Oecologia (2006) 148: 365–372
DOI 10.1007/s00442-006-0396-1

METHODS

Heather F. Sahli · Jeffrey K. Conner

Characterizing ecological generalization in plant-pollination systems

Received: 15 September 2005 / Accepted: 7 February 2006 / Published online: 3 March 2006

Abstract Despite the development of diversity indices in community ecology that incorporate both richness and evenness, pollination biologists commonly use only pollinator richness to estimate generalization. Similarly, while pollination biologists have stressed the utility of pollinator importance, incorporating both pollinator abundance and effectiveness, importance values have not been included in estimates of generalization in pollination systems. In this study, we estimated pollinator generalization for 17 plant species using Simpson's diversity index, which includes richness and evenness. We compared these estimates with estimates based on only pollinator richness, and compared diversity estimates calculated using importance data with those using only visitation data. We found that pollinator richness explains only 57–65% of the variation in diversity, and that, for most plant species, pollinator importance was determined primarily by differences in visitation rather than by differences in effectiveness. While simple richness may suffice for broad comparisons of pollinator generalization, measures that incorporate evenness will provide a much more accurate understanding of generalization. Although incorporating labor-intensive measurements of pollinator effectiveness are less necessary for broad surveys, effectiveness estimates will be important for detailed studies of some plant species. Unfortunately, at this point it is impossible to predict a priori which species these are.

Keywords Diversity · Effectiveness · Evenness · Pollinator importance · Specialization

Communicated by Jacqui Shykoff

H. F. Sahli (✉) · J. K. Conner
Kellogg Biological Station and Department of Plant Biology, Michigan State University, 3700 East Gull Lake Drive, Hickory Corners, MI 49060, USA
E-mail: sahlihea@msu.edu
Fax: +1-269-6712104

Introduction

Recent empirical studies have shown that many plant species are pollinator generalists; i.e., visited by many potential pollinator species (Herrera 1989; Waser et al. 1996; Olsen 1997; Memmott 1999; Kandori 2002). This observation sparked a debate over the relative frequency of generalization in plant-pollination systems in nature (Waser et al. 1996; Vazquez and Aizen 2003) and how to appropriately characterize generalization (Johnson and Steiner 2000; Vazquez and Aizen 2003; Kay and Schemske 2004; Herrera 2005). These questions are relevant for basic questions such as understanding plant-pollinator webs (Memmott 1999; Memmott and Waser 2002) and measuring spatio-temporal variation in plant-pollinator interactions (Feinsinger 1978; Waser et al. 1996; Gomez and Zamora 1999; Fenster and Dudash 2001). The debate has applied importance as well. The heavy reliance of many plants on animal pollinators for reproduction (Tepedino 1979; Burd 1994) has caused growing concern that pollinator declines will cause the extinction of specialized plant species or reduce crop yield of economically important plants (Allen-Wardell et al. 1998; Kearns et al. 1998). In addition, some weedy and invasive plants rely heavily upon pollinators for reproduction and population growth (Parker 1997; Barthell et al. 2001), and their spread may be influenced by how generalized their pollination is.

While virtually all previous studies of pollinator generalization have only measured generalization as the number of visiting taxa (i.e., pollinator richness; see Table 1 for definitions), visitors may not be equal in either their visitation rates or their ability to effect seed set (pollinator effectiveness). Thus, pollinator species can differ in their contribution to reproduction. Previous authors have suggested that many flower visitors are not actually pollinating, so are not contributing to plant reproduction (e.g., Spears 1983; Johnson and Steiner 2000; Fenster et al. 2004). Furthermore, to understand how generalized is a plant's pollinator assemblage,

Table 1 Definitions of terms used in this paper

Term	Definition
Pollinator visitation	The proportion of total flower, inflorescence, or plant visits made by a pollinator taxon during a unit of time
Pollinator effectiveness	The average number of seeds produced, percent fruit set, or pollen grains deposited by a pollinator taxon during a single visit to a plant
Pollinator importance	The proportion of the total number of seeds or fruits produced by a pollinator taxon, or the proportion of the total number of pollen grains deposited by a pollinator taxon. This is often estimated as the product of visitation rate and effectiveness
Visitation richness	The number of different genera that visit a plant species
Effective richness	The number of visiting pollinator genera that are effective pollinators of a plant species
Visitation diversity	The diversity of the pollinator community of a plant species calculated using the proportion of total visits made by each pollinator taxon
Importance diversity	The diversity of the pollinator community calculated using the proportion of total number of seeds or fruits produced, or pollen grains deposited, by each pollinator taxon

pollination biologists have pointed out the need to characterize both quantity (visitation rates) and quality (effectiveness) of different pollinators (Johnson and Steiner 2000). The product of visitation rate and effectiveness for each pollinator species is pollinator importance, a measure of a pollinator's contribution to plant reproduction (Primack and Silander 1975; Waser and Price 1983; Lindsey 1984; Schemske and Horvitz 1984; Inouye et al. 1994; Kearns and Inouye 1997). However, because pollinator importance is calculated for each visiting taxon separately, no one has previously suggested a method of combining estimates of importance for each visitor to produce one estimate of generalization for a plant species.

Although pollination biologists have discussed the need to measure visitation frequency and pollinator effectiveness when characterizing pollinator diversity, pollination studies rarely use diversity indices developed over five decades ago by community ecologists, which incorporate not only species richness, but also the relative abundance of each species (evenness) (Feinsinger et al. 1987; but see Parrish and Bazzaz 1979; Bosch et al. 1997; Balvanera et al. 2005). In a recent paper, Herrera (2005) pointed out that pollinator evenness deserves consideration in future studies of pollinator generalization. When visitation is uneven, diversity indices provide a more accurate depiction of pollinator generalization than species richness alone. If pollinator richness is increased mainly by the addition of infrequently visiting species, increasing richness may have little effect on pollinator diversity and plant reproduction.

Importance and diversity can be combined into a single measure by calculating diversity indices using pollinator importance values rather than pollinator visitation. We call this importance diversity as opposed to visitation diversity. Because pollinator importance characterizes each pollinator's contribution to plant reproduction, a diversity estimate calculated using the relative importance of each pollinator is the best estimate of the diversity of pollinators contributing to plant reproduction. If pollinator visitation data misrepresent a pollinator's actual importance, then visitation diversity will poorly predict importance diversity.

We used Simpson's diversity index to calculate pollinator diversity for 17 plant species. Visitation diversity, importance diversity, and visitation richness (the number of pollinator taxa visiting a plant species) were calculated to assess how well visitation richness, the typical measure in studies of pollinator generalization, predicts diversity. The evenness of pollinator assemblages was calculated for each plant species to understand differences between richness and diversity. Finally, to test the commonly held view that incorporating pollinator effectiveness provides a better understanding of a pollinator's contribution to plant reproduction than using only visitation rates, we estimated how visitation rates and effectiveness each contribute to variation in pollinator importance.

Materials and methods

Datasets that contained comprehensive estimates of both pollinator effectiveness (measured as pollen removal/deposition or number of seeds set during a single visit) and pollinator visitation frequency were reviewed for 17 plant species (Table 2). Pollinator diversity for each plant species was calculated using Simpson's (1949) diversity index:

$$\frac{1}{D} = \frac{1}{\sum_{i=1}^{S} p_i^2},$$

where p_i is the proportional visitation or importance for pollinator species i and S is richness, the number of pollinator taxa visiting or pollinating a plant species. If all pollinators are equally abundant or important (i.e., evenness = 1), diversity reaches a maximum of S. Simpson's index is commonly used to characterize diversity because it takes into account richness of the pollinating assemblage as well as pollinator evenness, but is weighted more heavily towards common species rather than rare ones (Magurran 1988). Other indices

Table 2 Plant species and studies for which pollinator data was used to calculate diversity and evenness

Plant species	Life habit	No. of years studied	Family	Location	Habitat	No. of locations	Reference
Asclepias incarnata[a]	P	2	Asclepiadaceae	USA	Wetland	1	Ivey et al. 2003
Asclepias tuberosa[c]	P	2	Asclepiadaceae	USA	Wetland	1	Fishbein and Venable 1996
Calathea ovandensis	P	3	Marantaceae	Mexico	Rainforest	4	Schemske and Horvitz 1988; Schemske and Horvitz 1984
Citrullus lanatus[d]	A	1	Curcurbitaceae	USA	Agricultural	3[b]	Kremen et al. 2002
Coffea canephora[d]	P	1	Rubiaceae	Indonesia	Agricultural	15	Klein et al. 2003
Dieffenbachia longispatha[c]	P	3	Araceae	Costa Rica	Rainforest	1	Young 1988
Geranium thunbergii	P	2	Geraniaceae	Japan	Temperate field	1	Kandori 2002
Heterotheca subaxillaris	A	1	Asteraceae	USA	Temperate field	1	Olsen 1997
Hormathophylla spinosa[a]	P	4	Brassicaceae	Spain	Montane	3[b]	Gomez and Zamora 1999
Ipomopsis aggregata[a]	P	5	Polemoniaceae	USA	Montane	3	Mayfield et al. 2001
Lavandula latifolia[a]	P	6	Lamiaceae	Spain	Mixed woodland	1	Herrera 1987; Herrera 1989
Lithophragma parviflora[a]	P	2	Saxifragaceae	USA	Steppe	2[b]	Thompson and Pellmyr 1992
Macromeria viridiflora[a]	P	1	Boraginaceae	USA	Montane	2[b]	Boyd 2004
Prosopis velutina	P	1	Fabaceae	USA	Desert	1	Keys et al. 1995
Raphanus raphanistrum[d]	A	1	Brassicaceae	USA	Temperate field	1	H.F. Sahli and J. K. Conner, unpublished
Satureja thymbra[a]	P	1	Lamiaceae	Israel	Phrygana	2[b]	Potts et al. 2001
Silene vulgaris[c]	P	4	Caryophyllaceae	Sweden	Temperate field	1	Pettersson 1991

P Perennial, *A* annual
[a]Pollinator effectiveness was only determined for a subset of the visiting taxa
[b]Diversity and evenness indices were calculated for each site and averaged over sites. Other studies for which multiple sites were used did not publish results from each site, but summed visits over all sites
[c]Pollinator visitation rate is the number of individuals per plant per unit time. All others are based on number of visits per flower or inflorescence
[d]Pollinator effectiveness and visitation data were collected at a site where the plant is non-native

measuring niche breadth or generalization incorporate relative abundances of the resources (e.g., pollinators) in a given community (see Krebs 1989 for a review) because a pollinator may visit a plant more than others simply because it is more abundant in that community. We chose Simpson's index for our study because very little pollinator community data is currently available to calculate such niche breadth indices, and such indices can misrepresent how reproduction is impacted by pollinator generalization. For example, if very few pollinator taxa are present in a community, but a plant uses all of them, it would be generalized according to a niche breadth index. However, in terms of how plant reproduction is impacted by a loss of just one of those pollinators, it would be relatively specialized because a loss of one pollinator taxon might greatly reduce plant reproduction.

Pollinator evenness was calculated for all plant species by dividing Simpson's diversity index by pollinator richness:

$$E_{1/D} = \frac{1/D}{S}.$$

Estimating $E_{1/D}$ allows the examination of the two components of diversity (evenness and richness) separately (Smith and Wilson 1996). Evenness reaches a maximum of one when $S = 1/D$, and diversity declines for a given S when evenness declines. Because the taxonomic level at which pollinators were identified varied between studies, pollinators were grouped at the genus level when possible.

Diversity and evenness for studies that published visitation data from multiple sites was calculated for each site separately, then averaged to estimate the pollinator diversity contributing to a single population's reproduction. Visitation data for *Calathea, Coffea*, and *Ipomopsis* were published as a sum across multiple sites (Table 2), so estimates for these species overestimate diversity in any one population. When visitation data were collected for multiple years (only done for perennial species), data were summed across years to provide one total diversity estimate. For perennial plants, characterizing the diversity of the pollinating assemblage over multiple years more accurately estimates the diversity of pollinators affecting lifetime plant reproduction. Differences among studies in sampling intensity, as well as different ways of handling multiple years, multiple populations, and different taxonomic groupings, do not affect the conclusions of this paper because our aim is not to understand the actual distribution of generalization, but to compare methods of estimating generalization (see Discussion). We note that annuals are under-represented in this study so this may potentially bias our results.

Visitation versus importance

To examine how including pollinator effectiveness alters estimates of pollinator diversity based only on visitation, pollinator diversity was calculated using both visitation and importance. Pollinator richness was determined for each plant species using visitation (visitation richness) and importance data (effective richness), where effective richness is the number of taxa actually pollinating a plant species. Effectiveness was not determined for 16–40% of the taxa visiting *Asclepias incarnata, Hormathophylla*, and *Ipomopsis* so these pollinator taxa were not included in comparisons of richness and evenness and richness and visitation. Leaving out the pollinator taxa for which effectiveness was not determined did not change evenness by more than 0.10, and thus resulted in little change in the relationship between richness and diversity. Because pollinator effectiveness was determined for less than half of the visiting taxa to *Satureja, Lithophragma*, and *Lavandula*, and leaving out these visiting taxa resulted in increases in evenness greater than 0.10, these three studies were not included in comparisons of richness and importance diversity. However, because they obtained comprehensive visitation data, these studies were included in comparisons of visitation diversity and visitation richness.

Results

Pollinator diversity across 17 plant species

Visitation richness ranged from 2 to 45 genera (Table 3). Because importance diversity includes richness, evenness, and effectiveness of pollinators contributing to plant reproductive success, it is the most comprehensive estimate of generalization. To determine how well the most common measure of generalization, pollinator richness, predicts pollinator diversity as calculated using either visitation rates or importance values, visitation and importance diversity were each regressed on pollinator richness among species. An inherent correlation between richness and diversity exists because richness is included in diversity (DeBenedictis 1973; Stirling and Wilsey 2001). Still, richness alone explained just 57% of the variation in visitation diversity and 65% of the variation in importance diversity (Fig. 1). The slope of the relationship between diversity and richness was much less than one due to a significant negative relationship between evenness and visitation richness (Fig. 2). Furthermore, there were many changes in rank among plant species when richness was used as compared to visitation diversity, and these rank changes were due to differences in the evenness of pollinator assemblages (Table 3).

Visitation versus importance

In roughly two-thirds of the plant species, and all of the more specialized ones (visitation richness <7 taxa), all visiting taxa were effective pollinators. For the other five plant species, an average of three genera of visitors were not effective pollinators, representing 7–43% of the visiting taxa (Table 3). Richness, diversity, and evenness calculated using only visitation data were all highly significantly correlated with their corresponding estimates calculated using importance data (richness $r=0.98$; diversity $r=0.84$; evenness $r=0.80$).

To determine how variation in pollinator importance is determined by effectiveness versus visitation, importance for each pollinator taxon was regressed on effectiveness and visitation separately for each plant species, and the resulting R^2 values were compared using a

Table 3 Estimates of richness, diversity, and evenness of each plant's pollinator assemblage calculated using visitation data versus importance data

Plant species	Visitation			Importance		
	Richness	Diversity	Evenness	Richness	Diversity	Evenness
Ipomopsis aggregata	2	1.09	0.55	2	1.15	0.58
Dieffenbachia longispatha	2	1.90	0.95	2	1.75	0.88
Macromeria viridiflora	3	1.48	0.49	3	1.19	0.40
Prosopis velutina	5	4.39	0.88	5	2.89	0.58
Asclepias incarnata	6	2.14	0.36	6	2.99	0.50
Citrullus lanatus	6.33	2.46	0.39	6.33	2.90	0.46
Asclepias tuberosa	7	3.89	0.56	4	3.60	0.90
Calathea ovandensis	9	3.10	0.34	6	2.23	0.37
Coffea canephora	9	3.72	0.41	9	4.10	0.46
Heterotheca subaxillaris	10	4.43	0.44	10	4.74	0.47
Satureja thymbra	11	5.03	0.46			
Hormathophylla spinosa	12.7	2.5	0.2			
Lithophragma parviflora	13	1.52	0.12			
Silene vulgaris	13	5.60	0.43	10	6.20	0.62
Raphanus raphanistrum	15	3.90	0.26	14	3.91	0.28
Geranium thunbergii	29	12.48	0.43	24	6.46	0.27
Lavandula latifolia	45	7.51	0.17			

Diversity and evenness were calculated using Simpson's diversity index ($1/D$) and $E_{1/D}$, respectively. Plant species are ordered by visitation richness. Data for *Citrullus, Hormathophylla, Satureja, Macromeria*, and *Lithophragma* are averaged over multiple populations, while *Ipomopsis, Calathea*, and *Coffea* are summed over multiple populations (Table 1). Importance data for *Satureja, Lithophragma, Hormathophylla*, and *Lavandula* are not included due to the lack of effectiveness data for the majority of the pollinating taxa

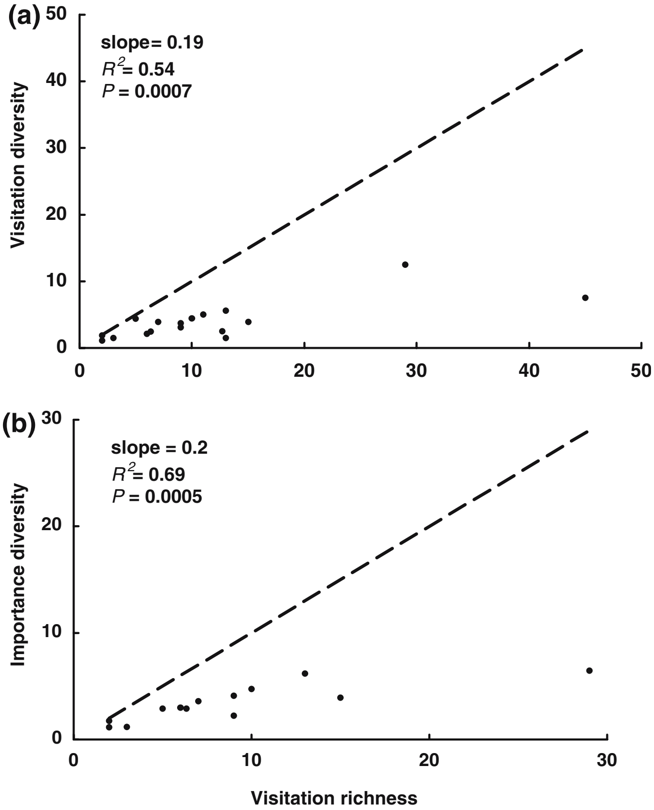

Fig. 1 Regression of **a** visitation diversity and **b** importance diversity on visitation richness, where each point represents a different plant species. The *dashed line* represents the maximum diversity for each plant's pollinator assemblage if all pollinators were equal in their visitation rates (**a**) and importance (**b**); *circles* are the actual diversity estimates for each plant's pollinator assemblage. Values for **a** include indices for *Satureja, Lithophragma, Hormathophylla*, and *Lavandula* which are not included in **b** due to the lack of effectiveness data for the majority of the pollinating taxa

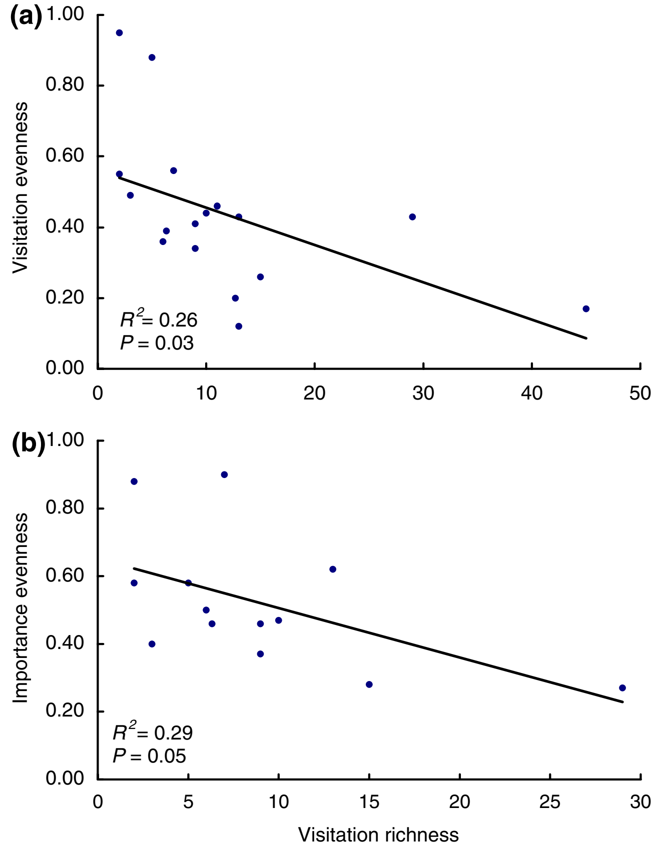

Fig. 2 Regression of **a** visitation evenness and **b** importance evenness on visitation richness, where each point represents a different plant species. **a** Includes indices for *Satureja, Lithophragma, Hormathophylla*, and *Lavandula* which are not included in **b** (see Fig. 1)

paired *t*-test. In most plant species, visitation rates were a far better predictor of pollinator importance than pollinator effectiveness (Table 4). Although there was more variance among pollinators in their visitation rates than in their effectiveness for more than half of the plant species included in this analysis (Table 4), the contribution of visitation and effectiveness to importance was not simply a function of the variance in each variable. And although visitation was the main determinant of importance overall, effectiveness proved to be more important in determining variation in pollinator importance than visitation rates for *A. incarnata* and *Prosopis* (Table 4).

Discussion

Due to the inherent correlation between richness and diversity, richness will always be a general surrogate for diversity. However, the present study revealed that estimates of pollinator diversity are only moderately well predicted by pollinator richness (Fig. 1). The inability of richness measures alone to accurately predict pollinator diversity is further shown by the change in rank of several plants when richness versus diversity is used to estimate generalization. Increasing numbers of pollinator taxa resulted in a less even assemblage because many of the visiting taxa are rare, as noted previously by Herrera (1989). While pollinator richness provides some understanding of generalization in pollination systems, accounting for evenness is a much more accurate approach.

Understanding the diversity of pollinators can influence conservation and management decisions because plant reproduction and plant population growth may be greatly impacted by a reduction in pollinator availability (Kearns et al. 1998; Havens 1999; Larsen et al. 2005). For example, Ricketts (2004) found that, in a population with low bee richness, a decrease in honeybee visitation to coffee plants led to a reduction in crop yield. However, in a population with high bee richness, native bees compensated for a reduction in honeybee visitation to coffee plants, causing little reduction in reproduction. Thus, a more rich or diverse pollinator assemblage might lead to more stable plant reproduction, despite

Table 4 Variation in pollinator importance explained by effectiveness versus visitation and coefficients of variation of effectiveness and visitation for each plant

Plant species	R^2		CV	
	Visitation	Effectiveness	Visitation	Effectiveness
Silene vulgaris	0.68**	0.0003	1.20	1.50
Raphanus raphanistrum	0.94***	0.003	1.74	0.71
Satureja thymbra	0.78*	0.005	0.62	0.29
Heterotheca subaxillaris	0.86***	0.02	1.18	0.46
Hormathophylla spinosa	0.96**	0.02	1.13	0.21
Lithophragma parviflora	0.99***	0.06	1.77	0.60
Citrullus lanatus	0.40	0.07	1.50	0.43
Calathea ovandensis	0.81**	0.09	1.46	2.05
Geranium thunbergii	0.82***	0.11	0.43	1.05
Coffea canephora	0.99***	0.25	1.26	0.14
Lavandula latifolia	0.94***	0.26*	1.42	0.61
Asclepias tuberosa	0.83*	0.30	0.96	1.08
Asclepias incarnata	0.02	0.40	1.47	1.03
Prosopis velutina	0.63	0.81*	0.42	0.53
Macromeria viridiflora	0.99*	0.82	0.99	0.32

Visitation and effectiveness were regressed on importance separately; a multiple regression including both is overparameterized because the product of visitation and effectiveness is importance. Regressions could not be performed for *Dieffenbachia* and *Ipomopsis* because they were visited by only two pollinator genera. One average value for visitation, effectiveness, and importance was calculated for each pollinator of each plant species. Plant species are ordered by effectiveness R^2. Visitation explained a significantly greater proportion of variance in importance than did effectiveness (mean difference = 0.56; paired $t = -5.37$, $P < 0.0001$)
*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.0001$

losses in pollinator species. Whether richness or diversity estimates are more predictive of stability remains to be tested. Studies examining the relationship between pollinator diversity and plant reproduction in the face of shifting pollinator assemblages are greatly needed.

Despite the widely held idea that pollinator effectiveness is crucial and should always be taken into account, the present study indicates that visitation rather than effectiveness is the main driving factor in determining pollinator importance. This was partly because the majority of visiting taxa were true pollinators, in contrast with the view that effective pollinators make up only a small fraction of floral visitors. Previous studies on single plant species noted that pollinator visitation seems to play a larger role in pollinator importance than pollinator effectiveness (Motten et al. 1981; Olsen 1997), while other studies have suggested that effectiveness was important (Armbruster et al. 1989; Fenster et al. 2004). Past studies, however, did not quantify the value of visitation versus effectiveness. Similar to our findings, a recent meta-analysis (Vazquez et al. 2005) showed that visitation rates play a more important role in plant reproduction than effectiveness.

However, effectiveness did explain a substantial amount of the variation in pollinator importance in approximately one-third of the plant species for which we could make this comparison. Still, visitation was a better predictor of importance for all species but *A. incarnata* and *Prosopis*, and only for *Prosopis* was the effectiveness significant (Table 4). It is interesting to note that effectiveness was important for both species of *Asclepias*, which have specialized modes of pollen removal/deposition. Pollinator effectiveness may be important for such species because many visitors may be unable to pollinate effectively. Due to the limited number of species included in our analysis, we could not address whether effectiveness is more important for species with specialized pollen removal/deposition mechanisms. Because we have no way of predicting for which plant species effectiveness will be important, pollination biologists should continue to measure effectiveness on the majority of pollinators whenever possible for a full understanding of how different pollinators contribute to a plant's reproductive success.

Thus far we have only addressed the ecological importance of measuring pollinator effectiveness. Many pollination studies examining pollinator effectiveness are motivated by the idea that effectiveness can provide insight into which pollinators are responsible for floral evolution (e.g., Grant and Grant 1965; Primack and Silander 1975; Schemske and Horvitz 1984; Herrera 1989; Fishbein and Venable 1996; Olsen 1997; Ivey et al. 2003). However, more efficient or abundant pollinators may not necessarily be those that are selecting on any given floral trait (Aigner 2001; Fenster et al. 2004; Aigner 2005). Without knowing how seed production from an important visitor is affected by variation in some floral trait, we cannot understand how a visitor influences the evolution of floral traits (Strauss et al. 2005). To date, few studies have measured selection by individual pollinator taxa in a generalized plant and have related this to pollinator effectiveness.

This study is not meant to provide a characterization of generalization in pollination systems because it is based on data sets gathered with different levels of sampling effort and with different numbers of populations. Future studies characterizing pollinator generalization of several species should take into account differences in sampling intensity since diversity indices are sensitive to sampling effort (Ollerton and Cranmer 2002). Herrera (2005) suggests using rarefaction to account for differences in sampling, although we were unable to use such a technique due to insufficient published data on sampling regime. In addition, because of the difficulty in estimating effectiveness for a large number of pollinator taxa, the plants included in this study may be biased toward specialization. What this study does suggest is that diversity indices should be incorporated into any study addressing pollinator generalization rather than simply estimating pollinator richness. Our study also indicates that pollinator effectiveness may not be as important as it is commonly believed to be, although more studies on plant species with high visitation richness are certainly needed.

Acknowledgements We thank S. Armbruster, C. Brassil, M. Duffy, S. Emery, C. Herrera, F. Knapczyk, A. Roles, D. Schemske, D. Vazquez, and P. Wilson for helpful comments on the manuscript. Funding was provided by a Lauff Scholarship, Sigma-Xi Grant-in-Aid, NSF DEB-9903880, and NSF DDIG DEB-0408055. This is KBS contribution no. 1214.

References

Aigner PA (2001) Optimality modeling and fitness trade-offs: when should plants become pollintor specialists? Oikos 95:177–184

Aigner PA (2005) The evolution of specialized floral phenotypes in a fine-grained pollination environment. In: Waser NM, Ollerton J (eds) Specialization and generalization in plant-pollinator interactions. University of Chicago Press, Chicago

Allen-Wardell G et al (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conserv Biol 12:8–17

Armbruster WS, Keller S, Matsuki M, Clausen TP (1989) Pollination of *Dalechampia magnoliifolia* (Euphorbiaceae) by male euglossine bees. Am J Bot 76:1279–1285

Balvanera P, Kremen C, Martinez-Ramos M (2005) Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. Ecol Appl 15:360–375

Barthell JF, Randall JM, Thorp RW, Wenner AM (2001) Promotion of seed set in yellow star-thistle by honey bees: evidence of an invasive mutualism. Ecol Appl 11:1870–1883

Bosch J, Retana J, Cerda X (1997) Flowering phenology, floral traits, and pollinator composition in a herbaceous Mediterranean plant community. Oecologia 109:583–591

Boyd EA (2004) Breeding system of *Macromeria viridiflora* (Boraginaceae) and geographic variation in pollinator assemblages. Am J Bot 91:1809

Burd M (1994) Bateman's principle and plant reproduction—the role of pollen limitation in fruit and seed set. Bot Rev 60:83–139

DeBenedictis PA (1973) Correlations between certain diversity indexes. Am Nat 107:295–302

Feinsinger P (1978) Ecological interactions between plants and hummingbirds in a successional tropical community. Ecol Monogr 48:269–287

Feinsinger P, Beach JH, Linhart YB, Busby WH, Murray KG (1987) Disturbance, pollinator predictability, and pollination success among Costa Rican cloud forest plants. Ecology 68:1294–1305

Fenster CB, Dudash MR (2001) Spatiotemporal variation in the role of hummingbirds as pollinators of *Silene virginica*. Ecology 82:844

Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD (2004) Pollination syndromes and floral specialization. Annu Rev Ecol Evol Syst 35:375–403

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

Gomez JM, Zamora R (1999) Generalization vs. specialization in the pollination system of *Hormathophylla spinosa* (Cruciferae). Ecology 80:796–805

Grant V, Grant KA (1965) Pollination in the Phlox family. Columbia University Press, New York

Havens K (1999) Pollination biology: implications for restoring rare plants. Ecol Restor 17:216–218

Herrera CM (1987) Components of pollinator "quality": comparative analysis of a diverse insect assemblage. Oikos 50:79–90

Herrera CM (1989) Pollinator abundance, morphology, and flower visitation rate: analysis of the "quantity" component in a plant-pollinator system. Oecologia 80:241–248

Herrera CM (2005) Plant generalization on pollinators: species property or local phenomenon? Am J Bot 92:13–20

Inouye DW, Gill DE, Dudash MR, Fenster CB (1994) A model and lexicon for pollen fate. Am J Bot 81:1517–1530

Ivey CT, Martinez P, Wyatt R (2003) Variation in pollinator effectiveness in swamp milkweed, *Asclepias incarnata* (Apocynaceae). Am J Bot 90:214

Johnson SD, Steiner KE (2000) Generalization versus specialization plant pollination systems. Trends Ecol Evol 15:140–143

Kandori I (2002) Diverse visitors with various pollinator importance and temporal change in the important pollinators of *Geranium thunbergii* (Geraniaceae). Ecol Res 17:283–294

Kay KM, Schemske DW (2004) Geographic patterns in plant-pollinator mutualistic networks: comment. Ecology 85:875–878

Kearns C, Inouye D (1997) Pollinators, flowering plants, and conservation biology. BioScience 47:297–307

Kearns C, Inouye D, Waser N (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. Annu Rev Ecol Evol Syst 29:83–112

Keys RN, Buchmann SL, Smith SE (1995) Pollination effectiveness and pollination efficiency of insects foraging *Prosopis velutina* in South-eastern Arizona. J Appl Ecol 32:519

Klein AM, Steffan-Dewenter I, Tscharntke T (2003) Pollination of *Coffea canephora* in relation to local and regional agroforestry management. J Appl Ecol 40:837–845

Krebs CJ (1989) Ecological methodology. Harper and Row, New York

Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. Proc Natl Acad Sci USA 99:16812–16816

Larsen T, Williams NM, Kremen C (2005) Extincion order and altered community structure rapidly disrupt ecosystem functioning. Ecol Lett 8:538–547

Lindsey AH (1984) Reproductive biology of Apiaceae. I. Floral visitors to *Thaspium* and *Zizia* and their importance in pollination. Am J Bot 71:375–387

Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton

Mayfield MM, Waser NM, Price MV (2001) Exploring the 'most effective pollinator principle' with complex flowers: bumblebees and *Ipomopsis aggregata*. Ann Bot 88:591–596

Memmott J (1999) The structure of a plant-pollinator food web. Ecol Lett 2:276–280

Memmott J, Waser NM (2002) Integration of alien plants into a native flower-pollinator visitation web. Proc R Soc Lond B 269:2395–2399

Motten AF, Campbell DR, Alexander DE, Miller HL (1981) Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. Ecology 62:1278–1287

Ollerton J, Cranmer L (2002) Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? Oikos 98:340

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

Parker IM (1997) Pollinator limitation of *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. Ecology 78:1457–1470

Parrish JAD, Bazzaz FA (1979) Difference in pollination niche relationships in early and late successional plant-communities. Ecology 60:597–610

Pettersson MW (1991) Pollination by a guild of fluctuating moth populations: option for unspecialization in *Silene vulgaris*. J Ecol 79:591–604

Potts SG, Dafni A, Ne'eman G (2001) Pollination of a core flowering shrub species in Mediterranean phrygana: variation in pollinator diversity, abundance and effectiveness in response to fire. Oikos 92:71

Primack RB, Silander JA Jr (1975) Measuring the relative importance of different pollinators to plants. Nature 255:143–144

Ricketts TH (2004) Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conserv Biol 18:1262

Schemske DW, Horvitz CC (1984) Variation among floral visitors in pollination ability: a precondition for mutualism specialization. Science 225:519–521

Schemske DW, Horvitz CC (1988) Plant animal interactions and fruit production in a neotropical herb—a path-analysis. Ecology 69:1128–1137

Simpson EH (1949) Measurement of diversity. Nature 163:688

Smith B, Wilson JB (1996) A consumer's guide to evenness indices. Oikos 76:70

Spears EE Jr (1983) A direct measure of pollinator effectiveness. Oecologia 57:196–199

Stirling G, Wilsey B (2001) Empirical relationships between species richness, evenness, and proportional diversity. Am Nat 158:286–299

Strauss SY, Sahli H, Conner JK (2005) Toward a more trait-centered approach to diffuse (co)evolution. New Phytol 165:81–89

Tepedino VJ (1979) The importance of bees and other insect pollinators in maintaining floral species composition. Great Basin Nat Memoirs 3:139–150

Thompson JN, Pellmyr O (1992) Mutualism with pollinating seed parasites amid co-pollinators: constraints on specialization. Ecology 73:1780–1791

Vazquez DP, Aizen MA (2003) Null model analyses of specialization in plant-pollinator interactions. Ecology 84:2493–2501

Vazquez DP, Morris WF, Jordano P (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. Ecol Lett 9:1088–1094

Waser NM, Price MV (1983) Pollinator behavior and natural selection for flower colour in *Delphinium nelsonii*. Nature 302:422–424

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77:1043–1060

Young HJ (1988) Differential importance of beetle species pollinting *Dieffenbachia longispatha* (Araceae). Ecology 69:832–844