proportion of potential links, specifically indicating a decline in the overall connections between pollinators and plants within the studied networks. This suggests a lower connectivity between pollinators and plants. This trend may stem from heightened sampling efforts for pollinators within these networks. Web asymmetry (r = −0.44) also showed a negative correlation, albeit weaker than connectance, suggesting an imbalance in plants and pollinators numbers across trophic levels with increasing latitude in the Southern Hemisphere.

Furthermore, we found a positive correlation between the nestedness metric and latitude in the Southern Hemisphere. Lower values of nestedness indicate a higher degree of specialization within the network. This positive statistical relationship suggests that as latitude increases in the Southern Hemisphere, there is decrease in network specialization. Nestedness, as a metric, implies two critical aspects:

Table 4 Correlation between bipartite metrics and latitude in the Northern and Southern Hemisphere

	North Hemisphere	*p*-value	South Hemisphere	*p*-value
Connectance	0.34	0.17	−0.63	< 0.01
Web asymmetry	0.15	0.54	−0.44	< 0.01
Links per species	−0.12	0.63	−0.47	< 0.01
Nestedness	0.32	0.20	0.53	< 0.01
NODF	0.38	0.12	0.31	< 0.01
Interaction strength asymmetry	0.39	0.12	−0.10	0.36
Specialization asymmetry	−0.47	0.05	−0.10	0.39
Linkage density	−0.27	0.29	−0.45	< 0.01
H2	−0.23	0.37	−0.21	0.05
Robustness HL	0.01	0.96	−0.54	< 0.01
Robustness LL	−0.39	0.12	−0.40	< 0.01

Abbreviations are seen in Table 2.

firstly, the presence of a core group of generalist plants and pollinators that are highly interconnected among themselves; secondly, specialists tend to interact predominantly with generalists (Bascompte and Jordano 2007; Bastolla et al. 2009; Burgos et al. 2007). The nested pattern indicates that generalist species interact more frequently with each other, while interactions between specialists are less common. This structure is beneficial because species with fewer connections are less susceptible to extinction, thus enhancing the network's resilience to disturbances. The nested configuration reduces competition, facilitates species coexistence, and bolsters community robustness against random extinctions.

In the Northern Hemisphere, our investigation uncovered diverse connections between latitude and network metrics. The sole notable correlation observed was with Specialization asymmetry ($r = -0.47$) and latitude. This negative correlation indicates an increased specialization at higher trophic level, suggesting that as latitude increases in the Northern Hemisphere, there tends to be a greater specialization towards pollinators within the studied networks. However, the metrics mentioned earlier possess certain limitations and may not provide a clear depiction of network specialization. To address this, Blüthgen et al. (2006) introduced the H2 metric, which mitigates the impacts of abundance, richness, and sampling effects on measuring the level of network specialization. H2 quantifies the deviation of observed interaction frequencies from those expected under neutral conditions, with random interactions yielding an H2 value of zero. Notably, H2 is unaffected by the size, shape, or sampling effects of the network and decreases with increasing specialization. Ranging between 0 and 1, an H2 value of 1 indicates maximum specialization. Regardless of whether the network structure is based on abundance or pollination syndrome, H2 enables the comparison of fundamental specialization among species and networks against random matrices (Blüthgen et al. 2008). The lack of latitudinal trends in network specialization (H2) in both Hemispheres suggests the absence of attractiveness between plants and pollinators remains consistent across different latitudes.

Schleuning et al. (2016) observed that the degree of specialization of plant-pollinator networks decreases towards lower latitudes, while Pauw and Stanway (2015) noted that the specialization of plant-pollinator networks increases with increasing latitude, but only in the Southern Hemisphere. In contrast, our study found no relationship between latitude and network specialization (H2), with some significant relationships observed in the Southern Hemisphere. However, Wang et al. (2024), in their examination of 87 networks, found no effects of latitude on network specialization and nestedness, which aligns with our findings.

Conclusions

Our exploration of the link between latitude and plant-pollinator networks identified notable correlations with bipartite metrics primarily in the Southern Hemisphere. However, the lack of correlation between H2 metric and latitude implies stable network structures irrespective of geographical location. Comparative analysis with previous studies underscored the variability in conclusions regarding the effects of latitude on plant-pollinator networks. While our findings align with some studies, in observing no direct effects of latitude on network specialization, discrepancies remain. These variations emphasize the need for comprehensive, context-specific investigations into the drivers of plant-pollinator network structure. Future research should delve deeper into the underlying mechanisms driving these patterns to inform conservation efforts and enhance our understanding of ecosystem functioning across diverse environments.

Abbreviations
Not applicable.

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Authors' contributions
ER conceptualization, software, validation, formal analysis, investigation, resources, writing - original draft, preparation, and writing - review and editing. CJ methodology, formal analysis, investigation, data curation, visualization, supervision, project administration, and funding acquisition. All authors have read and agreed to the published version of the manuscript.

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The authors declare that they have no competing interests.

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