Report

Specialization, Constraints, and Conflicting Interests in Mutualistic Networks

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Summary

The topology of ecological interaction webs holds important information for theories of coevolution, biodiversity, and ecosystem stability [1–6]. However, most previous network analyses solely counted the number of links and ignored variation in link strength. Because of this crude resolution, results vary with scale and sampling intensity, thus hampering a comparison of network patterns at different levels [7–9]. We applied a recently developed [10] quantitative and scale-independent analysis based on information theory to 51 mutualistic plant-animal networks, with interaction frequency as measure of link strength. Most networks were highly structured, deviating significantly from random associations. The degree of specialization was independent of network size. Pollination webs were significantly more specialized than seed-dispersal webs, and obligate symbiotic ant-plant mutualisms were more specialized than nectar-mediated facultative ones. Across networks, the average specialization of animal and plants was correlated, but is constrained by the ratio of plant to animal species involved. In pollination webs, rarely visited plants were on average more specialized than frequently attended ones, whereas specialization of pollinators was positively correlated with their interaction frequency. We conclude that quantitative specialization in ecological communities mirrors evolutionary trade-offs and constraints of web architecture. This approach can be easily expanded to other types of biological interactions.

Results and Discussion

Ecological specialization in a food web or other interaction networks is commonly defined by the number of

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realized "links." For instance, predators are specialized if they attack only a few prey species, and specialized flowers are those that are visited by few pollinator species only. This concept has been extended to measure the degree of specialization of entire networks ("connectance"), where associations are classified as "present" or "absent," but all links are considered equally important [1–3, 6, 8, 11–13]. However, such qualitative measures ignore the importance of variation in interaction strength for community dynamics [5, 14, 15]. Moreover, they are highly sensitive to sampling intensity and network size [7–10, 15]. Therefore, weighted links have been included in quantitative descriptors of different types of webs [5, 14, 16]. In bipartite ecological networks, the frequency of an interaction between two species is a meaningful measure of its strength (Figure 1) and has been shown to represent a suitable surrogate for mutualistic services such as pollination success [17]. In this article, we use two measures inspired by information theory to quantify specialization within and across networks. Technical properties of these indices have been explored in a recent methodology article [10] showing that—in contrast to other quantitative measures—they are scale independent and largely insensitive to sampling effort. Unlike previous measures, we define the overall degree of specialization in each web as the deviation from an expected probability distribution of interactions (evaluated by the standardized two-dimensional entropy H'_2), and individual species' specialization as the deviation from a conformity expected by the overall utilization of potential partners (standardized Kullback-Leibler distance, d'_i) [10]. The expected null distribution assumes that all species interact with their partners in proportion to their total frequencies, whereas the heterogeneity (evenness) of interactions in previously proposed quantitative metrics such as diversity indices [16, 18] varies with the partner availabilities in an uncontrolled way and is thus less suitable in the context of network analyses (see also [10, 19]). On the basis of these standardized quantitative measures, we explored 51 networks, covering four types of mutualistic plant-animal associations, for patterns of specialization on the level of the entire network [2, 8], the community of each of the two parties (guild level) [5], and the level of species [9].

Network Level

Across all networks, the overall degree of specialization (H'_2) covered a broad range (Table S1 in the Supplemental Data available online). All networks showed a significantly higher degree of organization than simulated networks, where partners were associated randomly (all $p \leq 0.001$), except for a single network of loosely associated ants and bromeliads [20] (p = 0.31). Pollination mutualisms were significantly more specialized than seed-dispersal mutualisms (Figure 2), corroborating a previous qualitative analysis [2] and expected on the basis of evolutionary considerations [21]. Plants may
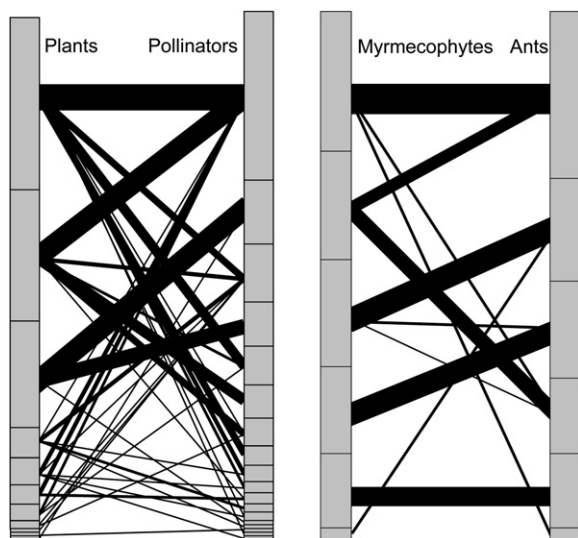
Figure 1. Visualization of Two Quantitative Networks

A pollinator web and an ant-plant association are displayed (webs 6 and 37 in Table S1). Widths of links are scaled in relation to interaction frequencies, bar sizes to total interaction frequencies. Both webs are regarded specialized, but the degree of specialization is lower in the pollinator web (H'_2 = 0.46) compared to the myrmecophyte web (H'_2 = 0.84). Note that the former web is asymmetric (more pollinator than plant species), whereas the latter is symmetric.

benefit disproportionately more from specialized pollinators, corresponding to the likelihood that each individual pollinator successively visits conspecific plants to maintain both male and female reproductive success of a plant, thereby reducing maladaptive heterospecific pollen transfer ([22, 23], but see [11]). In contrast to pollination, the efficacy of seed dispersal to suitable sites does not depend on the specialization of the dispersal agent [21]. A broader spectrum of seed dispersers may even be profitable from the plant's perspective to avoid aggregation of seeds [24] and generate fat-tailed dispersal kernels [25], which should be favored by natural selection under many conditions [26]. Correspondingly, obligate specialized mutualisms are known from a number of pollination systems [23] but seem to be largely absent in seed-disperser systems [21].

In ant-plant networks, there is an important distinction between completely facultative associations, based on extrafloral nectaries, and symbiotic associations, where ant colonies, often obligatory, inhabit plants (myrmecophytes) [27, 28]. For obligate and symbiotic mutualisms, a higher degree of specialization is generally expected [4, 29]. This differentiation is supported by our analysis: Ant-plant mutualisms involving myrmecophytes were significantly more specialized than those involving extrafloral nectaries (Figure 2). Obligate associations are common among myrmecophytic associations, sometimes causing irreversible dependence on a single partner species. Myrmecophytes represent a gradient from plants that offer neither specific structures nor specific food rewards to support their facultative ant inhabitants [20, 28] to cases where only few ant species are adapted to actively bite small entrance holes into preformed domatia and where colonies are fully supplied by nutritious plant-produced food bodies and never forage outside their host plants [27, 30]. Obligate-myrmecophytic symbioses represent the most specialized networks across all systems examined in this study. In contrast to other networks, such associations often remain uninterrupted for several generations, opening the opportunity for the evolution of tight specialization. In contrast, extrafloral nectaries usually attract a spectrum of largely opportunistic ants, where the accessible nectaries seem to offer little structural plasticity to facilitate specialization except for some degree of biochemical differentiation [31, 32]. This dissimilarity between the two types of ant-plant mutualisms is particularly evident between nectary-bearing and myrmecophytic species from the same genus [27, 32]. The gradient from facultative to obligate mutualisms is thus largely associated with an increasing H'_2.

The degree of specialization did not show a significant trend across networks of different dimensions (Figure 3) (Spearman rank correlations for each of the four network types, all $-0.48 \leq r_S \leq -0.10$, p $\geq$ 0.15). Given that H'_2 is mathematically independent of web size [10], the lack of a correlation between web size and H'_2 indicates that species-rich and species-poor real biological systems (or smaller fractions of a system) do not inherently differ in their degree of specialization between partners. This novel finding contrasts with the hyperbolic decline of
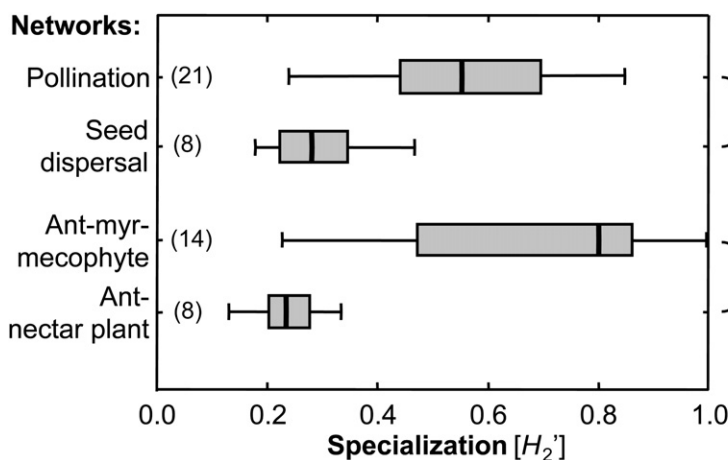

Figure 2. Network-Level Specialization

Overall specialization (H'_2) in 51 mutualistic networks. Box plots show median, quartiles, and range of the networks analyzed (number of networks in parentheses). Asterisks show significant difference between types according to a t test (*** p < 0.0001, both $t \geq$ 5.2, Welsh corrected for unequal variances).

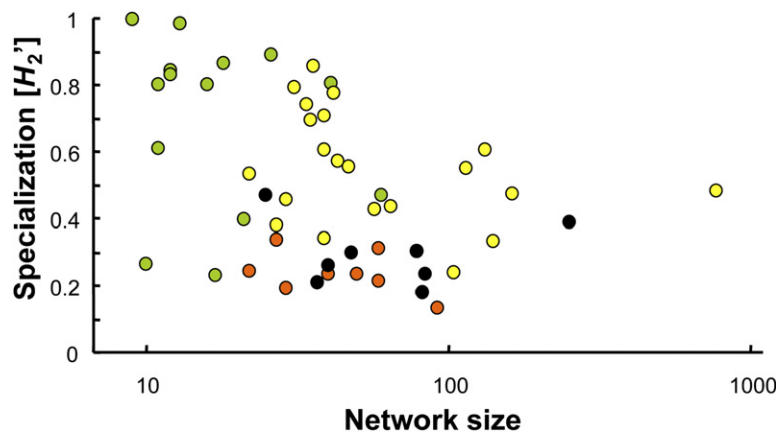the qualitative connectance index over increasing network size in different studies [2, 8, 33, 34], a decline that was also found if applied to the dataset used here (see Supplemental Data).

Guild Level

Within mutualistic networks, differences between the average degree of specialization of both parties (i.e., plants versus animals) could be a consequence of conflicting interests. Consumers would only benefit from increased specialization if this process went along with greater resource-use efficacy and/or reduced interspecific competition, e.g., by improved resource detoxification, reduced handling effort, or specific search images, and outweighed the costs of increased foraging time. If resources were very similar, optimal foraging theory would thus predict selection for generalization in both frugivores and pollinators [11, 21, 23]—the latter conflicting with the plant's interest in specialized pollinators. However, both parties did not vary independently in their degree of specialization, and average specialization of plants $\langle d'_i \rangle$ and animals $\langle d'_j \rangle$ was largely reciprocal (Pearson's $r^2 = 0.71$, p < 0.0001, n = 51 webs). Moreover, differences between $\langle d'_i \rangle$ and $\langle d'_j \rangle$ are strongly predicted by the asymmetry of the matrix ($r^2 = 0.62$, p < 0.0001) (Figure 4). In those webs where animal species were more numerous than plants, animals showed a lower degree of specialization ($\langle d'_j \rangle < \langle d'_i \rangle$) and vice versa. This effect was even stronger ($r^2 = 0.93$) for simulated networks with randomly assigned associations (Figure S2). Pollinator and ant-nectar webs were highly asymmetric, involving a much higher number of
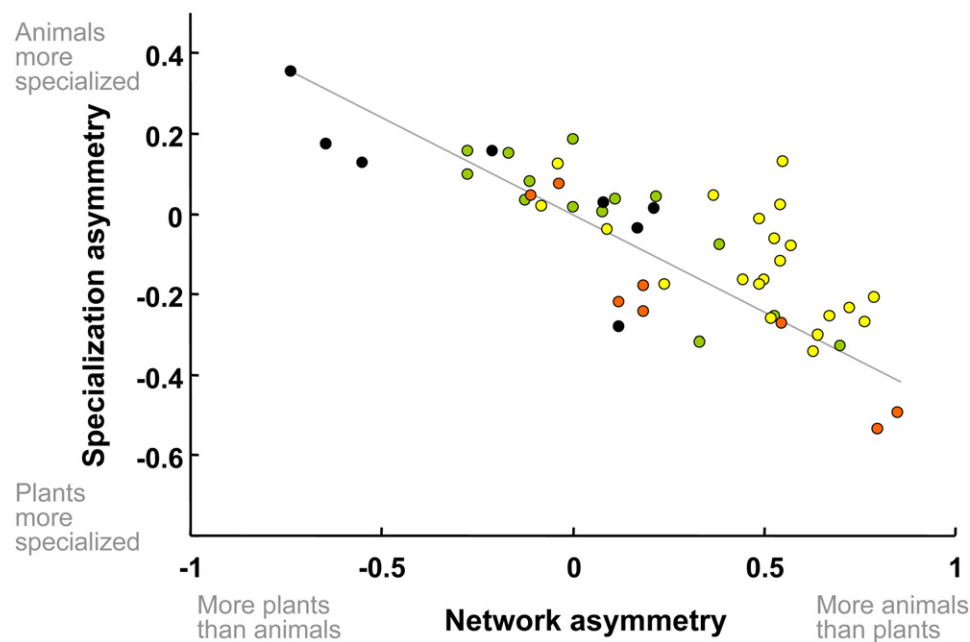

Figure 4. Relationship between Network Asymmetry and Specialization

Asymmetry of the number of plant (I) and animal (J) species in each web (network asymmetry) is given as ($J - I$) / ($I + J$) and equals zero for balanced webs (same number of animal and plant species). Specialization asymmetry between plants and animals is given as ($\langle d'_j \rangle - \langle d'_i \rangle$) / ($\langle d'_j \rangle + \langle d'_i \rangle$), based on weighted means across all species (plants i or animals j) in a web. Real networks include pollination (yellow), seed-dispersal (black), ant-myrmecophyte (green), and ant-nectar plant (red) associations. The regression line is plotted for randomly generated networks (fixed total interactions per species, mean values from 100 randomizations per web, $r = -0.97$).

pollinator species (usually insects) or ant species than plant species (on average 3.6:1 and 3.8:1, respectively). Consequently, pollinators were significantly less specialized on plants than plants on pollinators, and ants were significantly less specialized on plants with nectaries than vice versa (paired t test; pollinators: t = 3.8, p = 0.001; ants: t = 3.2, p = 0.01). In contrast, networks involving seed dispersers (mostly vertebrates) as well as ant-myrmecophyte associations were usually more symmetric (1.2:1 and 1.6:1, respectively) and did not show significant unequal specialization of both mutualists (both p $\geq$ 0.38). Hence, the network architecture severely constrains average specialization between two parties irrespective of the type of association, a result that is expected given the mathematical relationships of the indices in their unstandardized form [10]. Such constraints on specialization have been largely overlooked so far, but are important in other network metrics as well, including the "number of links" or quantitative "dependences" used elsewhere [5] (see Supplemental Data). However, with architectural constraints accounted for, residual variation from the linear regression (line shown in Figure 4) depicted differences between networks depending on the type of association. Pollinators were significantly more specialized than expected by the asymmetry (mean residuals > 0, t = 4.7, p < 0.001), whereas ants visiting extrafloral nectaries were more generalized than expected (residuals < 0, t = −2.4, p < 0.05). In seed-dispersal and ant-myrmecophyte networks, differences between animals and plants in specialization did not deviate significantly from the expected on the basis of asymmetry (both p $\geq$ 0.10). The increased residual specialization observed in pollinators, but not seed dispersers, thus corresponds to the plant's differential interest in these types of mutualists.

Species Level

Although the average degree of specialization in a community may be constrained to a large degree, this does not apply to single elements of the network, i.e., the local population of each species. For example, disparities in specialization of pollinators and plants were particularly pronounced for the rarely interacting species in a network. Across pollination networks, there was a significantly positive correlation between pollinator frequency and specialization, but a significant negative correlation between plant frequency and specialization (Table 1). We also found a significantly positive correlation between ant frequency and specialization in ant-myrmecophyte webs but not in any of the other networks investigated. Previous qualitative network analyses showed an invariable negative correlation between frequency and specialization (estimated as the inverse of the number of links), a correlation that can be explained by a null model [9] and is strongly affected by sampling effort. In contrast, our quantitative analysis demonstrates a highly variable relationship between frequency and quantitative specialization, one that differs between network types. Our results suggest that plant populations with low visitation frequencies, presumably those that occur in low densities in a community, have a particularly unconventional spectrum of visitors. Rare plants may be particularly sensitive for two fitness costs: subsequent

Table 1. Relationship between Frequency and Specialization of Plant and Animal Species

	Plants	Animals
Pollination	−0.20* (−0.30 − −0.11) (n = 20)	0.27* (0.15 − 0.37) (n = 21)
Seed dispersal	0.06 (−0.19 − 0.23) (n = 7)	0.00 (−0.27 − 0.24) (n = 8)
Ant-myrmecophyte	0.14 (−0.16 − 0.40) (n = 14)	0.51* (0.24 − 0.71) (n = 13)
Ant-nectar plant	−0.10 (−0.23 − 0.02) (n = 7)	−0.04 (−0.27 − 0.16) (n = 8)

Effect sizes derived from linear correlation coefficients for each network by using meta analysis based on Fisher's z-transformation. Mean back-transformed r values are shown with range of 95% bootstrap confidence intervals and number of webs (n) in parentheses. Asterisks indicate significant deviation from $r = 0$.

pollen deposition on (more common) plants and clogging of the stigma by pollen from (common) plants [22]. Increased specialization and reduced overlap with visitors of common flowers may reduce such costs. The positive correlation between animal abundance and specialization indicates that resource partitioning is particularly pronounced among the most active species, whereas rarely interacting species use their resources more opportunistically.

Conclusions

Three general conclusions can be drawn from the results. (1) The network-level specialization is unaffected by network size and form and depicts biologically meaningful system-specific differences. Our results demonstrate that the plant's interest in specialized pollen transfer but generalized fruit dispersal conformed to the overall specialization of the respective networks. Networks involving facultative associations were less specialized than more obligate ones, particularly in ant-plant webs. (2) The average degree of specialization of both network parties is highly reciprocal, i.e., one party cannot specialize or generalize on the other party without concomitant changes in the specialization within the other party itself. Moreover, differences between network parties are largely driven by constraints in the network architecture (unequal species numbers). Such constraints cause unequal degrees of specialization as well as asymmetric dependences between both parties. Residual differences in specialization still contain meaningful information, e.g., pollinators were more specialized than expected from architectural constraints only. (3) Species-level specialization is less affected by these constraints and may indicate differential roles of rare and common species in a network. Such patterns may potentially unveil density-dependent selection pressures or feedback mechanisms between frequency and specialization.

The hypothesis that natural selection drives specialization between interacting mutualists or antagonists has been debated for a long time [4, 11, 35]. Whereas generalists are obviously much less limited by resource or partner availability, specialists are usually better adapted to effectively use their selected resources. For antagonistic relationships (e.g., predator-prey, host-parasite, and plant-herbivore interactions), defensive

mechanisms of hosts or prey substantially constrain the choices of their enemies, enforcing specialization [36]. Trade-offs between specialization and generalization may occur in food webs [6], but are also complex among mutualists [37], where selective pressures on partner choices may be variable and shaped by coevolutionary complementarity or convergence [4]. Refined analyses and more fine-grained empirical data, particularly at the level of individuals, may reveal additional insights into the evolution of a broad spectrum of interaction webs and their ecological fragility.

Experimental Procedures

We analyzed the degree of specialization for 51 published and un-published interaction webs that included frequency data, representing a broad range of mutualistic relationships between plant-based resources and their consumers or inhabitants and covering six continents (Supplemental Data). Although all webs were obviously dominated by mutualists, several datasets may contain nonmutualistic species, e.g., nectar robbers and seed predators. Twenty-seven datasets were obtained from the Interaction Web Database (http://www.nceas.ucsb.edu/interactionweb). For each network containing a total of I plant and J animal species, we obtained the two-dimensional Shannon entropy for the observed association matrix [10] as

$$H_2 = -\sum_{i=1}^{I}\sum_{j=1}^{J}(p_{ij} \cdot \ln p_{ij}), \quad \text{with} \sum_{i=1}^{I}\sum_{j=1}^{J} p_{ij} = 1.$$

In this equation, i represents one plant species and j one animal species. The number of interactions between i and j (a_{ij}), e.g., the number of recorded visits of pollinator j on plant i, is divided by the total interaction frequencies recorded for the entire web, thus

$$p_{ij} = a_{ij} \Big/ \sum_{i=1}^{I}\sum_{j=1}^{J} a_{ij}.$$

Our specialization index H'_2 normalized H_2 between the minimum and maximum entropy for associations leading to the same matrix row and column totals as

$$H'_2 = \frac{H_{2\max} - H_2}{H_{2\max} - H_{2\min}}.$$

For quantification of the degree of specialization of each species (say plant i), the proportional distribution of the interactions with each animal (j), p'_{ij}, was compared with the proportion of the total number of interactions where j was involved, q_j, by using the Kullback-Leibler measure

$$d_i = \sum_{j=1}^{J}\left(p'_{ij} \cdot \ln \frac{p'_{ij}}{q_j}\right),$$

where $p'_{ij} = a_{ij} \Big/ \sum_{j=1}^{J} a_{ij}, \quad \text{thus} \sum_{j=1}^{J} p'_{ij} = 1,$

and $q_j = \sum_{i=1}^{I} a_{ij} \Big/ \sum_{i=1}^{I}\sum_{j=1}^{J} a_{ij}, \quad \text{thus} \sum_{j=1}^{J} q_j = 1.$

This measure was normalized as

$$d'_i = \frac{d_i - d_{\min}}{d_{\max} - d_{\min}}.$$

Specialization of the plant community (guild level) was obtained as the weighted mean $\langle d'_i \rangle$, for which each plant species i was weighted by its total number of interactions. Specialization of animals was calculated in the same way (d'_j and $\langle d'_j \rangle$). Maximum and minimum values for H_2, d_i, and d_j were computed algorithmically by using the fixed total number of interactions of each species as a constraint [10]. Resulting H'_2, d'_i, and d'_j range between 0.0 for extreme generalization and 1.0 for extreme specialization. For each network, H_2

was compared to a null model (randomly associating all species with the total number of interactions being fixed per species, 10^4 permutations) by using an established algorithm ([38], see [10]). Fixed marginals have been advocated as suitable constraints for null hypotheses in qualitative webs [6, 39]. In addition, we suggest that total interaction frequencies may better reflect variation in animal activity or plant resource availability for the actual associations than would external estimates of local population densities [10]. Such independent measures of the species' local abundances for both parties have not been provided by most empirical studies so far. All calculations can be performed online at http://itb.biologie.hu-berlin.de/~nils/stat/.

To analyze the relationship between specialization and interaction frequency at the species level, we calculated linear correlation coefficients between log(total number of interactions) and $\arcsin(\sqrt{d'_i})$ across all species of a guild per network and then quantified the combined mean effect size from all networks of the same type by using standard meta-analysis tools (MetaWin 2.0; Fisher's z-transformation, sample size as number of species, fixed effects); 95% confidence intervals were based on bootstrapping with 999 iterations, bias-corrected. To reduce a bias due to single, very large networks, we removed, prior to analysis, datasets where the number of species was more than twice as large as in the second-largest network (four cases).

Supplemental Data

Supplemental Data include additional results and data sources, three figures, and one table and are available with this article online at: http://www.current-biology.com/cgi/content/full/17/4/341/DC1/.

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