ASYMMETRIC SPECIALIZATION: A PERVASIVE FEATURE OF PLANT–POLLINATOR INTERACTIONS

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Abstract. Although specialization in species interactions has usually been equated to reciprocal specialization, asymmetric specialization (i.e., a specialist interacting with a generalist) is also likely. Recent studies have suggested that asymmetric specialization in species interactions could be more common than previously thought. We contrasted patterns of asymmetric specialization observed in 18 plant–pollinator interaction webs with predictions based on null models. We found that asymmetric specialization is common in plant–pollinator interactions, and that its occurrence is more frequent than expected under a simple null model that assumed random interactions among species; furthermore, large assemblages with many pairs of interacting species tend to have more asymmetric interactions than smaller assemblages. A second null model, which incorporated a correlation between species frequency of interaction and degree of specialization observed in most data sets produced patterns that were generally closer to those present in the data. At least three kinds of explanations could account for the observed asymmetric specialization, including random interactions among individuals (rather than species), adaptive consequences of specialization, and artifacts, such as data aggregation and sampling biases. Future studies should be aimed at understanding the relative importance of each of these alternative explanations in generating asymmetric specialization in species interactions.

Key words: asymmetric specialization; generalization; network organization; null models; plant–pollinator interactions.

Introduction

Biologists have frequently assumed symmetric specialization in species interactions: either specialists interact with specialists or generalists with generalists (see Schemske 1983, Thompson 1994, Renner 1998, Vázquez and Simberloff 2002). Under this scenario, reciprocally specialized interactions are more likely to lead to coupled ecological dynamics and coevolutionary change than reciprocally generalized interactions. However, interactions in nature may not follow this tidy pattern. Rather, only a fraction of specialists may interact with specialists, the rest interacting with moderate to extreme generalists.

Three studies have used correlation analysis to quantify asymmetric specialization in species interaction networks, two of them in plant–pollinator webs (Petanidou and Ellis 1996, Vázquez and Simberloff 2002) and the third in food webs (Melián and Bascompte 2002). These studies examined the association between the number of interaction partners of a species i (s_i, a measure of degree of specialization) and the average value of s of the interaction partners of species i (p_i) as a measure of specialization asymmetry; a positive correlation would indicate symmetric specialization, whereas a negative correlation would indicate asymmetric specialization (the variables used by Petanidou and Ellis to quantify asymmetry are not s and p, but they are conceptually related). In the three cases, negative, albeit weak, correlations were found. Furthermore, the analysis in food webs revealed that the slope of the regression between s and p changed at a threshold value as s increased (Melián and Bascompte 2002).

As with many other ecological variables (e.g., Brown and Maurer 1989, Thomson et al. 1996), the distribution of species throughout the s-p parameter space for a given community is unlikely to follow a linear pattern. Rather, it is likely to follow a triangular-like distribution, with the values of p occupying an increasingly smaller section of the parameter space with increasing s (Fig. 1). For example, an extreme generalist that interacts with most other species in the community will necessarily interact with some extreme specialists, which will constrain the range of possible values of p that generalists can exhibit (in the extreme, if a generalist interacts with all species in the community, there will be only one possible value of p that it can have). Conversely, the possible values of p available to an extreme specialist range from the highest to the lowest degree of specialization of potential interaction partners.
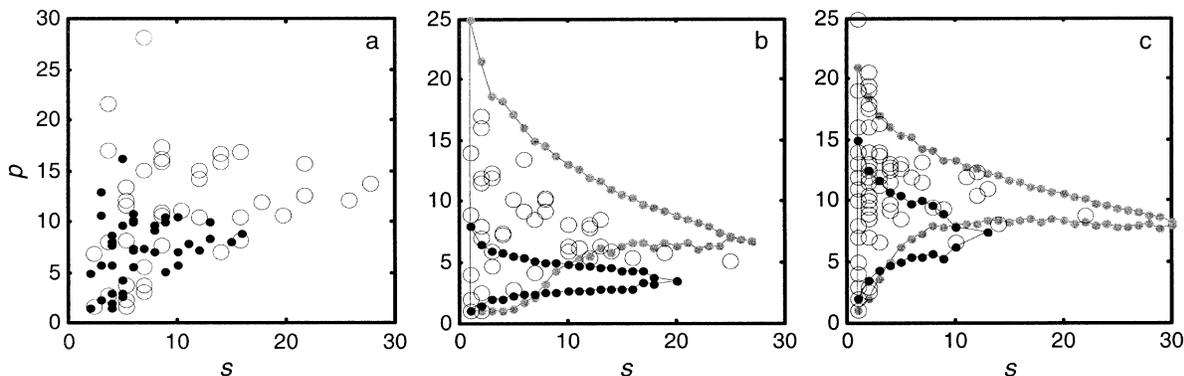
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FIG. 1. Distribution of asymmetric specialization in plant–pollinator interaction networks. Plots show the average specialization of interaction partners (p) vs. the degree of specialization (s). (a) An example to illustrate the inability of the correlation coefficient to characterize asymmetric specialization. Heuristic data are shown for two communities with identical correlation coefficients ($r = 0.4265$), one with higher values of s and p (large open circles) than the other (black dots). Data for the Inouye and Pyke (1988) data set are shown for plants (b) and pollinators (c). Large open circles represent observed s-p values; black dots and line indicate the null space for model 1; gray dots and line indicate the null space for model 2. Notice that most extreme specialists (species with low values of s) do not have reciprocally specialized interaction partners (low values of p); a similar pattern was observed for all data sets (see Appendix B).

The existence of such structure in randomly generated assemblages makes it necessary to contrast the observed patterns of asymmetry with some kind of null model, so as to generate an expected distribution in the absence of a hypothesized mechanism (e.g., coevolution between plants and pollinators or dynamical constraints to food-web stability). Furthermore, such random structure makes the very use of the correlation coefficient to characterize asymmetric specialization inappropriate. As shown in Fig. 1a, two interaction networks with very different distributions of s and p values may have exactly the same correlation coefficient; arguably, most species in one of the communities (shown with empty circles) are less symmetrically specialized than those in the other community.

Here we use an alternative method based on null models to study the distribution of asymmetric specialization in eighteen plant–pollinator interaction webs from around the world, in which interactions between all plant species (or a substantial subset) and their animal pollinators were recorded. In particular, we address the following questions: (1) whether asymmetric specialization is common in pollination systems, (2) whether the occurrence of asymmetric specialization is higher than expected from simple null models of species interactions, and (3) whether the observed asymmetry is explained by properties of the assemblages, such as total number of species, total number of interactions, and connectance.

METHODS

Data sets

We used 18 data sets from published community-wide studies of plant–pollinator interactions (throughout the manuscript, we refer to data sets by the authors'

names; complete references are given in Appendix A). 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). In these matrices, a cell ij containing a ''1'' represents an interaction between pollinator species i and plant species j, while a cell with a ''0'' represents no interaction. In addition, eleven data sets contained information on the frequency of interaction between pairs of species (either total number of pollinator visits recorded per unit time, or number of collected individuals per insect species for each plant species; Appendix A). For these data sets we constructed ''interaction frequency matrices,'' in which 1's in the binary matrix are replaced by positive integers representing the number of times a pair of species were observed interacting. One of the data sets (Vázquez and Simberloff 2002, 2003) consisted of data from eight sites with the same community type within a 25-km radius; since analysis done separately for each site and for all sites pooled gave similar results, we report results for the pooled data only. Data sets are available online through the Interaction Web Database.[4]

Quantification of degree of specialization, specialization of interaction partners, and frequency of interaction

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 (see Vázquez and

Aizen 2003). Average *s* of interaction partners (*p*) was used as a measure of degree of specialization of all species interacting with a given species (see Melián and Bascompte 2002, Vázquez and Simberloff 2002). Frequency of interaction (*f,* the total number of times a species was observed interacting with any other species) for plants and pollinators was calculated from the sum of columns and rows, respectively, in the interaction-frequency matrix.

Null models

We used simple computer algorithms written in Matlab (MathWorks 1999) to randomize plant–pollinator interactions in the data sets; these algorithms are based on those used in a previous analysis (Vázquez and Aizen 2003). Briefly, the number of pair-wise species interactions originally observed in the interaction matrix was randomly distributed among species of plants and pollinators, with the only restriction that each species had at least one interaction (i.e., the criterion for inclusion of plant and pollinator species in the data sets). Connectance (i.e., the number of observed interactions over the maximum number of potential interactions) in the randomized data sets was the same as in the original data sets.

We used two null models. In null model 1, interactions were randomly distributed among pairs of plant and pollinator species; all plant or animal species had the same probability of interacting, independently of their frequency of interaction, thus assuming neutrality at the species level (i.e., all species are equal, regardless of their characteristics). Conversely, in null model 2 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. (Notice that frequency of interaction was used only to calculate probabilities in null model 2, but not for the calculation of *s* and *p*.) Thus, assuming a link between species frequency of interaction and abundance, null model 2 represents neutrality at the individual level rather than at the species level, in the spirit of recent neutral models of community structure (Bell 2000, Hubbell 2001). (A fuller description of null models is given in Vázquez and Aizen [2003].)

We overlapped the *s-p* values from each of 1000 randomized interaction matrices, and used the 99% least extreme values of *p* for each category of *s* as boundaries of the null space generated by the null model (hereafter "null space"). Species with observed *s-p* combinations falling above or to the right of the null space are regarded as more asymmetrically specialized than expected from the null model, either because they are specialists interacting with extreme generalists or because they are extreme generalists themselves (which implies that they interact with at least some specialists); conversely, species falling under the lower limit of the null space (i.e., in the lower-left corner of the *s-p* graph)

would be more symmetrically specialized than expected from the null model. For each data set we counted the number of species below, within, and above the null space. We used null model 1 as a benchmark for comparison, and null model 2 as a way of incorporating a possible mechanism to explain observed patterns of asymmetry (i.e., species interaction frequency determines their degree of specialization).

RESULTS

The distribution of specialization among interacting species is highly asymmetric, as most specialists do not have specialized interaction partners (Fig. 1b and c). Therefore, the answer to our first question (i.e., Is asymmetric specialization common in pollination systems?) appears to be "yes."

Is the observed asymmetric specialization different from what is expected if species interacted randomly? In most data sets, a substantial proportion of plant and pollinator species had *s-p* combinations falling outside the null space of model 1 (Fig. 1b and c, Fig. 2). The mean number of species inside the null space was 40% (range 8–90%) for plants, and 43% (range 9–100%) for pollinators. With rare exceptions, species did not fall below the null space of model 1 (Fig. 1b and c, Fig. 2). Thus in most data sets a substantial number of species is more asymmetrically specialized than expected from model 1. This asymmetry is a consequence of specialists being specialized on generalists, or of species being extreme generalists themselves.

The percentage of species inside the null space for model 1 was significantly and negatively correlated with the total number of species in the assemblage and total number of links, and slightly positively correlated with connectance for pollinators but not for plants (Appendix C). Thus, communities with more species and with more pairs of interacting species tend to have more asymmetric interactions than smaller communities with fewer links.

In agreement with a previous analysis (Vázquez and Aizen 2003), there was a high correlation between *f* (frequency of interaction) and *s* (total number of species with which a grim species interacted) in most data sets, except for Olesen et al.'s Île aux Aigrettes and for Small's peat bog data (Appendix D). Thus, more frequently interacting species appear more generalized than rarely interacting species.

Does the observed correlation between *f* and *s* account for the distribution of asymmetric specialization observed in the data sets? Incorporating such correlation into the null model (i.e., model 2) results in a pattern that is, in most cases, strikingly similar to that observed in the data (Fig. 1b and c), generating a pattern much closer to the data than model 1 (Fig. 2). The mean number of species inside the null space of model 2 was 88% (range 71–100%) for plants, and 76% (30–100%) for pollinators, substantially higher than for model 1. Thus, the asymmetry observed in most data
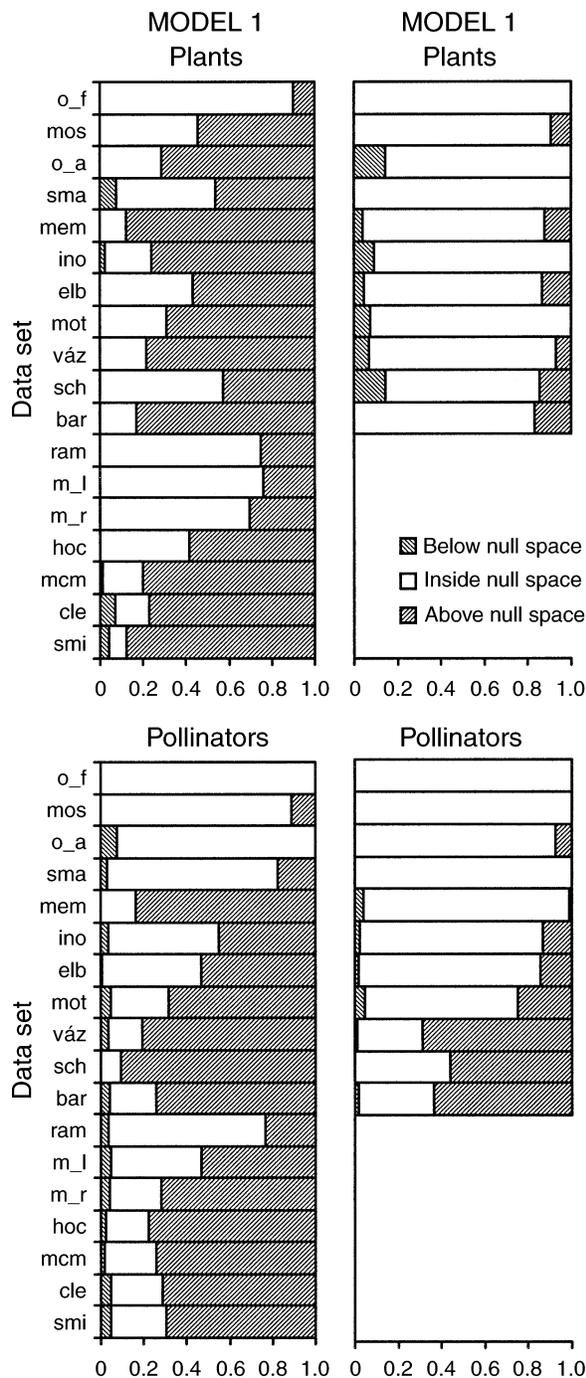
FIG. 2. Summary of comparisons between two null models for 18 plant–pollinator interaction data sets. Categories along ordinates are data-set codes (see Appendix A for complete references). Values along abscissas represent the proportion of species with *s-p* values (where *s* = number of species of interaction partners, and *p* = average *s* of all interaction partners) falling below (left), inside (middle), and above (right) the null space of the null models. Model 1 assumes random interactions among species; model 2 assumes interactions proportional to a species' observed interaction frequency. Seven data sets did not include data on interaction frequency, so model 2 could not be run in these cases (bottom of graphs).

sets can be partly accounted for by the relationship between species' frequency of interaction and their estimated degree of specialization. There are, however, several "outliers"—species falling outside the null space of model 2, whose asymmetry is not explained by the *f-s* correlation. A pattern common to several data sets is that one extremely generalized plant species falls beyond (i.e., to the right of) the null space of model 2, which in turn causes several specialized or moderately generalized insect species to fall above the null space (see Appendix B: panels o–t). This situation appears to be the reason for model 2 being, in general, a much better predictor for plants than for pollinators (compare the percentages above the null space of model 2 between plants and pollinators in Fig. 2).

DISCUSSION

The analysis presented here suggests that asymmetric specialization is common in plant–pollinator interaction webs, occurring more frequently than expected under a simple null model that assumes random interactions among species (model 1). Furthermore, our null model 2 reveals that much of the observed asymmetry can be attributed to random interactions between individuals rather than species. Our analysis also suggests that large assemblages with many pairs of interacting species tend to have a higher proportion of asymmetric interactions than smaller assemblages with fewer pairs of interacting species.

It is important to mention that a recent study by Bascompte et al. (2003) has independently reached similar conclusions to those reached in the present analysis. These authors have used similar null models to analyze patterns of interaction in plant–animal mutualistic networks (i.e., pollination and seed dispersal). They elegantly show that most networks have a nested structure, whereby specialized species always interact with a subset of the interaction partners of more generalized species. A nested pattern of interactions necessarily means asymmetric specialization between interaction partners. However, Bascompte et al.'s analysis has some important differences with our study. First, although the existence of a nested structure necessarily implies asymmetric specialization, the converse is not necessarily true. Thus, if we concluded that a particular assemblage is not nested, we would still be left with the question of whether interactions are asymmetrically specialized. Such a situation could occur, for example, when two or more generalized plant species with nonoverlapping phenologies interact with many specialized pollinators. Thus, in this sense our analysis is more general, because it allows us to detect other kinds of asymmetry besides nested interactions. Second, our null model 2 allows us to evaluate a specific mechanism as a potential cause of the observed patterns; such considerations were absent from Bascompte et al.'s study.

Our findings (and those of Bascompte et al. 2003) may have important implications for understanding the

structure of plant–pollinator interaction networks. Although extreme specialization appears to be common in plant–pollinator interactions (Vázquez and Aizen 2003), our analysis shows that reciprocal specialization is rare, since most specialists are asymmetrically specialized on generalists. Provided that the pattern observed in the data reflects underlying biological processes and not sampling biases (see below), our results suggest a low potential for ecological and coevolutionary coupling of the dynamics of interacting populations of plants and pollinators. Rather, rare specialists are likely to "track" their super-abundant, super-generalist partners. Many of the species interacting with extreme generalists are themselves specialized; thus, their interactions with the generalist are likely to be strong, and this interaction may represent an important selective pressure for them.

Our results may also be applicable at scales that transcend the local communities in which most studies of plant–pollinator interactions have been conducted to date. Because locally abundant species tend to be geographically widespread (Gaston et al. 1997), the asymmetries found in local communities are likely to occur over vast geographical scales. For example, *Larrea tridentata* is the most locally abundant and most geographically widespread plant in North American deserts; over its range, *L. tridentata* is visited by more than 120 species of bees, second only to the sunflower *Helianthus annuus*; many of these bee species are specialists on *L. tridentata* (Minckley et al. 1999). Thus, asymmetric specialization may not just be a local phenomenon, but one that extends over broad geographical scales.

Although super-abundant, super-generalized species interact with many other species, they do not interact equally strongly with all of them. Thus, generalists are likely to be effectively influenced by a small subset of their partners with whom they maintain strong interactions. Population-level interaction strength is a function of per capita interaction strength and frequency of interaction. Thus, frequent visitors that are also efficient pollinators will interact more strongly with a particular plant species than rare visitors or than frequent, inefficient visitors. Likewise, pollinators will interact more strongly with frequently visited plants that provide high food profit per visit than with rare plants or with frequently visited plants that offer poor rewards. For example, in the Vázquez and Simberloff (2002, 2003) data set the most generalized plant species (the "outlier" in Appendix B:panel o) is *Alstroemeria aurea*, an understory, summer-flowering plant visited by a broad assemblage of flower visitors (Vázquez and Simberloff 2002). *A. aurea* interacts strongly with the most generalized and most abundant pollinator, *Bombus dahlbomii*, which accounts for >90% of the pollen deposited in the stigmas of *A. aurea* (Aizen 2001); in turn, *B. dahlbomii* is virtually restricted to *A. aurea* during its flowering period (late spring–summer). Thus,

the two most abundant, most generalized plant and pollinator species likely represent strong selective agents for each other, and the many other species that interact with them may be relatively unimportant. As a consequence, asymmetry may be lower when interactions are described in functional terms than when they are described just in terms of who interacts with whom.

So far we have discussed the consequences of the observed asymmetric specialization. We now need to ask the more fundamental question of what is the cause of such asymmetry. We discuss three kinds of alternative explanations below. These mechanisms are not mutually exclusive, and all are likely contributors to the observed patterns.

One possible set of explanations is artifactual. First, asymmetric specialization observed in the data sets could be exacerbated by data aggregation. The information usually available in these data sets typically does not include phenological or spatial patterns in the distribution of abundance. As an example of temporal data aggregation, consider a generalist pollinator that interacts sequentially with several specialist plants throughout the flowering season. In Nahuel Huapi National Park, Argentina, *Bombus dahlbomii* is not only the most abundant and most generalized pollinator, but also the species with the longest activity period (D. P. Vázquez, *unpublished data*). Although *B. dahlbomii* interacts with many species throughout the entire flowering season, the number of species with which it interacts at any given time is much smaller. Spatial aggregation of data can occur when a widespread species interacts with different species at different locations; if data for such a species are pooled into a single data set, the species may appear more generalized than it actually is at each locality. Thompson (1994) argues that widespread species could have geographically structured subpopulations, so that they are more specialized than they appear (see also Fox and Morrow 1981). However, because most data sets used in the present analysis come from local communities, even if Thompson's conjecture were correct, our findings suggest that abundant generalists have the potential to interact asymmetrically with many rare specialists at a local scale.

Second, as we argued in a recent analysis (Vázquez and Aizen 2003), the observed patterns could be simply a result of a sampling bias, whereby frequently interacting species appear more generalized than rare species. Petanidou and Ellis (1996:213) pointed out that "despite intensive fieldwork we cannot exclude that the high level of oligolecty [i.e., specialization] should be accounted for at least partially by insufficient sampling." Specifically, we must ask whether the observed correlation between s and f (frequency of interaction) is a result of a sampling bias or one or more biological mechanisms (Vázquez and Aizen 2003). If it is a sampling bias, then part of the asymmetric specialization observed in the data may also be a result of such bias,

as model 2 suggests. Thus, as we concluded in a recent analysis (Vázquez and Aizen 2003), the question of what causes the *f-s* correlation remains key to the understanding of patterns of specialization in plant–pollinator interactions.

Another possible explanation concerns neutrality and the level at which it occurs. Our null model 2 assumes that random interaction occurs at the individual level, rather than at the species level, as it is implicit in model 1. This assumption implies that species that interact more frequently do it with more species than rarely interacting species. The fact that for most data sets null model 2 provides a better fit to the data than model 1 gives some support for this explanation. Neutrality at the individual level rather than at the species level is also central to recent neutral models of community structure (Bell 2000, Hubbell 2001).

A final set of explanations is adaptive. High reciprocal specialization could mean high risk of extinction (Renner 1998, Vázquez and Simberloff 2002), which would explain the absence of species with low values of *s* and *p* (i.e., at the lower left corner of the graph in Fig. 2). In addition, high reciprocal specialization could mean, for most species and under most circumstances, low fitness. Waser et al. (1996), using simple models of plant and pollinator fitness, showed that when the abundance, per capita visitation rates, or quality of interaction partners vary strongly over time, it should be more beneficial to be a generalist than a specialist; specialization on a single species should be beneficial only when the abundance and efficiency of the interaction partner are constant in time. Waser et al. (1996: 1051) concluded that ''We might therefore expect [plant] specialization on one or a few pollinators mostly in species that are large, long-lived, have many reproductive episodes, and/or have pollinators whose populations, for whatever mysterious reason, fluctuate little, so that the identity of the 'best' pollinator tends to remain constant across years.'' Super-abundant, super-generalist species may provide a more predictable opportunity for specialization than rare specialists.

Uncovering the role played by each of the above explanations will be necessary to improve our understanding of the causes and consequences of interaction specialization, both for the particular case of plant–pollinator interaction webs considered here, as well as for other kinds of interaction networks such as food webs. Future studies should be aimed at assessing the relative contribution of each of these alternative explanations to the generation of asymmetric specialization. As shown here, the use of null models is a useful approach to fulfill this goal.

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APPENDIX A

A description of the 18 data sets included in the study is available in ESA's Electronic Data Archive: *Ecological Archives* E085-031-A1.

APPENDIX B

Plots of degree of specialization (s) vs. average specialization of interaction partners (p) for each of the data sets are available in ESA's Electronic Data Archive: *Ecological Archives* E085-031-A2.

APPENDIX C

The relation between the percentage of species inside the null space of both models and several community characteristics is available in ESA's Electronic Data Archive: *Ecological Archives* E085-031-A3.

APPENDIX D

The correlation between frequency of interaction (f) and estimated degree of specialization (s) of plants and pollinators in 11 data sets is available in ESA's Electronic Data Archive: *Ecological Archives* E085-031-A4.

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