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NULL MODEL ANALYSES OF SPECIALIZATION IN PLANT–POLLINATOR INTERACTIONS

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Abstract. Recent studies have suggested that plant–pollinator interactions may be less specialized than previously thought. We contrasted patterns of specialization observed in five plant–pollinator interaction webs with predictions based on null models. In the five data sets, the observed number of extreme specialists and extreme generalists was significantly higher than the null expectation. This pattern was mostly due to a positive correlation between species frequency of interaction (f) and their estimated degree of generalization (s). After accounting for this association, the expected frequency distribution of degree of specialization generated by the null model closely matched the observed frequency distribution in the five data sets. A second null model, which explicitly incorporated the correlation between f and s, also generated expected frequency distributions of specialization that closely resemble those observed in the data sets. To make progress in understanding the distribution of degree of specialization in pollination systems it will be necessary not only to improve the quality of the data and to refine methods used to quantify specialization, but also to answer the question of why more frequently interacting species appear to be more generalized.

Key words: frequency of interaction; generalization; mutualism; null models; plant–pollinator interactions; pollination; sampling bias; specialization.

INTRODUCTION

Biologists have long been aware of the importance of interspecific interactions in shaping evolutionary processes. Interacting species can have tremendous reciprocal influences on their ecological and evolutionary dynamics. However, not all interactions have the same potential to drive reciprocal evolutionary change. Highly specialized interactions are more likely to lead to coevolution than generalized ones (Thompson 1994, Waser et al. 1996; but see Gómez 2002). Plant–pollinator interactions have often been regarded as highly coevolved and specialized, and some evolutionary biologists have suggested a general evolutionary trend from generalization to specialization, with increasingly tight coevolution of interacting partners (Schluter 2000).

Traditionally, most research in the field of pollination biology involved detailed studies of small groups of species. However, biologists are increasingly emphasizing a broader community-level perspective, in which patterns of interaction among all the plants and pollinators in a given area, or substantial subsets, are studied simultaneously (Jordano 1987, Waser et al. 1996). In many cases, this approach is revealing a greater degree of generalization in interactions than previously thought (Herrera 1988, Ollerton 1996, Waser et al. 1996, Gómez and Zamora 1999; but see Johnson and Steiner 2000). For example, Waser et al. (1996) have analyzed several community-wide data sets to show that, contrary to the traditional view, pollination systems contain many generalist species of plants and pollinators, and that relatively few species are specialized with one or a few interacting partners.

We propose that any statement about an observed pattern should be considered in light of a null expectation. Many of our current questions about specialization in plant–pollinator interactions cannot be answered without such consideration. For example, is the number of specialists or generalists in a given community high or low compared to what would be expected in an assemblage where interactions are assigned randomly among species? Null models (e.g., the generation of randomized data sets in the absence of a hypothesized mechanism) represent a useful tool to address the above questions. Null models have played an important role in many areas of community ecology and biogeography (Gotelli and Graves 1996, Gotelli 2001). However, to our knowledge, there have been no previous attempts to use null models to test patterns of specialization in pollination systems. Here we report the results of a comparison between observed patterns

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TABLE 1. Data sets included in the study.

Data set	Habitat type	Location	*f* data†	*m*‡	*n*§
Clements and Long (1923)	montane forest and grassland	Pikes Peak, Colorado, USA.	none	96	276
Inouye and Pyke (1988)	montane forest	Kosciusko National Park, New South Wales, Australia	no. individuals caught	42	91
Memmott (1999)	meadow	England	visit frequency	25	79
Motten (1982)	deciduous forest	Durham and Orange counties, North Carolina, USA	visit frequency	13	44
Vázquez (2002)	evergreen montane forest	Nahuel Huapi National Park, Argentina	visit frequency	14	93

† Type of data on frequency of interactions included in the data set.
‡ Number of plant species.
§ Number of pollinator species.

in five published data sets against those generated by null models.

METHODS

Data sets

We used five data sets from published community-wide studies of plant–pollinator interactions (Table 1). Each data set consisted of a binary interaction matrix, in which rows represented pollinator species and columns represented plant species (i.e., a plant–pollinator interaction web; see Plate 1). In these matrices, a cell ij containing a ''1'' represents an interaction between pollinator species i and plant species j, while a cell with ''0'' represents no interaction. In addition, four data sets contained information on the frequency of interaction between pairs of species (either visitation frequency of each pollinator species to each plant species, or number of individuals of each pollinator species caught while visiting flowers of each plant species; Table 1). Thus, if ones in the binary matrix are replaced by integer, positive numbers representing the number of times a pair of species was observed interacting, we obtain the so-called ''interaction frequency matrix.''

Quantification of degree of specialization and interaction frequency

Because of limited information available in the data sets, we used a simple measure of specialization: the total number of species with which a given species was observed interacting (s), obtained from the binary interaction matrix as the sum of the columns or rows for plants and pollinators, respectively. Frequency of interaction (f) for plants and pollinators was calculated from the sum of columns and rows, respectively, in the interaction frequency matrix, for the four communities for which this information was available.

Null models

We used simple computer algorithms written in MATLAB (MathWorks, Natick, Massachusetts, USA) to randomize plant–pollinator interactions in the five data sets (see Appendix A). Randomizations were performed by randomly distributing the observed total number of interactions among species of plants and pollinators, with the only restriction that each species had at least one interaction (as was the case for all plant and pollinator species included in the data sets). Because our randomization routine conserved the total number of observed interactions, connectance (i.e., the number of observed interactions divided by the maximum number of potential interactions; Jordano 1987) in the randomized data sets was the same as in the original data sets.

We used two basic models. In null model 1, every species was assigned an interaction by randomly selecting a species from the pool of possible interaction partners. Once every species had been assigned one (and only one) interaction, the remaining interactions were assigned by randomly selecting pairs of plant and pollinator species. Thus, in this model all plant or animal species had a priori the same probability to interact, independent of their interaction frequency. The expected value of s for plants will be $E\{s\} = nC = L/m$, where C is the connectance of the interaction matrix (proportion of cells with ones), L is the number of links, and m and n are the numbers of plants and pollinators, respectively. Similarly, for pollinators the expected value of s will be $E\{s\} = mC = L/n$.

In null model 2, every species was assigned an interaction by randomly selecting a species from the pool of possible interaction partners. Once every species had been assigned one (and only one) interaction, the remaining interactions were assigned proportionally to a species' observed interaction frequency, so that frequently interacting species had a higher probability of being assigned an interaction than rarely interacting species. The expected value of s for plant species i will be $E\{s_i\} = \varphi_i L$, where φ_i is the proportional frequency of interaction of plant species i (i.e., $\varphi_i = f_i/\Sigma_{k=1}^{m} f_k$); thus frequently interacting plant species had a higher expected number of interactions than rarely interacting species. Similarly, the expected value of s for pollinator species j is $E\{s_j\} = \varphi_j L$.

The algorithm then compared the observed frequency distribution of degree of specialization (s) with the expected frequency distribution under each null model, calculated as the mean frequency over 1000 iterations. We used a difference statistic, D, to compare the observed and expected distributions (see Manly 1997, Veech 2000). The statistic computes the difference between the frequency distribution of s in the original data or in each of the 1000 randomized data sets and the expected frequency distribution of s (i.e., the mean frequency distribution of the 1000 randomized data sets). Thus, $D = \Sigma_{i=1}^{k}|d_i|$, where $|d_i|$ is the absolute value of the difference between the expected and the observed (or randomized) frequency for category i of the frequency histogram, and k is the total number of categories (the total number of pollinator species for plants, and the total number of plant species for pollinators). We then compared the D statistic calculated for the original data with the 1000 D statistics calculated for the randomized data. The significance of the D statistic for the original data is assessed by means of a one-tailed P value, calculated as the proportion of randomized D values greater than the observed D.

In addition, our algorithm estimated the 95% and 99% confidence limits of the expected frequency distribution. Confidence intervals were used to test whether the frequency observed for a particular category of s was statistically different from the expected frequency generated by the null model.

Removing the correlation between f and s

To account for the positive correlation between frequency of interaction (f) and estimated specialization (s) (see *Results*), we used the residuals of the linear regression between the natural logarithms of s and f as an adjusted measure of specialization. This procedure factors out much of the correlated effect of f on s. We then added a constant (positive integer) to the residuals, back transforming and rounding the resulting values to avoid fractional numbers of interactions. The resulting mathematical relationship between the uncorrected (s) and corrected (s_c) estimates of specialization is $s_c = [e^{r+c}]$, where r represents the residuals of the regression between ln s and ln f (i.e., $r = \ln s - \ln \hat{s}$, where $\hat{s}$ are the predicted values of s), c is a constant, e is the base of the natural logarithm, and the brackets indicate rounding to the nearest integer. The constant c was added so that the total number of interactions added up to the original number of interactions, and was found using an iterative process. Parameter estimates and significance testing of regressions are in Appendix B.

When incorporating the correction for the relationship between f and s we excluded plant and pollinator species for which we detected less than eight interactions. The reason for such exclusion was to avoid forcing the regression through the origin (if a species is observed only once, its s_c value will be necessarily 1). However, to make sure that excluding rare species did not affect our results, we also performed the correction and ran null model 1 including rare species; results were not affected. We therefore report only results excluding rare species.

PLATE 1. Bumble bee *Bombus dahlbomii* visiting *Vicia nigricans* in Nahuel Huapi National Park, Argentina. *Bombus dahlbomii* is the most generalized pollinator species recorded in the Vázquez (2002) dataset; *V. nigricans* is a specialist, interacting almost exclusively with *B. dahlbomii*. Photo by Diego P. Vázquez.

RESULTS

The observed frequency distribution of s significantly differs from the expected frequency distribution under null model 1 for all data sets (Fig. 1). The observed number of extreme specialists (i.e., species with extremely low s values) was in 8 of 10 cases higher than the upper confidence limit of the null model expectation. The two exceptions to this pattern are (1) plants in the Motten (1982) data set, where the observed frequency of s overlapped with the upper confidence limit for the lowest two categories of s; and (2) plants in the Vázquez (2002) data set, where the observed frequency for the lowest category of s overlapped with the upper confidence limit (Fig. 1). In the two cases, however, the observed frequency for the second lowest category (i.e., $s = 3, 4$) was above the 95% confidence limit of the expected frequency. The observed frequency of extreme generalists (i.e., species with extremely high s values) was higher than the upper 99% confidence limit of the expected frequency for plants and pollinators in the five data sets. Thus, in most cases for extreme specialists, and in all cases for extreme generalists, the observed frequency of s is significantly higher than expected under null model 1.

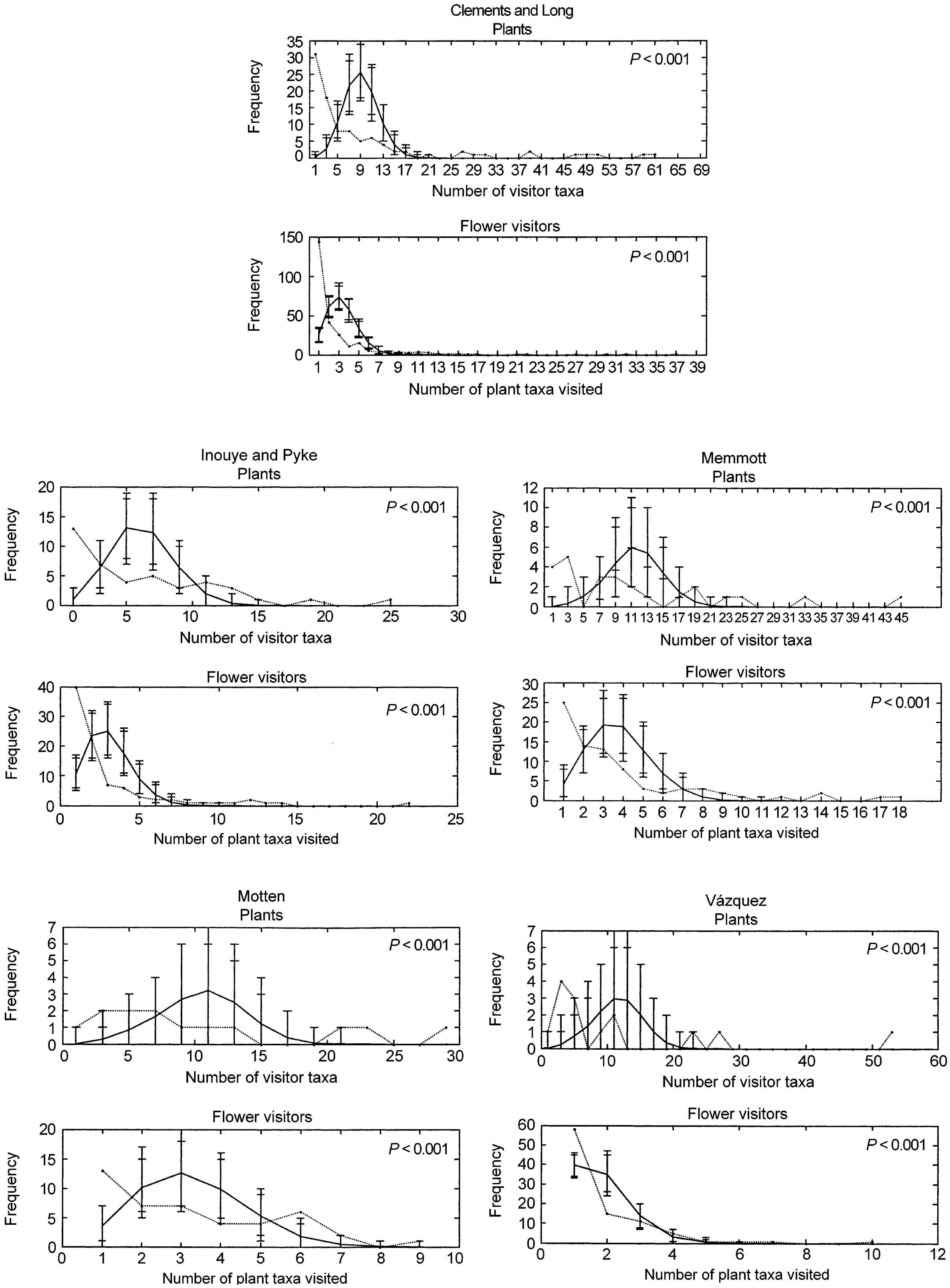

FIG. 1. Results of null model 1 simulations and comparison with five data sets, using original (uncorrected) data. Figures represent observed (dashed line) and expected (continuous line) frequency of number of interacting partners per species (number of pollinator species for plants, or number of plants species visited for pollinators). Expected frequency is the mean

Results presented in Fig. 1 suggest that extreme specialization and extreme generalization are unusually common in the data sets. However, a closer look at the data reveals a disturbing fact about our estimate of specialization: in the four data sets that provided an estimate of frequency of interaction (see Table 1), there is a positive correlation between the estimated degree of specialization (*s*) and the observed frequency of interaction (*f*) (Fig. 2). In other words, more frequently interacting species appear more generalized than less frequently interacting species.

To eliminate the correlation between *s* and *f* we applied the correction described above (see *Methods*: *Removing the correlation between f and* s), and then re-ran null model 1 using s_c. The observed frequency distribution of s_c did not differ significantly from the expected frequency distribution generated by the null model in any data set except Vázquez, plants (Fig. 3). Furthermore, in most s_c categories the observed frequency fell within the confidence intervals generated by the null model, with the sole exception of the highest category in plants in the Vázquez data set, which was above the 99% confidence limit (Fig. 3).

As another way of taking into account the correlation between *s* and *f*, we used null model 2 (see *Methods*: *Removing the correlation between f and s*). This approach allowed us to incorporate such correlation while still using the untransformed (original) *s* values. The results from this model were closer to the observed patterns of the distribution of specialization than with model 1 for the uncorrected data, although there were significant differences between the observed and expected distributions in two cases (Inouye and Pyke, plants, and Vázquez, plants; Fig. 4). The most important result from this model is that, unlike model 1 (Fig. 1), in most cases it predicts a number of specialists as high, or even higher, than observed (with the two exceptions just mentioned, where the number of plant species with extreme specialization is higher than expected from the null model).

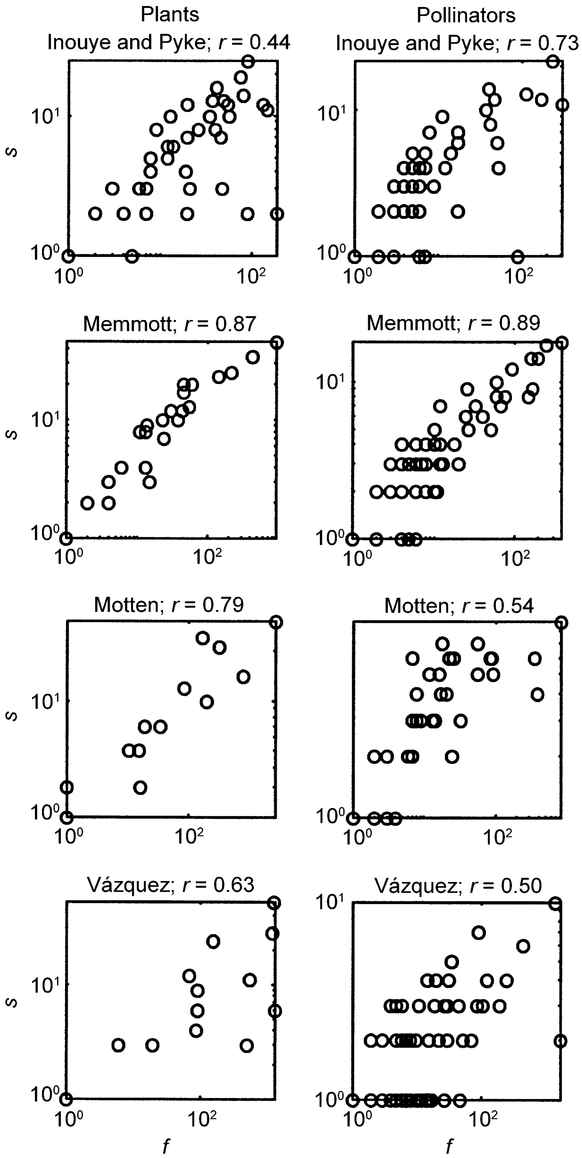

FIG. 2. Relationship between estimated degree of specialization (*s*) and total frequency of interaction (*f*) for plants and pollinators for the four data sets that included information on frequency of interaction (see Table 1). Notice logarithmic scale in abscissa and ordinates.

DISCUSSION

Results presented here have important implications for our understanding of patterns of specialization in pollination systems. Our analysis revealed that patterns in the distribution of the degree of specialization in five plant–pollinator interaction webs differ significantly from the expected patterns generated by our simplest null model (i.e., model 1). Recent studies (e.g., Waser et al. 1996) have suggested that pollination systems are not unusually specialized or generalized, and that moderate generalization is more common than previously thought. Our results show exactly the opposite: there are an unusually high number of extreme specialists and extreme generalists in these data sets. Therefore, our first conclusion is a methodological one: it is difficult to answer questions about community-wide pat-

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of 1000 randomizations, and error bars represent the 95% (inner) and 99% (outer) confidence limits of expected frequency. (Because frequencies are discrete, confidence intervals for the two significance levels overlap in many cases.) Numbers at upper right corner of plots are the *P* values of the difference test.

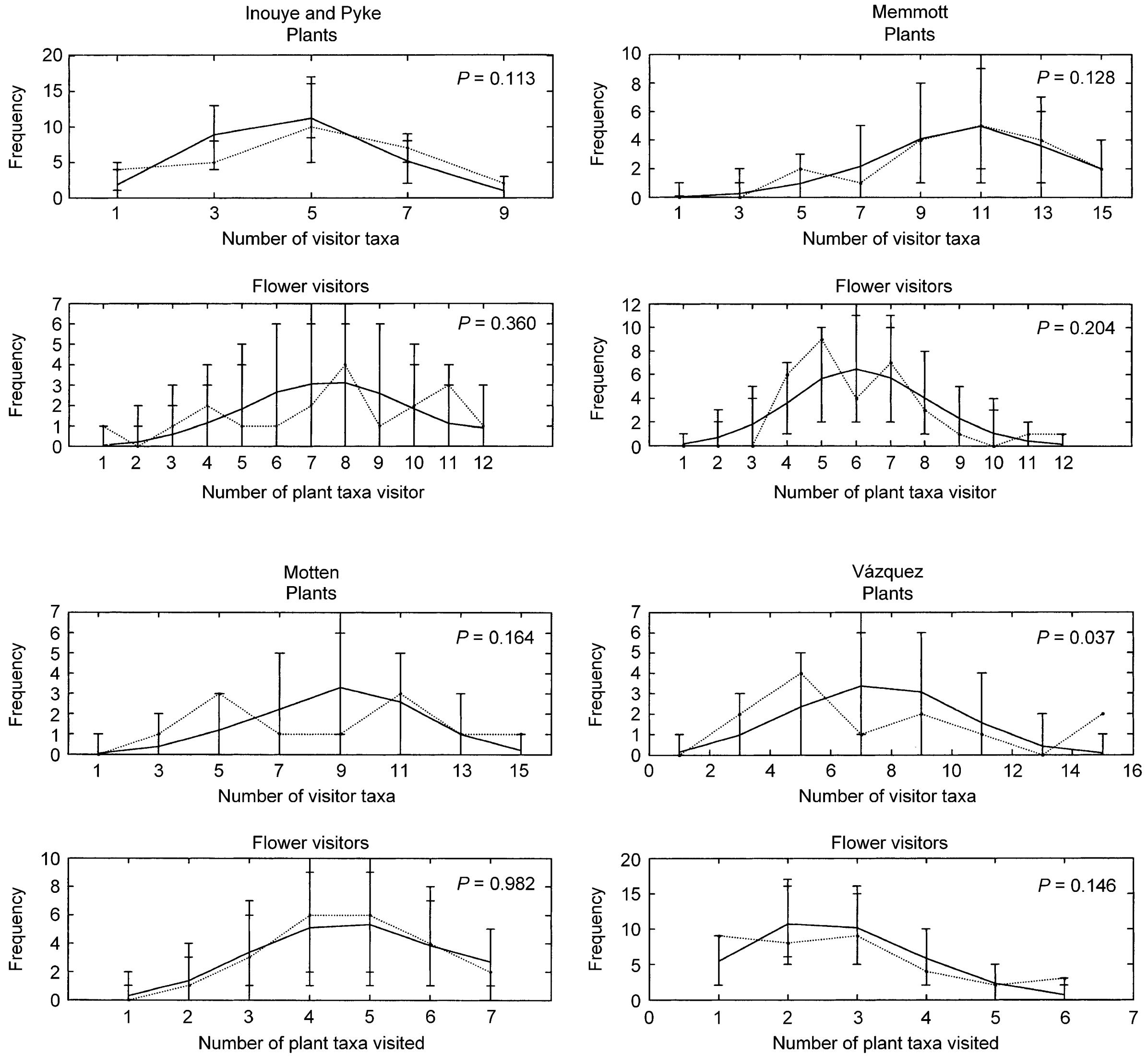

FIG. 3. Results of null model 1 simulations and comparison for the four data sets that included information on frequency of interaction (see Table 1) after applying the correction to account for correlation between *f* and *s* (see *Methods*: *Removing the correlation between f and s*). Conventions follow Fig. 1, except that scales differ.

terns of specialization in pollination systems without contrasting observed patterns against some null expectation. The null models used in our analysis are a way of providing such contrast.

The striking patterns found in the five data sets might suggest that even though species are distributed along a continuum, extreme specialization and generalization may represent two highly adaptive alternative strategies (Bronstein 1995). However, these patterns could be mostly attributed to a correlation between species interaction frequency (*f*) and their estimated degree of specialization, (*s*). The effect of the correlation between *f* and *s* is suggested both by the disappearance of the nonrandom pattern after extracting this association from the data (Fig. 3), and by the closer fit between the observed and the expected frequencies after explicitly incorporating the correlation into the null model (model 2, Fig. 4). The crucial question then becomes whether this correlation represents simply a sampling artifact or whether there is a biological mechanism responsible for generating it.

A sampling artifact can occur because rare (or rarely interacting) species are less likely to be observed than abundant (or frequently interacting) species. For example, a rarely interacting pollinator is unlikely to be seen visiting flowers of many species of plants, even if it does visit many species. A similar situation occurs in many analyses of the relationship between local abundance and geographic range, where the observed positive relationship between these two variables may be frequently attributed to a sampling artifact; for a given sampling effort locally rare species are likely to

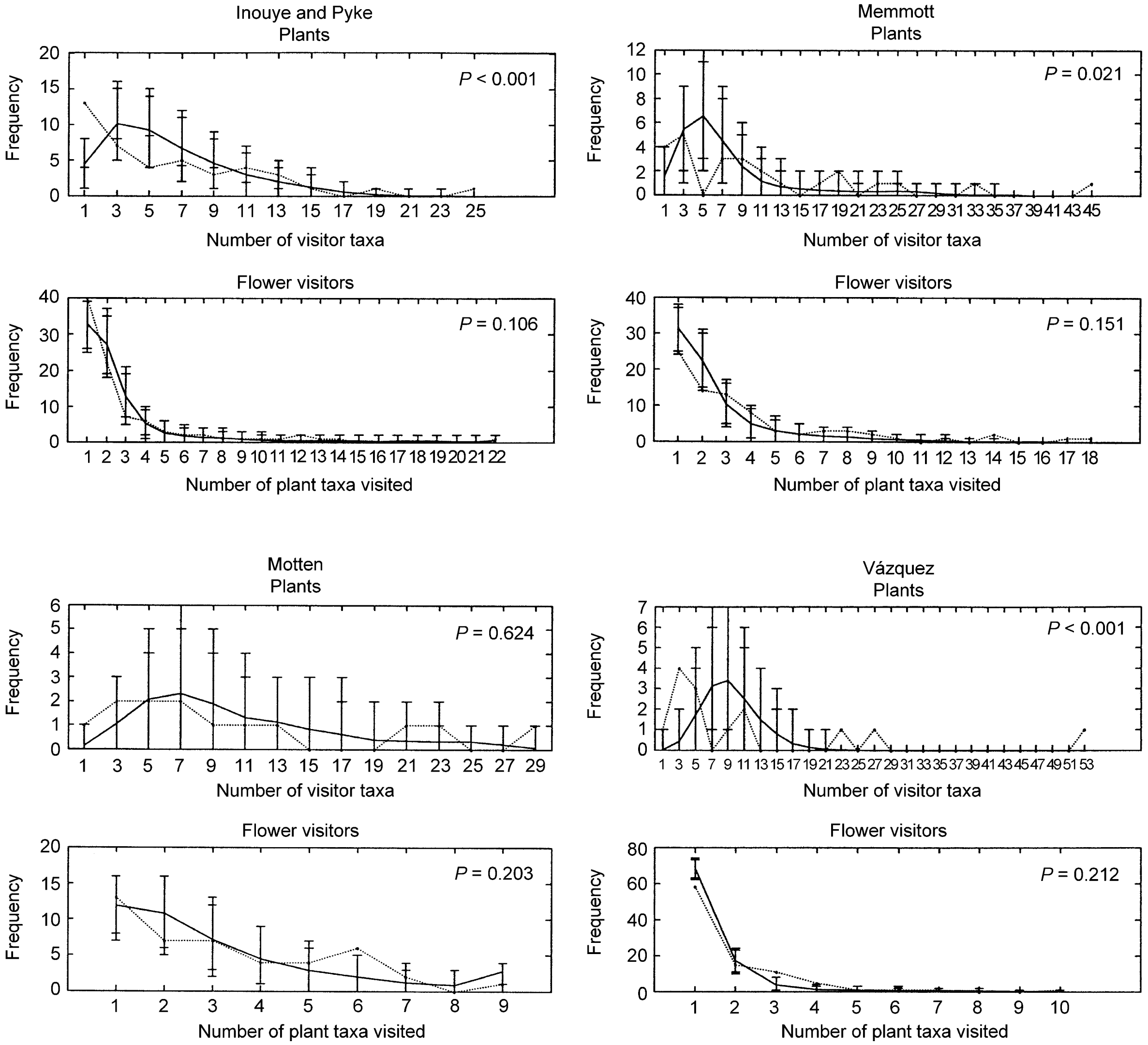

FIG. 4. Results of null model 2 simulations and comparison for the four data sets that included information on frequency of interaction (see Table 1), using original (uncorrected) data. Conventions follow Fig. 1, except that scales differ.

be detected in fewer sites than locally abundant species (Gaston et al. 1997). Effects of sampling bias on community properties have also been identified in food web studies. Goldwasser and Roughgarden (1997) specifically studied the effects of sampling bias in food web properties; they concluded that "both the incompleteness of the existing data and our focus on properties that are sensitive to that incompleteness may be giving us a misleading picture of the trophic structure of ecological communities." The situation in studies of plant–pollinator interaction webs is strikingly similar.

It must be considered, however, that part of the correlation between *f* and *s* might be owing to true biological mechanisms. For instance, highly abundant plants could interact with a high number of pollinators simply because they are more likely to be encountered than rare plants. Many of the pollinators interacting with these super-abundant, super-generalist plants may be themselves rare and specialized. Furthermore, a positive correlation between *s* and *f* can be accentuated by a nonrandom distribution of species abundance in time and/or space. For example, if abundant species had longer phenologies than rare species, rare species would tend to interact with fewer species than commoner species simply because their activity periods are shorter. In the Vázquez (2002) data set, the most generalized pollinator is the bumblebee *Bombus dahlbomii* (see Vázquez and Simberloff 2002). This species also has the longest period of activity, being active from the start of the flowering season in the early spring to the end of the flowering season in the late summer. In contrast, many infrequent flower visitors were recorded only on the summer-flowering herb *Alstroemeria aurea*.

A related idea was proposed by Thompson (1994), who argued that species with wider geographical ranges tend to interact with a broader set of species than range-restricted species (see also Southwood 1961, Strong et al. 1984, Leather 1991, Poulin 1999). Given the positive correlation between range size and local abundance (Gaston et al. 1997), it is possible that the pattern suggested by Thompson is also occurring at the local scale at which most studies of plant–pollinator interactions have been conducted so far.

Lastly, we cannot discard the possibility that low interaction frequency and abundance are a direct consequence of specialization and not the opposite. After all, low abundance can result from specialization, as this trait implies a more restricted use of available resources. Although this idea has been dismissed on theoretical grounds (Gaston 1994:124), empirical testing is lacking. In summary, we cannot discount that the positive correlation between f and s is, at least in part, due to one or more biological mechanisms.

Another caveat is that the rough estimate of specialization used in our study (as well as in all other community-wide studies conducted to date) may not be a true depiction of the degree of specialization among plants and pollinators. First, mere interaction, or even high frequency of interaction, does not necessarily mean that the interaction is functionally important. For example, the most important pollinator species is not necessarily the most frequent flower visitor (e.g., Schemske and Horwitz 1984). Furthermore, at least for predator–prey interactions, interaction strength varies greatly among pairs of species in communities, with most interactions weak and only a few strong (Paine 1992, Berlow et al. 1999). A similar situation appears to occur in plant–pollinator interactions. For example, several studies show that plants visited by a broad assemblage of pollinators are effectively pollinated only by a small subset of those visitors (e.g., Schemske and Horwitz 1984, Pettersson 1991, Fishbein and Venable 1996, Olsen 1997, Aizen 2001).

Like Goldwasser and Roughgarden (1997), we feel that the incompleteness of the data and our poor understanding of specialization among interacting species may be giving us a misleading picture of the community structure of pollination systems. To make progress in understanding the distribution of degree of specialization in pollination systems it will be necessary to improve the quality of the data and to refine methods used to quantify specialization. Furthermore, the use of null models of increasing complexity may assist in identifying potential factors generating observed patters in plant–pollinator interactions (see also Armbruster et al. 1994, Stone et al. 1998). We conclude that an association between frequency of interaction and degree of specialization is mostly responsible for generating observed patterns in pollination webs. Future studies should focus on the processes and mechanisms, whether truly biological or sampling artifacts, that are behind this relationship. We hope the work presented here will stimulate others to continue these important steps towards a better understanding of specialization in plant–pollinator interactions.

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LITERATURE CITED

Aizen, M. A. 2001. Flower sex ratio, pollinator abundance, and the seasonal pollination dynamics of a protandrous plant. Ecology **82**:127–144.

Armbruster, W. S., M. E. Edwards, and E. M. Debevec. 1994. Floral character displacement generates assemblage structure of western Australian triggerplants (*Stylidium*). Ecology **75**:315–329.

Berlow, E. L., S. A. Navarrete, C. J. Briggs, M. E. Power, and B. A. Menge. 1999. Quantifying variation in the strengths of species interactions. Ecology **80**:2206–2224.

Bronstein, J. L. 1995. The plant–pollinator landscape. Pages 256–288 *in* L. Hansson, L. Fahrig, and G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman and Hall, London, UK.

Clements, R. E., and F. L. Long. 1923. Experimental pollination. An outline of the ecology of flowers and insects. Carnegie Institute of Washington, Washington, D.C., USA.

Fishbein, M., and D. L. Venable. 1996. Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. Ecology **77**:1061–1073.

Gaston, K. J. 1994. Rarity. Chapman and Hall, London, UK.

Gaston, K. J., T. M. Blackburn, and J. H. Lawton. 1997. Interspecific abundance–range size relationships: an appraisal of mechanisms. Journal of Animal Ecology **66**:579–601.

Goldwasser, L., and J. Roughgarden. 1997. Sampling effects and the estimation of food-web properties. Ecology **78**:41–54.

Gómez, J. M. 2002. Generalización en las interacciones entre plantas y polinizadores. Revista Chilena de Historia Natural **75**:105–116.

Gómez, J. M., and R. Zamora. 1999. Generalization vs. specialization in the pollination system of *Hormathophylla spinosa* (Cruciferae). Ecology **80**:796–806.

Gotelli, N. 2001. Research frontiers in null model analysis. Global Ecology and Biogeography **10**:337–343.

Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C., USA.

Herrera, C. M. 1988. Variation in mutualisms: the spatiotemporal mosaic of a pollinator assemblage. Biological Journal of the Linnean Society **35**:95–125.

Inouye, D. W., and G. H. Pyke. 1988. Pollination biology in the Snowy Mountains of Australia: comparisons with montane Colorado, USA. Australian Journal of Ecology **13**: 191–210.

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

Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. American Naturalist **129**: 657–677.

Leather, S. R. 1991. Feeding specialization and host distribution of British and Finnish *Prunus* feeding macrolepidoptera. Oikos **60**:40–48.

Manly, B. F. J. 1997. Randomization, bootstrap, and Monte Carlo methods in biology. Chapman and Hall, London, UK.

Memmott, J. 1999. The structure of a plant–pollinator food web. Ecology Letters **2**:276–280.

Motten, A. F. 1982. Pollination ecology of the spring wildflower community in the deciduous forests of piedmont North Carolina. Dissertation. Duke University, Durham, North Carolina, USA.

Ollerton, J. 1996. Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant–pollinator systems. Journal of Ecology **84**:767–769.

Olsen, K. M. 1997. Pollination effectiveness and pollinator importance in a population of *Heterotheca subaxillaris* (Asteraceae). Oecologia **109**:114–121.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature **355**:73–75.

Pettersson, M. W. 1991. Pollination by a guild of fluctuating moth populations: option for unspecialization in *Silence vulgaris*. Journal of Ecology **79**:591–604.

Poulin, R. 1999. The intra- and interspecific relationships between abundance and distribution in helminth parasites of birds. Journal of Animal Ecology **68**:719–725.

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

Schluter, D. 2000. The ecology of adaptive radiations. Oxford University Press, Oxford, UK.

Southwood, T. R. E. 1961. The number of species of insect associated with various trees. Journal of Animal Ecology **30**:1–8.

Stone, G. N., P. Willmer, and J. A. Rowe. 1998. Partitioning of pollinators during flowering in an African *Acacia* community. Ecology **79**:2808–2827.

Strong, D. R., J. H. Lawton, and T. R. E. Southwood, editors. 1984. Insects on plants. Blackwell, Oxford, UK.

Thompson, J. N. 1994. The coevolutionary process. Chicago University Press, Chicago, Illinois, USA.

Vázquez, D. P. 2002. Interactions among introduced ungulates, plants, and pollinators: a field study in the temperate forest of the southern Andes. Dissertation. University of Tennessee, Knoxville, Tennessee, USA.

Vázquez, D. P., and D. Simberloff. 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. American Naturalist **159**:606–623.

Veech, J. A. 2000. A null model for detecting nonrandom patterns of species richness along spatial gradients. Ecology **81**:1143–1149.

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.

APPENDIX A

MATLAB code of null models is available in ESA's Electronic Data Archive: *Ecological Archives* E084-062-A1.

APPENDIX B

Parameter estimates and fit statistics for the linear regression between the natural logarithm of the frequency of interactions (ln *f*) and the natural logarithm of the observed degree of specialization (ln *s*) are available in ESA's Electronic Data Archive: *Ecological Archives* E084-062-A2.