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The future of plant–pollinator diversity: Understanding interaction networks across time, space, and global change[1]

Laura A. Burkle[2,4] and Ruben Alarcón[3]

[2]Department of Biology, Washington University, St. Louis, Missouri 63130 USA; and
[3]Biology Program, California State University Channel Islands, Camarillo, California 93012 USA

Structural analysis of plant–pollinator networks has revealed remarkably high species and interaction diversity and highlighted the species important for pollination services. Although techniques to analyze plant–pollinator networks began to emerge a decade ago, the characterization of spatiotemporal variation of interactions is still in its infancy. Understanding the ecological and evolutionary causes and consequences of spatial and temporal variation in plant–pollinator interactions is important for both basic and applied questions in community structure and function, the evolution of floral traits, and the development of optimal conservation strategies. Here we review observational, theoretical, and experimental studies of temporal and spatial variation in plant–pollinator interaction networks to establish a foundation for future studies to incorporate perspectives in spatiotemporal variation. Such perspectives are crucial given the rapid environmental changes associated with habitat loss, climate change, and biological invasions, which we discuss in this context. The inherent plasticity of plant–pollinator interactions and network structure suggests that many species should be able to persist by responding to environmental changes quickly, even though the identity of their mutualistic partners may change.

Key words: community composition; community dynamics; connectance; mutualism; phenology; pollination; specialization–generalization continuum; species interactions.

The ecological interactions between plants and pollinators make important contributions to global diversity. Through their nested architecture, plant–pollinator networks reduce competition and increase biodiversity (Bastolla et al., 2009). At least 300 000 plant species and over 200 000 vertebrate and insect species are involved in mutualistic plant-pollinator interactions worldwide (NRC, 2007; Ollerton et al., in press). Furthermore, diverse pollinator assemblages can lead to increased ecosystem function through enhanced pollination services, plant reproduction, and persistence (e.g., Klein et al., 2003; Fontaine et al., 2006). This diversity and the accompanying community-level maintenance of pollination services are being challenged by environmental change and population declines of plants and pollinators (Biesmeijer et al., 2006). Given rapid environmental changes, including habitat destruction, climate change, and biological invasions, it is essential to consider the natural spatiotemporal variation in plant–pollinator interaction networks as a foundation for developing solid conservation and management options.

Traditionally, pollination ecologists studied plant–pollinator systems with a single focal plant species and usually one or a few closely associated visitor taxa, such as bumblebees or hummingbirds, rather than entire ecological communities. This approach may be ideal for species pairs that have coevolved with one another, but not for species that interact with diverse groups of mutualistic partners across space and time (Thompson, 2005). Furthermore, this traditional view assumed that plant–pollinator mutualisms were ecologically and evolutionarily specialized, such that plant species are pollinated by, and coevolved with, their current pollinating taxa (Waser et al., 1996; Aigner, 2001). However, in the late 1990s, biologists began to question the assumption of ecological specialization and instead argued that pollination systems are relatively generalized, largely because of perceived spatiotemporal variation in pollinator visits (Herrera, 1996; Ollerton, 1996; Waser et al., 1996; Waser, 1998). This prompted a renewed interest in the study of entire communities over the past decade in which ecologists sought to characterize the diversity of plant–pollinator interactions and the degree of specificity in pollination systems (e.g., Waser and Ollerton, 2006).

These efforts were further fueled by computational advances from several areas of science and by the realization that entire ecological communities can be profitably viewed as complex interaction networks (Strogatz, 2001; Proulx et al., 2005). These "network" analyses have revealed several interesting patterns, including (truncated) power-law degree distributions, with most species having few partners, but some having many (Jordano et al., 2003; Vázquez and Aizen, 2003). Other studies have revealed that plant–pollinator relationships are highly asymmetric (Vázquez and Aizen, 2004) and nested (Bascompte et al., 2003), such that species with few partners primarily interact with hierarchical subsets of a generalized core group of partners. And although some pollination networks may also contain small subgroups of tightly linked species (Dicks et al., 2002; Olesen et al., 2007), such compartmentalization is not necessarily a dominant feature of all plant–pollinator networks

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[4] Author for correspondence (e-mail: laura.burkle@montana.edu); present address: Ecology Department, Montana State University, Bozeman, MT 59717 USA

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(e.g., Alarcón et al., 2008). These and other studies highlight the value of analyzing plant–pollinator communities as interaction networks and have furthered our understanding of community-scale ecological patterns and the mechanisms generating them (for a thorough review, see Vázquez et al., 2009a).

However, much less attention has been paid to the characterization of spatiotemporal variation within plant–pollinator interaction networks. This lack is likely due to the significant effort required to construct a single network, let alone the time and resources required to construct multiple networks across multiple sites and/or seasons (Hegland et al., 2009). But, such studies are sorely needed given the unprecedented levels of land use change (Wilcove et al., 1998), which may create dramatic spatial variation. Seasonal, annual and long-term (e.g., successional) patterns of species interactions are also likely to be altered given the potential effects of climate change on plant abundances, flowering phenology (Inouye, 2008; Miller-Rushing and Primack, 2008), and pollinator phenology (Gordo and Sanz, 2006). Such changes could result in the decoupling of mutualistic plant–pollinator interactions and negatively impact plant and pollinator populations (Gordo and Sanz, 2005; Devoto et al., 2007; Memmott et al., 2007; Hegland et al., 2009; Schweiger et al., 2010). Furthermore, a thorough understanding of the scale and patterns of spatial and temporal variation of interaction networks is necessary to understand the evolutionary consequences of plant–pollinator interactions (Thompson, 2005; Waser, 2006). For example, how will floral traits evolve in nested communities when the identity of the generalized core group of pollinators varies among years (e.g., Alarcón et al., 2008)? And at what spatial scales are interaction networks biologically relevant, such that their structure potentially influences mating events and gene flow among plants (e.g., Fortuna et al., 2008)?

Our goals here are to (1) synthesize the recent studies that have described spatial and temporal variation in plant–pollinator interaction networks, particularly in the context of changing environmental conditions and (2) propose ways to incorporate such perspectives in future studies, through our analyses and discussion presented here.

PLANT–POLLINATOR INTERACTIONS ACROSS TIME

Although previous publications have documented temporally variable pollinator environments for specific plant species (e.g., Herrera, 1988) and have described intra-annual variation in plant and bee composition (e.g., Petanidou and Ellis, 1993, 1996), temporal analyses of entire plant–pollinator interaction networks are still in their infancy. This limitation is largely due to the lack of available data sets with a temporal component, which is understandable given the effort required to complete such tasks. For example, many of the earlier pollination network analyses were based on observations derived from a single season (e.g., Memmott, 1999) or were aggregated across multiple seasons without regard to time scales (see references in Jordano et al., 2003). Understanding the patterns and scale of temporal variation is necessary to gauge the long term effects of global change on plant–pollinator interaction networks. Only in the last few years have ecologists specifically addressed daily, seasonal, and annual temporal patterns in network structure (e.g., Olesen et al., 2008). In general, these studies have attempted to characterize intra- or inter-annual patterns of network structure, which is how we will summarize the findings. Here we will focus on describing empirical studies rather than studies that simulate network dynamics following species removal (e.g., Valdovinos et al., 2009; Kaiser-Bunbury et al., 2010).

Intra-annual variation in plant–pollinator networks—The few recent studies that have focused on intra-annual patterns have analyzed network structure over various sampling intervals to determine the optimal time scales to characterize them or to describe seasonal changes. For example, would a single pollination network accurately describe the community structure of a year-long system, or would several shorter consecutive time intervals be more appropriate? Medan et al. (2006) addressed this issue by analyzing connectance values, the proportion of plant–pollinator links actually observed, for monthly and cumulative, consecutive monthly time periods for the Talar, a xeric forest from Argentina, and a Phryganic community in Greece. For both systems, not surprisingly, the authors found that aggregating observations into longer time periods decreased connectance values. In further analysis of the year-long Talar system, ordination of monthly groups of the active taxa revealed temporal subassemblages, with compositional similarity typically greatest among months from the same season (Basilio et al., 2006). These results suggest that analysis of year-long systems should be done at shorter, biologically relevant periods because analyses of observations aggregated over longer periods introduces "forbidden links" (Jordano et al., 2003) created by noncoincidental plant and pollinator phenologies, resulting in apparent (but inaccurate) decreased network cohesion and increased specialization (Petanidou et al., 2008). Though these results are obvious in hindsight, it should now be recognized that the time scale of the network considered should reflect the time scale of the system, i.e., the flowering phenology and flight periods of the constituent plants and pollinators.

Olesen et al. (2008) investigated intra-annual temporal variation on a shorter intra-annual time scale, by following the day-to-day dynamics of an arctic pollination network in Greenland for the entire flowering seasons (snowmelt to snowfall) in each of two consecutive years. Construction of daily interaction matrices revealed significant turnover in species composition, which resulted in ever-changing species interactions and network topology. In addition, the linkage degree of both plant and pollinator species was positively correlated with the length of their phenophase, such that species active for longer periods interacted with more partner species. Furthermore, new plants and pollinators expressed partial preferential attachment to the most linked mutualistic partners already present in the system the day before.

Together these results suggest that plant–pollinator networks are highly dynamic due to changes in species composition and should be analyzed at the time scales that reflect the biology of the constituent species, specifically when attempting to characterize inter-annual variation, rather than lumping observations across entire "spring" or "summer" seasons. Analysis over such long time frames alters estimates of generalization by grouping together plant and animal species that are not active at the same time and, hence, cannot interact with each other. Thus, constructing networks at the appropriate time scales will also provide biologists with the resolution necessary to characterize structural patterns, such as nestedness and modularity, without the inclusion of "forbidden links." Given that plant–pollinator networks appear to be built up following a simple mechanism of new species preferentially interacting with established

generalists in the system, more studies like Olesen et al.'s (2008) are needed to improve our understanding of how network topology changes over biologically relevant time scales (e.g., days to weeks). Such time scales are also more likely to correspond to the effects climate change is having on flowering phenology and pollinator activity. Resolving interaction networks at weekly or biweekly intervals would aid in the comparison of climate change effects across communities, given that growing seasons at high elevation sites are usually much shorter in duration than at lower elevation sites. Hence, a 1-wk shift in flowering at a subalpine meadow with a 6-wk flowering period may have a more significant effect on network structure compared to the same shift in a lower elevation site with a 12-wk long flowering season.

Annual variation in plant–pollinator networks—In the last few years, several studies have described the temporal patterns of pollination networks across 2–4 years of sampling to reveal interesting similarities. For example, most networks were highly nested, with the degree of nestedness being relatively invariant across years (Alarcón et al., 2008; Petanidou et al., 2008; Burkle and Irwin, 2009; Dupont et al., 2009). Similarly, the levels of connectance, modularity (or compartmentalization), number of plant and pollinator species, and number of interactions were highly conserved across years (Alarcón et al., 2008; Petanidou et al., 2008; Burkle and Irwin, 2009; Dupont et al., 2009). In general, linkage degree distributions also remained unchanged, typically following truncated power-law distributions for plants and power-law distributions for animals (Olesen et al., 2008; Dupont et al., 2009).

In all of these networks, however, the composition of the plant and pollinator assemblage differed significantly among years. For example, Alarcón et al. (2008) reported that nearly one-third of the plant species and more than half of the animal species recorded over their 3-year study were only observed to interact with a partner in a single season. Similarly, Dupont et al. (2009) report that between-year persistence of animal visitors was generally much lower than of plant species, such that only about one third of the animal species encountered in 1 year were observed in a consecutive year, while 46–97% of plants species persisted between years. Olesen et al.'s (2008) analysis over two seasons found that about 80% of the pollinators detected in one season were observed in the other, while Petanidou et al. (2008) reported that only 20.5% of pollinator species were detected across all 4 years of their study.

The similarity in the identity of the plant–pollinator interactions was also low among the annual networks. Petanidou et al. (2008) estimated interaction similarity among their four annual networks using the Jaccard index and found values <0.2 between any 2 years. In 30% of the cases when interactions were lost, plants and pollinators species were present but did not interact with each other, suggesting that pollinators are extremely plastic in resource use, resulting in network "rewiring." Understanding the conditions under which rewiring occurs, possibly involving the relative abundances of plants and pollinators and subsequent influences on foraging choices, is an important topic ripe for empirical and theoretical consideration. Dupont et al. (2009) also report drastic changes in the identity of the species interactions, with less than 25% of the interactions present in 1 year being observed in the next. Using the Procrustes analysis, a matrix comparison method, both Alarcón et al. (2008) and Burkle and Irwin (2009) found that network topology was not consistent across years, such that the frequency and identity of plant–pollinator interactions differed. Similarly, in a seminatural meadow system in Norway, Lazaro et al. (2010) found that the degree of generalization of the 20 most common plants was not correlated between years, but instead related to changes in flowering duration, synchrony with other plant species, and abundance, further highlighting the plastic nature of plant–pollinator interactions.

Albrecht et al. (2010) recently compared the network structural properties of a chronological sequence of succession sites exposed by receding glaciers in Switzerland. Although this approach confounds spatial and temporal variation, it does provide insight for gauging long-term changes in network structure. Overall, Albrecht et al. (2010) found that plant and animal species richness increased through the chronological sequence. However, species composition varied across the chronological sequence, with bees dominating younger sites and flies at older sites. Furthermore, measures of pollinator generalization and nestedness increased, while network-level specialization decreased though succession sequence. It would be interesting to determine if early or later successional stages are more likely to exhibit temporal variation or be resilient to disturbances, such as species introductions and losses, given their differences in species composition and network structure. For example, will early successional stages be affected more strongly by species loss because specialists have fewer mutualistic partners to interact with compared to older successional stages that are dominated by generalist species? And are introduced generalist species more likely to establish in early successional stages than later stages? These and other similar questions need to be addressed to understand the assembly of plant–pollinator networks and to develop long-term conservation plans.

The overall similarity of findings across studies is all the more striking given differences in habitat, methods, level of taxonomic resolution, and the nature of the observations, i.e., qualitative vs. quantitative data. Together these studies suggest that most plant–pollinator systems are likely to be more generalized than previously perceived, given the high degree of annual turnover in species composition and rewiring of interactions among species that co-occur across multiple years. Why species that are observed to frequently interact in one year do not interact in another is still not understood and requires additional attention, requiring ecologists to consider competitive interactions among plants for pollinator services. Both insect populations and flower production can vary dramatically among years, often in relation to drought, grazing, and other factors, and such variation in abundance likely plays a large role in the frequency (or absence) of interactions. A great deal of caution must be used when interpreting the results of single season studies to try to infer patterns of ecological specialization or its evolutionary significance, because such studies will surely underestimate the degree of plasticity inherent to interaction networks and overestimate the importance of apparently specialized interactions. For example, pollinators might shift their foraging to use less-preferred floral resources when a preferred resource is rare or absent. Thus, complementary behavioral assays (e.g., Junker et al., 2010) could be useful in determining pollinator preferences and possibly help explain why interactions rewire. Additionally, studies that incorporate measures of pollinator services are needed to determine what such rewiring could mean in terms of plant fitness and pollinator mediated selection. For example, Alarcón (2010) found that a large fraction of floral visitors do not carry conspecific pollen and thus are not pollinators.

Thus, it could be possible that much of the perceived temporal variation in species interactions would have a small impact on plant reproduction if most of the interactions that are being rewired or lost are those with opportunistic "cheaters" as opposed to true pollen vectors.

It is also apparent that although plant–pollinator systems are highly dynamic, interaction networks are structurally stable across all time scales studied. In particular, network structural properties such as nestedness, degree distributions, modularity, and connectance, remain relatively conserved. This suggests that the mechanisms governing the assembly of pollination networks are likely independent of species composition, thereby preserving ecosystem function, across seasons, years or decades. Such opportunism in species interactions should increase the resilience of pollination networks to species loss or shifts in phenology, perhaps rendering some conclusions (Memmott et al., 2007) overly pessimistic. However, as Albrecht et al.'s (2010) study suggests, long-term successional changes will not only alter species composition but could affect structural properties as well with sufficient changes to the component species. Future studies that consider temporal perspectives should strive to relate how changes in species composition impact network structure.

***Case study 1: The impact of species turnover on patterns of network topology*—**The fact that descriptors of network structure are not sensitive to the temporal compositional changes in plant–pollinator communities suggests that ecologists need to perform additional analyses to characterize the extent of species turnover and interaction rewiring. For example, recent studies have used similarity indices (e.g., Petanidou et al., 2008) and ordination techniques (Basilio et al., 2006) to gauge such changes. The use of matrix comparative methods, such as the likelihood analysis of pairwise interaction probabilities (Vázquez et al., 2009b) and the Procrustes analysis (Alarcón et al., 2008; Burkle and Irwin, 2009; Alarcón, 2010), seem to be promising techniques for comparing network topology, given that these approaches consider the identity and pattern of interactions among plant and pollinator species, as well as make use of permutation tests to calculate the statistical significance of network resemblance.

Here we present an example of how species turnover can influence network topology and the pattern in the frequency and identity of plant–pollinator interactions in a montane meadow system in California, United States. This system is one of the few well-studied pollination networks to be surveyed for three consecutive years (2001–2003; see Alarcón et al., 2008 for details) and was originally chosen because the peak summer flowering period was relatively short and thus believed not to experience much interannual variation compared with other systems of longer duration. For each of the three seasons, observed plant–pollinator interactions were subdivided into six intervals that correspond to weekly floral surveys of 120 plots of 1 m^2. We pooled floral abundances across the plots for each week and then calculated pairwise dissimilarity values among weeks using the Bray–Curtis index. To estimate the overall congruence between weekly quantitative plant-by-pollinator interaction matrices (i.e., networks), we performed an orthogonal, least-squares Procrustes analysis using the FATHOM toolbox (Jones, 2002) implemented in the program MatLab 7.1. This analysis produces the m^2 goodness-of-fit statistic that varies from 0 to 1, with 0 indicating that the matrices are identical.

Correlations between the Bray–Curtis index values based on floral composition and the m^2 statistic reveal that the degree of similarity in topology among weekly interaction networks is positively related to the degree of similarity in floral composition in two out of the three seasons (Fig. 1; 2001: $r = 0.715$, $P = 0.001$; 2002: $r = 0.341$, $P = 0.213$; 2003: $r = 0.876$, $P < 0.001$), with 2002 being the outlier; a year with significant drought and reduced flower production (Alarcón et al., 2008) . These results show that as plant species turn over during the course of a single season, so do the pattern of species interactions, such that the resemblance in network topology between any two weeks typically mirrors that of the plant assemblage. Such dynamic "rewiring" also suggests that temporally distinct interaction networks might succeed one another during the course of a single season. To verify this, we searched for a homogeneous network topology by applying Ward's hierarchical clustering algorithm to the m^2 values. Based on this analysis, it appears that each season is subdivided into three successive phases, comprising early, middle, and late summer interaction networks, typically lasting 2 wk (Fig. 2). Thus, arbitrary comparison of "monthly" or "seasonal" interaction networks masks the dynamic rewiring occurring at significantly shorter time scales.

PLANT–POLLINATOR INTERACTIONS ACROSS SPACE

Given that plant and pollinator taxa vary in their spatial distributions, spatial processes also likely influence their interactions (Olesen and Jordano, 2002; Vázquez et al., 2009a), but only recently have spatial effects in interaction networks been addressed explicitly in empirical studies and models incorporating spatial variation. In studies focusing on plant populations

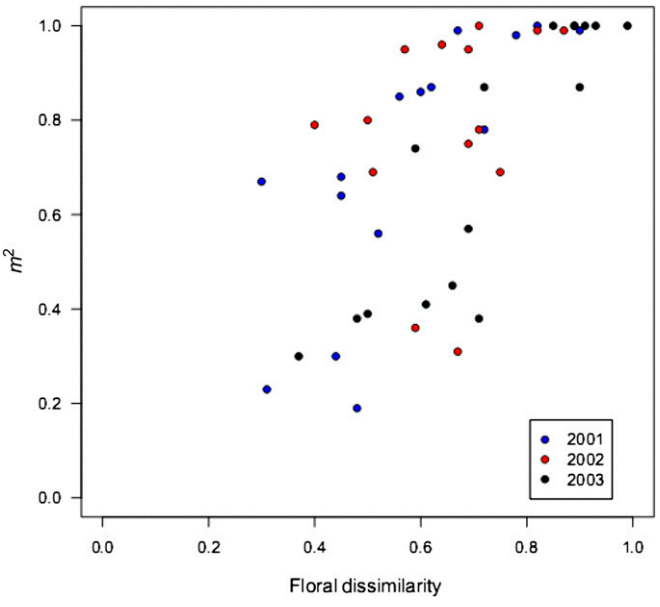

Fig. 1. Scatter-plot depicting the relationship between Bray–Curtis dissimilarity values comparing weekly floral surveys and the Procrustes' m^2 goodness-of-fit statistic, that varies from 0 to 1, with 0 indicating that the matrices are identical, used for compare the resemblance among weekly pollination networks. Procrustes' m^2 are positively correlated with floral dissimilarity values for 2001 (blue circles, $r = 0.715$, $P = 0.001$) and 2003 (black circles, $r = 0.876$, $P < 0.001$).

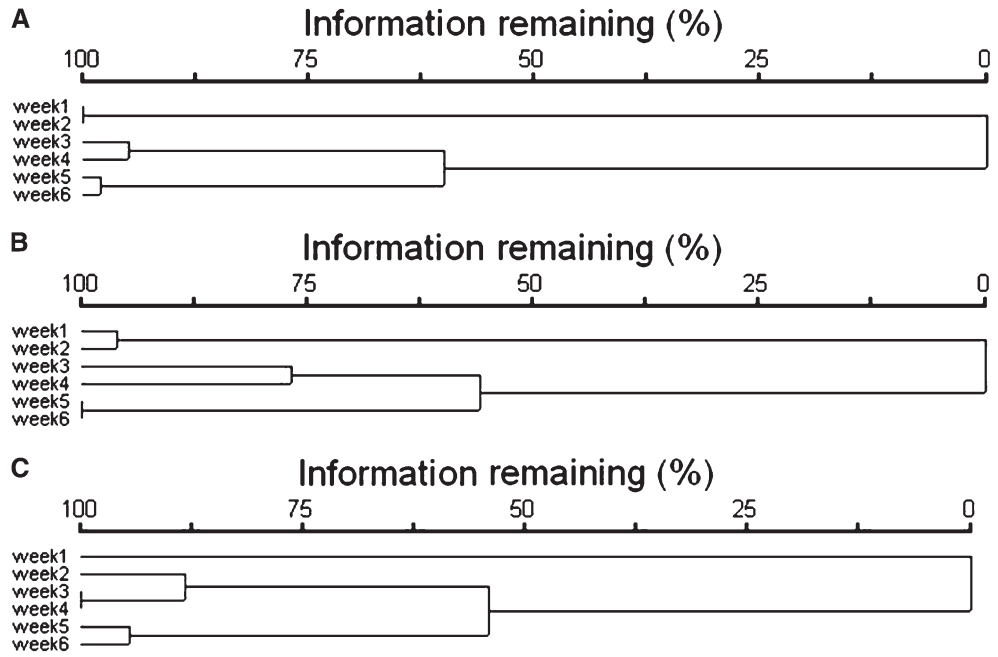

Fig. 2. Dendrograms showing the relationships among weekly interaction networks based on Ward's hierarchical clustering algorithm of the Procrustes m^2 goodness of fit statistic for (A) 2001, (B) 2002, and (C) 2003 seasons. Each season is subdivided into three successive phases, with homogenous network topology, that typically lasts 2 weeks.

of a single species, spatial variation in the assemblages of visiting pollinators is frequently found (e.g., Eckhart, 1992; Guitian et al., 1996; Fenster and Dudash, 2001; Moeller, 2005) and can lead to differences in pollen limitation and plant reproduction (e.g., Mustajarvi et al., 2001; Gomez et al., 2010). Additionally, landscape traits, including habitat fragmentation and quality, are known to have strong effects on pollinator communities and plant visitation (e.g., Steffan-Dewenter and Tscharntke, 1999; Klein, 2009). Very little work, however, has been scaled up to ask whether community-level plant–pollinator interaction networks vary spatially, and the underlying processes influencing network-level variation across space are virtually unknown. Understanding the causes and consequences of such spatial variation is important for answering fundamental ecological and evolutionary questions of coevolution and specialization in plant–pollinator interactions and as well as for applied questions of their conservation, restoration and management. Here, we summarize and expand with some new analyses.

Spatial variation in plant–pollinator networks—Plants and pollinators must meet in space (and time) to interact. "Forbidden links" include those plants and pollinators that cannot interact due to the lack of overlap in spatial distributions, including situations as local as a canopy-dwelling plant and a ground foraging pollinator or spatial separation of ranges at much larger geographic scales (Jordano et al., 2003). Sampling of plant–pollinator interactions is often performed at one site; if multiple sites are used, the interaction data are often pooled to create one interaction matrix. Sampling plant–pollinator interactions over space may involve more habitat types, heterogeneity of environmental factors (both biotic and abiotic), and may include a specific environmental gradient of interest (e.g., elevation, rainfall). The use of interaction data at multiple sites can be used to test for the dominant factors contributing to spatial variation in interaction composition, diversity, and structure in different systems.

Spatial influences on species interactions have been addressed primarily in the context of food webs, despite their potential importance on the outcome of plant–pollinator interactions within and among communities. Investigators of mutualistic networks have been slow to incorporate spatially explicit modeling of interactions and effects on network structure, but there are some notable exceptions. For instance, in a plant–frugivore interaction simulation model, Morales and Vázquez (2008) found strong effects of spatial aggregation and lack of mobility on connectance, nestedness, and the strength and identity of interactions. To our knowledge, similar modeling has not been done thus far for plant–pollinator networks. However, in an empirical study, Burkle and Irwin (2009) found that although plant and pollinator community composition and abundance differed among subalpine sites 0.8 to 2.7 km apart, interaction network structure was not significantly different across this geographic space. In case study 2, we expand these analyses and introduce a framework to allow environmental factors to be tested for their contribution to network interactions across space in biologically relevant ways.

Habitat area—To move forward in our fundamental understanding of how interaction networks vary across space, we might first consider how the habitat area and the species that are represented to varying degrees in habitats of different sizes contribute to the assembly of plant–pollinator interactions. Species-area curves and the theory of island biogeography have been instrumental to our understanding of communities. Now we need to ask whether interactions between species accumulate with area in the same way that species do, because answering this question has important implications for the maintenance of biodiversity, functioning of ecosystems, and conservation and management decisions.

Species richness typically accumulates with area, but whether total species and total interactions accumulate with area at the

same rate is not well understood. As the size of an interaction network increases (i.e., total number of species increases), the average number of links per species, and thus connectance, tend to decrease (reviewed in Vázquez et al., 2009a). In the first study to document differences in network structure on islands of different sizes, Sugiura (2010) found connectance of plant–ant interactions to decrease with island area. Whether these patterns result from the incorporation of more forbidden links in larger, lumped networks is not known. We currently lack information in other systems about the relationship between network size and the area sampled and whether these statistical properties of networks represent an effect of area and the shape of species-area curves. Moreover, these relationships with network size may result from increased average trophic specialization due to an increase in the number of rare specialist species and/or behavioral changes among generalists in which their preferred food plants are more readily available by chance in a larger species pool (i.e., they are fulfilling their trophic niche). Thus, we might expect the slope of the species–area line to be steeper than the slope of the interaction–area line (i.e., species accumulate faster with area than do interactions). Such hypotheses have implications for the maintenance of biodiversity and functioning of ecosystems; the conservation or restoration of an area containing focal species may not necessarily also result in the maintenance or restoration of their expected interactions. Small conservation areas may contain a core group of species and a limited number of important interactions, while only large areas may support all the interactions needed for a fully functioning system. Sabatino et al. (2010) have begun to investigate the relationships between habitat area and plant–pollinator interaction diversity and found a trend opposite to this prediction—the number of interactions increased faster with area than species richness did. Whether this relationship holds across systems is not known and deserves additional study.

Moving beyond the fundamental consideration of habitat area and how plant–pollinator interactions accumulate with increasing sampling area, there is the more mechanistic approach of determining which biotic and abiotic factors explain the majority of variation in interaction diversity and structure at different spatial scales. At local scales, variation in microclimate (e.g., soil properties, moisture, sunlight) may be most important for spatial overlap of plants and their pollinators, while at larger scales, the effects of rainfall, elevation, slope and aspect, land cover, and subsequent effects on plant and pollinator community composition may dominate. We explore some of these local and landscape effects on plant–pollinator interactions in case study 2. Given that pollinator individuals are more mobile than plant individuals across the landscape in their daily activities, pollinators and plants may respond to environmental variation across spatial scales differently, depending on the degree of dispersal limitation and the spatial distribution of required resources.

Habitat loss, fragmentation, and land-use change—Understanding the spatial component of plant–pollinator interactions is increasingly important because space, or suitable habitat of appropriate size and distribution, is disappearing rapidly. Habitat destruction is the leading threat to biodiversity (Wilcove et al., 1998). Plant–pollinator interaction webs appear to be robust to species extinctions and loss, largely due to asymmetric interactions and their nested structure (Bascompte and Jordano, 2007). Fortuna and Bascompte (2006) modeled the effects of habitat loss on plant–pollinator network structure, finding that even low levels of habitat destruction have discernable effects on species loss, but persist in the face of higher destruction levels than randomly assembled communities until reaching a threshold at which the community collapses. Additional empirical work is needed to understand the implications of habitat loss, fragmentation, and different types of changing land use on plant–pollinator interaction networks.

We need to move beyond the vision of a community as merely an assemblage of species to incorporate how interactions accumulate with species, with area, and over time. The challenge is to unite these processes occurring at different spatial and temporal scales to understand the relative importance of different biotic and abiotic factors acting on plant–pollinator interactions. Additional consideration of merging metacommunity concepts with measurement and analysis of plant–pollinator interactions will also contribute to our understanding of the factors contributing to interaction diversity and function.

Case study 2: The impact of environmental factors on plant–pollinator interactions across space—Here we introduce a framework to test the contribution of local and landscape factors to the spatial patterning of network interactions. As a case study, we used plant–pollinator networks collected from 24 different plots in subalpine meadows in Colorado, United States (see Burkle and Irwin 2009, 2010 for details). We measured 17 local and landscape environmental factors associated with each of the plots, including soil pH, aboveground plant primary productivity, flower production, and pollinator behavior metrics (e.g., time spent per flower). For landscape factors, 30-m resolution elevation, canopy, and land cover data were obtained from the National Map Seamless Server (U. S. Geological Survey, http://seamless.usgs.gov/). The program ArcGIS 9 was used to determine the elevation, slope, and aspect as well as canopy and land cover within a 300-m radius of each study site.

We calculated the environmental distance between all pairwise combinations of plots in each of 3 years using the principle components of the local and landscape factors. Geographic distances (in m) between plots were also calculated. We then compared plant and pollinator communities of each plot using Bray–Curtis dissimilarity and determined the similarity (m^2) of all pairwise combinations of plant–pollinator interaction networks for each plot in each year using Procrustes analysis. With Mantel tests, we investigated the relationships between geographic or environmental distance and plant or pollinator community similarity or similarity in network topology for each year and investigated which of the original environmental variables explained most of the variation in these relationships.

We found that local and landscape environmental factors were important in explaining variation in community structure, and substantial variation in plant–pollinator interactions occurred across a relatively small geographic space. Geographic distance between study sites explained very little of the variation in community similarity for plants, pollinators, and their interactions (Fig. 3, Mantel test: $-0.06 < r < 0.54$, $0.80 > P > 0.001$), relative to environmental factors (Fig. 4, Mantel test: $0.25 < r < 0.78$, $0.004 > P > 0.001$). Interestingly, the steepness of these relationships were similar for plants and pollinators, indicating that although pollinators are mobile, they respond to environmental gradients at the same scale that plants do or that plant and pollinator communities are very tightly associated in this system. In general, however, there was the most scatter in the relationship between environmental distance and plant–pollinator

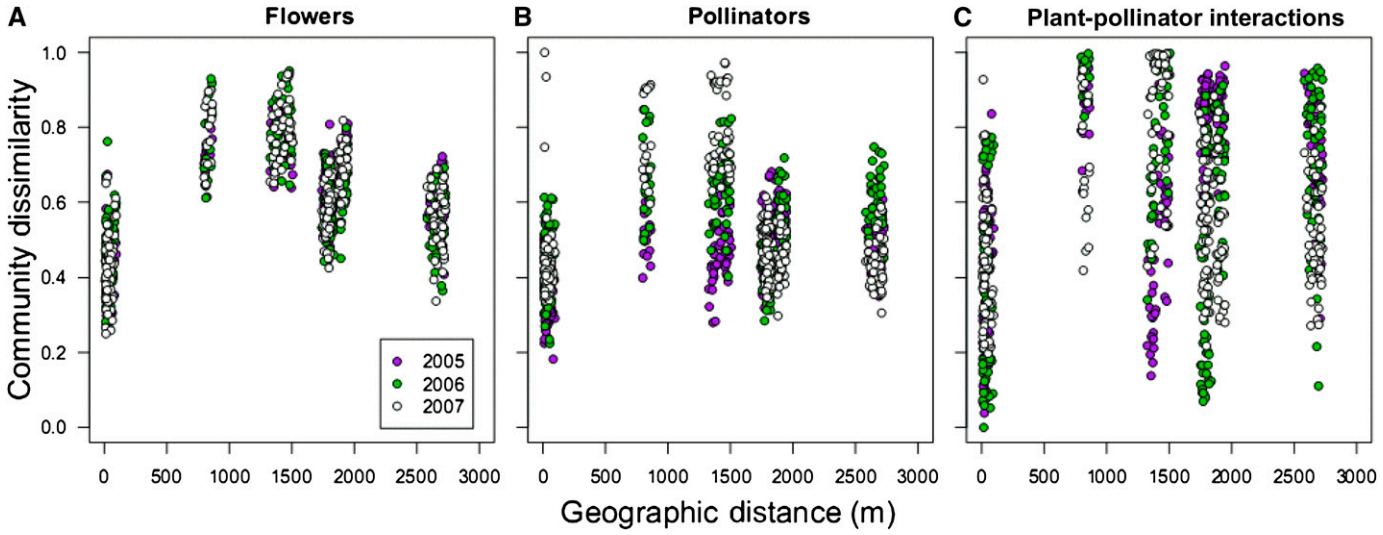

Fig. 3. There were no clear relationships between measures of community dissimilarity of (A) flowers, (B) pollinators, or (C) plant–pollinator interactions and geographic distance. Each circle is one pairwise plot–plot comparison. Year 2005: purple circles, 2006: green circles, 2007: white circles.

interactions (Fig. 4C, $r > 0.25$, $P < 0.004$), suggesting that additional biotic or abiotic factors contribute to the structuring of interactions even when similar communities of plants and pollinators are present. The relationships between environmental or geographic distance and measures of community similarity differed among years, due to variation in both local environmental factors and community composition. In this topographically complex area, slope of the study site was the single factor most consistently and strongly correlated to flower and pollinator community similarities ($r > 0.48$, $P < 0.001$). Slope may encompass a variety of local environmental conditions, such as soil substrate and stability and incident sunlight and heat accumulation, which could easily influence plant community composition and recruitment as well as pollinator behavior. For plant–pollinator interaction dissimilarity, elevation was positively correlated in 2005 ($r = 0.37$, $P < 0.001$), pollinator visitation rate in 2006 ($r = 0.66$, $P < 0.001$), and slope in 2007 ($r = 0.54$, $P < 0.001$). Thoughtful study site choice and manipulation of abiotic factors could help separate environmental influences on plant and pollinator communities at different scales in this and other systems.

FUTURE DIRECTIONS

Experimental approaches for plant–pollinator networks—Our basic understanding of plant–pollinator interaction networks can be used to approach applied questions in community ecology (Memmott, 2009). For instance, when we consider conservation from a community ecology perspective, it becomes apparent that restoring a community requires more than just restoring species, but also restoring interactions and ecosystem functions, like pollination, that accompany those interactions. In hay meadows and healthlands in the United Kingdom, plant and pollinator communities have been restored in terms of species richness and abundance, but there is variation in the degree to which network interactions have been restored (Forup and Memmott, 2005; Forup et al., 2008).

To inform conservation, restoration, and management practices for plant–pollinator interactions across time and space, we need an experimental approach. We have excellent theory and models of plant–pollinator interaction networks that have contributed to our knowledge of the causes and consequences of network structure. These theoretical models are generating numerous predictions of the effects of biotic and abiotic factors on networks. However, experimental approaches to interaction networks are necessary to test these predictions (Proulx et al., 2005; de Ruiter et al., 2005). For example, experimental manipulation of nitrogen enrichment at small scales had important effects on the plant community and plant traits important to pollinators, but the effects were not strong enough at the spatial and temporal scale to fundamentally change plant–pollinator associations throughout the network (Burkle and Irwin, 2009). Manipulation of nitrogen availability (or other environmental factors) at larger spatial scales or the use of the "natural experiments," such as gradients of anthropogenic nitrogen deposition is necessary to broaden our understanding of these effects.

To understand how community-level plant–pollinator interactions assemble and are fundamentally structured, we can establish artificial plant communities, systematically adding or removing plant species, and tracking the frequency and composition of pollinator visitation as the community develops. Ideally, a parallel experimental introduction (or removal) of pollinators would provide additional insights, but also present huge design challenges. Fontaine et al. (2006) experimentally manipulated the diversity of both plants and pollinators in a small network, finding that high functional diversity contributed to the recruitment and maintenance of more species-rich plant communities. This approach is congruent to those employed to understand community structure for restoration through the investigation of community assembly rules.

Understanding the effects of global change—Human activities, through habitat fragmentation, climate change, and biological invasions for example, have the potential to strongly influence spatiotemporal patterns of plant–pollinator networks. We know very little about how plant–pollinator interactions are being disrupted by global change (Hegland et al., 2009), yet these interactions may be more susceptible to global change than simple biodiversity measures because interactions are

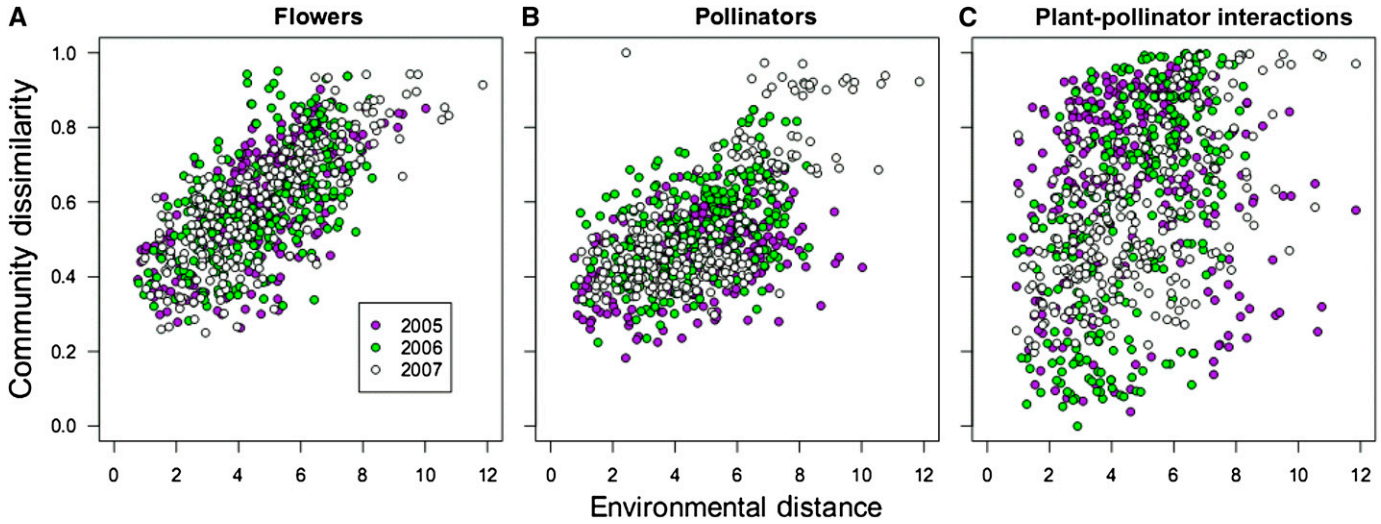

Fig. 4. With increasing environmental distance, measures of community dissimilarity of (A) flowers, (B) pollinators, and (C) plant–pollinator interactions increase in all years. Each circle is one pairwise plot–plot comparison. Year 2005: purple circles, 2006: green circles, 2007: white circles.

sensitive to the phenology, behavior, physiology, and relative abundances of multiple species (Tylianakis et al., 2008). Because foraging pollinators respond to the composition and abundance of community-level floral rewards, the response of some plant species to environmental change could indirectly affect other plants through competition or facilitation for pollinators. Thus, global change may have unexpected effects unless we study interactions at the community level. Earlier in this paper, we touched on the effects of habitat loss and nitrogen enrichment on networks, and here we focus on invasive species and climate change in plant–pollinator interaction networks—both summarizing recent work and highlighting directions forward (see Schweiger et al., 2010 for a comprehensive review the interactive effects of species invasions and climate change on pollination).

Invasive species—Of the dominant elements of global change, the most is known about the influence of alien and naturalized species on plant–pollinator interaction networks. Observational studies have shown that alien mutualist species can integrate into plant–pollinator interaction networks (Olesen et al., 2002; Morales and Aizen, 2006; Bartomeus et al., 2008), but have little effect on the overall connectivity and other structural properties of the network (Memmott and Waser, 2002; Olesen et al., 2002; Padrón et al., 2009; Vila et al., 2009). However, Aizen et al. (2008) found structural and functional changes in the network: supergeneralist alien species can usurp links formerly held by natives, weakening the degree of mutualism and increasing network stability. Our current cumulative understanding of the effects of alien species in plant–pollinator networks does not necessarily illuminate straightforward conservation or management directions, which may be system and objective specific.

Models and experiments can provide valuable insight into the potential effects of alien species on interaction networks over time—from the initial invasion process, to integration, to removal and restoration. Valdovinos et al. (2009) simulated the removal of alien plant species from an empirical plant–pollinator interaction network and found, not surprisingly, that the presence of the alien plants was important for the structure and function of the network and that their removal could lead to species extinctions, under the assumption that species could not reorganize or redistribute their interactions after alien plants were removed. Lopezaraiza-Mikel et al. (2007) provide a unique, experimental approach to understanding the effects of an alien plant on the plant–pollinator interaction network. By comparing invaded plots with experimental plots in which the flowers of the invasive species had been removed, they found that the presence of the alien plant facilitated pollinator visitation to natives but that pollen transport networks were dominated by alien pollen, possibly negating any positive effects of increased visitation to natives.

Overall, these studies suggest that plant–pollinator interaction networks are quite plastic and permeable to invasion by alien species, but the structure of networks is relatively robust to invasion. However, there is some evidence to suggest the function of invaded networks in terms of pollination services may be compromised. Even less is known about the effects of alien pollinators on network structure and function or of alien species on plant and pollinator reproduction. Additional empirical work, ideally with interaction data pre-invasion, during invasion, and post-removal, is sorely needed. In particular, we may be facing unexpected consequences for plant–pollinator networks from management and removal of invaders. The magnitude and direction of the effects of invader removal may depend on the density and spatiotemporal extent of invasion and removal, the degree of invader integration into community interactions, and effects on native plant and pollinator population dynamics since invasion.

Climate effects—To understand how climate change is affecting plant–pollinator interactions and predict future changes, the influence of climatic variables, such as temperature and precipitation, on plant and pollinator communities and their interactions along natural gradients may provide critical insight. Gonzalez et al. (2009) found that rainfall was important in explaining variation in bee and fly interactions with plants. Similarly, precipitation was found to influence species prevalence and turnover in Patagonian plant–pollinator communities as well as the percentage of interactions established

by each taxon (Devoto et al., 2005, 2009). In the West Indies, increased rainfall and decreased temperature with elevation are accompanied by phenotypic and ecological specialization of plant species on hummingbird pollination (Dalsgaard et al., 2009). Because water availability through patterns of rainfall and snowmelt can influence the timing and abundance of flowers and floral rewards (e.g., Inouye et al., 2003; Lambert et al., 2010), the potential links between increased frequency and intensity of droughts with climate change and subsequent effects on plant–pollinator interactions are clear (Alarcón et al., 2008).

Plants are very sensitive to the seasonality of their environment, and phenological shifts in plants provide undeniable evidence that climate change is affecting species and ecosystems (Cleland et al., 2007). For instance, over 500 plant taxa from Massachusetts, United States, first studied by Henry David Thoreau in the mid 19th century, have been shown to be affected by global warming, with plants blooming earlier now than historically (Miller-Rushing and Primack, 2008). In addition to plants blooming earlier, warmer temperatures are also correlated with earlier activity in some insect pollinators (reviewed in Hegland et al., 2009). Especially concerning is that pollinators appear to be experiencing a greater degree of phenological advancement than plants, potentially leading to interaction mismatches.

Studies simulating the effects of climate change on plant–pollinator interaction webs provide expectations and hypotheses to test under observed or experimentally induced climate change. Memmott et al. (2007) modeled the potential effects of phenological shifts on plant–pollinator interactions, finding reduced or eliminated floral resource availability for many pollinators and thus potential extinction cascades. In addition to the temporal model of Memmott et al. (2007), Devoto et al. (2007) considered spatial movement of pollinators by simulating a range shift over a steep rainfall gradient, similar to predictions of decreased precipitation with climate change. In this model, they found plant–pollinator interaction networks to be fairly robust to these range shifts. Neither of these models account for behavioral flexibility of pollinator foraging. As species go extinct, alter their range distributions, or no longer overlap in phenology, pollinators may alter their behavior to forage on and pollinate new plant species. Thus, models that do not account for behavioral flexibility will likely overestimate the overall network effects of phenological change on plant–pollinator interactions.

Pollination ecologists have come a long way in describing the structure of plant–pollinator interaction networks; however, there is still much to do to better understand patterns and processes related to spatiotemporal variation in pollination systems. For example, additional long-term studies across diverse habitats are sorely needed given that the best available data set is from a ca. 4-yr survey (Petanidou, 1991) of a Phryganic community in Greece. These data have contributed significantly to our understanding of temporal patterns (Petanidou and Ellis, 1993, 1996; Petanidou et al., 1995, 2008; Medan et al., 2006; Petanidou and Potts, 2006); however, the time frame is still too short to document the long-term effects of climate change, species introduction, or succession. To increase our understanding of long-term temporal patterns, pollination ecologists, or their students, could return to their former study sites at 5–10-yr intervals or to sites of historic studies to resurvey plant–pollinator interactions and build upon existing data sets.

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