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Source: *Ecology*, Vol. 97, No. 6 (June 2016), pp. 1431–1441

Published by: Wiley on behalf of the Ecological Society of America

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Flexible foraging shapes the topology of plant–pollinator interaction networks

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Abstract. In plant–pollinator networks, foraging choices by pollinators help form the connecting links between species. Flexible foraging should therefore play an important role in defining network topology. Factors such as morphological trait complementarity limit a pollinator's pool of potential floral resources, but which potential resource species are actually utilized at a location depends on local environmental and ecological context. Pollinators can be highly flexible foragers, but the effect of this flexibility on network topology remains unclear. To understand how flexible foraging affects network topology, we examined differences between sets of locally realized interactions and corresponding sets of potential interactions within 25 weighted plant–pollinator networks in two different regions of the United States. We examined two possible mechanisms for flexible foraging effects on realized networks: (1) preferential targeting of higher-density plant resources, which should increase network nestedness, and (2) context-dependent resource partitioning driven by interspecific competition, which should increase modularity and complementary specialization. We found that flexible foraging has strong effects on realized network topology. Realized connectance was much lower than connectance based on potential interactions, indicating a local narrowing of diet breadth. Moreover, the foraging choices pollinators made, which particular plant species to visit and at what rates, resulted in networks that were significantly less nested and significantly more modular and specialized than their corresponding networks of potential interactions. Preferentially foraging on locally abundant resources was not a strong driver of the realization of potential interactions. However, the degree of modularity and complementary specialization both increased with the number of competing pollinator species and with niche availability. We therefore conclude that flexible foraging affects realized network topology more strongly through resource partitioning than through focusing on high-density resources.

Key words: *adaptive foraging; competition; complementary specialization; complex adaptive system; flexible foraging; interaction switching; modularity; nestedness; niche partitioning; optimal foraging.*

INTRODUCTION

The choices foraging pollinators make, which plant species to visit and at what rates, form the essence of plant–pollinator interaction networks. These foraging decisions result in nonrandom network topologies that may be important for biodiversity, stability, and ecosystem function (May 1972, Okuyama and Holland 2008, Bastolla et al. 2009, Allesina and Tang 2012, Brosi and Briggs 2013). For example, nestedness is a topological pattern in which relative specialists interact with subsets of the partners of more generalized species (Bascompte et al. 2003). Nestedness may benefit biodiversity by enhancing facilitation among species (Okuyama and Holland 2008, Bastolla et al. 2009, Rohr et al. 2014, but see James et al. 2012, Staniczenko et al. 2013). Modularity, another type of pattern, describes the degree

to which species form groups, or modules, with interactions frequent within and rare among modules (Olesen et al. 2007, Schleuning et al. 2014). Modularity is thought to result from niche organization and similarity of resource use (Guimerà et al. 2010), which may promote biodiversity through niche partitioning and complementary specialization (Blüthgen and Klein 2011). Most theory and empirical studies have assumed interaction partners are static. However, pollinators can be highly flexible in resource use (Inouye 1978, Fründ et al. 2010, 2013, Brosi and Briggs 2013), which allows for plasticity of network topology. At a network scale, this flexibility can result in turnover of interactions (in addition to species turnover) among locations (Simanonok and Burkle 2014, Trøjelsgaard et al. 2015), but it is unclear how this flexibility helps shape local network topology.

A pollinator species' foraging choices are bounded by a set of potential interaction partners, or its fundamental niche (at least the portion related to food resources), which is determined by the evolution of trait complementarity (reviewed in Santamaría and Rodríguez-Gironés 2007). For example, flowers with a long corolla are

Manuscript received 28 September 2015; revised 11 December 2015; accepted 6 January 2016; final version received 3 February 2016. Corresponding Editor: N. M. Williams.

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usually only visited by animals with a long proboscis (Stang et al. 2006). But the plant resources that a pollinator species actually uses at a given location, its realized niche, will further depend on local environmental and ecological conditions. For instance, the local abundance of resources or the presence of competitors may shift pollinators' local foraging preferences so that realized network topology differs from its potential topology (i.e., the topology based on species' fundamental niches). Including flexible and adaptive foraging in model networks can account for realistic topologies (Beckerman et al. 2006, Zhang et al. 2011). Moreover, such adaptive flexibility can be crucial for maintaining network diversity (Kondoh 2003, Abrams 2010, Ramos-Jiliberto et al. 2012), which may become more important in an increasingly variable environment. It is therefore important to develop a better understanding of how foraging flexibility contributes to realized network topology in empirical systems.

Flexible foraging behavior should affect network topology in predictable ways. For example, species often do not utilize their entire fundamental niche and therefore network connectance necessarily declines as species restrict interactions to fewer partners. But the rates at which a particular subset of resources are used will determine realized network patterns such as nestedness and modularity. Nestedness will increase, for instance, if a specialist pollinator reduces its rate of interaction with a specialist plant in favor of interactions with a more generalized plant. Generalists tend to be more abundant than specialists so a greater neutral encounter rate of more abundant species may explain patterns of nestedness (Dupont et al. 2003, Vázquez et al. 2009). However, optimal foraging theory suggests that in order to maximize net energy intake, pollinators may choose to focus their effort on the most abundant species (MacArthur and Pianka 1966, Waser 1986). Along these lines Zhang et al. (2011) showed that nestedness can emerge from a non-neutral process when effort-limited foragers actively focused on resources that provided a greater benefit for population growth (i.e., those in higher abundance) while ceasing interactions with resources that provided little benefit. Thus, if foraging pollinator species give preference to plant species of greater local abundance, we would expect realized nestedness to increase relative to networks composed of all potential interactions.

Modularity will increase if interactions between species in different modules are reduced in favor of interactions within modules. If interspecific competition among pollinators increases with pollinator (competitor) species richness, flexibility in foraging may allow pollinators to shuffle interaction partners and partition niches in order to minimize competition for floral resources (Pianka 1974). An increase in plant resource species richness may provide for more dimensions in which niches can be partitioned (MacArthur and Levins 1967) and an increase in resource density may better sustain pollinators within those niches. Thus, if niche partitioning among flexible

foragers results from interspecific competition, we would expect realized networks to be more modular and with greater complementary specialization relative to networks formed of potential interactions. Furthermore, relative modularity and specialization should increase with pollinator and plant species richness and with plant resource density because of the greater need (stronger competition) and opportunity (greater availability of resources in more niche dimensions). These scenarios show how realized network topology may be affected by the adaptive choices made by foraging pollinators.

At any given location it is relatively straightforward to observe a set of interactions between plants and pollinators. But to what extent are locally realized interactions a departure from the set of all potential interactions between the same species and a result of flexible foraging? One way to quantify this, in the absence of extensive individual feeding trials, is to first establish the range of resources that pollinators can potentially utilize by making observations of plant–pollinator interactions at multiple sites and across a range of ecological conditions within a region, and then compare those potential interactions to the set of locally realized interactions (Laliberte and Tylianakis 2010, Poisot et al. 2012; Fig. 1). Thus, differences between species' locally realized and potential interactions can indicate how flexible foraging shapes realized network topology.

We use this approach along with a set of null model analyses to examine how and to what extent flexible foraging shapes the realized topology of 25 plant–pollinator networks. We then examine two possible mechanisms for the observed differences between realized and potential network topologies: focused foraging on abundant resources and niche partitioning driven by interspecific

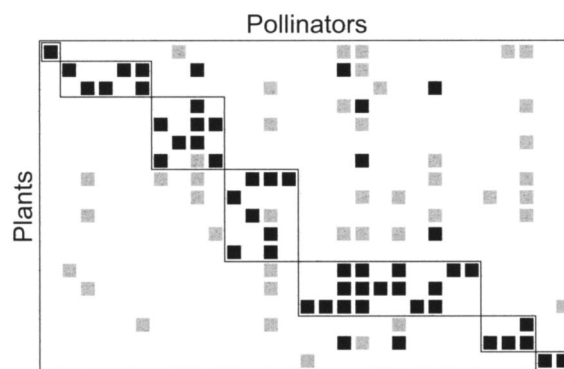


FIG. 1. Realized and potential interactions for Florida site 13. Black squares represent the presence of locally realized interactions, while gray (and black) squares represent the presence of potential interactions, i.e., the set of interactions that occurred between the same species at all Florida sites. Plant species in rows and pollinator species in columns are ordered based on realized modularity and black boxes delimit the interactions that occur between species in the same module. This network is presented in unweighted (presence/absence of interactions) form here for clarity of illustration but all network indices except connectance were calculated from weighted interactions.

competition. By conducting our study in different ecological contexts, in two different habitat types that occur in two different regions (pine savannah in Florida and seminatural grassland in Wisconsin, USA), we are able to assess the generality of flexible foraging effects on network topology.

METHODS

Study areas

Observations of plant–pollinator interactions were conducted in the sandhills of northern Florida and grasslands of southern Wisconsin, USA (see photos of habitats and a map of locations in Appendix S1). In Florida, sandhill habitat is an upland pine savannah composed of an open canopy of longleaf pine (*Pinus palustris*), with an understory of turkey oak (*Quercus laevis*), wiregrass (*Aristida stricta*), and a diverse mix of forbs. Wisconsin grassland sites are seminatural prairies composed of switchgrass (*Panicum virgatum*) and other grasses, as well as a diversity of forbs. In Florida, 15 60 × 60 m sites, each separated by at least 1.2 km, were established within a region of the Apalachicola National Forest, just south of Tallahassee, Florida (30.35° N, 84.29° W). Florida sites were imbedded within a patchwork of loosely connected sandhill and surrounded by a landscape matrix of mainly lands disturbed by timber harvesting, pine flatwoods, and wetlands. In Wisconsin, 10 50 × 100 m sites, each separated by at least 2.4 km, were established on U.S. Fish and Wildlife and Wisconsin Department of Natural Resource lands in a region surrounding Madison, Wisconsin (43.07° N, 89.41° W). Wisconsin sites were imbedded within larger restored grassland fields (5.2–23.3 ha) and surrounded by a matrix of mainly agriculture, deciduous woodlands, and wetlands.

Pollinator observations

In Florida, four sets of standardized observations were conducted monthly at each site between June and September 2010 (Spiesman and Inouye 2013). In Wisconsin, three sets of observations were conducted monthly at each site between June and August 2013. During each observation period in both study regions, three to four individuals of each plant species in flower were observed for 15–25 min. On average, 8.4 ± 3.6 (mean \pm SD; Florida) and 10.4 ± 4.3 (Wisconsin) plant species were flowering at a given site and during a given sampling period. All pollinator observations were made between the hours of 09:00 and 17:00 local time on sunny days with low wind. Within a sampling period, observations at each site were usually completed in 1 d, but occasionally poor weather required finishing observations on another day.

Plant–pollinator interactions in Florida were recorded on high definition video and flower visitors were then identified to morphospecies and to the finest taxonomic

level possible with the help of a reference collection. Wisconsin observations were conducted visually in the field where easily identified flower visitors were identified on the fly or collected for later identification in the lab with the help of expert taxonomists (see *Acknowledgments*). Only flower visitors that came into contact with reproductive flower parts were recorded. Although we recognize that not all visits result in pollination and species vary in their effectiveness as pollinators, we hereafter refer to flower visitors as pollinators.

We estimated the relative density of floral resources for each plant species in flower during each sampling period. At Florida sites, we counted and identified to species all individual plants in flower within six 3 × 60 m belt transects. At Wisconsin sites, we estimated floral resource density within two 2 × 100 m belt transects by counting the number of nonoverlapping 0.5-m² quadrats that flowers of each plant species occurred in along the belt transect. Additional detail about the Florida study sites and sampling methodology can be found in Spiesman and Inouye (2013).

We combined the visitation data from each sampling period to assemble 25 weighted (or quantitative) bipartite networks of realized plant–pollinator interactions (one network per site). In bipartite networks, species are separated into two trophic levels (plants and pollinators) and it is assumed that interactions occur exclusively between species in different trophic levels. Interaction strengths between each plant and pollinator species were weighted by the visitation rate (number of visits per minute of observation).

For each of the two regions, visitation data comprising the locally observed networks were pooled to form a regional network (i.e., a metanetwork). A regional network was composed of all of the interactions observed between all species in the region with interaction strengths weighted by the visitation rates calculated from observations across all sites and sampling periods. We treated the regional networks from Florida and Wisconsin each as an estimate of the full set of potential interactions (i.e., species' fundamental niches) between all plant and pollinator species in the region and treated the locally observed interactions at each site as an estimate of the realized subset of all potential interactions (i.e., realized niches). However, we recognize that some rare interactions were likely missed (Chacoff et al. 2012), both locally and regionally.

To compare the topologies of networks formed by locally realized interactions and locally potential interactions, we assembled two versions of each network (Laliberte and Tylianakis 2010, Poisot et al. 2012). First, for each site a “realized” network was composed of the locally observed species and interaction rates (e.g., a binary version of a realized network is represented by the black squares in Fig. 1). Second, for each site we assembled a “potential” network, which was composed of the same species observed locally, but retained the set of regionally observed, or potential, interaction rates

between those species (e.g., a binary version of a potential network is represented by the gray and black squares in Fig. 1). Each potential network was generated by starting with the regional network and then pruning the plant and pollinator species down to the set of locally observed species, thereby maintaining their regional interaction rates. It is important to note that variation in phenological synchrony between plants and pollinators among sites can account for some of the potential interactions that are not locally realized. For example, a plant and pollinator that are observed interacting at site A may both be present at site B but not active in the same sampling period, resulting in an apparent mismatch in phenology at one site (B) but not another (A). We therefore excluded these interactions from potential networks corresponding to sites where the apparent phenological mismatch occurred.

Realized and potential networks were each analyzed as a matrix A with plant species in P rows and pollinator species in V columns. For realized networks, elements of A (a_{ij}) indicated the number of visits of pollinator j to plant i expected in 10 h of local observation (rounded to the nearest whole number), based on locally observed visitation rates. For potential networks, a_{ij} is the regionally observed number of visits by pollinator j to plant i expected in 10 h of regional observation, based on regional visitation rates. The expected numbers of visits in realized and potential networks are therefore weighted by the scale-specific sample effort (observation time) of each plant species. We make a distinction between *interactions* and *links* in our analyses. We define an *interaction* as a single visit of pollinator j to plant i . We define a *link* as the binary presence of interactions between plant i and pollinator j . Therefore, a link is present when $a_{ij} > 0$ and the number of interactions defines the weight of the link between plant i and pollinator j .

Binary connectance was calculated as the number of realized (or potential) links divided by the $P \times V$ possible links. Weighted versions of nestedness, modularity, and complementary specialization were calculated in R v3.2.0 (R Development Core Team 2015) for each of the realized and potential networks. We used the *vegan* package v2.3-2 (Oksanen et al. 2015) to calculate nestedness based on the weighted version of the NODF metric (Almeida-Neto and Ulrich 2011). Modularity, based on Newman and Girvan's (2004) formulation, was calculated using the *igraph* package v0.7.0 (Csardi and Nepusz 2006). We used the *fastgreedy* and *walktrap* module detection algorithms to find the network conformation that maximized the value of modularity and, for each site, used the output that resulted in the highest modularity. Though it may be preferable to calculate bipartite modularity (Dormann and Strauss 2014), the only algorithm for weighted networks to our knowledge (*computeModules* in the *bipartite* package v2.04; Dormann et al. 2009) is prohibitively slow. However, a test using the 15 Florida realized networks indicated that values of

modularity obtained using the *igraph* algorithms and the bipartite algorithm (maximum value of 5 runs, each with 1×10^7 steps and a tolerance of 1×10^{-10}) are nearly identical (Pearson's $r = 0.9993$). Specialization (H'_2 ; Blüthgen et al. 2006) was calculated using the *H2fun* algorithm in the *bipartite* package. Each network index was scaled 0 to 100, with 100 being the theoretical maximum value of connectance, nestedness, modularity, or specialization.

Null model analysis

We used two different null models for weighted networks to determine whether differences between realized and potential network topologies were greater than expected by chance. That is, we compared the topology of a realized network with randomized versions of its potential network, rather than randomized versions of itself. Null model 1 maintains the exact connectance, number of interactions, and number of plant and pollinator species of each *realized* network. It also ensures that species only interact with potential interaction partners, so interactions with non-potential partners are forbidden. This constraint differs from other models that generally assume each pollinator species can interact with all plant species, and vice versa. The probability of a link between a given plant and pollinator depends on the number of *potential* binary links the plant and pollinator have with other species. The number of interactions one species has with another depends on their *potential* number of interactions.

For each randomized network we began with the plant and pollinator species present locally and then filled out the binary links between species by randomly selecting (but with selection probabilities weighted by the *potential* binary row and column totals) links from the *potential* network, until the connectance of the randomized network equaled the connectance of the *realized* network. In this way, the binary degree distribution of each random network is similar to the corresponding potential network. Interactions were then randomly selected from the *potential* network (but with selection probabilities weighted by potential row and column interaction totals) and added to links (i.e., entries greater than zero) in the randomized network until the total number of interactions in the randomized network equaled the number of interactions in the *realized* network. In this way, the species strength distribution of each random network is similar to the corresponding potential network. Each plant and pollinator species' level of generalization in random networks will therefore reflect what was observed regionally, so differences between the unadjusted (i.e., for sample effort) number of interactions observed in the field and the number of interactions expected in 10 h of observation (which are used to construct realized and potential networks for analysis) will not bias the distribution of interactions in random networks.

In setting the connectance of randomized networks to that of realized networks, we are, in effect, rarifying the number of links in potential networks to the level of realized networks. A similar rarifying effect occurs by fixing the number of interactions in randomized networks to that of realized networks. These features of our null model are important for helping to control for the inherently greater sample effort used to generate the data for potential networks, which we discuss in more detail below.

By weighting the random selection of links and interactions using row and column totals, the degree and strength distributions of potential networks are probabilistically maintained in null model 1. This is similar to the behavior of the CE model (Guimarães and Guimarães 2006), which is commonly used for unweighted networks (e.g., Bascompte et al. 2003, Olesen et al. 2007, Zhang et al. 2011). We used a second null model (null model 2) in which this weighting is relaxed so that all links and interactions have equal probability of selection. Null model 2 is otherwise the same as null model 1. However, because non-potential interactions are forbidden in randomized networks, random selection of links and interactions of species that have more potential links and interactions is more likely. Therefore, there is still some correlation between randomized and potential networks in their degree and strength distributions in null model 2.

For null models 1 and 2, in order to assess whether realized network indices were significantly different from potential networks, we compared them to indices calculated from a set of 1000 randomized networks. Realized values were considered significantly different than expected by chance if they were greater or less than 95% of the values in randomized networks, respectively (i.e., if $P \leq 0.025$ or $P \geq 0.975$). We calculated relative nestedness, modularity, and complementary specialization for comparison among networks that differ in factors such as connectance and number of species by generating z scores, $z = (n - \bar{r})/\sigma_r$, where n is the realized value of the network index, and \bar{r} and σ_r are the mean and standard deviation, respectively of the index values for the 1000 replicate null model randomizations. R code for running null models 1 and 2 is included in Appendix S5.

Examining potential mechanisms

We examined two possible drivers of flexible foraging and differences between realized and potential networks. The first is preferentially foraging on locally abundant resources. We used binomial regression (rms package; Harrell 2014) in order to examine how the relative density of each plant resource species predicts the presence or absence of potential interactions with pollinators. However, this analysis may be biased when there is a local mismatch in phenology between plants and pollinators. Following Vázquez et al. (2009), we therefore used sample period-specific plant densities and sample period-specific pollinator presence/absence data to

remove potential interactions from the analysis that could not occur locally due to mismatches in the activity of each plant-pollinator species pair. This also accounts for differences in each plant species' abundance among sample periods.

A second potential mechanism that may drive flexible foraging is niche partitioning resulting from interspecific competition. We used linear models in R to examine relationships between relative network indices and niche availability. As a measure of niche availability we use the product of plant species richness and \log_{10} total resource density (i.e., the site-level sum of the relative densities of all plant species). Our index of niche availability therefore encompasses the number of available niche dimensions and the amount of available resources at a location.

Methodological caveats

There are two important methodological limitations of our study. First, an unavoidable consequence of our approach is that the sampling effort (i.e., the total time length of observation of each plant species) for constructing potential networks was inherently greater than the sampling effort for realized networks. We equalize visitation rates for potential and realized networks in our analyses (number of visits expected in 10 h of observation) but the greater regional sample effort could result in the observation of a greater number of rare potential interactions regionally. However, our null model approaches help to account for this by rarifying the number of links and interactions in randomized potential networks to that of realized networks. Moreover, our use of weighted networks, instead of unweighted networks, makes this sampling artifact much less likely to affect our nestedness, modularity, and specialization results. For example, if a potential interaction is rare regionally and not observed locally, the rare potential interaction would be given too much influence in an unweighted analysis. On the other hand, if a rare regional interaction was observed as common locally, the common local interaction would be given too little influence in an unweighted analysis.

To further increase confidence in our analyses, we used binomial regression to determine the effect of observation time (local sample effort) on the probability that a potential interaction was realized. That is, does greater local sample effort increase the likelihood of detecting the realization of a potential link? For each network in this analysis, potential interactions that were locally realized were assigned 1, while unrealized potential interactions were assigned 0. Non-potential interactions were excluded.

Second, our use of morphospecies for some pollinators has the potential to confuse our results. For example, if morphospecies A is actually two different taxonomic species, then apparent differences in foraging behavior among sites may actually be a result of confused identity

rather than foraging flexibility. However, we are confident that our use of morphospecies did not affect our results qualitatively. Although 30 of the 169 total pollinator species (3.04% of all individuals) observed in Wisconsin were identified only to morphospecies level (mainly sarcophagid and tachinid flies), most of these morphospecies were composed of a single individual, leaving only seven morphospecies (0.79% of individuals) capable of confusing our results. The removal of these seven morphospecies had no qualitative effect and only a very slight quantitative effect on our Wisconsin analysis (results not shown). The use of recorded HD video observations in Florida required greater use of morphospecies-level identifications. However, to minimize this bias in our Florida data set, the same person (B. J. Spiesman) provided consistent identification of all flower visitors. Moreover, a preliminary analysis of the Wisconsin data before species-level identifications were made on many abundant bee species (i.e., containing many morphospecies-level identifications) yielded results qualitatively similar to those we present here. In fact, five realized Wisconsin networks switched from nonsignificant to significantly more nested than their corresponding potential networks, and the correlation between relative nestedness and niche availability was strengthened with the use of greater taxonomic resolution. This suggests that our Florida morphospecies identifications produce conservative yet qualitatively reliable results.

RESULTS

Regionally, networks were made up of 70 plant and 155 pollinator species in Florida, and 61 plant and 169 pollinator species in Wisconsin. Locally, there was a mean of 23.1 ± 7.8 (SD) plant and 46.4 ± 18.4 pollinator species per site in Florida, and 17.3 ± 4.6 plant and 44.5 ± 14.4 pollinator species per site in Wisconsin. Although a number of plant and pollinator genera were shared between regions, species compositions were dissimilar with very few plant and pollinator species shared in common. However, because some of the pollinators in our study were identified only to morphospecies, we cannot be certain that more species did not occur in common between the two regions. Therefore, in addition to differences in local habitat types, regional habitat compositions (Appendix S1), and climate zones, Florida and Wisconsin networks show differences in community structure. Nevertheless, the two regions show consistent differences between realized and potential network topologies.

Pollinators in both regions visited far fewer plant species than their potential. On average, only 56.8% \pm 7.9% of potential links were realized; realized connectance was therefore much lower than potential connectance (Fig. 2). It is likely that some of the potential links were not observed locally because they are generally rare and only detected in the regional networks because of the inherently greater regional sample effort (minutes of

observation per plant species), so connectance results should be interpreted with caution. However, sample effort had no significant effect on whether potential interactions were realized in most (21 of 25) networks (see Appendix S2: Table S1). Four networks had a statistically significant relationship between sample effort and whether potential interactions were observed ($P < 0.05$), but sample effort explained only 5.2–9.8% of the variation (pseudo R^2 values). Thus, the differences we observed between realized and potential interaction networks are unlikely to be driven by differences in sampling effort and suggests that the lower connectance of realized networks is at least partly due to flexible foraging.

Realized networks were all less nested and more modular with greater complementary specialization than their corresponding networks of potential interactions (Fig. 2, Appendix S2: Table S2) and, based on null model 1, these differences are all greater than expected by chance (Fig. 3, Appendix S2: Table S2). Results based on null model 2 agree (Appendix S3): all realized networks were significantly less nested, more modular, and more specialized than their corresponding potential networks. Hereafter, we focus our presentation of results and discussion based on null model 1 because we feel it is more conservative than null model 2. We assume that pollinator populations are well mixed within regions (maximum distance to a nearest site is <15 km) so that differences between realized and potential network topologies are a result of flexible foraging behaviors and not due to intraspecific genetic variation that causes differences in trait matching among sites.

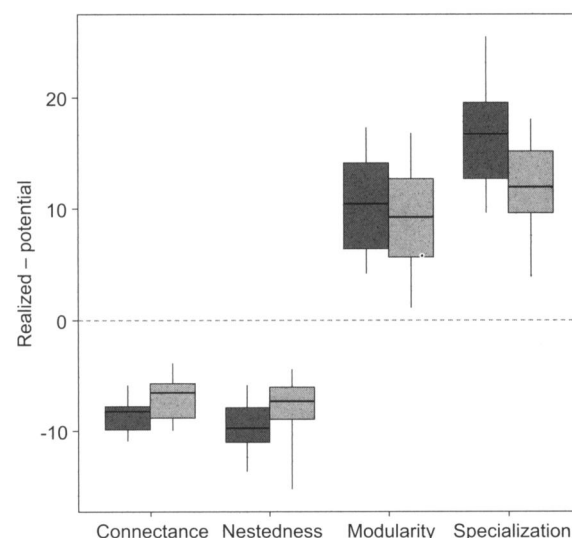


FIG. 2. Observed differences between realized and potential connectance, nestedness, modularity, and specialization, for the Florida (dark gray) and Wisconsin (light gray) networks. Horizontal lines within boxes indicate the medians, boxes indicate first and third quartiles, and error bars indicate the range. Each network index was scaled 0 to 100.

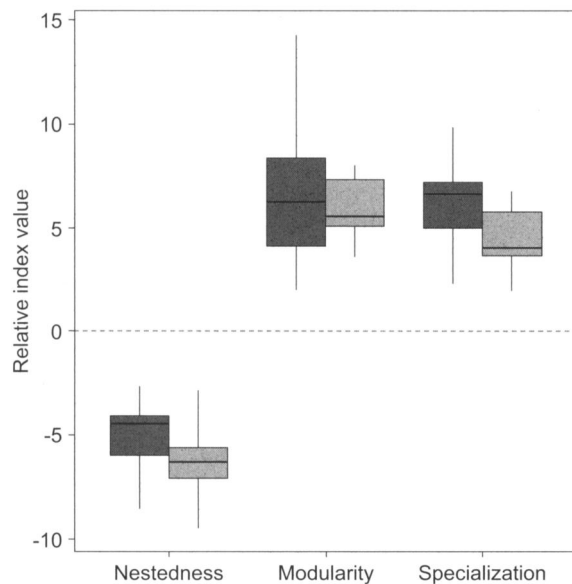


FIG. 3. Relative nestedness, modularity, and complementary specialization, for Florida (dark gray) and Wisconsin (light gray) networks determined using null model 1.

Based on null model 1, relative nestedness, modularity, and specialization all varied with niche availability (the product of plant species richness and total relative plant resource density) and the number of pollinator species (potential competitors; Fig. 4). We analyzed relative network index responses to niche availability because the relationships were stronger for niche availability than for other potential explanatory variables, such as pollinator species richness, and because plant and pollinator species richness are positively correlated in both Florida (FL; $t = 3.92$, $df = 13$, $P < 0.0018$, Pearson's $r = 0.736$) and Wisconsin (WI; $t = 4.61$, $df = 13$, $P < 0.0017$, Pearson's $r = 0.852$). Based on null model 1, relative nestedness decreased with niche availability (FL $F_{1,13} = 10.86$, $P = 0.0058$, $R^2 = 0.455$; WI $F_{1,8} = 24.95$, $P = 0.0010$, $R^2 = 0.757$) and the number of pollinator species (FL $F_{1,13} = 23.02$, $P = 0.0004$, $R^2 = 0.639$; WI $F_{1,8} = 14.89$, $P = 0.0048$, $R^2 = 0.651$). Relative modularity, on the other hand, increased with niche availability (FL $F_{1,13} = 26.21$, $P = 0.0002$, $R^2 = 0.669$; WI $F_{1,8} = 5.78$, $P = 0.0429$, $R^2 = 0.419$) and the number of pollinator species (FL $F_{1,13} = 12.28$, $P = 0.0039$, $R^2 = 0.486$; WI $F_{1,8} = 3.51$, $P = 0.0977$, $R^2 = 0.305$). Similarly, relative specialization increased with niche availability (FL $F_{1,13} = 19.3$, $P = 0.0007$, $R^2 = 0.598$; WI $F_{1,8} = 12.64$, $P = 0.0074$, $R^2 = 0.613$) and the number of pollinator species (FL $F_{1,13} = 11.33$, $P = 0.0051$, $R^2 = 0.466$; WI $F_{1,8} = 9.91$, $P = 0.0136$, $R^2 = 0.553$). Additionally, the observed number of modules within realized networks (separate from modularity per se) increased with plant species richness ($F_{1,23} = 13.76$, $P = 0.0012$, $R^2 = 0.374$), while the mean number of pollinator species per module did not vary with the number of modules ($F_{1,23} = 0.57$, $P = 0.4554$,

$R^2 = 0.025$), nor did the number of plant species per module ($F_{1,23} = 0.15$, $P = 0.6981$, $R^2 = 0.007$).

Binomial regression revealed that the relative density of each plant species is a poor predictor of the realization of potential interactions. Only 3 of 25 sites showed a significant relationship between the resource density-based likelihood of interaction and the realization of potential interactions (Table 1). Moreover, the variation explained by resource densities at these 3 sites, as

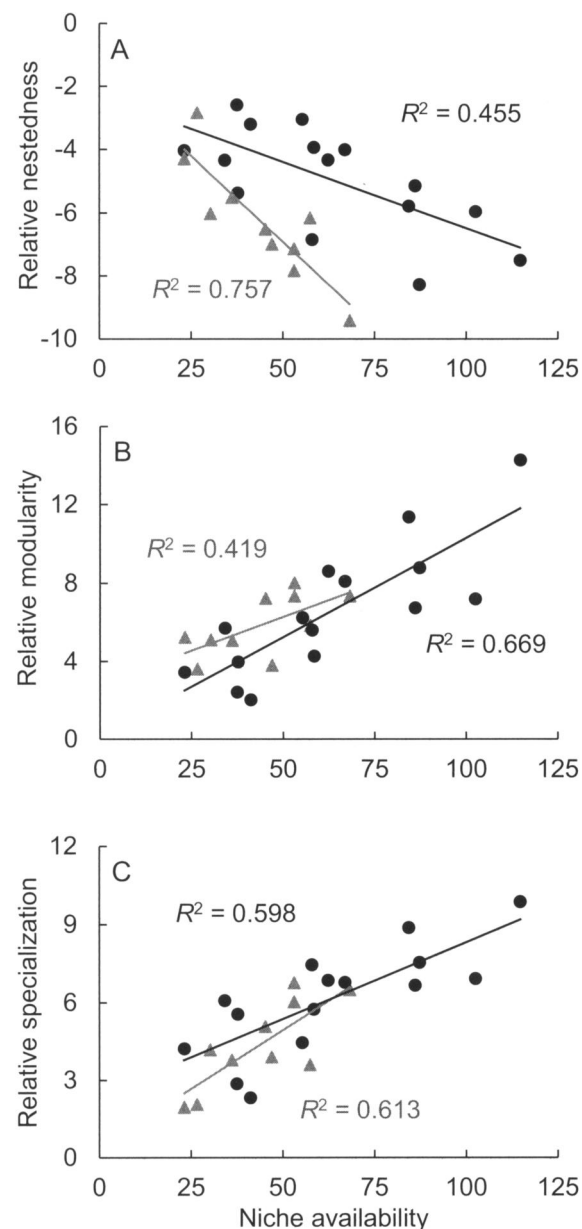


FIG. 4. Relationships between (A) relative nestedness, (B) modularity, and (C) specialization (H_2') and niche availability (plant richness \times \log [resource density]). Relative network indices are based on null model 1. Florida networks are represented by black circles and Wisconsin networks are represented by gray triangles.

TABLE 1. Binomial regression results showing the effect of plant resource density on the probability that potential interactions were locally realized.

Site	State	Estimate	SE	Wald z	P	Pseudo R^2	Sample size
1	FL	0.0009	0.0014	0.61	0.5399	0.002	321
2	FL	0.0044	0.0087	0.50	0.6145	0.002	204
5	FL	-0.0029	0.0116	-0.25	0.8033	0.002	53
10	FL	0.0097	0.0192	0.51	0.6122	0.003	112
11	FL	0.0007	0.0061	0.11	0.9102	0.000	111
12	FL	0.0028	0.0025	1.11	0.2684	0.012	147
13	FL	0.0011	0.0186	0.06	0.9508	0.000	96
14	FL	0.0782	0.0257	3.04	0.0024	0.110	187
15	FL	-0.0015	0.0027	-0.54	0.5878	0.001	338
16	FL	0.0101	0.0098	1.03	0.3038	0.006	221
17	FL	0.0053	0.0064	0.84	0.4031	0.003	285
18	FL	0.0175	0.0145	1.21	0.2269	0.016	134
19	FL	0.0075	0.0029	2.59	0.0095	0.038	283
20	FL	0.0090	0.0140	0.65	0.5189	0.007	76
21	FL	-0.0010	0.0009	-1.08	0.2790	0.005	322
Becker	WI	0.0143	0.0224	0.64	0.5238	0.007	85
Brooklyn	WI	-0.0009	0.0026	-0.33	0.7434	0.001	150
Harvey's Marsh	WI	0.0856	0.0597	1.44	0.1511	0.068	73
Hook Lake	WI	0.0002	0.0083	0.02	0.9848	0.000	176
Jackson	WI	0.0024	0.0043	0.57	0.5706	0.002	203
Lodi Marsh	WI	0.0099	0.0042	2.38	0.0172	0.044	196
Northrup King	WI	0.0053	0.0041	1.29	0.1968	0.025	99
Rowe	WI	0.0202	0.0120	1.68	0.0926	0.067	74
Schoenberg	WI	-0.0049	0.0037	-1.31	0.1917	0.014	161
Swan Pond	WI	0.0012	0.0051	0.24	0.8104	0.001	144

Notes: States are FL, Florida, and WI, Wisconsin. Sample size is equal to the number of potential binary links in each a network. Significant *P* values are shown in boldface type.

determined by pseudo R^2 values, was low, ranging from 3.8% to 11.0%. Therefore, a greater plant resource density did not strongly increase the likelihood of a potential interaction being realized.

DISCUSSION

Within the bounds of their potential interaction partners, the great flexibility in resource use by pollinators has strong effects on the realized topology of plant–pollinator networks. We found that pollinator species forage on only a subset of their potential flower resources that are present locally, resulting in a reduction of niche breadth and realized networks with much lower connectance than their corresponding networks of potential interactions. However, the particular subset of resource species that are utilized also greatly affects the pattern of interactions. As foraging effort on flower resources is dropped for some species, and shuffled among others, networks converge on a much more modular pattern with high complementary specialization, and a much less nested pattern than their potential. Furthermore, differences between realized and potential topologies are similar across regions that vary greatly in climate, habitat, and species composition, suggesting that our results are generally

representative of a wide variety of plant–pollinator communities.

A number of mechanisms could contribute to a reorganization of network topology through flexible foraging. Pollinators may locally adapt their foraging effort in response to interspecific competition for plant resources, which may drive resource partitioning, leading to modular networks. If interspecific competition increases with pollinator (competitor) species richness, the corresponding increase in resource diversity (niche dimension) should allow pollinators more options to partition resources and avoid competitive exclusion (MacArthur and Levins 1967, Pianka 1974). Along these lines, Fründ et al. (2013) showed that bee species can partition niches by switching to alternative, even non-preferred, plant resources in the presence of a competitor; the presence of an alternative resource allowed for this competition-induced switch. Supporting this idea, we found that relative modularity and complementary specialization increased with pollinator species richness and with niche availability (Fig. 4). Moreover, the number of modules (separate from the degree of modularity per se) within networks increased with plant species richness, while the number of pollinator and plant species comprising each module remained constant. This suggests that a greater diversity of resources allowed for more

partitions (modules) while pollinators were able to utilize similar ranges of resources locally.

Another possible mechanism to explain flexible foraging effects on network topology involves adaption to variation in local resource densities. For example, optimal foraging theory (MacArthur and Pianka 1966) or related ideas like flower constancy (Waser 1986) suggest that focusing foraging effort on the most locally abundant resource species may reduce search and handling time, increasing foraging efficiency and net energy gain. However, binomial regression results (Table 1) suggest that the probability of potential interactions being realized is not strongly dependent on plant relative densities. These results fall in line with the network-scale differences between realized and potential networks. Although focusing on abundant resources should increase specialization within species, network-level specialization should decrease and nestedness should increase because more pollinator species would be focusing on the same highly abundant plant species while ignoring the same low-abundance species, and this was not observed in our study. Zhang et al. (2011) found that flexible foraging increased network nestedness as adaptive foragers focused on more abundant resources, however their model did not include interspecific competition as a factor in population growth or adaptive foraging decisions.

Our results suggest that resource partitioning is a much more likely driver of differences between realized and potential network topology than targeted foraging on high-density resource species. We did not measure differences among plant species in their attractiveness or quality of floral rewards, which can also affect foraging decisions (Makino and Sakai 2007). However, if pollinators focused on highly rewarding plant species we would have expected realized networks to converge on a more nested topology, as with our expectation of a resource density effect. If resource densities are not a strong driver of the realization of potential interactions, it implies that some pollinator species bypass high-density potential resources for lower-density resources. This is not surprising as competition is known to result in foraging that is otherwise suboptimal (Werner and Hall 1979).

Implications of modularity for the maintenance of diversity in plant–pollinator networks

Modularity has long been thought to generate stability in complex networks (Simon 1962, May 1972) and has since been shown to be important for many different types of systems, including predator–prey networks (Stouffer and Bascompte 2011), financial systems (Haldane and May 2011), and brain networks (Meunier et al. 2010). In ecological networks, modularity follows niche partitioning, which has well-documented benefits for biodiversity and, increasingly, ecosystem functioning (Poisot et al. 2013, Peralta et al. 2014). But, as

in many types of systems, modularity can also allow for efficient, specialized transfer of information or resources. From a plant's perspective, the realized specialization of its pollinators means that it has dedicated partners and stigmas less likely to be clogged with nontarget pollen. Reduced specialization can therefore have a negative effect on plant reproductive function (Brosi and Briggs 2013). Also the effect of a disturbance, like species loss, is better contained within modules so that it does not spread among them leading to system-wide collapse (Stouffer and Bascompte 2011). The spread of pathogens, an increasingly significant area of study for pollinators (reviewed in McArt et al. 2014), is another form of disturbance that can be limited by a modular network topology (Griffin and Nunn 2012). Transmission of pathogens among pollinators frequently occurs at flowers (McArt et al. 2014) so modularity and specialization of resource use may help limit system-wide contagion. Adaptive flexibility, in which species can continuously reevaluate foraging choices, in combination with an emergent modular network topology, may therefore be vital for maintaining biodiversity in variable environments.

CONCLUSIONS

The flexible foraging behavior of pollinators affects the realized topology of plant–pollinator interaction networks. We found that, locally, pollinators restrict their diet breadth to a subset of their potential despite the fact that usable plant resources are present. Foraging flexibility allows pollinators to focus on a particular subset of their resource base resulting in patterns of realized interactions that are significantly less nested and a significantly more modular and specialized topology than networks based on all potential interactions. Moreover, the relative modularity and complementary specialization of networks increases with niche availability, a function of plant species richness and abundance. These results are consistent with a hypothesis that pollinators adjust their foraging strategies to minimize interspecific competition for food resources. This partitioning becomes stronger in increasingly diverse networks as more different resources are available and more competing species are present. These results are consistent across two widely separated geographic areas and across different habitat types with dissimilar communities of pollinators and plants, indicating that adaptive flexibility and resource partitioning are generally important for realized network topology.

We have focused on pollinators as drivers of a shifting network topology because of their ability to rapidly alter their foraging choices. However, plants can also experience interspecific competition for pollinators (reviewed in Mitchell et al. 2009) that may help drive phenotypic plasticity in floral display or rewards. These factors certainly affect pollinator foraging decisions (Mitchell 1992) and thus network topology.

ACKNOWLEDGMENTS

We thank C. Bergstrom, S. Hyson, T. Kim, I. McCrie, and A. Wenninger for help in the field and the lab. T. Kim, R. Mallinger, and H. Gaines provided helpful feedback on the manuscript. J. Gibbs and K. Johnson helped with the identification of bees and Lepidoptera, respectively. We thank B. Inouye for his support on the development of the Florida data set. Research was funded in part by grants from the National Science Foundation (DEB-0816838) and USDA (NIFA/AFRI 2012-67009-20146).

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