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Measuring partner choice in plant–pollinator networks: using null models to separate rewiring and fidelity from chance

MOLLY MACLEOD, MARK A. GENUNG,¹ JOHN S. ASCHER, AND RACHAEL WINFREE

Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, New Jersey 08901 USA

Abstract. Recent studies of mutualistic networks show that interactions between partners change across years. Both biological mechanisms and chance could drive these patterns, but the relative importance of these factors has not been separated. We established a field experiment consisting of 102 monospecific plots of 17 native plant species, from which we collected 6713 specimens of 52 bee species over four years. We used these data and a null model to determine whether bee species' foraging choices varied more or less over time beyond the variation expected by chance. Thus we provide the first quantitative definition of rewiring and fidelity as these terms are used in the literature on interaction networks. All 52 bee species varied in plant partner choice across years, but for 27 species this variation was indistinguishable from random partner choice. Another 11 species showed rewiring, varying more across years than expected by chance, while 14 species showed fidelity, indicating that they both prefer certain plant species and are consistent in those preferences across years. Our study shows that rewiring and fidelity both exist in mutualist networks, but that once sampling effects have been accounted for, they are less common than has been reported in the ecological literature.

Key words: *bipartite network; choice experiment; diet breadth; generalization; mutualism; native bee; sampling effect; specialization.*

INTRODUCTION

Interactions between mutualist partners influence the structure and functioning of ecological communities and make an important contribution to global biodiversity (Bronstein 2015). For many types of mutualisms, the interactions that take place on a community level can be described as networks, and the distribution of links (interactions) between nodes (species) can be used to study community structure and dynamics (Ings et al. 2009). Plant–pollinator networks have become a model system for the study of mutualist networks in terms of their structure, evolution, and resilience to human disturbance (Bascompte and Jordano 2007). The few studies that have explored plant–pollinator networks over multiple years have found that they are highly dynamic, meaning pollinator species often visit different plant species in different years (Alarcón et al. 2008, Petanidou et al. 2008, Dupont et al. 2009, Fang and Huang 2012), or across time in the same year (Olesen et al. 2008, Kaiser-Bunbury et al. 2010, Simanonok and Burkle 2014).

Observed variation in partner choice over time could be caused by either deterministic factors such as species interactions, or stochastic factors related to the relative abundances of plant and pollinator species. An inexact analogy can be drawn with the “niche vs. neutral” debate in ecology; very briefly, niche (deterministic) and neutral (stochastic) effects are contrasting, but not mutually exclusive, explanations for patterns found in ecological communities (Hubbell 2001, Chase and Leibold 2003). In studies of plant–pollinator networks, niche effects include species traits of both plants and pollinators as well as pollinator behaviors such as foraging plasticity that respond to changing resources (Vázquez et al. 2009a, Beckerman et al. 2010, Brosi and Briggs 2013). Neutral effects, in contrast, result from demographic and sampling processes that are not dependent on species identities, such as the richness and abundance of plants and pollinators (Vázquez et al. 2009a, Blüthgen 2010, Fründ et al. 2015). If only neutral effects operate, the resulting pattern is known as interaction neutrality, in which plants and pollinators interact randomly with respect to their abundances (Vázquez 2005, Santamaría and Rodríguez-Gironés 2007, Stang et al. 2007, Vázquez et al. 2009a). Many studies of ecological networks have separated niche and

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¹E-mail: mark.a.genung@rutgers.edu

neutral effects as drivers of various interaction patterns between plants and pollinators (e.g., Santamaría and Rodríguez-Gironés 2007, Stang et al. 2007, Vázquez et al. 2009b).

However, a similarly rigorous analysis of variation in partner choice over time is lacking, and existing terminology does not properly differentiate niche and neutral effects. The term “rewiring” is used to mean the ability of pollinator species to change its foraging preferences over time, presumably in an adaptive way, i.e., as a niche effect (Kaiser-Bunbury et al. 2010). However, rewiring has been previously defined to occur when both members of a plant-pollinator species pair are present from year to year, but do not interact every year (Alarcón et al. 2008, Petanidou et al. 2008, Dupont et al. 2009, Kaiser-Bunbury et al. 2010, Olesen et al. 2011, Carstensen et al. 2014), an outcome that includes both niche and neutral effects. In particular, previous definitions of rewiring do not account for how yearly shifts in the abundance of plants and pollinators affect the probability of detecting an interaction in each year.

Similarly, the term “fidelity” has been used in multiple ways in the literature, and lacks a quantitative, statistically testable definition. Fidelity can mean consistent choice of partner(s) over space (“partner fidelity”; Trøjelsgaard et al. 2015), the tendency of individual bees to repeatedly visit the same plant species over short time scales (“floral fidelity”; Brosi and Briggs 2013), or the proportion of pollen on a bee’s body that originates from a given plant (“pollen fidelity”; Forup et al. 2008, Burkle et al. 2013). In all cases, fidelity would result from niche effects. However, these previous definitions of fidelity have not accounted for how variable abundance of plants or pollinators could influence the patterns observed. Thus previous definitions allow fidelity to result from a combination of niche and neutral effects.

Here we use a four-year field experiment along with a null model to separate the biological phenomena of rewiring and fidelity from random partner choice. Specifically, we define rewiring as changes in pollinator species’ partner choice over time that are greater than those predicted by a null model that assumes random interactions between plant and pollinator species within each year, conditioned on the relative abundance of each plant and pollinator species in each year. In the broad sense, this definition is consistent with previous work defining rewiring as coexisting species forming new interactions over time (Dupont et al. 2009, Kaiser-Bunbury et al. 2010, Olesen et al. 2011, Carstensen et al. 2014). However, we differ from most of the previous literature by defining rewiring in terms of the frequency of interactions between pairs of plants and pollinators, rather than simply the presence of an interaction. This definition has two strengths. First, it recognizes the important role of sampling limitations as drivers of observed network structure (Vázquez et al. 2009a, Blüthgen 2010). Specifically, observing turnover in interactions between rare plant and pollinator species has limited value because

these changes could reasonably be due to chance. Second, definitions based on the presence of interactions would not capture the fact that pollinators can change their foraging behavior significantly even without forming new links or losing old links. In other words, a pollinator species’ preference for a plant species is a continuum, and the loss of an interaction is the endpoint of a continuum.

We define fidelity (more specifically, “interaction fidelity”) as changes in pollinator species’ preferences over time that are less than those changes predicted by a null model, again as conditioned by relative abundances in each year. Thus, fidelity operates at the species level, which is appropriate within the context of bipartite networks, within which species are nodes. This species-level definition is broader than previous, individual-level, definitions that have focused on the sequence of plant species visited by an individual pollinator, or on pollen transfer (Forup et al. 2008, Brosi and Briggs 2013, Burkle et al. 2013). Our definition of fidelity requires both preference, meaning individual of a given bee species prefer the same host plants within years, and low change in preference over time. Thus, as for other definitions, under our definition, bees with high fidelity should be superior pollen vectors, but in our case, we have the additional and stronger requirement that preference is consistent across most individuals of a species.

Our plant–pollinator network data came from a field experiment in which we established a native plant community with a perfectly even species abundance distribution (on a per-area basis) and maintained this consistently across four years. This experimental design removes variation in partner choice driven by variation in plant abundance; such variation is ubiquitous in natural networks and makes it difficult to measure partner choice in non-experimental systems an unbiased way. Specifically, we answer the following questions: (1) Do bee species show significant rewiring (variation in partner choice) over time? (2) Do bee species show significant fidelity (consistency in partner choice) over time? (3) How does a bee species’ abundance affect our ability to detect rewiring or fidelity?

MATERIALS AND METHODS

The field experiment

In the fall of 2009, we established an experimental array of 20 native, perennial, plant species (of which 17 survived all four years and were used in our analyses; for plant species names, see Data S1) located in a former old field in southern New Jersey, USA (39.1237° N, 74.7814° W). Our experiment was a randomized block of 120 plots in a 20 × 6 grid. Each plot had an area of 1 m², initially included nine mature plants, and was separated from its neighbors by 3 m (Appendix S1: Fig. S1). Thus, the total experiment covered an area of 77 m by 21 m. Given that the bee species in our study forage over

distances of 100 to 10,000 m (Greenleaf et al. 2007) and our entire experimental array was 21×77 m, our design creates a choice experiment for foraging bees. In preliminary analyses of the complete data set, we found no evidence of edge effects, and no evidence of spatial autocorrelation in pollinator visitation across plots.

We hereafter use the term “even species abundance distribution” for our experimental plant community because we standardized the total area covered by each monospecific plot to 1 m^2 both within and across years. All plots were originally planted with nine individual plants, and at the start of each year’s experiment, we replaced any over-winter losses such that every plot always had at least nine plants, but did not grow outside of the 1-m^2 area. Thus each plant species developed as per its own habit, with some species spreading more within their plots and/or producing more flowers than others. We considered these traits to be a characteristic of the plant species and to be one possible factor influencing bees’ foraging preferences.

Our data collection proceeded as follows. From May to September in each of 2010–2013, we netted all flower-visiting bees (for pollen, nectar, or both) to each of the 102 plots on three separate days during the peak bloom of that plot. In order to capture bee species that forage at different times of day, plots were netted twice on each day, for 10 min in the morning (08:00–12:00) and 10 min in the afternoon (12:00–17:00). Within a single day, the order of plot sampling was randomized. We limited data collection to times when weather was sunny or partly cloudy, temperatures $\geq 16^\circ\text{C}$, and mean wind speed was ≤ 3 m/s, with rare exceptions (fewer than 1% of sampling events occurred at greater wind speeds). All bee specimens were fully curated, assigned unique specimen identifier (USI) codes, and identified to species level by two professional taxonomists (J. S. Ascher and Jason Gibbs).

Null models for rewiring and fidelity

The purpose of our null modeling approach is to evaluate whether each bee species shows rewiring (change in partner choice over time), fidelity (consistency in partner choice over time), or neither. Our null model begins with the year by plant ($Y \times P$) matrix for each bee species, with plant species in rows and years in columns, and cell values that represent the number of individuals of that bee species that were collected from each of the 17 plant species in our field experiment in each year. From this empirical matrix, we generated randomly resampled null matrices while maintaining yearly abundances of the given bee species, which prevents our null model from confounding changes in bee abundance with changes in partner choice. This restriction was accomplished using function `permatfull` with `fixedmar = “column”` in package `vegan` (Oksanen et al. 2015, R Core Team 2015), which takes all of the interactions within a given column of the $Y \times P$ matrix, and randomly assigns each interaction across plant species (rows). This maintains each bee

species’ temporal variation in abundance while removing any preference for particular plant species. We repeated the resampling process 1000 times, yielding 1000 “null” $Y \times P$ matrices for each bee species. We assume that all bee species could have interacted with all plant species, because the bee species we analyze have long flight seasons that should extend throughout our entire study period and because we do not have any independent data (i.e., records of our study bee species at our site that were not collected from our study plants) that would allow us to truncate bees’ flight seasons in an unbiased way. However, an alternate null model would permit bees to be randomly assigned to plant species only if they had been collected in our study during the peak bloom of that plant. We applied the alternate null model to our data and found it produced similar results (Appendix S2).

We next determined, separately for each bee species, the year-to-year dissimilarity in plant species visited. Specifically, for each bee species, we calculated the mean Morisita-Horn dissimilarity (Horn 1966) in the plant community visited for all possible pairwise comparisons of years. In further analyses, we used the mean value of the index across all 1000 iterations, and 95% confidence intervals were found using the 2.5 and 97.5 percentile values from the 1000 iterations.

We chose the Morisita-Horn index because it matches our definition that fidelity requires both significant preference within years and little to no change in preference over time. Morisita-Horn dissimilarity is ideal because it allows us to ask: For any bee species, what is the chance that two flower visits, drawn from different years, would be to the same plant? When this probability is high, Morisita-Horn dissimilarity is low and represents fidelity. When this probability is low, dissimilarity is high and represents rewiring.

Comparing empirical results to the null model

For each bee species, we compared the empirical result to the null model’s 95% confidence interval. An empirical result above the null confidence interval indicates rewiring. An empirical result beneath the null confidence interval indicates fidelity. Lastly, we visualized the extent to which rewiring or fidelity occurs more or less frequently among common or rare species by plotting how much the empirical data deviated from null expectation, as a function of the number of individuals collected per species. Descriptions of pollinator species as common or rare are based on visitation rates, which are the abundance metric to which sampling effects would apply in our study, rather than on background abundance, which we did not measure.

RESULTS

In our four-year field experiment we completed 2,448 separate per-plot collection events totaling 409 h, and collected 6,713 individual bees of 52 species that were

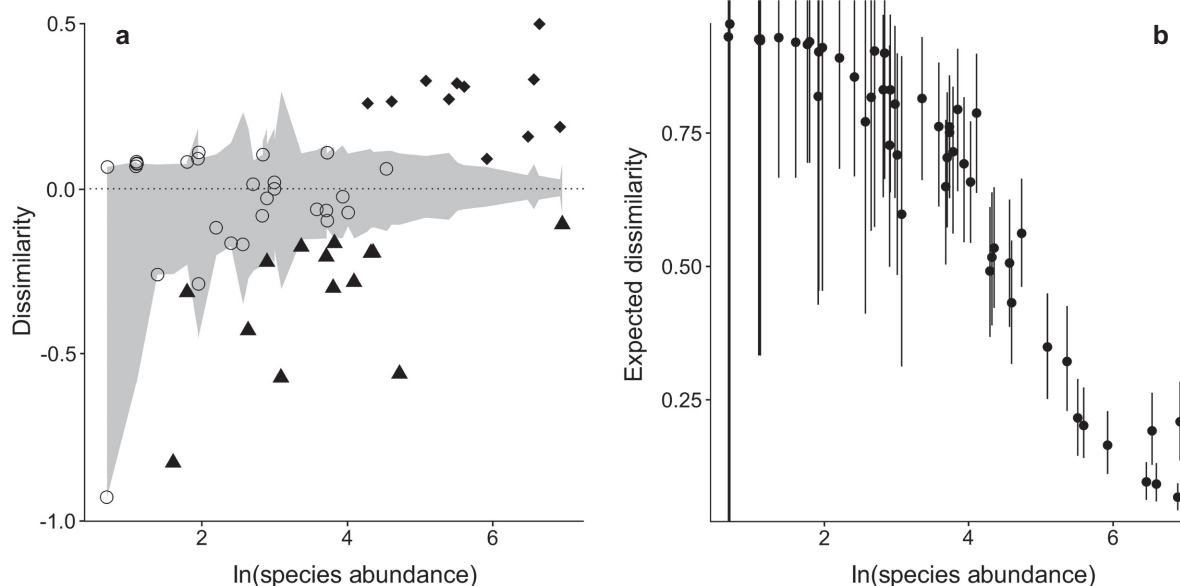


FIG. 1. (a) Results of null model analysis of field data for 52 bee species, ranked in increasing order of overall (across-year) abundance on the x -axis. The shaded area is bounded by each bee species' empirical across-year change in preference, subtracted from either the upper or lower bound of the null model 95% confidence intervals for across-year changes in preference. Across-year changes in preference were measured as mean Morisita-Horn dissimilarity across all pairwise comparisons of years. The points show how much each species diverged from the mean Morisita-Horn dissimilarity produced by the null model (observed – expected). Thus points in the shaded area indicate no difference from random (open circles), points below the shaded area indicate fidelity (solid triangles), and points above the shaded area indicate rewiring (solid diamonds). CI are jagged because each null model was based on the data for a particular bee species. (b) Expected dissimilarity produced by the null model alone (observed values are not plotted), which assumes that bees visit plant species at random in each year. Points represent the mean, and error bars the 95% confidence interval, of the across-year Morisita-Horn dissimilarity in the plant species visited by each bee species. Bee species are ordered on the x -axis by increasing abundance, as for Fig. 1a. Expected dissimilarity tends to decline, and confidence intervals decrease in size, with increasing abundance, resulting in greater power to detect nonrandom changes in preference across years.

usable in our analyses (we were unable to use an additional 25 species that were observed in only one year).

1. *Do bee species show significant rewiring (variation in partner choice) over time?*—For 27 of 52 bee species, this variation was not significantly different from what would be expected by chance. In contrast, 11 species rewired, meaning that they varied more across years than what would be expected by chance (Fig. 1a).

2. *Do bee species show significant fidelity (consistency in partner choice) over time?*—Fourteen species showed significant fidelity over time, indicating that they both have strong preferences and that those preferences do not vary significantly across years (Fig. 1a).

3. *How does a species' abundance affect our ability to detect rewiring or fidelity?*—Rewiring is easier to detect at large sample sizes, and fidelity at small to moderate sample sizes, for reasons related to both the CI and the mean produced by the null model. Rewiring is impossible to detect for many species with small sample sizes (<20 specimens collected), because the CI include 1 (Fig. 1b). The null model predicts high mean dissimilarity and large CI in this situation because it distributes a small number of individuals randomly across all 17 plant

species in each year, thereby creating “communities” of visited plants that vary both within and between years. As sample size increases, the null communities become more similar both across iterations within a year, leading to a smaller CI, and between years, leading to both a smaller mean dissimilarity and a smaller CI. Both trends make rewiring easier to detect, as indicated visually by increasing white space above the CI as one moves from left to right in Fig. 1b. Using simulated data we show that our null model detects rewiring (Appendix S3: Fig. S1) as expected.

Conversely, fidelity is easier to detect when sample sizes are small to moderate, and becomes more difficult to detect when sample sizes are large. This is indicated visually by the decreasing white space below the CI as one moves from left to right in Fig. 1b. Unlike the case for rewiring, for fidelity the trends in the mean and CI as abundance increases produce opposing effects: the smaller CI make detection easier, but the smaller mean makes detection harder. The net effect, though, is that as sample size increases it becomes harder to discriminate fidelity, which means greater-than-expected similarity in the visited plant community across years, from the null expectation, because the null converges on highly similar plant communities representing equal visitation to each plant species in each year. However, because the null

model is based on Morisita-Horn dissimilarity, fidelity is still detectable at large sample sizes, because it includes a component of specialization in addition to the component of consistency across years. A bee species that consistently prefers a smaller number of plant species will show statistically significant fidelity as compared with the null that assumes consistent but equal preference for all plant species (Appendix S4).

DISCUSSION

Previous studies of temporal variation in pollination networks have found that many pollinator species, including bees, rewire, or change partners over time (Alarcón et al. 2008, Olesen et al. 2008, Petanidou et al. 2008, Dupont et al. 2009, Trøjelsgaard et al. 2015). However, previous work has accounted for neither the species abundance distributions of the plants and pollinators, nor how these abundances change over time, and therefore confounds neutral (stochastic) changes in partner choice with biologically driven rewiring. Here, we controlled the plant species-abundance distribution experimentally, and used a null model to account for changes in the pollinator species-abundance distribution over time. We found that pollinator species that were rare in our study change partners frequently, as reported in the literature, but in contrast to previous work, we also determine that these changes are largely expected by chance due to poor sampling and/or low abundance of those rare species. In contrast, most common bee species showed significant rewiring, in that their plant preferences varied more over the four years of the experiment than would be expected by chance (Fig. 1a). At the same time, many bee species, including both rare and highly abundant species, varied less in partner choice across time than expected, which is evidence of fidelity. However, in contrast with previous studies which tend to find that rare species either have high fidelity (are “specialists”) or rewire frequently, our null model revealed that most rare species’ preferences were not separable from chance.

Several features of our study make it a particularly robust test of the rewiring and fidelity concepts. First, because our experimental design controlled year-to-year variation in plant relative abundance, and the phenologies of plant species were relatively constant across years, we were able to isolate the pollinators’ choice of plant species, rather than variation in the identity and abundance of flowering species available, in our empirical measurement of both rewiring and fidelity. Second, any changes in how pollinators forage as a function of plant abundance (Dauber et al. 2010) is also controlled by our standardization of the relative abundance (per-plot area) across plant species. While it is possible to use statistical methods to account for the different abundances across plant species that result from sampling non-experimental communities (Dorado et al. 2011, Chacoff et al. 2012), these corrections are still uncertain because pollinators may respond non-linearly to plant abundance.

It is consistent with bee biology that we found multiple bee species that showed fidelity, or preference for particular plant species that is consistent over time. Many bee species are known to prefer particular types or families of plants, even though only a small percentage of bee species in temperate biomes such as ours specialize exclusively on the pollen of one to a few plant species (oligolecty; Minckley and Roulston 2006). In our study, only one of the 14 species showing fidelity is a known oligolectic: *Melissodes subillata* is a pollen specialist on plants in the Asteraceae family and in our study consistently preferred *Rudbeckia hirta*. Three more species that showed fidelity, *Bombus pensylvanicus*, *Hoplitis pilosifrons*, and *Nomada articulata*, are not oligolectic but are well known to prefer particular types of plants.

Ecologically, it is not surprising to find that several species rewire, or change their floral preferences over time, even after accounting for sampling effects. Bees should be selected to forage adaptively on the changing floral resources available to them. At the seasonal scale, within years, it is well known that species with long flight seasons will need to forage on different plant species as each species blooms (Menz et al. 2011), even if individual bees display some level of short-term foraging specialization, or floral fidelity (Brosi and Briggs 2013). Even bee species that are oligolectic, defined as female bees’ restriction to collecting and provisioning larvae with pollen from only one or a few plant taxa (Williams et al. 2010, Roulston and Goodell 2011), could have annual variation in preferences for nectar source plants.

The ecologically driven rewiring that we detected could be caused by multiple factors related to plant species attractiveness, phenology, and/or bee foraging behavior. First, even though our study design standardized area per plant species across years, a plant species might vary across years in the number of flowers it produces, due to plant age, or to site or weather conditions (Aizen et al. 2006), and floral abundance is a primary factor in determining factor in pollinator visitation patterns (Potts et al. 2003, Veddeler et al. 2006). Second, and for similar reasons, plants might vary across years in the amount of nectar or pollen they produce (Aizen et al. 2006). Third, most bee species forage over areas of many hectares (Greenleaf et al. 2007) and thus the attractiveness of any one plant species is evaluated relative to the alternative resources available, which are also fluctuating. We did not collect data on predatory, parasitic, or competitive interactions. However, given that floral resources are likely more limiting to bee communities than other factors (Roulston and Goodell 2011), we expect that variation in plant attractiveness over time, including attractiveness relative to the background availability of other foraging resources, is tracked by bees (Pyke et al. 1977, Pleasants 1981, Potts et al. 2003, Roulston and Goodell 2011) and observed by researchers as changing preferences over time.

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LITERATURE CITED

- Aizen, M. A., D. P. Vazquez, L. Harder, and S. Barrett. 2006. Flower performance in human-altered habitats. *Ecology and Evolution of Flowers*:159–179.
- Alarcón, R., N. M. Waser, and J. Ollerton. 2008. Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos* 117:1796–1807.
- Bascompte, J., and P. Jordano. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 37:567–593.
- Beckerman, A., O. L. Petchey, and P. J. Morin. 2010. Adaptive foragers and community ecology: linking individuals to communities and ecosystems. *Functional Ecology* 24:1–6.
- Blüthgen, N. 2010. Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. *Basic and Applied Ecology* 11:185–195.
- Bronstein, J. 2015. *Mutualism*. Oxford University Press, Oxford, UK.
- Brosi, B. J., and H. M. Briggs. 2013. Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proceedings of the National Academy of Sciences USA* 110:13044–13048.
- Burkle, L. A., J. C. Marlin, and T. M. Knight. 2013. Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* 339:1611–1615.
- Carstensen, D. W., M. Sabatino, K. Trøjelsgaard, and L. P. C. Morellato. 2014. Beta diversity of plant–pollinator networks and the spatial turnover of pairwise interactions. *PLoS ONE* 9:e112903.
- Chacoff, N. P., D. P. Vazquez, S. B. Lomascolo, E. L. Stevani, J. Dorado, and B. Padron. 2012. Evaluating sampling completeness in a desert plant–pollinator network. *Journal of Animal Ecology* 81:190–200.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago, Illinois, USA.
- Dauber, J., J. C. Biesmeijer, D. Gabriel, W. E. Kunin, E. Lamborn, B. Meyer, A. Nielsen, S. G. Potts, S. P. Roberts, and V. Sober. 2010. Effects of patch size and density on flower visitation and seed set of wild plants: a pan-European approach. *Journal of Ecology* 98:188–196.
- Dorado, J., D. P. Vázquez, E. L. Stevani, and N. P. Chacoff. 2011. Rareness and specialization in plant–pollinator networks. *Ecology* 92:19–25.
- Dupont, Y. L., B. Padrón, J. M. Olesen, and T. Petanidou. 2009. Spatio-temporal variation in the structure of pollination networks. *Oikos* 118:1261–1269.
- Fang, Q., and S.-Q. Huang. 2012. Relative stability of core groups in pollination networks in a biodiversity hotspot over four years. *PLoS ONE* 7:e32663.
- Forup, M. L., K. S. Henson, P. G. Craze, and J. Memmott. 2008. The restoration of ecological interactions: plant–pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology* 45:742–752.
- Fründ, J., K. S. McCann, and N. M. Williams. 2015. Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. *Oikos* 125:502–513.
- Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153:589–596.
- Horn, H. S. 1966. Measurement of “overlap” in comparative ecological studies. *American Naturalist* 100:419–424.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography (MPB-32)*. Princeton University Press, Princeton, New Jersey, USA.
- Ings, T. C., J. M. Montoya, J. Bascompte, N. Blüthgen, L. Brown, C. F. Dormann, F. Edwards, D. Figueroa, U. Jacob, and J. I. Jones. 2009. Review: ecological networks—beyond food webs. *Journal of Animal Ecology* 78:253–269.
- Kaiser-Bunbury, C. N., S. Muff, J. Memmott, C. B. Müller, and A. Caffisch. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecology Letters* 13:442–452.
- Menz, M. H., R. D. Phillips, R. Winfree, C. Kremen, M. A. Aizen, S. D. Johnson, and K. W. Dixon. 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends in Plant Science* 16:4–12.
- Minckley, R. L., and T. Roulston. 2006. Incidental mutualisms and pollen specialization among bees. Plant–pollinator interactions: from specialization to generalization. The University of Chicago Press, Chicago, Illinois, USA. Pages 69–98.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. *vegan: Community Ecology Package*.
- Olesen, J. M., J. Bascompte, H. Elberling, and P. Jordano. 2008. Temporal dynamics in a pollination network. *Ecology* 89:1573–1582.
- Olesen, J. M., C. Stefanescu, and A. Traveset. 2011. Strong, long-term temporal dynamics of an ecological network. *PLoS ONE* 6:e26455.
- Petanidou, T., A. S. Kallimanis, J. Tzanopoulos, S. P. Sgardelis, and J. D. Pantis. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters* 11:564–575.
- Pleasants, J. M. 1981. Bumblebee response to variation in nectar availability. *Ecology* 62:1648–1661.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* 84:2628–2642.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* 52:137–154.
- R Core Team. 2015. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Roulston, T. A. H., and K. Goodell. 2011. The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology* 56:293–312.
- Santamaria, L., and M. A. Rodríguez-Gironés. 2007. Linkage rules for plant–pollinator networks: Trait complementarity or exploitation barriers? *PLoS Biology* 5:e31.
- Simanonok, M. P., and L. A. Burkle. 2014. Partitioning interaction turnover among alpine pollination networks: spatial, temporal, and environmental patterns. *Ecosphere* 5:1–17.

- Stang, M., P. G. Klinkhamer, and E. Van der Meijden. 2007. Asymmetric specialization and extinction risk in plant–flower visitor webs: A matter of morphology or abundance? *Oecologia* 151:442–453.
- Trøjelsgaard, K., P. Jordano, D. W. Carstensen, and J. M. Olesen. 2015. Geographical variation in mutualistic networks: similarity, turnover and partner fidelity. *Proceedings of the Royal Society B* 282:20142925.
- Vázquez, D. P. 2005. Degree distribution in plant–animal mutualistic networks: Forbidden links or random interactions? *Oikos* 108:421–426.
- Vázquez, D. P., N. Blüthgen, L. Cagnolo, and N. P. Chacoff. 2009a. Uniting pattern and process in plant–animal mutualistic networks: a review. *Annals of Botany* 103:1445–1457.
- Vázquez, D. P., N. P. Chacoff, and L. Cagnolo. 2009b. Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology* 90:2039–2046.
- Veddeler, D., A. M. Klein, and T. Tschardt. 2006. Contrasting responses of bee communities to coffee flowering at different spatial scales. *Oikos* 112:594–601.
- Williams, N. M., E. E. Crone, H. R. Tai, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation* 143: 2280–2291.

SUPPORTING INFORMATION

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