Report

Specialization of Mutualistic Interaction Networks Decreases toward Tropical Latitudes

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Summary

Species-rich tropical communities are expected to be more specialized than their temperate counterparts [1–3]. Several studies have reported increasing biotic specialization toward the tropics [4–7], whereas others have not found latitudinal trends once accounting for sampling bias [8, 9] or differences in plant diversity [10, 11]. Thus, the direction of the latitudinal specialization gradient remains contentious. With an unprecedented global data set, we investigated how biotic specialization between plants and animal pollinators or seed dispersers is associated with latitude, past and contemporary climate, and plant diversity. We show that in contrast to expectation, biotic specialization of mutualistic networks is significantly lower at tropical than at temperate latitudes. Specialization was more closely related to contemporary climate than to past climate stability, suggesting that current conditions have a stronger effect on biotic specialization than historical community stability. Biotic specialization decreased with increasing local and regional plant diversity. This suggests that high specialization of mutualistic interactions is a response of pollinators and seed dispersers to low plant diversity. This could explain why the latitudinal specialization gradient is reversed relative to the latitudinal diversity gradient. Low mutualistic network specialization in the tropics suggests higher tolerance against extinctions in tropical than in temperate communities.

Results and Discussion

Latitudinal Specialization Gradient
In order to test the direction of the latitudinal specialization gradient, we gathered a global data set comprising a total of

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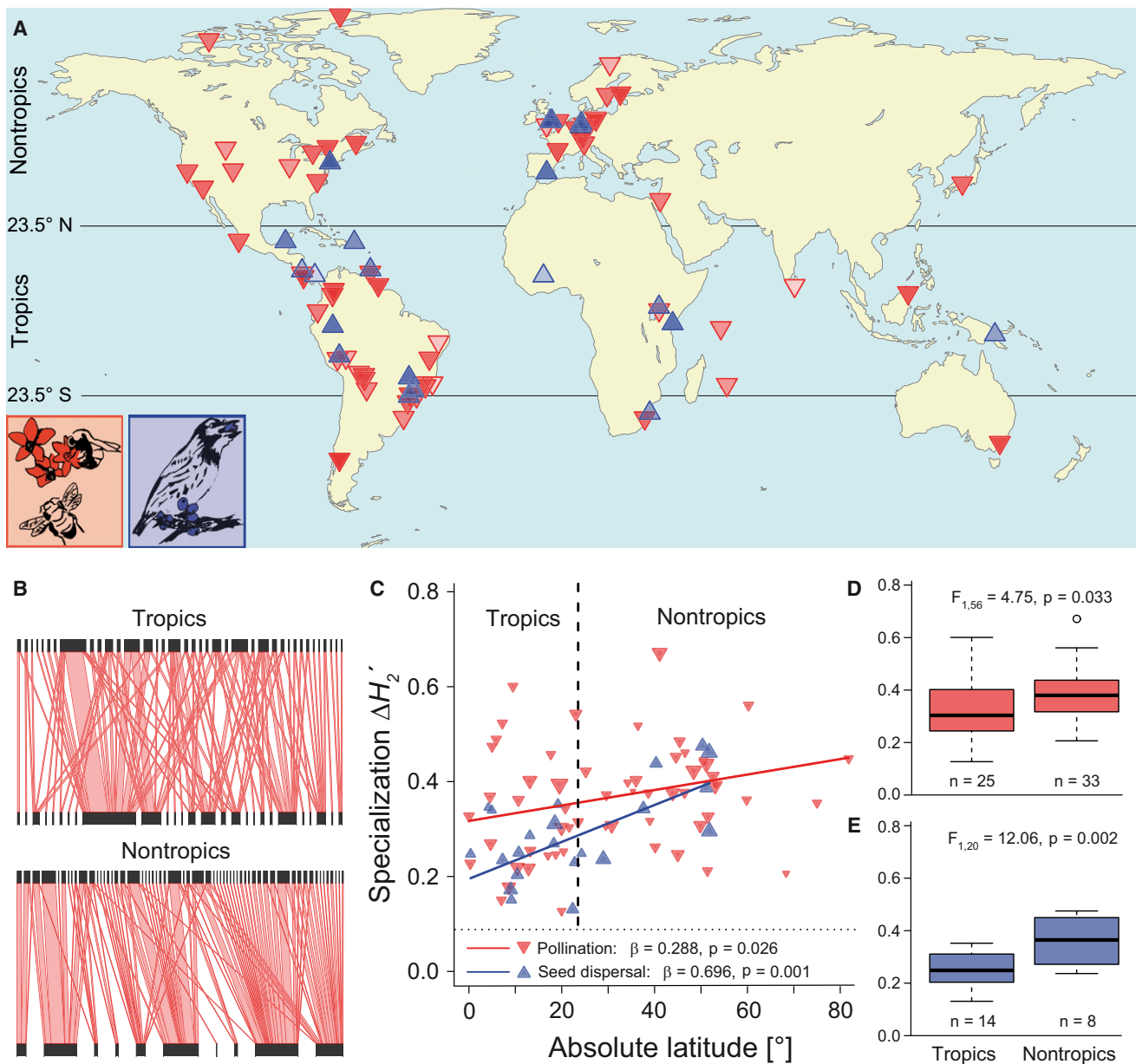*Correspondence: matthias.schleuning@senckenberg.de

Figure 1. Latitudinal Trends in Specialization of Pollination and Seed Dispersal Networks

(A) Global distribution of pollination (red) and seed dispersal (blue) networks. Color intensities of triangles reflect mean network specialization ($\Delta H_2'$) in each study region: color intensity increases with $\Delta H_2'$.

(B) Examples of a generalized pollination network with functionally redundant pollinators (top: $\Delta H_2' = 0.18$, 13°S) and a specialized network with functionally distinct pollinators (bottom: $\Delta H_2' = 0.51$, 51°N). Pollinators are shown at top and plants at bottom of the networks.

(C) The relationship between $\Delta H_2'$ and latitude. Symbol size corresponds to weights by sampling intensity in each region.

(D and E) The difference in $\Delta H_2'$ between tropical ($\leq 23.5°$) and nontropical ($>23.5°$) regions. Thick horizontal lines are medians, boxes indicate 25th and 75th percentiles, whiskers indicate the data range, and the circle is an outlier. See Figure S1 for consistent latitudinal trends in alternative indices of biotic specialization and Table S1 for an overview of the data set.

282 quantitative pollination and seed dispersal networks from 80 sampling regions (58 for pollination, 22 for seed dispersal) ranging in absolute latitude from 0° to 82° (Figures 1A and 1B; see also Table S1 available online). Original studies reported the number of pollinator or seed disperser individuals feeding on a plant species or the number of individuals of a consumer species carrying pollen or seeds of a plant species. Although pollinator and seed disperser species differ in the efficiency of mutualistic services provided to plant species

[12, 13], because original studies did not report interaction efficiencies, we relied on estimates of interaction strength as a surrogate for the mutualistic importance of a consumer species for a plant species [12].

We estimated specialization of the interacting species by assessing patterns of niche partitioning and resource overlap among pollinator or seed disperser species [14–16]. We exploited recent advances in the analysis of quantitative interaction networks that facilitate the comparison of network-wide

Table 1. Minimal Adequate Linear Models for Relationships between Network Specialization $\Delta H_2'$ and Predictor Variables

Predictor	β	t	p
Absolute Latitude (n = 80, R^2 = 0.24, p < 0.001)			
Network type (pollination)	0.122	2.70	0.009
Absolute latitude	0.696	3.40	0.001
Network type (pollination) × absolute latitude	−0.408	−1.67	0.098
Past Climate Stability (n = 80, R^2 = 0.19, p = 0.003)			
Network type (pollination)	0.160	3.09	0.003
Glaciated during LGM	0.072	1.95	0.055
Climate-change velocity	0.555	2.59	0.012
Network type (pollination) × climate-change velocity	−0.564	−2.36	0.021
Contemporary Climate (n = 80, R^2 = 0.27, p < 0.001)			
Network type (pollination)	0.464	1.93	0.057
Growing degree days	−0.456	−4.54	<0.001
Regional Plant Diversity (n = 78, R^2 = 0.13, p = 0.004)			
Network type (pollination)	0.065	2.50	0.015
Regional plant diversity	−0.250	−2.13	0.036
Local Plant Diversity (n = 232, R^2 and p values not applicable for mixed effects models)			
Network type (pollination)	0.058	1.96	0.052
Local plant diversity	−0.233	−2.49	0.014

Models correspond to relationships in Figures 1C, 2, and 3. See Figure S4 for spatial autocorrelation in model residuals and Table S3 for independence of $\Delta H_2'$ from sampling effort and network size. For analyses of latitude, past climate stability, contemporary climate, and regional plant diversity, least squares of linear models were weighted according to the sampling intensity within a region. For analysis of local plant diversity, we accounted for the spatial structure in the data by fitting mixed-effects models with region as random effect. For analyses of latitude, contemporary climate, and regional and local plant diversity, we compared five models (including main and interaction effects of the respective predictor variable and network type), and for analysis of past climate stability, we compared nine models (including main and interaction effects of climate-change velocity and network type plus the additional covariate glaciated during last glacial maximum [LGM]). Minimal adequate models were those with the lowest Akaike information criterion, corrected for small sample size, AICc.

specialization among communities differing in species richness [16]. This approach aims at integrating specialization across individual species to the community level, providing information about functional complementarity and redundancy among species [17]. The specialization metric gives more weight to frequently observed rather than rarely observed species and is weighted by interaction frequencies [16]. This mitigates potential biases in estimates of specialization by giving low weights to accidental observations of consumers on plants with which they are rarely associated.

We found that specialization of both pollination and seed dispersal networks decreased significantly toward tropical latitudes (Figure 1C; Table 1). The same pattern was found in a categorical approach: specialization of both network types was significantly lower in the tropics than in temperate regions (Figures 1D and 1E); this pattern was also found when we restricted the analysis to the New World ($F_{1,44}$ = 4.2, p = 0.047) or the Old World ($F_{1,29}$ = 11.0, p = 0.002). We emphasize that alternative indices of biotic specialization (i.e., connectance, unweighted and weighted generality), as well as guild-specific analyses for plants and animals, showed corresponding latitudinal trends, all confirming a lower degree of specialization in the tropics (Figure S1). This finding contradicts the long-standing assumption that biotic

interactions are more specialized in species-rich tropical communities [1–7], which appears to be reversed for mutualistic interactions involving mobile pollinators and seed dispersers.

Effects of Climate and Plant Diversity

In order to identify climatic factors that may determine the latitudinal specialization gradient, we tested for effects of past climate stability (i.e., climate-change velocity [18]) and contemporary climate on network specialization. To describe the latitudinal gradient in contemporary climate, we focused on cumulative annual temperature [19], which was closely associated with potential and actual evapotranspiration (Figure S2). Both past climate stability and contemporary climate have been postulated to influence biotic specialization [3, 5]. Past climate stability reflects the temporal stability of local communities and the available time for coevolution [20]. Effects of contemporary climate on network specialization might be mediated by an increase in plant diversity in warm climates [21] because high plant diversity reduces relative abundances and densities of resource species. Consistent with optimal foraging theory, reduced densities of resource plants lead to longer search times [22] and constrain the specialization of consumer species [23].

Specialization of seed dispersal networks increased with increasing climate-change velocity (Figure 2A), suggesting that coevolutionary processes have led to more generalized seed dispersal systems in regions with stable climates. This is in line with recent ideas that diffuse coevolutionary processes in mutualistic networks favor trait convergence [24]. On the other hand, specialization of pollination networks was unaffected by climate-change velocity (Figure 2A), possibly due to multiple trade-offs between the benefits of low and high degrees of specialization for the fitness of plants and pollinators that preclude general specialization trends over evolutionary timescales [25]. In contrast, increasing specialization with increasing past climate stability has been shown for plant-hummingbird networks [5]. Reasons for these divergent findings may include strong direct competition between hummingbirds [26] and tight coadaptations between hummingbirds and their food plants [27], leading to increased network specialization where species composition is relatively stable. Effects of past climate fluctuations on hummingbird range-size dynamics may have caused the breakup of coadapting plant-hummingbird species pairs in areas with low past climate stability [5, 20]. Other types of pollinators may be more flexibly linked to their resource plants [28], resulting in weak effects of community stability on network specialization.

Specialization of both pollination and seed dispersal networks consistently decreased with increasing cumulative annual temperature (Figure 2B; Table 1). The effect of contemporary climate on network specialization was much stronger than that of past climate stability (cf. R^2 values in Table 1 and Akaike weights from multipredictor models in Table S2), showing that current conditions, rather than historical processes, have influenced associations among consumer and resource species in mutualistic networks. Consistent with the effect of contemporary climate, network specialization also decreased with increasing plant diversity both regionally and locally (Figures 3A and 3B; Table 1). Differences in plant diversity and associated changes in relative resource abundances provide a generic explanation for decreasing network specialization with decreasing latitude because both regional
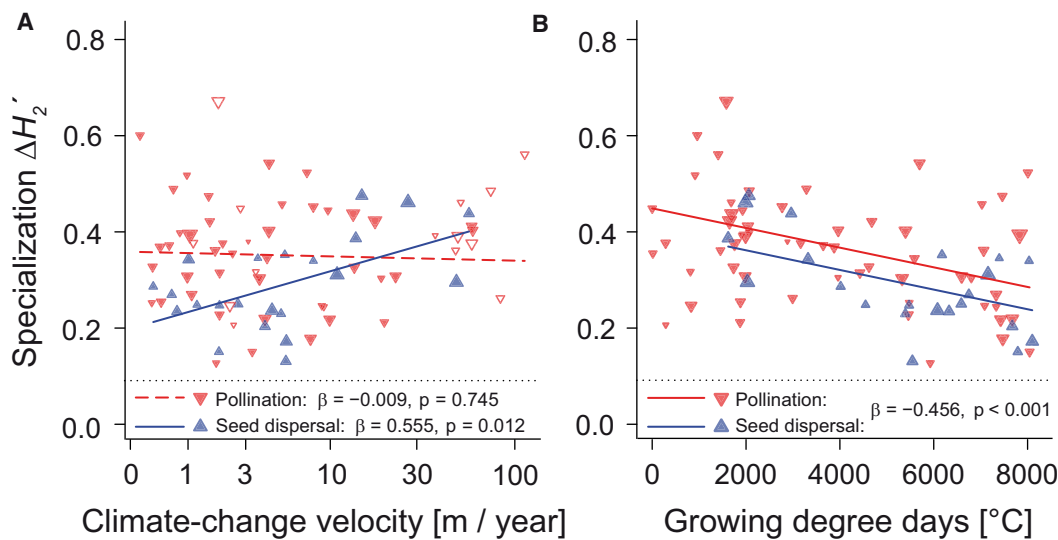
Figure 2. Effects of Past Climate Stability and Contemporary Climate on Specialization of Pollination and Seed Dispersal Networks

(A) Relationship between network specialization $\Delta H_2'$ and climate-change velocity (m/year; log scale), i.e., climate stability from the LGM to contemporary climate. Open triangles indicate glaciated regions during the LGM.

(B) Relationship between network specialization $\Delta H_2'$ and growing degree days (°C), i.e., current cumulative annual temperature.

See Figure S2 for correlations between cumulative annual temperature and other climatic predictor variables and Table S2 for multiple predictor models including past climate stability and contemporary climate.

and local plant species richness decreased with latitude (Figure S3). The latitudinal gradient in the diversity of animal-pollinated flowers and animal-dispersed fruits is even stronger than the overall plant diversity gradient [29]. Previous studies have shown that increasing plant diversity in the tropics is also associated with both a wider range of resource traits [4, 30] and a larger number of distinct pollination systems [11]. In response to high functional resource diversity, generalist consumer species may evolve traits [28, 30] that enable them to use resources from a wide trait spectrum [24], whereas consumer species associated with a specific pollination or seed dispersal syndrome may utilize various plant species within that syndrome [28, 30]. Consistent with previous work at the local scale [23], our findings suggest that high resource diversity may represent a key driver of generalization of consumer species in mutualistic networks.

Influence of Guild Structure and Network Sampling

Latitudinal trends in guild structure could also influence latitudinal differences in specialization. Whereas most tropical seed dispersers feed on fruits throughout the year, most seed dispersers in temperate systems switch diet between fruits and invertebrates [31]. Frugivore species appear to be more generalized than omnivores in seed dispersal networks [32]. In our data set, frugivores were more numerous in tropical than in temperate systems (ANOVA: $F_{1,20}$ = 7.0, p = 0.015), and network specialization was negatively associated with their proportion in the network (Pearson correlation: r = −0.60, p = 0.003). Pollinator communities also differed between tropical and temperate latitudes: the proportion of long-lived pollinator species (vertebrate pollinators and social insects with perennial colonies, such as honeybees, stingless bees, and ants) was higher in tropical than in temperate systems (ANOVA: $F_{1,51}$ = 79.7, p < 0.001). Long-lived species might use more different resources during their life span than short-lived species. The latitudinal difference in longevity, however,

could not be assigned unequivocally to network specialization (Pearson correlation: r = −0.26, p = 0.056). Differences in guild structure among tropical and temperate consumer communities may supplement effects of climate and plant diversity on network specialization, and future studies should aim at separating the relative role of changes in consumer communities from that of climate and plant diversity.

Despite the fact that we compiled the most comprehensive global database of quantitative mutualistic networks thus far, we are aware that the data set is heterogeneous, combining interaction data from different studies. We assessed the sensitivity of our results to potentially confounding latitudinal differences in network sampling. Specifically, we tested the effects of time span of observation (number of observation days), habitat type (forest versus nonforest habitats), and taxonomic completeness of sampling (entire species community versus single plant and/or animal family) together with the effects of past climate stability and contemporary climate on network specialization. This multipredictor analysis supported our conclusion that contemporary climate was the best predictor to explain the latitudinal specialization gradient (Table S2).

Conclusions

We found that specialization of pollination and seed dispersal networks decreases toward tropical latitudes. This finding calls for a careful rethinking of the role of specialized biotic interactions as a cause of high tropical diversity. Furthermore, we showed that past climate stability is related to specialization only in seed dispersal networks, whereas specialization in both pollination and seed dispersal networks is associated with contemporary climate and plant diversity. We propose that the latitudinal specialization gradient is to a large extent mediated by the latitudinal gradient in plant diversity because high resource diversity requires consumer species to generalize their diet.
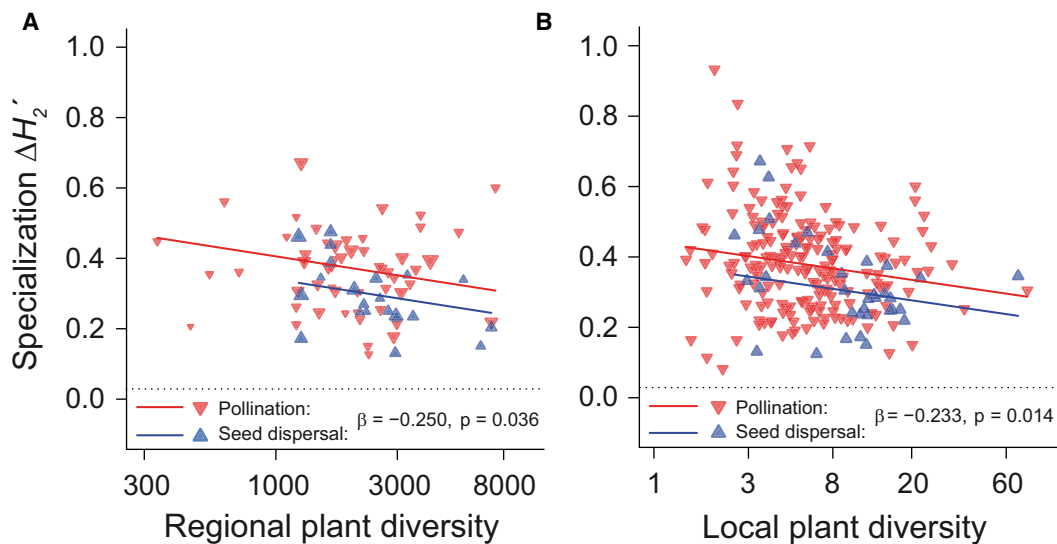
Figure 3. Effects of Regional and Local Plant Diversity on Specialization of Pollination and Seed Dispersal Networks

(A) Relationship between network specialization $\Delta H_2'$ and regional plant diversity, i.e., the number of vascular plant species (log scale) in equal-area grids of $\approx 12,100$ km^2.

(B) Relationship between network specialization $\Delta H_2'$ and local plant diversity, i.e., the effective number of plant species (log scale) in each network (e to the power of Shannon diversity of plant species interaction frequencies).

Regional diversity of vascular plant species and average local plant diversity were not correlated (n = 78, r = 0.077, p = 0.505). Regional plant diversity could not be derived for small islands (<2,000 km^2, i.e., Seychelles and Mauritius were excluded from this part of the analysis) and was set to the species pool of the entire Canadian Arctic Archipelago (340 species) for the northernmost point (Ellesmere Island). See Figure S3 for negative latitudinal trends in regional and local plant diversity.

Our findings also have important implications for the robustness of pollination and seed dispersal functions to disturbance in tropical and temperate ecosystems. Low specialization of tropical plant-animal communities is likely to increase their functional redundancy and resistance against secondary extinctions [33], whereas high diversity and functional complementarity of consumer species may be crucial for maintaining ecosystem functions in the more specialized temperate communities [17].

Experimental Procedures

Network Metrics

For each of the 282 networks, interactions among animal and plant species were summarized in a bipartite interaction matrix between I animal species in rows and J plant species in columns (data collection is described in the Supplemental Experimental Procedures). Species represent the nodes of the network, and interaction strength per link is given by the number of interaction events between an animal and a plant species. All network analyses were performed with the software R [34] and the bipartite 1.17 package [35].

To quantify specialization for a weighted network, we first calculated interaction diversity (Shannon entropy) H_2 across all I animal and J plant species [36]. In order to disentangle different degrees of specialization from differences in species frequencies, a standardized network specialization metric has been proposed, in which the actual H_2 value is compared with the range (H_{2min} to H_{2max}) of possible H_2 from any distribution of interaction events with the same number of events per species [36]. H_2' ranges from 0.0 for the most generalized (i.e., maximum niche overlap) to 1.0 for the most specialized network (i.e., maximum niche divergence). In poorly sampled networks, higher values of H_2' can be reached by chance as expected values of nonselective foraging deviate more strongly from 0 and may get closer to 1 [36]. Because we aimed at comparing the most unbiased estimates of network specialization, we used a modified specialization index $\Delta H_2' = H_2' - H_{2ran}$, where H_{2ran} represents the mean H_2' from 1,000 randomized networks. Randomizations were performed with the Patefield algorithm, which randomly redistributes interaction events among all cells of the network while constraining total interaction

strength per species. $\Delta H_2'$ differs only slightly from H_2', and the latitudinal trends in both metrics were qualitatively identical (compare Figures 1C and S1A).

We also examined latitudinal trends in biotic specialization with other specialization indices. We calculated two alternative indices for binary networks: connectance, i.e., the realized proportion of possible links, and unweighted generality, i.e., the average number of links (species degree) per consumer species. We also determined weighted generality, i.e., the average effective number of links per consumer species, accounting for interaction strength [35]. Furthermore, we tested specialization trends separately for plants and animals by calculating weighted and unweighted means of species-level specialization d' [36]. Because network asymmetry, i.e., the balance between plant and animal diversity in a network, strongly affects guild-level specialization [16], we accounted for differences in network asymmetry, i.e., we included network asymmetry as a covariate in guild-level analyses. In the main manuscript, we focus on $\Delta H_2'$ because it integrates specialization across the entire community [16] and was the only metric that was affected by neither the number of interaction events nor the number of species in the network (Table S3).

Predictor Variables

For each network location, we obtained climate-change velocity since the last glacial maximum (LGM, 21,000 years ago) as an estimate of past climate stability [18]. The measure describes the rate at which temperature conditions have moved over the Earth's surface since the LGM (here in m/year), based on 2.5 min resolution maps of contemporary climate [37] and paleoclimate projections (CCSM3 model in [38]). The spatial pattern of climate-change velocity since the LGM is representative of the last several hundred thousand years [39]. We also identified locations that were glaciated at the LGM with maps of glacial extent [40]. We additionally obtained information on contemporary climate (monthly temperatures, annual precipitation) for each network location at a 2.5 min resolution [37]. We calculated estimates of the cumulative annual temperature above 5°C (i.e., growing degree days) as a measure of available thermal energy during the growing season [19]. The regional plant diversity for each network location was derived from spatial interpolation of global plant richness data at a spatial resolution of $\approx 12,100$ km^2 [21]. The local plant diversity was derived from each network as the Shannon index of the plant species marginal totals. This takes into account the number of observed plant species in a network

and the evenness of their abundance distribution. Local plant diversity was averaged over networks from the same location (n = 232 locations).

Statistical Analyses

Each of the 282 networks was assigned to a sampling region (n = 80 regions). Regions were defined by the original studies that focused on a particular habitat type in a given area (see Supplemental Experimental Procedures). Region-level analyses were conservative because they prevented pseudoreplication of networks with almost identical climatic conditions and overrepresentation of regions with many replicate networks.

At the global scale, we related network specialization $\Delta H_2'$ to absolute latitude, past climate stability, contemporary climate, and regional plant diversity in linear models. We used the sampling region as the unit of replication and calculated mean $\Delta H_2'$ of all networks within a region. At the local scale, we tested the effect of local plant diversity on $\Delta H_2'$ with a random-intercept model with sampling region as random factor. For each predictor, we fitted reduced and full models (including main effects and interaction effects with network type) and identified the minimal adequate model according to the lowest Akaike information criterion, corrected for small sample size, AICc (Table 1).

In analyses at the global scale, we accounted for differences in sampling intensities among regions with least squares weighted by sampling intensity,

$$Intensity_{web} = \frac{\sqrt{N_i}}{\sqrt{size_i}};$$

$$Intensity_{region} = \log_{10}\left(Intensity_{web\_mean} \times \sqrt{n} + 1\right),$$

where N_i is the number of interactions in network i and $size_i$ is the product of the number of plant species and the number of animal species in network i. $Intensity_{web}$ reflects the number of interactions observed per species. Sampling intensity per region ($Intensity_{region}$) combines mean network sampling intensity in a region ($Intensity_{web\_mean}$) with the number of networks sampled per region (n). Analyses of the relationship between $\Delta H_2'$ and latitude with each network as a replicate ($\beta = 0.262$, $p < 0.001$) and with unweighted least squares at the regional scale ($\beta = 0.326$, $p = 0.003$) resulted in the same latitudinal trend as the weighted regional analysis. We visually examined spatial dependences (Moran's I) in the residuals of all minimal adequate models. Spatial autocorrelation was negligibly small in all cases (Figure S4).

Supplemental Information

Supplemental Information includes four figures, three tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.08.015.

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