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Comments

GEOGRAPHIC PATTERNS IN PLANT–POLLINATOR MUTUALISTIC NETWORKS: COMMENT

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Throughout the history of the field of pollination biology, biologists have disagreed over the extent of adaptation between flowers and pollinators (reviewed in Herrera 1996, Vogel 1996), and in recent years, specialization in plant–pollinator interactions has been the focus of much discussion and debate (e.g., Waser et al. 1996, Johnson and Steiner 2000). There are well-documented examples of both highly specialized and highly generalized plant–pollinator interactions. However, the distribution of these interactions along the generalization–specialization spectrum is much less understood. This distribution has profound implications for plant biology, specifically concerning the processes of floral adaptation and reproductive isolation through pollinator preference. From a zoological perspective, the degree of specialization in plant use by pollinating animals elucidates important behavioral preferences and patterns of resource utilization. Furthermore, the distribution of plant–pollinator interactions in a community could affect emergent properties such as stability and resilience (May 1973).

The collection of empirical data and the development of standardized measures of specialization are imperative for resolving the debate over specialization and generalization in plant–pollinator interactions. Moreover, information on the ecological correlates of generalization in plant–pollinator interactions would help to illuminate the conditions under which specialization or generalization are likely to occur. Olesen and Jordano (2002) recently contributed to this discussion by using a network approach to evaluate a range of published and unpublished studies of community plant–pollinator interactions. They calculated the covariance between generalization and species richness, latitude, elevation, and insularity, concluding that "extensive generalization in plant–pollinator interactions is the rule" and "very few plant or pollinator taxa are indeed specialized." We suggest that their results and interpretation are not well supported, and that their network approach is inappropriately applied to the issue of specialization.

Olesen and Jordano view a community as a matrix of potentially interacting plant (P) and animal (A) species, and then calculate the connectance value (C) as the percentage of all possible interactions (M) that are actually observed (I), where $C = 100\ I/M$. Both C and I are considered network-level measures of generalization, whereas the mean number of interactions per plant and per animal species are taken as species-level measures. Most of their analyses focus on connectance as an overall measure of generalization in a given community. Olesen and Jordano present the network analysis as a fruitful new way to compare community-level data on plant–pollinator interactions. We believe that their approach actually obscures the issue of generalization in plant–pollinator interactions.

Both the potential range and the magnitude of C are heavily influenced by network size, and therefore its use as an index of generalization is questionable. Consider a hypothetical community consisting of 100 plants and 100 animals, with each plant completely specialized on one animal and vice versa, so that there are a total of 100 observed interactions, giving a connectance value of 1. Next consider a community of only five plants and five animals, with each species exhibiting the same extreme specialization. This community has a connectance of 20. In fact, for a given community, $C_{\mathrm{min}} = 100 \times \max(P, A)/(PA)$, so that the minimum value of C is never zero, although it approaches zero with increasing species richness.

Some of the relationships that Olesen and Jordano find between connectance and community attributes are expected even with the same level of generalization per species. For example, they report an exponential decrease in C with total number of species ($A + P$; Olesen and Jordano 2002: Fig. 1) as evidence for lower generalization in species-rich communities. To examine this relationship, we constructed hypothetical communities consisting of equal numbers of plants and animals and spanning the range of species richness in the communities analyzed by Olesen and Jordano. We then calculated connectance values assuming two, four, or eight interactions per species. When plotted against the total number of species, the hypothetical communities

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FIG. 1. Relationship between connectance and species richness for the total number of animal and plant species, as reproduced from Olesen and Jordano (2002), and from hypothetical communities with constant levels of generalization per species.
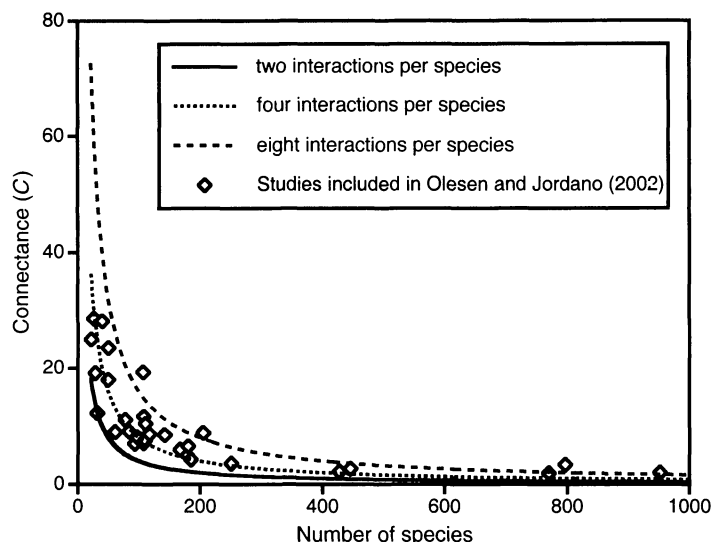
with constant levels of interactions per species show the same exponential decrease in connectance with species richness (Fig. 1). These hypothetical communities also show similar relationships between C and both network size (M) and number of interactions (I), after transformation, as do the reviewed studies (Olesen and Jordano 2002: Fig. 2). Clearly, a better measure of generalization than connectance is needed to evaluate the ecological correlates of generalization.

To be sure, the authors do control for variation in matrix size by including it along with their ecological correlate of interest in multiple regression analyses of their various measures of generalization. If one accepts all of the problems with varying methods of data collection and uneven sampling across the various geographic factors, these results do suggest some interesting patterns, such as higher generalization at higher latitudes and lower elevations and in mainland environments. Perhaps the most interesting results are those for the mean number of interactions per plant or animal species, because they are independent of the network-level properties and do not obscure any differences in generalization between the plants and animals. Even so, the distribution of studies across the ecological factors is highly uneven, and the analyses only examine one ecological factor at a time. For example, they investigate whether tropical interactions are more specialized than those at higher latitudes, but the analysis comprises only four tropical studies, including two from oceanic islands, one from high elevation, and one from "coastal scrub." These are not the types of communities that generated the hypothesis of higher specialization in the tropics. We suggest that far more studies are needed in a variety of tropical communities before any conclusions can be reached regarding lati-

tudinal differences in the degree of plant–pollinator specialization.

We propose moving away from the network approach and toward more direct measures of specialization. Given the limitations of the available community-wide data reviewed by Olesen and Jordano, the degree of plant–pollinator generalization is best estimated from the frequency distribution of interactions. This follows a more traditional presentation of generalization in plant–pollinator interactions as the distribution of both the number of visitor taxa per plant taxon and the number of plant taxa per visitor taxon (e.g., Waser et al. 1996). To demonstrate, we reanalyzed three of the studies included in Olesen and Jordano (Fig. 2). Although these studies span a range of C from 2.2 to 26.3, the shapes of their frequency distributions of plants per visitor and visitors per plant are, in most cases, remarkably similar. The one exception is the plant community studied by Primack (1983) that shows a pattern of pervasive generalization, indicated by both the high median and overall distribution of visitors per plant. Yet connectance in this case is much lower than that of the community studied by Schemske et al. (1978), which has lower median values for both plants and visitors (Fig. 2). The median number of interactions per taxon is an easily interpretable measure of specialization, and can reveal differences in the level of specialization between the plants and animals. Nevertheless, reducing the distribution of interactions to any single parameter results unavoidably in the loss of valuable information. The distributions of interactions can be compared between a pair of communities using nonparametric statistics, and we urge the further development of measures to compare communities across a range of ecological correlates.
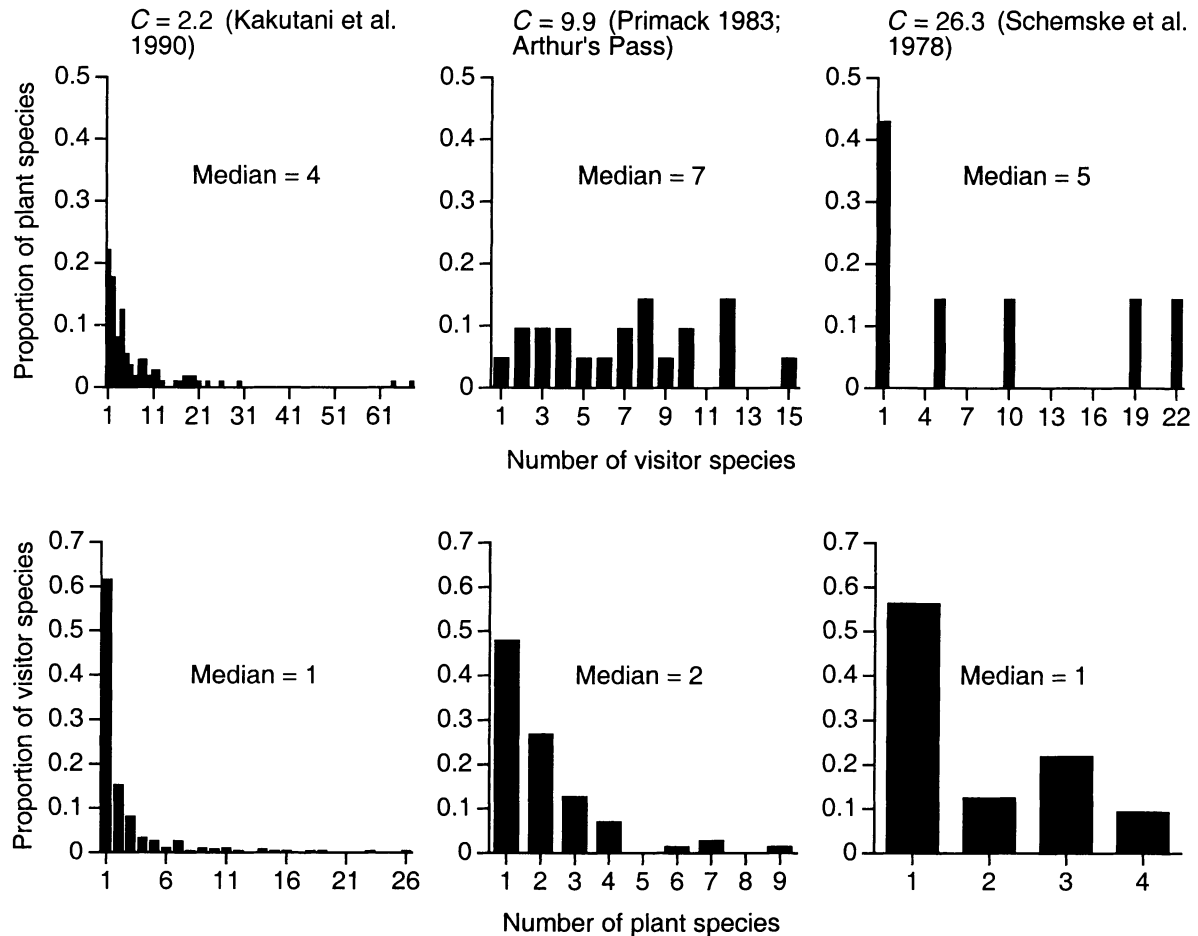
FIG. 2. Frequency distributions of the number of visitor species per plant species and the number of plant species per visitor species for three of the studies reviewed in Olesen and Jordano (2002). Connectance values (C) were calculated by reanalyzing the original studies, and they differ slightly from the values of 2.2, 11.1, and 28.1 calculated by Olesen and Jordano (2002).

From our limited reanalysis, it also is apparent that Olesen and Jordano's conclusions that highly generalized interactions are the norm and that very few plant or animal species are specialized are unsupported by the data. Overall, some taxa are indeed highly generalized, yet across all animal species in the three studies that we reanalyzed, 59% visited only one plant species, and across all plant species, 21% are visited by only one animal species. Extreme specialization is far from rare in these communities. Extreme generalization, on the other hand, is less common, with only 3% of the animal species visiting >10 plant species and 19% of the plant species visited by >10 animals species.

We suggest that the network approach of Olesen and Jordano does not provide a meaningful measure of specialization, but also acknowledge that the proper measurement of specialization in plant–pollinator interactions is problematic. Many of these issues are discussed

elsewhere (Johnson and Steiner 2000), but a few merit particular attention. First, it is overly simplistic to categorize an interaction as either present or absent when there is important variability in the nature and strength of interactions. It is necessary to distinguish effective pollen vectors from nonpollinating visitors, because they will have very different effects on plant fitness, and therefore on the evolution of the interaction, yet most of the studies reviewed by Olesen and Jordano do not estimate the pollination efficiency of flower visitors. Ideally, plant specialization could be evaluated by quantifying the percentage of pollen removal and fertilization caused by each pollinator (e.g., Schemske and Horvitz 1984). Specialization could then be compared between plants or communities by estimating the number of pollinator taxa that, taken together, effect a given percentage of pollination for each plant species. For example, a plant species that achieves 95% of seed

set with three pollinator taxa would be judged more specialized than one that requires more than three taxa to effect the same percentage of seed set, even if the total number of visiting taxa is the same. More feasible across a community would be quantification of the relative frequency of visitation by animals observed to regularly contact the anthers and stigma. Second, one needs to clarify the taxonomic level at which specialization is measured. To illustrate, most would consider a plant pollinated by four species of bumblebee more specialized than one pollinated by four species spanning four different insect orders (Johnson and Steiner 2000). Much floral specialization is thought to occur on higher taxonomic groupings of pollinators that presumably exert similar selection pressures, such as bees, hummingbirds, or moths. Quantifying specialization only at the species level would miss any important patterns at these levels. A recent community study of plant–visitor interaction webs (Dicks et al. 2002) attempted to address these first two issues by including quantitative measures of visitation and considering higher taxonomic groupings of flower visitors. Although the study did not make comparisons between communities, within communities they found strong evidence for compartmentalization of the interaction web based on insect orders associated with pollination syndromes. Finally, broad community surveys may overestimate specialization because of the likelihood of not observing an interaction that actually occurs. This is especially important in species-rich communities where comprehensive surveys are difficult. Many of these problems might be overcome by intensive sampling of a random subset of species in a community instead of broadly surveying an entire community for the simple presence or absence of each possible interaction.

In the case of plant–pollinator interactions, Olesen and Jordano's new methods of analysis cannot compensate for a lack of data on community-wide interactions. Progress toward understanding the ecology and evolution of plant–pollinator interactions will require increased sampling of underrepresented communities, particularly in lowland tropical forests, and measures of the relative frequency and strength of interactions.

Literature cited

Dicks, L. V., S. A. Corbet, and R. F. Pywell. 2002. Compartmentalization in plant–insect flower visitor webs. Journal of Animal Ecology 71:32–43.

Herrera, C. M. 1996. Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. Pages 65–87 *in* D. G. Lloyd and S. C. H. Barrett, editors. Floral biology: studies on floral evolution in animal-pollinated plants. Chapman and Hall, New York, New York, USA.

Johnson, S. D., and K. E. Steiner. 2000. Generalization versus specialization in plant pollination systems. Trends in Ecology and Evolution 15:140–143.

Kakutani, T., T. Inoue, M. Kato, and H. Ichihashi. 1990. Insect–flower relationships in the campus of Kyoto University, Kyoto: an overview of the flowering phenology and the seasonal pattern of insect visits. Contributions of the Biological Laboratory, Kyoto University 27:465–521.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Olesen, J. M., and P. Jordano. 2002. Geographic patterns in plant–pollinator mutualistic networks. Ecology 83:2416–2424.

Primack, R. B. 1983. Insect pollination in the New Zealand mountain flora. New Zealand Journal of Botany 21:317–333.

Schemske, D. W., and C. C. Horvitz. 1984. Variation among floral visitors in pollination ability: a precondition for mutualism specialization. Science 225:519–521.

Schemske, D. W., M. F. Willson, M. N. Melampy, L. J. Miller, L. Verner, K. M. Schemske, and L. B. Best. 1978. Flowering ecology of some spring woodland herbs. Ecology 59:351–366.

Vogel, S. 1996. Christian Konrad Sprengel's theory of the flower: the cradle of floral ecology. Pages 44–62 *in* D. G. Lloyd and S. C. H. Barrett, editors. Floral biology: studies on floral evolution in animal-pollinated plants. Chapman and Hall, New York, New York, USA.

Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. Ecology 77:1043–1060.