Shifts in pollinator composition and behavior cause slow interaction accumulation with area in plant–pollinator networks

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Abstract. Although ecologists have a solid understanding of the positive species–area relationship, little is known about how and why variation in habitat area influences the richness, structure, and function of species interaction networks. To address this, we investigated plant–pollinator interaction networks of the herbaceous rocky outcrop communities in Ozark glades (Missouri, USA) of different areas. We quantified the degree to which the increase in the number of species interactions with area differed from a null model based on sampling, where numbers of individuals increase with area. Although plant–pollinator interactions were expected to increase more steeply with area than species richness as a result of sampling, the observed rate of increase was considerably lower than expected. Two mechanisms could lead to this pattern: a higher proportion of specialist species in larger glades or generalist pollinators becoming more selective in their diets in larger glades. We found support for the former hypothesis, and those changes in species composition were strong enough to outweigh behavioral changes in the opposite direction; generalist pollinators were more selective in smaller glades. If these results are general, larger habitats may be needed to conserve interactions than would be thought based on species accumulation curves.

Key words: connectance; ecosystem service; generalization; habitat fragmentation; Missouri, USA; Ozark glades; pollination; specialization.

Introduction

One of the most robust relationships in ecology is the observation that species accumulate with increasing area, which can result from increased habitat heterogeneity, lower extinction rates in larger populations, and/or passive sampling (Rosenzweig 1995). With the increasing loss of natural habitats, there is heightened interest in using this relationship to understand species loss and to optimize the size of conservation areas (e.g., Rosenzweig 2003, He and Hubbell 2011). However, if plant–animal interactions are critical to species' persistence (e.g., Bastolla et al. 2009), then the preservation of biodiversity also requires reserves that are large enough to maintain the structure of these interactions (Forup and Memmott 2005, Forup et al. 2008, Tylianakis et al. 2010). Despite the importance of species interactions for maintaining diversity, surprisingly little is known about their relationship with habitat area.

In food web and plant–pollinator interaction networks, quantitative syntheses across studies have found that the overall connectance within a web typically decreases as the size of the web (i.e., the total number of species) increases (Banašek-Richter et al. 2009, Vázquez

et al. 2009, Petchey et al. 2010). The degree to which diet specialists interact with subsets of increasingly diet generalist species (i.e., nestedness) generally increases with species richness in mutualistic networks (Guimaraes et al. 2006). However, much less is known about the relationship between the mean number of interactions per species (linkage density) and web size or area. Some studies have shown linkage density to be scale invariant or weakly positively related to species richness in food webs (Banašek-Richter et al. 2009), but to our knowledge, only two studies have tested the relationship between links per species and habitat area, and both found the relationship to be positive. Sabatino et al. (2010) investigated plant–pollinator interactions on isolated hills in Argentina and found that interaction richness increased twice as fast as species richness with increasing area. Likewise, Spencer and Warren (1996) found that in experimental microcosms, larger habitats supported more complex food web, containing more species, more interactions per species, and longer food chain lengths than smaller habitats.

Prior to ascribing biological mechanism to the pattern of increasing linkage density with area, it is important to recognize that this relationship can result simply from differences in the number of individuals, and thus species richness (Preston 1962), in communities that vary in area (a sampling effect). Deviations from the null-expected changes in interaction richness with area could result in either steeper or shallower increases in

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links per species with area than expected by sampling. It is these deviations that are biologically meaningful beyond the probabilistic expectation of increased interactions with increased species. Previous studies on the influence of habitat area on linkage density in interaction webs (Spencer and Warren 1996, Sabatino et al. 2010) did not explicitly test the degree to which their results deviated from a null expectation, so it is unclear whether biological mechanisms other than sampling contributed to their results.

At least two non-mutually exclusive mechanisms could contribute to any deviations in the rise of interaction richness with increasing area beyond sampling, including the overall degree of diet generalization and specialization, which is a property of the species, and the degree of flexibility in diet selectivity, which can differ across individuals within a species. First, if the proportion of diet specialist vs. diet generalist species in the pollinator community changes with increasing area, this could lead to steeper (proportionately more generalist species in larger habitats) or shallower (proportionately more specialist species in larger habitats) slopes of interaction richness with increasing area than expected by sampling. Second, foraging flexibility and food selectivity may also change with area (MacArthur and Pianka 1966, Stephens and Krebs 1986, Fontaine et al. 2008). A species may become less selective in its diet in larger habitats if, for example, different individuals specialize on different resources such that more individuals in larger habitats cumulatively utilize a higher number of resources, or if other constraints (e.g., interspecific interactions) are relaxed in larger relative to smaller habitats. If species become less selective in their diets, this would lead to a steeper slope of interaction richness increasing with area than expected by chance. Alternatively, species could become more selective in their diets in larger habitats, if, for example, species are able to focus on their preferred resources when they are more locally abundant, leading to a shallower slope between interaction richness and area than expected. A third possibility is that larger networks might have lower connectance as a by-product of lumping across space or time, which could introduce "forbidden links" (Jordano et al. 2003) of noninteracting species; we removed this possibility by utilizing a sampling design that minimized such lumping (see *Methods*).

In this study, we examined how species interactions accumulated relative to species richness in plant–pollinator networks from habitat islands that varied in size by over two orders of magnitude. We sampled plants and pollinators in Ozark glades in Missouri, USA, which are insular rock outcrop patches of herbaceous vegetation within a forested matrix and contain many endemic plants and pollinators (Ware 2002). These communities historically stretched over large expanses of limestone bedrock in this region (Nelson and Ladd 1980), but have been considerably reduced in area due to fire suppression over the last century. This ecosystem is ideal for examining area

effects on species and species interactions because recent restoration efforts have created a wide variety of habitat sizes among otherwise similar environments. We first examined whether the rate at which plant–pollinator interactions accumulate with glade area deviates from the accumulation of plant and pollinator species, leading to differences in plant–pollinator network structure (e.g., links per species) among glades of different sizes. We also investigated the effects of glade area on an additional component of network structure, interaction nestedness, which is indicative of functional robustness to perturbations (e.g., Bascompte et al. 2003) beyond the influence of shifts in the identity and abundance of species. Next, we devised a null model to account for the expected variation in interaction richness due to the increase in individuals and species richness with sampling from larger areas. Finally, we evaluated deviations from that null expectation in the context of possible biological mechanisms, such as differences in the relative richness of specialist vs. generalist species or in pollinator behavior and diet selectivity in glades of different areas.

METHODS

Field methods

We sampled plants and pollinators in 10 patchily distributed dolomite Ozark glades in Missouri, USA that ranged in size from 450 to 71 000 m^2. These glades contained similar plant communities, although smaller glades were not as species rich as larger glades. We intensively sampled the plant–pollinator interactions of each glade during peak bloom (3.5 weeks, totaling 84 hours of sampling time) in the summer of 2010 to minimize the possibility of introducing forbidden links between plants and pollinators into our glade networks. In each glade, we established a nonlinear transect from which we could observe the entire glade area. Each observer continuously walked the transect, capturing any insect visitors observed contacting the reproductive parts of a flower (see Plate 1). We sampled pollinators in proportion to the relative abundances of open flowers, and we calculated pollinator visitation rate for each glade. We spent more total time observing larger glades (regression, $F_{1,8} = 35.45$, $P = 0.0003$, $r^2 = 0.79$) because additional time is required to thoroughly investigate larger areas (Sugiura 2010). Sampling took place during peak pollinator activity (0800–1430 hours) on sunny, windless days. Each insect was swabbed for pollen with a cube of fuschin dye to evaluate pollinator fidelity (e.g., Alarcón 2010). All pollinators were identified to species. Across all glades, we recorded 45 flowering plant and 127 pollinator species (Appendix).

Relationships between species richness, number of interactions, and network structure with area

We investigated the relationships between the number of plant species, pollinator species, and plant–pollinator interactions vs. glade area using linear regressions on

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log-transformed variables. Because we observed larger glades for more time than smaller glades and found higher pollinator visitation rates in larger glades ($F_{1,8} = 12.01$, $P = 0.0085$, $r^2 = 0.55$), we rarefied pollinator species richness and plant–pollinator interaction richness for some analyses (Ecosim version 7; Gotelli and Entsminger 2004). Interaction nestedness (discrepancy, robust to differences in network size; Ulrich and Gotelli 2007) was calculated to investigate the degree to which specialists interacted with subsets of more generalist species in each glade. We determined the relationships between these network metrics using R 2.12.1 with the bipartite package version 1.14 (see Supplement 1; Dormann et al. 2008) and glade area using regressions.

Null model

To address the null hypothesis that observed patterns in plant–pollinator interaction accumulation with area result from changes in species richness and abundance of individuals in the absence of any other differences among glades, we employed a null model to simulate the predicted relationship between the richness of pollinator species or plant–pollinator interactions and area (pollinator individuals; Supplement 2). We parameterized the model with the observed plant : pollinator ratio and the slope and intercept of the observed species–area relationship. Species and interaction richness were output for the values of pollinator abundances observed in each glade, and the resulting null-expected network metrics were compared to those observed; deviations indicate that biological mechanisms influence the relationship between the observed number of interactions and habitat area. To determine whether the slope of the null-expected pattern in interaction richness with habitat area was statistically different than the observed, we calculated the proportion of the replicated simulations that had a slope equal to or less than the observed slope.

Mechanism: area effects on pollinator species composition

Because the plant and pollinator species were nested subsets across glades (i.e., species-poor glades contain frequently occurring species, whereas glades that are more species rich contain both frequent and less common species; $P < 0.05$), we sought to determine whether glade area was a main contributing factor to this nestedness and the presence (or absence) of species. We investigated the degree to which small glades contained nested subsets of the plant and pollinator species present at large glades using regression analysis of the relationship between the rank order of nestedness of each glade site for plant or pollinator species and glade area. A significant, positive relationship between nestedness rank and glade area would indicate that small glades supported only the more widespread/common subset of species, while larger glades contained both widespread and more narrowly distributed species. To investigate the degree to which diet generalist pollinator

species varied across the area gradient, we tallied the overall diet breadth of each pollinator species across all glades, and calculated the mean diet breadth of pollinator species present in each glade. We used linear regression to determine the relationship between mean diet breadth (generalization level) of pollinator species and glade area.

Mechanism: area effects on pollinator behavior

To address area effects on pollinator foraging behavior and selectivity of generalist pollinators, we determined the top five pollinator species with the widest overall diet breadths that were also present in eight or more of the glades. For each of these species, we determined the proportion of possible interactions that were realized, given the identities of the plant species present (Laliberte and Tylianakis 2010; possible interactions were those found to occur in this system in at least one glade), and calculated the mean selectivity of these generalists in each glade. For each glade, we also calculated H_2', a network-level measure of interaction selectivity robust to network size and sampling effort, which indicates the degree to which species interactions deviate from the null expectation that they are interacting in proportion to their abundance (0 represents no selectivity and 1 represents complete selectivity; Blüthgen et al. 2006). We calculated d' as a species-level measure of interaction selectivity (Blüthgen et al. 2006) for *Augochlorella aurata* (Halictidae), a common bee present in all 10 glades. We investigated the relationships between H_2' and d' with glade area using regression. Additionally, using the richness of pollen species identified on the bodies of female *A. aurata*, we investigated the relationship between individual bee fidelity and glade area with regression. To control for differences in plant species richness across glades, we also tested this relationship using only *A. aurata* females captured on *Dalea purpurea*, a common plant species present in all glades. In all cases, the assumptions of regression were met, and regression analyses were performed in JMP 4.0.4 (SAS Institute 2001).

Results

Relationships between species richness, number of interactions, and network structure with area

There were strong positive relationships between plant ($F_{1,8} = 16.67$, $P = 0.0035$, $r^2 = 0.64$) and pollinator ($F_{1,8} = 8.80$, $P = 0.018$, $r^2 = 0.46$) species richness and glade size. More plant–pollinator interactions were found in larger glades ($F_{1,8} = 16.39$, $P = 0.0037$, $r^2 = 0.63$). These patterns were maintained when pollinator richness ($F_{1,8} = 6.93$, $P = 0.03$, $r^2 = 0.40$) and plant–pollinator interaction richness ($F_{1,8} = 22.84$, $P = 0.0014$, $r^2 = 0.71$) were rarefied to account for differences in sample size (Fig. 1A); rarefied interaction richness increased almost three times faster with glade area than did rarefied pollinator species richness. Plant–pollinator
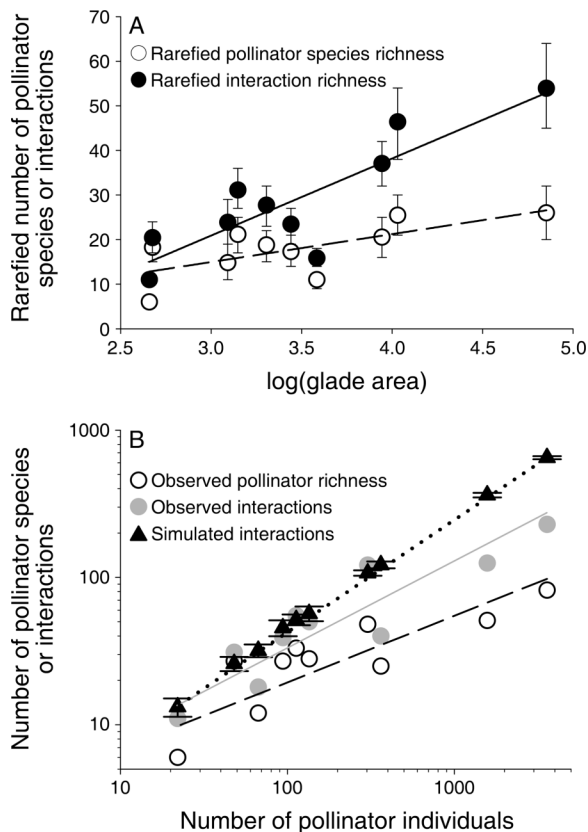
FIG. 1. (A) The rarefied richness of plant–pollinator interactions (solid circles, solid line) increased more steeply with glade area (originally measured in square meters) than did pollinator species richness (open circles, dashed line). Error bars are 95% confidence intervals. (B) Simulated values (solid triangles) for interaction richness were far greater than observed values (solid circles). Error bars show the 97.5% confidence intervals of simulated values and do not overlap observed values. Observed and simulated values for pollinator species richness were similar (open circles and dashed line, respectively).

interactions were more nested in larger glades ($F_{1,8} = 8.77$, $P = 0.018$, $r^2 = 0.46$).

Null model

Based on sampling alone, plant–pollinator interactions should increase more steeply with area than the do the number of species. However, this null model predicts a rate of interaction increase (slope = 0.76) far greater than that which was observed (slope = 0.53) ($P < 0.0001$; Fig. 1B). Confidence intervals (97.5%) for interaction richness do not overlap observed values.

Mechanism: area effects on pollinator species composition

The plant and pollinator species present at small glades were nested subsets of those species present at large glades (for plants, $F_{1,8} = 11.40$, $P = 0.0097$, $r^2 = 0.54$; for pollinators, $F_{1,8} = 11.16$, $P = 0.010$, $r^2 = 0.53$). The overall diet breadth of pollinator species decreased with glade area (Fig. 2A; $F_{1,8} = 8.60$, $P = 0.019$, $R^2 = 0.46$), indicating that specialist pollinators were proportionately richer in larger glades.

Mechanism: area effects on pollinator behavior

The mean selectivity of the top five generalist pollinators decreased with glade area (Fig. 2B; $F_{1,8} = 5.55$, $P = 0.046$, $R^2 = 0.34$). Quantitative metrics of selectivity illustrated the same patterns: both H_2' and d' (*A. aurata*) declined with glade area ($F_{1,8} = 5.28$, $P = 0.051$, $r^2 = 0.32$ and $F_{1,8} = 4.04$, $P = 0.079$, $r^2 = 0.25$, respectively). Together these results suggest that generalist pollinator species were more selective in smaller glades. However, the fidelity (mean pollen species richness) of female *A. aurata* individuals did not vary with glade area ($F_{1,8} = 1.64$, $P = 0.24$). This lack of pattern held for *A. aurata* individuals captured only from *D. purpurea* ($F_{1,8} = 0.034$, $P = 0.86$).

DISCUSSION

We found a strong influence of glade area on the richness of plants, pollinators, and their interactions. The richness of species interactions accumulated more steeply with area than did species richness, and thus the number of interactions per species increased with glade area. This
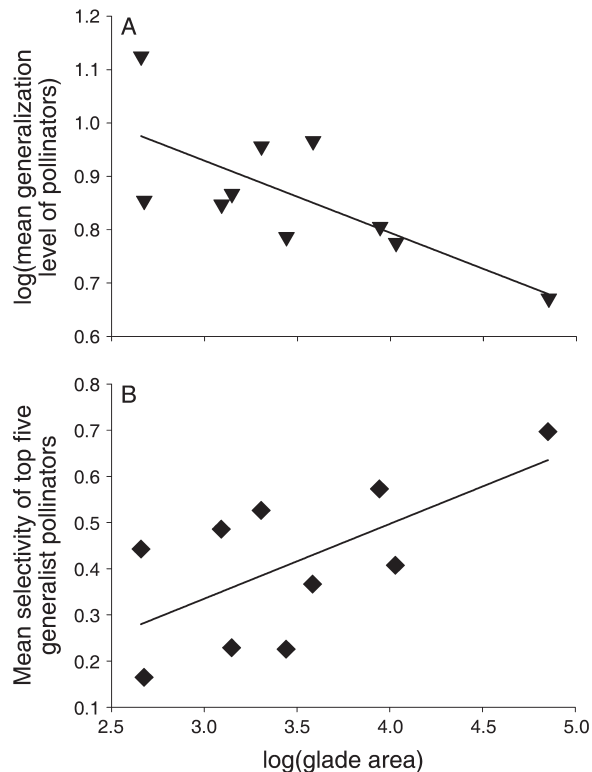

FIG. 2. Relationship between glade size and diet selectivity. (A) Smaller glades contained primarily diet generalist pollinators while larger glades contained both diet generalists and specialists. (B) The generalists present in smaller glades, however, exhibited more selective foraging behavior. Zero represents complete selectivity, and 1 represents no selectivity.

PLATE 1. Prickly pear cactus flower (*Opuntia humifusa*) visited by the bee *Agapostemon virescens* (Halictidae). Photo credit: L. A. Burkle.

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pattern is consistent with other empirical studies that examined how species interactions accumulated among habitats differing in size (Spencer and Warren 1996, Sabatino et al. 2010). However, this pattern is expected simply due to the fact that sampling more area leads to more individuals, sampling more individuals leads to more species found, and sampling more species leads to an increase in the number of links per species. Thus, in order to determine whether the observed shifts in plant–pollinator network structure across glades that varied in size resulted from something other than just sampling, a null model is necessary. The results from our null model analysis showed that the observed increase in the rate of interaction accumulation with area was considerably shallower than that expected, indicating that although sampling plays a role, biological mechanisms that influence the structure of plant–pollinator networks also strongly influence this pattern.

The pattern of shallower accumulation of species interactions with increasing habitat area than expected by chance could result from the presence of relatively more specialized species and/or more selective behavior in larger glades. Our results support the former hypothesis because plant and pollinator species in the

smaller glades were nested subsets of those present in larger glades. That is, common generalist species were present in both small and large glades, whereas rarer and more specialized species were only present in the larger glades. This is not a surprising pattern, given that small or fragmented areas often lack specialist species (e.g., Turner 1996, Cagnolo et al. 2009). Furthermore, the overall average diet breadth of pollinators decreased with glade area, suggesting that more specialist species were present in larger glades (Fig. 2A).

In opposition to the hypothesis that our results could be explained by species becoming more selective in larger glades, we instead found that pollinators were less selective in larger glades; the proportion of possible interactions realized increased with glade area (Fig. 2B). These results suggest that the species that were present in smaller glades behaved differently than those in large glades, and failed to fulfill their interaction potential (based on the species present) in smaller glades relative to the larger glades. This pattern was consistent across all pollinator species present in each glade, as well as for a subset of common generalist pollinators. Because these behavioral differences are in the opposite direction of what would have been expected, given our observation

of shallower increases in the accumulation of species interactions with area, we conclude that the shift in species composition to disproportionately more specialists in larger glades was particularly strong in order to outweigh the combined effects of sampling and pollinator selectivity.

Why might generalist pollinators have narrower than expected diets (be more selective) in small glades? Although our data do not allow us to explicitly discern these mechanisms, several possibilities exist. First, competition among pollinator species may be more intense in small glades than in larger glades, if for example, their densities are proportionately higher in smaller glades. Here, each pollinator may be forced to forage on only the subset of plants for which they are most competitive (Inouye 1978), even though there may be other plant species present that they are capable of foraging on under less competitive conditions. Second, if individuals in small glades are more limited by factors besides floral resources (e.g., nesting sites) in small relative to large glades, they might forage on only their most preferred foods in those smaller glades.

It is worth noting that the decreased selectivity of pollinators in large glades represents the summed population-level resource use of the species. The common halictid bee species, *Augochlorella aurata*, for example, exhibited a wider absolute and relative diet breadth in larger glades, but individuals did not display the full diet breadth of the species in large glades. The foraging behavior of *individual* pollinators is the important consideration for plant reproduction, given that the fidelity of individual bees will strongly influence the effectiveness of pollination. Further investigation of individual-level vs. species-level pollinator behavior and subsequent plant reproduction across habitat area gradients will enable us to better understand the consequences of these interactions.

In addition to altering the richness of species and interactions in the network, the overall structure of plant–pollinator networks was also influenced by glade area. The degree of nestedness of the networks increased with increasing glade area, suggesting that both the identity of the species that are maintained in large glades and the ways in which they interact contribute to the maintenance of these communities. This pattern is in agreement with other studies that have found that nestedness increases with network size in mutualistic networks (e.g., Bascompte et al. 2003, Vázquez and Aizen 2004, Guimaraes et al. 2006), suggesting that the redundancy of interactions typical of intact systems is maintained primarily in large, continuous habitats. Interestingly, previous studies on network size have compared across systems that covary in a number of characteristics other than species richness, such as productivity and latitude (e.g., Vázquez et al. 2009), whereas our study was conducted within one ecosystem type, but similar patterns emerged in plant–pollinator networks with

habitat area as a primary factor influencing patterns of species richness and their interactions.

The observation that species richness increases with area sampled has critically guided investigations of the effects of habitat loss and fragmentation. However, species conservation also requires maintenance of essential species interactions, such as plant–pollinator interactions (e.g., Bastolla et al. 2009). The accumulation of species interactions with area is a critical knowledge gap for long-term biodiversity conservation, and here we find that habitat area strongly influenced the structure and function of plant–pollinator interaction networks as a result of shifts in abundance of individuals, species richness and composition, and pollinator behavior. Additional investigations of these patterns in other systems with appropriate null models, as well as a more thorough understanding of individual-level pollinator behavior in diverse community contexts, coupled with assessments of plant and pollinator reproduction, will provide important insights into the effects of habitat loss and fragmentation on species interactions and the conservation and maintenance of biodiversity.

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Supplemental Material

Appendix

Species list of plants and pollinators in this study (*Ecological Archives* E093-219-A1).

Supplement 1

The R source code used to determine aspects of plant–pollinator network structure as described in this paper (*Ecological Archives* E093-219-S1).

Supplement 2

The R source code used in the null model analysis (*Ecological Archives* E093-219-S2).

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