Plant species dominance increases pollination complementarity and plant reproductive function

Jamie R. Stavert,[1,2,6] Ignasi Bartomeus,[3] Jacqueline R. Beggs,[1] Anne C. Gaskett,[4] and David E. Pattemore[4,5]

[1]*Centre for Biodiversity and Biosecurity, School of Biological Sciences, The University of Auckland, Auckland, New Zealand*
[2]*School of Environmental and Rural Science, University of New England (UNE), Armidale, New South Wales, Australia*
[3]*Integrative Ecology Department, Estación Biológica de Doñana (EBD-CSIC), Avenida Américo Vespucio 26, Isla de la Cartuja, Sevilla E-41092 Spain*
[4]*School of Biological Sciences, The University of Auckland, Auckland, New Zealand*
[5]*The New Zealand Institute for Plant & Food Research Limited, Hamilton, New Zealand*

Abstract. Worldwide, anthropogenic change is causing biodiversity loss, disrupting many critical ecosystem functions. Most studies investigating the relationship between biodiversity and ecosystem functioning focus on species richness, predominantly within the context of productivity-related functions. Consequently, there is limited understanding of how other biodiversity measures, such as species evenness (the distribution of abundance among species), affect complex multitrophic functions such as pollination. We explore the effect of species evenness on the ecosystem function of pollination using a controlled experiment with selected plants and insects in flight cages. We manipulated the relative abundances of plant and pollinator species, while holding species richness, composition, dominance order, and total abundance constant. Then, we tested how numerical species evenness affected network structure and consequently, seed production, in our artificial communities. Contrary to our expectation, numerical dominance in plant communities increased complementarity in pollinator use (reduced pollinator sharing) among plant species. As predicted by theory, this increased complementarity resulted in higher seed production for the most dominant and rare plant species in our cages. Our results show that in a controlled experimental setting, numerical species evenness can alter important aspects of plant–pollinator networks and plant reproduction, irrespective of species richness, composition, and total abundance. Extending this understanding of how species evenness affects ecosystem functioning to natural systems is crucial as anthropogenic disturbances continue to alter species' abundances, likely disrupting ecosystem functions long before extinctions occur.

Key words: anthropogenic change; biodiversity; complementarity; ecosystem function; floral display; interspecific competition; niche; plant reproduction; plant–pollinator network; pollination; species abundance distribution; species evenness.

Introduction

The accelerating rate of global biodiversity loss has prompted many experimental attempts to disentangle the relationship between biodiversity and ecosystem functioning (B-EF; Cardinale et al. 2012). In numerous studies, within natural and experimental conditions, plant communities that are more diverse have shown greater productivity, use resources more efficiently, and are more resistant to disturbances (Loreau et al. 2001, Hooper et al. 2005). This positive effect of biodiversity on ecosystem functioning is often driven by complementarity between species, such as increased resource partitioning

between plant species in diverse communities (Tilman et al. 2014). However, the way in which multitrophic ecosystem functions respond to biodiversity loss remains unclear. This is because most studies focus on how species richness affects productivity-based functions (e.g., plant biomass; Balvanera et al. 2006) rather than functions that involve multiple trophic levels, such as pollination and seed dispersal (Schleuning et al. 2015, but see Fründ et al. 2013). Furthermore, there is little research into how ecosystem functions are affected by less-conspicuous components of biodiversity, such as the distribution of abundance among species (species evenness; Lewandowska et al. 2016, Hillebrand et al. 2017).

Ecological communities universally have skewed species abundance distributions, where a few species are common and the rest are rare (McGill et al. 2007). The degree to which a community's abundance distribution is skewed is described as "species evenness" (Pielou 1977, Smith and Wilson 1996). Anthropogenic disturbances

[6] E-mail: jamie.stavert@gmail.com

generally reduce species evenness by homogenizing resources in ecosystems, favoring a subset of species that subsequently become dominant (Hillebrand et al. 2008, Stavert et al. 2018). Following Hillebrand et al. (2008), here we use the terms "dominance" of a community or a "dominant" species composition to refer to the opposites of "evenness" of a community or an "even" species composition. Species evenness often responds more rapidly to anthropogenic disturbance than other commonly used biodiversity measures (e.g., species richness; Hillebrand et al. 2017). This is because the relative abundance of different species can change long before local extinctions occur, while still having major consequences for ecosystem functioning. When a species becomes extinct, interactions between the extinct species and its interaction partners are also lost, but changes in the evenness of species' abundances may alter interactions in subtle ways that are different to changes detected by richness studies (Dangles and Malmqvist 2004).

Whether controlled B-EF experiments with high species evenness are relevant to real-world ecosystem functions is contentious (Wardle 1999, Dıaz et al. 2003, Thompson et al. 2005, Winfree et al. 2018). Most B-EF experiments are designed so that all species have equal abundance, which magnifies the positive effects of complementarity (two or more species contributing to a function in different ways; Loreau and Hector 2001). However, in nature, complementarity is typically less prominent than in experimental conditions because natural species' abundances vary widely, such that rare species contribute little to functioning (Winfree et al. 2015). Furthermore, in many B-EF experiments, function is driven by the selection (or sampling) effect, where some dominant species have a disproportionate influence on function (Reiss et al. 2009). This same issue may arise in evenness–function experiments if the direction and magnitude of change in community functional performance is driven by the dominant species' identity (Jiang et al. 2009). For example, in multitrophic systems (e.g., plant–pollinator networks), the order of species dominance could affect the evenness–function relationship because plant species often vary in attractiveness and pollinator species differ in both pollination effectiveness and floral preference. Nevertheless, in nature, there is no reason to expect an association between species dominance and functional performance, especially for multitrophic functions such as pollination (Larsen et al. 2005, Bartomeus et al. 2017).

From the few studies to date, there is no consensus on the relationship between species evenness and ecosystem functioning. Varying associations are reported, but most of the few available studies focus on productivity-based functions (Hillebrand et al. 2017). For example, plant communities with low productivity generally have extremely uneven species abundance distributions, whereas those with higher productivity also have higher evenness (Whittaker 1960, Grime 1998, Wilsey and Potvin 2000). However, in stream ecosystems, decomposition rate was higher where decomposer communities were more uneven (i.e., where there was greater dominance; Dangles and Malmqvist 2004). Similarly, increased pollinator community evenness, through the removal of the dominant pollinator species, caused reduced plant reproductive success (Brosi and Briggs 2013). Other studies have found that fluctuations in the abundance of dominant species are the main driver of ecosystem functioning (Smith and Knapp 2003), and this can occur irrespective of species richness and composition (Winfree et al. 2015). In multitrophic systems, factors driving the effect of evenness on function are difficult to identify because relative abundances of highly mobile animal species are challenging to manipulate in wild populations. Further, the flow of conspecific and heterospecific pollen from outside of study communities is difficult to control in natural systems. Thus, cage-based studies can facilitate manipulation of multiple factors in a controlled way, allowing some ecological principles to be tested, which could then be confirmed or disproven in natural systems.

Pollination systems provide an excellent model to explore the relationship between species numerical evenness and ecosystem function. Animal-mediated pollination is a critical ecosystem function; approximately 85% of wild plant species (Ollerton et al. 2011) and 75% of agricultural crops (Klein et al. 2007) require animal pollinators to some degree. Several studies have tested the effects of pollinator diversity on plant reproduction in controlled cage experiments, finding that seed production was enhanced by increased functional diversity (Fontaine et al. 2006, Albrecht et al. 2012) and species richness (Fründ et al. 2013) of pollinators, which is consistent with biodiversity–ecosystem function theory (Cardinale et al. 2012, Tilman et al. 2014). Other studies show that changes in plant diversity also affect plant reproduction, due to changes in competition between plant species for pollination services (Ghazoul 2006, Pauw 2013). However, these previous studies all manipulated only one trophic level, either plants or pollinators, and are therefore unable to test the relative effects of changes to plant vs. pollinator communities on plant reproduction. Nonetheless, anthropogenic disturbances continue to simultaneously alter both plant and pollinator communities and given the impact of both plant and pollinator diversity on plant reproduction, it seems probable that there will be dynamic feedback between these trophic levels as abundances change. This interaction effect is likely to vary depending on the degree of dominance in both plant and pollinator communities. Thus, experiments that simultaneously test the effects of changes in dominance of both plants and pollinators are needed.

Here, we investigate how changes in numerical species evenness alter plant–pollinator interactions, and whether this affects the ecosystem function of seed production within an experimental cage environment, where abundances can be precisely controlled. In large outdoor cages, we manipulated numerical evenness of seven plant and five pollinator species, independent of species richness, composition and total abundance. We then

recorded plant–pollinator interactions and quantified seed production. We predicted that increased evenness would increase complementary interactions between species within plant–pollinator networks, and consequently enhance seed production.

METHODS

Experimental design

We constructed 24 mesocosms (each 2.4 × 3 × 2 m = 14.4 m^3) with fine netting to ensure insect pollinators could not escape or enter the cages (0.58 mm; Cropsafe Protection Mesh, Cosio Industries, Auckland, New Zealand). The cages were closed when the first plant seedlings were introduced (beginning 30 November 2015) and were inspected every 2–3 d until the start of the experiment to ensure no pollinating insects were present. The experiment commenced on 26 December 2015 when pollinators were introduced into the cages. All pollinators were removed from cages on 11 January 2016. Fruits were harvested over a four-week period, from 28 January to 26 February 2016. The experiment was conducted outdoors in Hamilton, New Zealand (37°46′4″ S; 175°18′45″ E), during spring and summer. Cage experiments can produce behavioral artefacts (e.g., insects collecting on the cage walls) and isolate the study organisms inside from other ecological interactions (e.g., predation and herbivory). We aimed to reduce these artefacts by facilitating natural intraspecific interactions between pollinators. Specifically, we included a queen and nest box for the social bees and provided nesting resources for solitary bees and flies (see *Pollinator community*). Natural behaviors consistent with population establishment were observed including mating, foraging, and nest provisioning.

We used a factorial experimental design that included four evenness treatment levels, which were randomly assigned to five cages each: high pollinator dominance and high plant dominance (DomPoll—DomPlant); high pollinator dominance and high plant evenness (DomPoll—EvenPlant); high pollinator evenness and high plant dominance (EvenPoll—DomPlant) and high pollinator evenness and high plant evenness (EvenPoll—EvenPlant; Fig. 1a, b). All pollinator species (five species) and plant species (seven species) were present in all evenness treatment cages. The total abundance of pollinators (30 individuals of all species) and plants (140 individuals of all species) was the same in all 20 cages; 140 was the maximum number of plants that we could fit in realistic enclosures and pollinator numbers were then set at a half an order of magnitude lower to ensure they had enough food. We excluded all pollinators in the remaining four cages, allowing us to identify whether each plant species benefited from the presence of pollinators (in terms of seed production). These cages were inspected daily to ensure no pollinators were present. Although practical limitations restricted the parameter space that we could explore (i.e., four evenness treatments within a single species dominance order for plants and pollinators, respectively), this design enabled us to vary species evenness in both plant and pollinator communities simultaneously.

To choose appropriate patterns of dominance for the species in our dominant communities, we simulated species abundance distributions (SADs) using an algorithm that generates random partitions (i.e., abundance values for each species), constrained by the total sum of individuals (30 for pollinators and 140 for plants) and species richness (five for pollinators and seven for plants; Fig. 1a, b) using the rpartitions package (Locey and McGlinn 2012). We then retained a subset of simulated communities that had a SAD dominance skew in the 99th percentile of all simulated communities (i.e., the most dominant communities), and calculated average abundance values for each species in this subset. Thus,
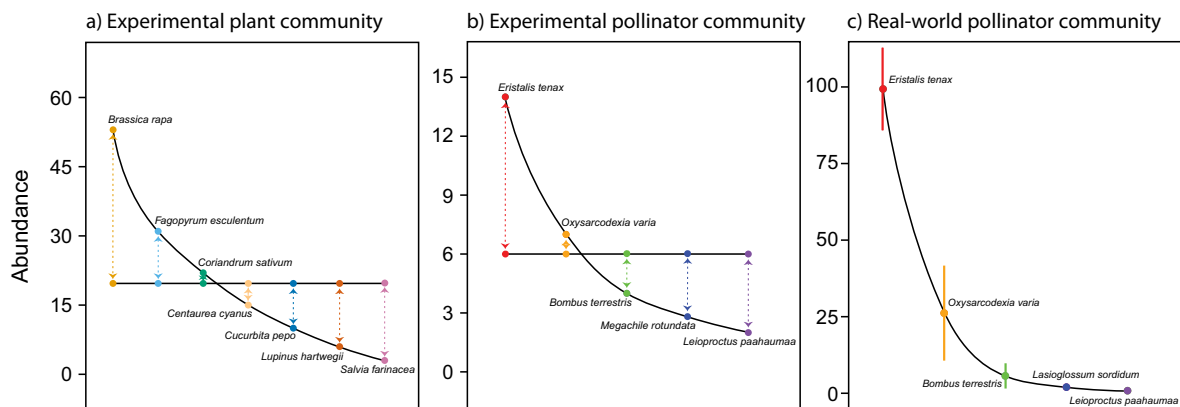

FIG. 1. Abundances of species in (a) even vs. dominant experimental plant communities; (b) even vs. dominant experimental pollinator communities; and (c) real-world pollinator communities with >85% agriculture at 2,000 m radius, wherein dots are the mean abundance for each species across sites and error bars are the standard error (see Stavert et al. 2017 for details). Note that *y*-axis scales are different for each community as total species abundances in real world communities were much higher than those included in cages. *Megachile rotundata* was substituted for *Lasioglossum sordidum* in cages because the latter species could not be collected in sufficient numbers.

dominant communities were representative of those with the highest probable numerical dominance in nature (Locey and White 2013). Even communities had equal numbers of individuals for each species.

Plant community

Seeds for the plants were purchased from commercial suppliers (Kings Seeds, Katikati, New Zealand; South Pacific Seeds, Canterbury, New Zealand; Awapuni Nurseries, Palmerston North, New Zealand; Egmont Seed Company, New Plymouth, New Zealand) and were initially sown into standard biodegradable seedling trays. Individual seedlings were later planted out into standardized 1.7-L pots with commercial grade organic soil (Top Soil and Sand, Hamilton, New Zealand) and transported into cages before they began flowering. The sowing date for different plant species was staggered, based on the estimated number of days to flowering, to ensure flowering synchrony among different plant species. Plants were watered every night for 20 min with an automatic watering system. We controlled unsown weedy plants by regularly removing these by hand.

We used seven insect-pollinated species in our plant communities: *Brassica rapa* (Brassicaceae), *Fagopyrum esculentum* (Polygonaceae), *Coriandrum sativum* (Apiaceae), *Centaurea cyanus* (Asteraceae), *Cucurbita pepo* (Cucurbitaceae), *Lupinus hartwegii* (Fabaceae), and *Salvia farinacea* (Lamiaceae). We validated their need for pollinators by growing them in pollinator-exclusion cages and testing for seed production. Five of these plant species produced some seed without insect presence, (e.g., via wind or passive within-flower pollen transfer: Appendix S1: Table S2), but all produced more seed when insects were present (Appendix S1: Table S1 and Fig. S10). These plant species were chosen because they represent diverse floral structures that vary in size, color, and accessibility to pollinators to be somewhat representative of a diverse community, and all produce seed within one growing season. The plants do not all co-occur in a natural community, but they are commonly grown in garden and agricultural contexts, where they are accessible and encountered by the insect species we selected for our study.

Brassica rapa has a yellow, cruciferous flower that is hermaphroditic with fully exposed reproductive organs (Dixon 2007). *F. esculentum* has white, actinomorphic flowers that are hermaphroditic with exposed reproductive organs (Cawoy et al. 2009). *Coriandrum sativum* has white/pink flowers arranged in umbels (Diederichsen 1996). The peripheral flowers are hermaphroditic and have exposed reproductive organs whereas the central flowers are staminate and often sterile. *Centaurea cyanus* has blue flowers aggregated in an inflorescence (Penet et al. 2012). The peripheral ray florets are sterile but the central disk florets are fertile and hermaphroditic with exposed reproductive organs. *Cucurbita pepo* has yellow monecious flowers; male flowers are produced 3–4 d

before female flowers (Abu-Hammour and Wittmann 2010). Staminate *Cucurbita pepo* flowers have three large anthers and pistillate flowers have a thick style and a large stigma, both have a showy corolla. *L. hartwegii* has a hermaphroditic papilionoid blue/purple flower with the reproductive organs enclosed within the corolla (Tucker 2003). *S. farinacea* has a labiate purple flower with the reproductive organs enclosed within the corolla (Claßen-Bockhoff et al. 2004).

Because our plant community was artificial, we did not have real-world data on dominance order. Therefore, we used theoretical principles drawn from the literature on natural patterns of dominance. Plant species with more specialized pollination structures are typically rarer in nature and have greater extinction risk due to loss of their specialist pollinators, whereas species with open pollinated flowers are typically more generalist and thus have lower extinction risk (Bond 1994, Johnson and Steiner 2000, Aguilar et al. 2006, Aizen et al. 2012). Correspondingly, we chose highly accessible (generalist) plant species to be dominants and less accessible (specialist) species to be rare (Fig. 1a).

Pollinator community

We selected pollinator species that were representative of real-world pollinator communities, based on a previous study that established the relative abundance of species in a community that included two fly species (*Eristalis tenax* and *Oxysarcodexia varia*), one social bee species (*Bombus terrestris*), and two solitary bee genera (*Lasioglossum* and *Leioproctus*; Fig. 1c; Stavert et al. 2017). However, we were unable to source adequate populations of *Lasioglossum*, so we used a similar-sized readily available bee species (*Megachile rotundata*) as a proxy. All pollinators were introduced into cages on the same day (26 December 2015). Flies (*E. tenax* and *O. varia*) were collected from nearby field sites and transferred directly into cages. Bumblebees (*B. terrestris*) were purchased in small colonies (Zonda Beneficials, Auckland, New Zealand) and included a queen and brood to encourage natural foraging behavior. Excess *B. terrestris* workers were removed daily to ensure that the target number of workers was maintained. We translocated native bee (*L. paahaumaa*) larvae from nearby nest aggregations to artificial nest boxes 3–4 d before the experiment commenced. We only translocated larvae that were in a late developmental stage (~1 week from emergence). Since *L. paahaumaa* are ground nesting (Donovan 2007), we provided bare soil nest sites within cages to encourage natural nesting behavior and regularly observed female bees provisioning nests during the experiment. *M. rotundata* larvae were incubated at 28°C for 30 d so that adult emergence was synchronized with the start date of the experiment. Within the cages, we provided wooden branches with pre-drilled 4-mm holes as nest sites for *M. rotundata* and observed females actively provisioning nests during the experiment. The order of

pollinator species dominance was determined based on relative species abundances for nearby sites with strong land-use change in the surrounding landscape (i.e., > 85% agriculture; Fig. 1; Stavert et al. 2017).

Plant–pollinator interaction rate

To approximate the contribution of pollinator taxa to pollination, we conducted plant–pollinator visitation observations for two weeks (27 December 2015 to 10 January 2016). The visitation rate of pollinators to flowers can be used as a proxy of pollination effectiveness (Vázquez et al. 2005); although more direct measures are possible they were beyond the scope of our study, which focused on patterns of plant–pollinator interactions in the artificial communities. To quantify plant–pollinator interaction rates, we recorded all visits from pollinator species to all flowers on each of the seven plant species, within a given cage, during 3 min observation sessions. A pollinator visit was recorded only when the insect made contact with the reproductive structures of the flower. We observed all pollinator visits to one plant species at a time and always observed visitation to each plant species in the same order. This resulted in a total observation time of 21 min (7 plant species × 3 min) per cage per observation session. Conducting observations of plant species in the same order was unlikely to result in strong temporal effects as all plant species were observed within a relatively short time period (21 min). We are confident that we recorded all visits from each pollinator species during observations, as total pollinator visitation was relatively low (mean per cage = 0.00–13.02 visits per observation session). At the end of each observation session we recorded the number of open flowers for each plant species. The visitation rate for each pollinator species to the different plant species was thus calculated as the number of visits per flower per 3 min. Five observation sessions were conducted per day (09:30–11:00; 11:00–13:00; 13:00–15:00; 15:00–17:00; 17:00–18:30). On any given sampling day within each cage, visitation was observed for two time periods and never at consecutive time periods. In each cage, each visitation observation session was sampled on at least three separate days. We randomly assigned identification numbers to cages to ensure that observation order was independent of cage treatment and spatial arrangement.

Seed production

We measured seed production per flower for each plant species in each cage, which provided an unambiguous measure of pollination success. To ensure that seeds we counted were a product of pollination during the experiment, we marked flowers that were open while pollinators were present in the cages. This was a process that varied substantially between plant taxa. For *B. rapa*, we marked racemes on individual plants so that markings on each raceme encompassed 10 flowers. Then, once seedpods

had ripened, we recorded whether each flower had produced a seedpod and counted the number of seeds in each pod. For *F. esculentum*, we marked inflorescences for which all flowers were closed and once the experiment ended, we counted the number of open flowers, flower buds, and fruits on each inflorescence. Later, when fruits had ripened, we counted the number of seeds and abscised flowers on each inflorescence and subtracted the number of open flowers and buds that we recorded at the end of the experiment. This allowed us to determine the number of seeds produced from flowers that were open during the experiment. For *C. sativum*, we marked individual umbels at the start of the experiment and used the same process described for *F. esculentum* to determine seed production per flower. For *C. cyanus*, we marked budding inflorescences and later recorded seed production for each floret on inflorescences. *C. pepo* flowers opened in the morning and were only open for half a day, so we marked female flowers at the start of each sampling day. We later identified whether flowers produced fruits, and where fruits were produced, we counted the number of seeds. Finally, for *L. hartwegii* and *S. farinacea* we determined seed production per flower using the same process as with *B. rapa*. Cages remained closed until all fruit had sufficiently ripened and once ripe, fruit from marked flowers were picked and dried (28 January to 26 February 2016). All seed from the harvested fruit were counted in the laboratory.

Statistical analyses

To account for the hierarchical nature of our experiment (i.e., plant species nested within cages), we used a mixed effects or multilevel modeling approach (Gelman and Hill 2006). Specifically, in our models, we account for non-independence in the data by allowing intercepts to vary among cages and plant species where necessary. This modeling approach, also known as partial-pooling, accounts for differences in variance and sample size across observations within levels.

How does numerical evenness of plant and pollinator species affect seed production?.—To test if there were differences in seed production within plant species between evenness treatments and among plant species within treatments, we constructed a linear mixed effects model (LMM) using the lme function in the nlme package (Pinheiro et al. 2017). Because seed production varied between plant species by several orders of magnitude, we scaled seed production values within each species. This was achieved by subtracting the mean seed production for each seed production value and dividing this by the standard deviation. Thus, for this model, the scaled number of seeds produced per flower or flower head was the response (total of 12,895 flowers from the seven plant species across all replicates of the evenness treatments). Plant species identity (categorical; seven levels), treatment level (categorical; four levels) and the plant species ×

treatment interaction were fixed effects. We included cage identity (categorical; 20 levels) as a random effect to account for non-independence of seed produced by plants within the same cage (Gelman and Hill 2006, Zuur et al. 2010). To determine the overall importance of treatment and the plant species × treatment interaction for seed production (as estimated by the model described above), we applied type III Wald test with a chi-square statistic in the car package (Fox et al. 2012). Finally, we compared seed production for each plant species among treatments and seed production among plant species within treatments using pairwise least squared means contrasts in the emmeans package (Length 2016) and determined significance using false discovery rate (FDR) corrected P values (at $\alpha = 0.05$; Verhoeven et al. 2005).

Additionally, we tested whether there were overall differences in seed production between pollinator exclusion cages and cages with pollinators, for each plant species, using the same LMM approach as outlined above. In this model, the scaled number of seeds produced per flower or flower head was the response, pollinators present/absent, plant species, and the pollinators present/absent × plant species interaction were the fixed effects, and cage identity was a random effect.

Does numerical species evenness affect plant–pollinator interactions?.—We calculated visitation rate, visitation evenness, pollinator niche overlap, pollinator sharing (inverse of complementarity in pollinator use among plant species), number of links per species, and selectivity for pollinator and/or plant species in each community (cage). Visitation rate can influence seed production for plants where multiple visits are required for sufficient pollen deposition to maximize seed production, as observed in the majority of published studies (Vázquez et al. 2005). Visitation evenness may affect seed production by increasing the probability of complementary floral visitation interactions occurring between pollinator species. "Pollinator niche overlap" measures the degree that different pollinator species visit the same plant species in a community. In contrast, "pollinator sharing" quantifies the degree to which different plant species are visited by shared pollinator species. Thus, pollinator niche overlap is an inverse measure of complementarity between pollinators in the plant species they use, whereas pollinator sharing is an inverse measure of complementarity between plant species in the pollinators they use. The number of links per species and species selectivity are important measures of niche breadth. We also calculated one network-level metric, interaction evenness, to determine if changes to numerical species evenness translated to changes in community-level evenness of interactions.

We calculated visitation rate as the number of pollinator visits per flower for each plant species per 3-min observation period. Visitation evenness of different pollinator species to each plant species was measured by calculating Hill's diversity ($\alpha = 1$; Hill 1973). Thus, visitation rate evenness is a measure of the equitability of visits from pollinator species to a given plant species, taking into account the total number of open flowers for that plant species. We calculated niche overlap for pollinators (inverse of complementarity among pollinators in their plant use) and pollinator sharing between plants (inverse of complementarity among plants in pollinator use) using the vegdist function in the vegan package (Oksanen et al. 2017). Plant–pollinator interaction matrices were created by summing the number of interactions between each plant and pollinator pair, in each cage. From interaction matrices, we computed dissimilarity matrices using the Bray-Curtis dissimilarity measure (Faith et al. 1987), which provided values of interaction dissimilarity between each species pair for plants and pollinators, respectively. Using these matrices, we calculated mean dissimilarity values for each plant and pollinator species; the inverse of this value (similarity) represents the mean niche overlap for pollinator species and/or the mean level of pollinator sharing for plant species in a community. We measured the number of links for each plant and pollinator species in each cage; a link represented the presence of one or more interaction(s) between a plant and pollinator species. We calculated species level selectivity (d') for plants and pollinators using the dfun function in the bipartite package (Dormann et al. 2008). Selectivity (d') measures how strongly a species deviates from random sampling of available interacting partners, given the availability of those partners (i.e., is weighted by the relative abundances of species in the corresponding trophic level; see Blüthgen et al. 2006 for further details). Selectivity values were computed for all plant and pollinator species in each cage. Finally, we calculated community-level interaction evenness for each cage using the networklevel function in the bipartite package.

To test if differences in numerical species evenness affected the species-level network metrics, we fitted LMMs using the nlme package (Pinheiro et al. 2017) or generalized linear mixed effects models (GLMMs) using the lme4 package (Bates et al. 2015). In each model, the response variables were the network metric values (7 plant species × 20 cages = 140 for plants, and 5 species × 20 cages = 100 for pollinators). Fixed effects were plant species (categorical; seven levels) or pollinator species (categorical; five levels) identity, treatment level (categorical; four levels) and the plant species × treatment interaction. Cage identity (categorical; 20 levels) and plant or pollinator species identity (categorical; seven or five levels) were included as crossed random effects to account for non-independence of metrics generated from species within the same cage. For the number of links per species and selectivity, two models were used (one for plants and one for pollinators). We used a gamma distribution for visitation rate, visitation evenness and pollinator selectivity, a Gaussian distribution for pollinator niche overlap, pollinator sharing, and plant selectivity, and a Poisson distribution for number

of links per species. To test for differences in network-level interaction evenness between treatments, we fitted a simple linear model where interaction evenness was the response (20 networks) and treatment (categorical; four levels) was the predictor. Finally, we tested for differences in metric values between treatments using pairwise least squared means contrasts in the emmeans package and determined significance using false discovery rate (FDR) corrected P values (at $\alpha = 0.05$).

How do changes to plant–pollinator network structure affect seed production?.—To investigate how network structure affected seed production, we fitted a LMM. In this model, the standardized number of seeds produced per flower was the response variable (12,895 flowers) and species level network metrics for plants (visitation rate, visitation evenness, pollinator sharing, number of links per plant species, and plant selectivity; all continuous) were fixed effects. Cage identity (categorical; 20 levels) and plant species (categorical; seven levels) were included as crossed random effects to account for non-independence of seed produced from species within the same cage. We did not include pollinator-specific network metrics in this model, as we were interested in network properties from a plant perspective. Further, plant species was not included as a fixed factor in this case because we were interested in general patterns of how a plants' position in the network is linked to its reproduction success. On the global model, we performed AIC_c model selection with the dredge function in the MuMIn package (Barton 2016). We then used model averaging to calculate estimates and P values for fixed effects for the best-ranked models with a cumulative Akaike weight ≥ 0.95 (Symonds and Moussalli 2011). We tested for covariance between fixed effects using the vif function in the car package (Fox et al. 2012). Variance inflation factor values were low (<2 in all models retained in the 95% confidence set). All fitted models were validated by examining the distribution of residuals plotted against fitted values (Crawley 2002, Zuur et al. 2010). All statistical analyses were conducted in R version 3.4.3 (R Core Team 2017).

RESULTS

How did numerical evenness of plant and pollinator species affect seed production?

We found no main effect of evenness treatment on seed production across plant species ($\chi^2 = 6.90$, df = 3, $P = 0.08$: Appendix S1: Table S4). However, there was a strong interaction between plant species identity and effect of evenness treatment ($\chi^2 = 67.91$, df = 18, $P < 0.0001$) indicating idiosyncratic responses in seed production among plant species to our evenness treatments. More specifically, we found differences in seed production among treatments for three of the seven plant species (*Brassica rapa*, *Fagopyrum esculentum*, and *Salvia farinacea*; Fig. 2). Interestingly, these three

species had largely different relative abundances in the dominant plant treatments (i.e., dominant, subdominant, and rare, respectively) and all had higher seed production when plant communities were uneven. When we assessed seed production among plant species within treatments we found that, in dominant plant treatments, some species increased their seed production relative to others, compared with even plant treatments (Fig. 3). Specifically, dominant (*B. rapa*) and rare (*S. farinacea*) plant species tended to produce more seed relative to other plant species in dominant plant treatments.

Did numerical species evenness affect plant–pollinator interactions?

In total, we recorded 32,480 plant–pollinator interactions across all evenness treatments. Interestingly, pollinator abundances did not always appear to directly correspond to their interaction frequencies (e.g., *Oxysarcodexia varia* had fewer interactions than expected given its abundance, whereas *Bombus terrestris* had more interactions than expected; Fig. 4). Further, interactions were dominated by the pollinator species *Eristalis tenax* and *B. terrestris* and the plant species *Brassica rapa* (Fig. 4). However, numerical species evenness altered the evenness of interactions and, as expected, we found substantially lower community-level interaction evenness in cages with dominant pollinator and plant communities (DomPoll—DomPlant and EvenPoll—DomPlant; Fig. 4; Appendix S1: Fig. S9). Conversely, interaction evenness was highest where plant communities were even (EvenPoll—EvenPlant and DomPoll—EvenPlant).

At the species level, we found differences between evenness treatments in pollinator selectivity (d'), plant selectivity (d'), pollinator sharing, pollinator niche overlap, and visitation rate (Fig. 5). Pollinator selectivity was highest in treatments with even plants, whereas plant selectivity was highest in treatments with even pollinators, and this trend was relatively uniform across species (Appendix S1: Fig. S6). Pollinator sharing was highest where plant communities were even, regardless of pollinator evenness, and this trend was relatively consistent across plant species (Appendix S1: Fig. S3). In contrast, pollinator niche overlap was highest where pollinator communities were even. Finally, pollinator visitation rate was highest in DomPoll—EvenPlant and lowest in EvenPoll—DomPlant treatments and was higher for dominant and rare plant species in even plant treatments (Appendix S1: Fig. S8).

How did plant–pollinator network structure affect seed production?

Pollinator sharing (the inverse of complementarity in pollinator use among plant species) had a strong negative effect on seed production and was present in six of the 10 top ranked models (conditional model-averaged estimate = -0.66, SE = 0.25, $z = 2.59$, $P = 0.01$: Appendix S1: Table S3; Fig. 6). Visitation rate had a weak
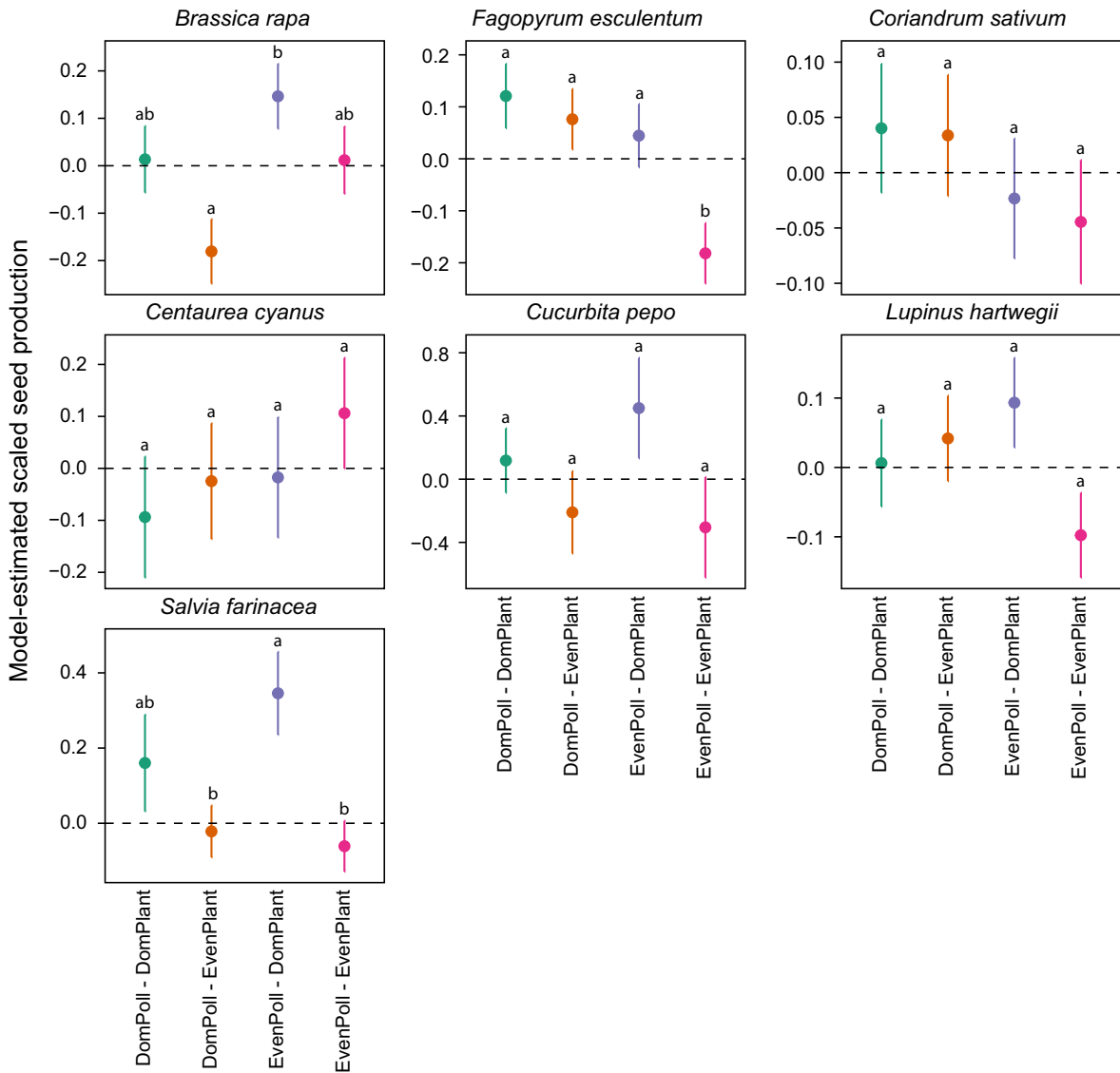
FIG. 2. Model estimates (± SE) for scaled seed production of each plant species across evenness treatments. Letters above estimates denote statistically significant differences (α = 0.05; false discovery rate [FDR] corrected) in seed production for each plant species between treatments. Note that *y*-axis scales differ among plant species. Treatments are described in *Methods: Experimental design*.

positive effect on seed production and was present in five of the top ranked models (conditional model-averaged estimate = 0.38, SE = 1.27, z = 0.30, P = 0.77: Appendix S1: Table S3; Fig. 6), although estimates varied widely. Visitation rate evenness and plant selectivity both had weak effects on seed production and the number of links per plant species was not included in the top ranked model set (Appendix S1: Table S3; Fig. 6).

DISCUSSION

We conducted one of the first experiments aiming to disentangle the effect of numerical species evenness on network structure and ecosystem function, independent

of species richness, composition and total abundance. Further, we simultaneously manipulated the evenness of two trophic levels (plants and pollinators) in artificial communities, whereas most previous biodiversity–ecosystem function experiments have focused on only one trophic level. We found that differences in evenness caused important changes to the plant–pollinator network structure, which consequently affected plant reproduction. Specifically, numerical dominance in our artificial plant communities increased complementarity in pollinator use among plant species (indicated by reduced pollinator sharing), and this network change was associated with increased seed production for dominant and rare species. This finding is important, because
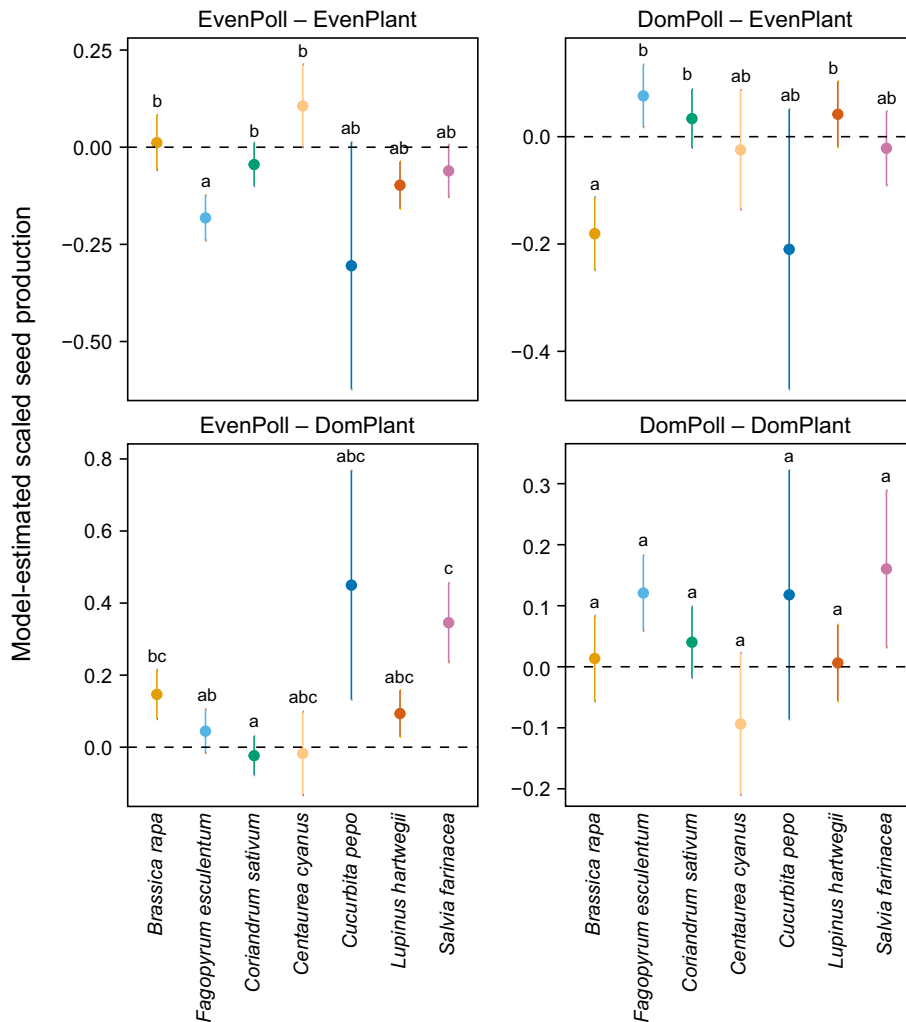
FIG. 3. Model estimates (± SE) for scaled seed production of each plant species within each evenness treatment. Letters above estimates denote statistically significant differences (α = 0.05; FDR corrected) in seed production between plant species within treatments.

although increased complementarity among species is expected to enhance ecosystem functioning in both natural and artificial systems (Nijs and Roy 2000, Wilsey and Potvin 2000, Kirwan et al. 2007), the effect of species evenness on complementarity is less obvious.

Numerical dominance increased complementarity in pollinator use among plant species

We show that across all evenness treatments, interaction frequencies between plants and pollinators were relatively uneven, mainly because pollinator species had different activity rates and strong floral preferences. Interestingly, relative abundances of the pollinator species did not necessarily correspond to their floral visitation rates. In all treatments, the majority of floral visits were by two pollinator species, a hoverfly (*Eristalis tenax*) and a bumblebee (*Bombus terrestris*). Both species were broad

generalists, with *B. terrestris* in particular performing the most visits to most plant species. In contrast, the fly, *Oxysarcodexia varia*, was second in the dominance order but contributed the fewest visits of any pollinator species.

Importantly, we assumed that all insects observed visiting flowers and contacting reproductive structures were pollinating those flowers. However, we did not explicitly test the pollination effectiveness of insects for each plant species in our experiment. Different pollinator species are likely to vary in their pollination effectiveness (defined as the quantity of viable, compatible and conspecific pollen transferred by an animal to a receptive stigma in a single visit; Ne'eman et al. 2010) when visiting different plant species. Thus, visitation frequency may not be entirely representative of pollinator contributions to pollination, because pollinator performance is a product of both their interaction rate and effectiveness (Mayfield et al. 2001, Kremen et al. 2002). This highlights the need to explore
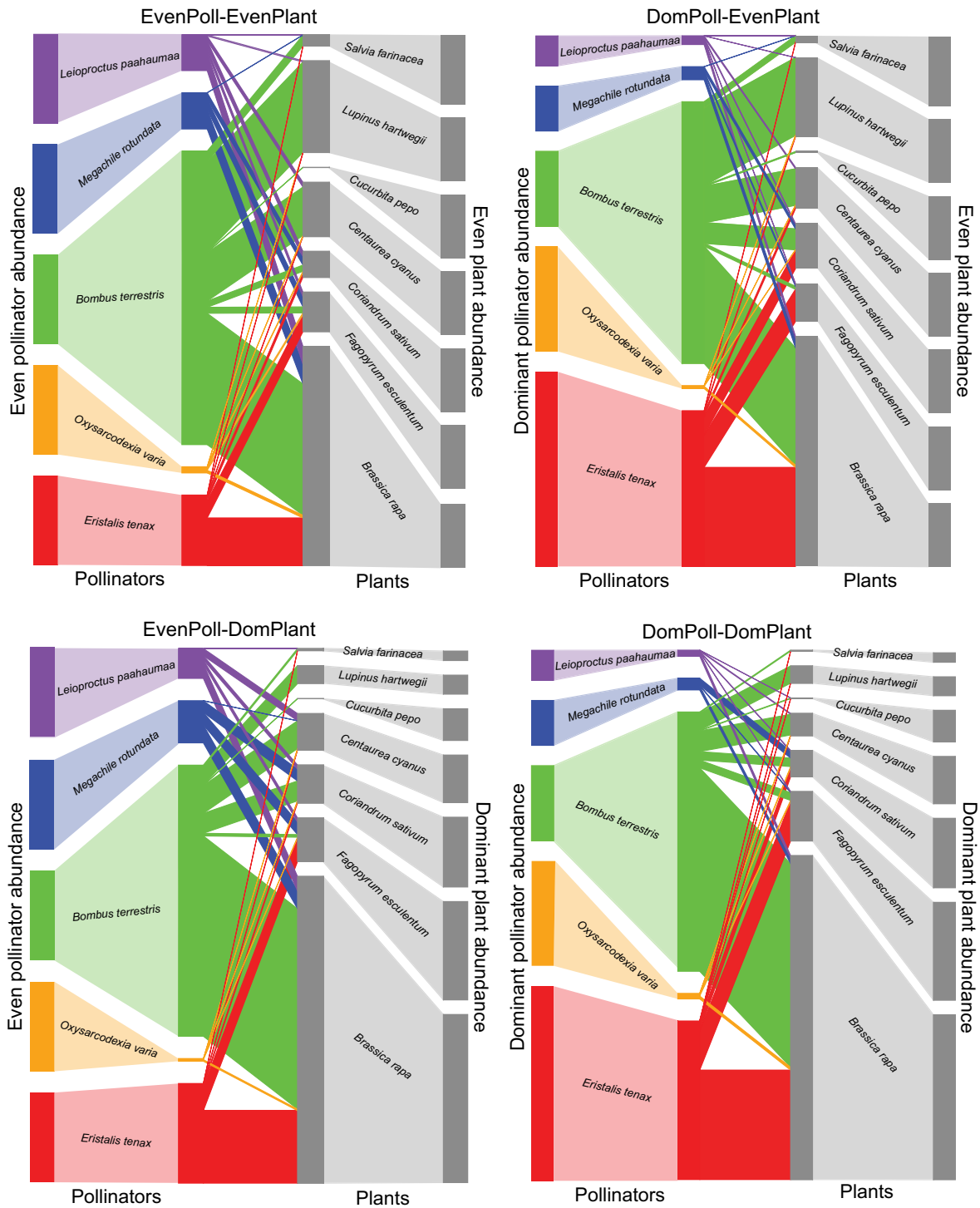
JAMIE R. STAVERT ET AL.

FIG. 4.   Bipartite networks of plant and pollinator communities for each evenness treatment. Boxes on the outside of network diagrams represent the relative numerical abundances of plant and pollinator species in each treatment. Boxes on the inside of the diagrams represent the interaction frequency of plants (gray) and pollinators (colored). Semi-transparent links between abundance and interaction frequency boxes depict the association between species' abundances and their interaction frequencies. Thickness of links between plant and pollinator partners represents the relative number of interactions (pollinator visits to flowers) between those species. Plants and pollinators are ordered according to dominance rank (for treatments with dominant communities), with the most dominant species at the bottom and the least dominant species on the top.
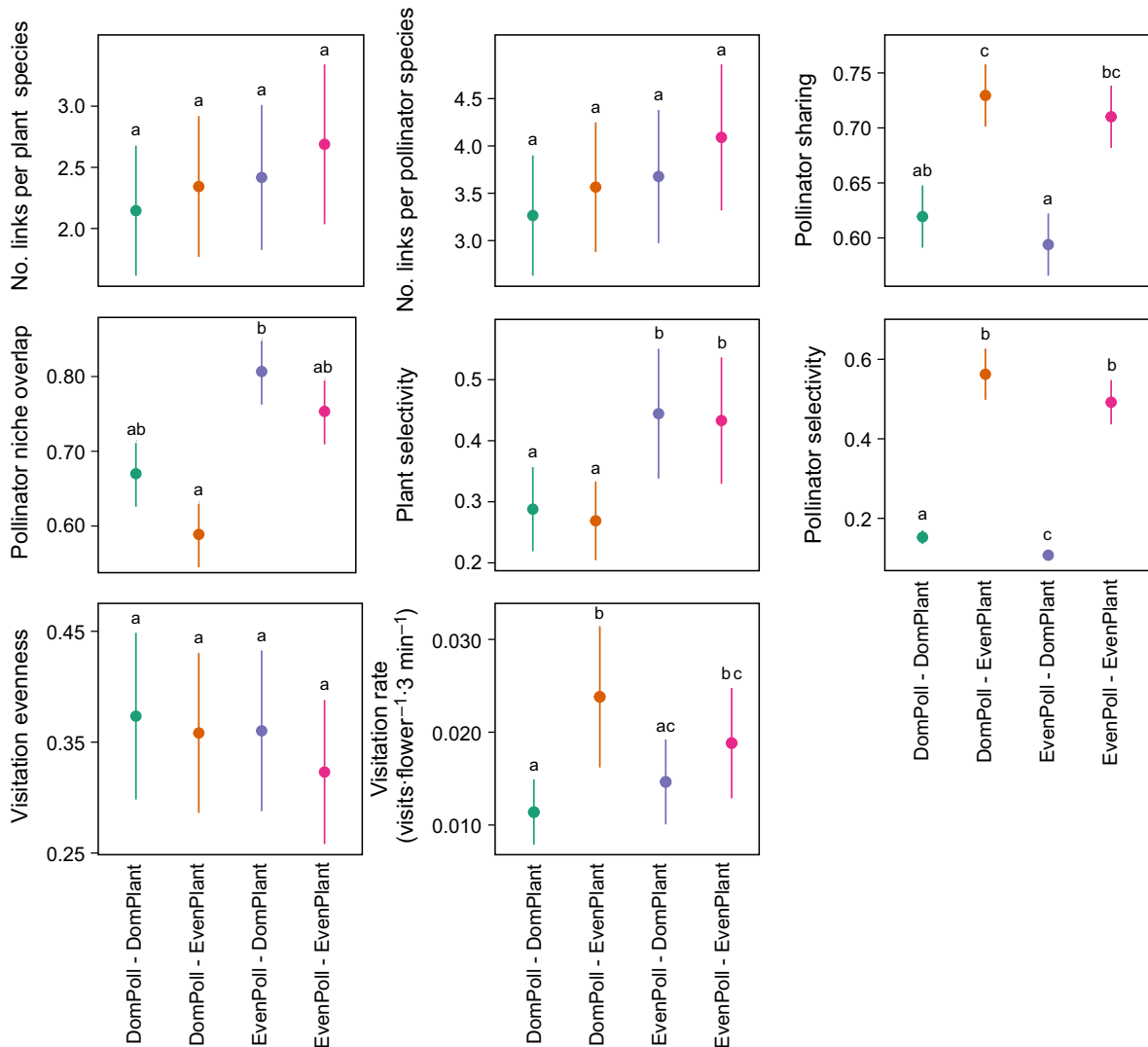
Fig. 5. Model estimates (± SE) for species-level network metrics for each evenness treatment. Letters above estimates denote statistically significant differences in network metric values (α = 0.05; FDR corrected) between treatments.

further numerical dominance scenarios and/or test the effect of functional evenness (the distribution of species traits that contribute to functional performance) on ecosystem functioning, particularly in natural systems where evenness will be more variable.

Varying network structures were apparent across our evenness treatments. These are likely due to the combination of differences in floral display size (as a product of numerical abundance) and differing floral attractiveness inherent to each plant species. Specifically, complementarity in pollinator use among plant species was lower in even compared to dominant plant treatments. This contrasts to previous work that suggests higher pollinator evenness should increase complementarity in pollinator use among plant species (i.e., reduce pollinator sharing), due to greater interspecific competition and subsequent niche separation between species (Magrach et al. 2017). However, we show

that changes to plant communities, rather than pollinator communities, can drive network structural changes and consequently, plant reproduction.

The increased complementarity in pollinator use that we observed in dominant plant communities could have arisen due to adaptive pollinator foraging and/or changes in the availability of the various floral resources. For example, adaptive foraging causes generalist pollinators to prefer specialist plants, which facilitates niche partitioning between generalist and specialist species (Valdovinos et al. 2016, Benadi and Gegear 2018). This niche partitioning can enhance pollination function because it makes generalist plant resources available to specialist pollinators, while also increasing pollination of specialist plants. Alternatively, in our dominant plant treatments, pollinators may not have needed to visit rare plants because the dominant plant, *B. rapa*, produced
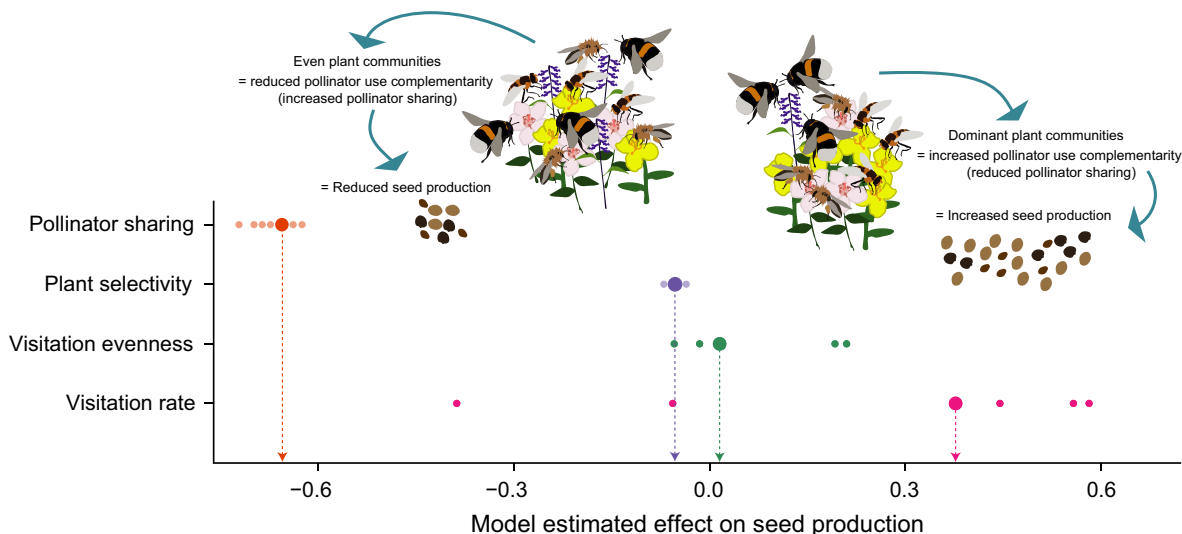
FIG. 6. Model estimates for the 10 best-ranked models that have a cumulative Akaike weight ≥0.95 for network metric effects on seed production. Small semi-transparent points are estimate values for each covariate from all best-ranked models (Appendix S1: Table S3). Large points are model-averaged estimates for each covariate. The illustration above depicts plant–pollinator interactions and resulting seed production in an even and dominant plant community. Communities have been simplified to three species per trophic level to aid interpretation.

many flowers and thus, abundant floral resources. Therefore, one major limitation of our study is that we tested only one dominance order scenario, and different dominance orders may reveal alternative evenness effects on complementarity.

Floral abundance is also likely to be an important factor driving complementarity. Theory predicts that larger floral displays, due to greater abundance of a plant species, should enhance attraction for pollinators, and/or reduce interspecific competition between plants to attract pollinators (Pauw 2013). In contrast, we found that greater floral abundance did not always result in higher visitation rate. Some plant species did receive more visits when they were more abundant: *Lupinus hartwegii* and *Salvia farinacea* had higher visitation rates in even treatments than when they were rare in dominant treatments. However, greater floral abundance did not increase visitation rate for the dominant plant species, *B. rapa*, which had a higher visitation rate per flower in even compared to dominant plant treatments. Thus, for *B. rapa*, increased conspecific density may have caused intraspecific competition for pollinators to exceed intraspecific facilitation, resulting in pollinators becoming satiated, which diluted per flower visitation rate (as often occurs in large conspecific floral displays; Rathcke 1983, Brys et al. 2008, Dauber et al. 2010).

Reduced complementarity in pollinator use among plant species decreased seed production

Overall, we found that lower complementarity in pollinator use among plant species (i.e., greater pollinator sharing) had a strong negative effect on seed production, while other aspects of network structure had weak effects. Lower complementarity in pollinator use is likely to reduce plant reproduction by compromising intraspecific pollen transfer due to pollen loss or misdelivery to heterospecifics in between conspecific visits (Muchhala and Thomson 2012). In particular, pollen loss can be a significant fitness cost, greatly reducing the pollen available for fertilization (Morales and Traveset 2008, Muchhala et al. 2010, Muchhala and Thomson 2012). The rate of intraspecific pollen transfer depends on pollinator constancy, the degree to which pollinators forage at a single plant species despite the availability of other suitable species, and this can be strongly influenced by floral display size (Levin and Anderson 1970, Goulson 1994, Morales and Traveset 2008). We did not specifically measure pollinator constancy in our study. However, field studies have shown that relative plant abundances affect pollinator constancy and intraspecific pollen transfer, whereby plant species with many flowers develop higher constancy (Kephart and Heiser 1980). Indeed, we found that *B. rapa* had greater seed production in treatments where it was the dominant plant species, possibly indicating higher floral constancy and greater rates of intraspecific pollen transfer. In addition to the loss/reduced rate of conspecific pollen transfer where pollinator sharing is high, heterospecific pollen transfer (the transfer of pollen among plant species) could reduce seed production. This often occurs through deposition of heterospecific pollen on stigmas, causing pollen clogging and/or allelopathy (Wilcock and Neiland 2002, Fang and Huang 2013). Clearly, these mechanisms are important for plant reproduction and need to be explored further in the context of varying plant and pollinator abundance distributions, particularly in

natural systems where disturbances often cause increased plant dominance (Hillebrand et al. 2008).

Changes to species numerical evenness favor some species over others

We found that the magnitude and direction of differences in seed production between plant species varied across evenness treatments. This indicates that in our artificial communities, increases in plant dominance favored some plant species over others, potentially due to changes in relative attractiveness to pollinators and thus, delivery of conspecific pollen. Importantly, this aligns with recent studies that show plant–pollinator interactions can alter competitive hierarchies among plant species (Pauw 2013, Lanuza et al. 2018). Extending this concept from our cage experiment to consider a natural system, we suggest that differences in plant species' competitive abilities to attract pollinators could well contribute to maintaining the skewed species abundance distributions that are common in natural plant communities (McGill et al. 2007). Nevertheless, our cage experiment does not consider other aspects of plant competition in natural systems, such as competition for nutrients and water, which can strongly affect plant reproduction and population dynamics (Tilman 1994, 2007). Thus, to gain a holistic understanding of how evenness drives functioning, studies are required that manipulate evenness of natural plant communities, recording changes to fitness and populations over multiple generations, while considering both multitrophic interactions and abiotic factors (Godoy et al. 2018, Lanuza et al. 2018).

Beyond the limitations imposed by using artificial rather than natural communities, one experimental limitation of our study is that we did not alter the order of species dominance. However, this would have required an experiment an order of magnitude larger than what we present here and thus, we focused on manipulating the degree of dominance rather than dominance order per se. In many richness–function experiments, functioning is driven by the selection (or sampling) effect, where the chances of including a species with high functional performance increase with increasing richness (Cardinale et al. 2012). Therefore, in a broader sense, it seems likely that changes in dominance order would also affect ecosystem function. In plant–pollinator systems, dominance order is likely to affect the evenness–function relationship because different plant species vary in relative attractiveness and pollinator species differ in pollination effectiveness and floral preference. Yet, testing the effect of dominance order on function would require assembling somewhat random communities with respect to the real world, with correspondingly less applicability to natural systems (Winfree 2013).

CONCLUSION

Here, we provide evidence from controlled artificial communities that suggests numerical species evenness can affect the structure of plant–pollinator networks, and subsequently alter plant reproduction. In particular, dominance increased complementarity in pollinator use (reduced pollinator sharing) among plant species, which increased plant reproduction. However, whether our findings are transferable to natural communities is unclear and studies are required to identify the evenness–ecosystem functioning relationship in natural plant–pollinator systems. Although species richness is the most commonly researched aspect of biodiversity, there is now a growing body of evidence showing that other components of biodiversity are important drivers of ecosystem functioning. This highlights the need for researchers to look beyond invasions or extinctions to more subtle changes in species abundances and interactions. Improving this understanding is critical as anthropogenic disturbances continue to alter the evenness structure of ecological communities, likely disrupting ecosystem functions long before changes in species richness occur. Although our study provides a step towards understanding the evenness–ecosystem functioning relationship, our use of numerical species evenness is a relatively coarse measure of community structure. Moving forward, research would benefit from studies that specifically manipulate the abundance of species with particular traits that are strongly linked to the function(s) of interest and assess the implications for ecosystem functioning. Such experiments would be especially valuable and transferable if they were conducted in real world ecological communities.

LITERATURE CITED

Abu-Hammour, K., and D. Wittmann. 2010. Pollination and pollinators of *Cucurbita pepo* (Cucurbitaceae) in the Jordan Valley to improve seed set. Advances in Horticultural Science 24:249–256.

Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecology Letters 9:968–980.

Aizen, M. A., M. Sabatino, and J. M. Tylianakis. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. Science 335:1486–1489.

Albrecht, M., B. Schmid, Y. Hautier, and C. B. Müller. 2012. Diverse pollinator communities enhance plant reproductive success. Proceedings of the Royal Society B 279:4845–4852.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9:1146–1156.

Bartomeus, I., D. P. Cariveau, T. Harrison, and R. Winfree. 2017. On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. Oikos 127:306–315.

Barton, K. 2016. Package MuMIn: multi-model inference. R package version 1.15.6. https://cran.r-project.org/web/packages/MuMIn/index.html

Bates, D., M. Maechler, and B. M. Bolker. 2015. lme4: Liner mixed-effects models using S4 classes. https://cran.r-project.org/web/packages/lme4/index.html

Benadi, G., and R. J. Gegear. 2018. Adaptive foraging of pollinators can promote pollination of a rare plant species. American Naturalist 192:E81–E92.

Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. BMC Ecology 6:9.

Bond, W. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society B 344:83–90.

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.

Brys, R., H. Jacquemyn, and M. Hermy. 2008. Pollination efficiency and reproductive patterns in relation to local plant density, population size, and floral display in the rewarding *Listera ovata* (Orchidaceae). Botanical Journal of the Linnean Society 157:713–721.

Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Cawoy, V., J.-F. Ledent, J.-M. Kinet, and A.-L. Jacquemart. 2009. Floral biology of common buckwheat (*Fagopyrum esculentum* Moench). European Journal of Plant Science and Biotechnology 3:1–9.

Claßen-Bockhoff, R., T. Speck, E. Tweraser, P. Wester, S. Thimm, and M. Reith. 2004. The staminal lever mechanism in *Salvia* L. (Lamiaceae): A key innovation for adaptive radiation? Organisms Diversity & Evolution 4:189–205.

Crawley, M. J. 2002. Statistical computing: an introduction to data analysis using S-Plus.–J. Statistical computing: an introduction to data analysis using S-Plus. John Wiley & Sons, Ltd, Chichester, UK.

Dangles, O., and B. Malmqvist. 2004. Species richness–decomposition relationships depend on species dominance. Ecology Letters 7:395–402.

Dauber, J., et al. 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.

Dıaz, S., A. J. Symstad, F. Stuart Chapin III, D. A. Wardle, and L. F. Huenneke. 2003. Functional diversity revealed by removal experiments. Trends in Ecology & Evolution 18:140–146.

Diederichsen, A. 1996. Coriander: *Coriandrum sativum* L. Bioversity International, Rome, Italy.

Dixon, G. R. 2007. Vegetable Brassicas and related crucifers. CABI, Wallingford, UK.

Donovan, B. J. 2007. Apoidea (Insecta: Hymenoptera). Fauna of New Zealand 57:295.

Dormann, C. F., B. Gruber, and J. Fründ. 2008. Introducing the bipartite Package: analysing ecological networks. R news 8:8–11.

Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57–68.

Fang, Q., and S.-Q. Huang. 2013. A directed network analysis of heterospecific pollen transfer in a biodiverse community. Ecology 94:1176–1185.

Fontaine, C., I. Dajoz, J. Meriguet, and M. Loreau. 2006. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. PLoS Biology 4:0129–0135.

Fox, J., S. Weisberg, D. Adler, D. Bates, G. Baud-Bovy, S. Ellison, D. Firth, M. Friendly, G. Gorjanc, and S. Graves. 2012. Package 'car'. R Foundation for Statistical Computing, Vienna, Austria.

Fründ, J., C. F. Dormann, A. Holzschuh, and T. Tscharntke. 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. Ecology 94:2042–2054.

Gelman, A., and J. Hill. 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.

Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. Journal of Ecology 94:295–304.

Godoy, O., I. Bartomeus, R. P. Rohr, and S. Saavedra. 2018. Towards the integration of niche and network theories. Trends in Ecology & Evolution 33:287–300.

Goulson, D. 1994. A model to predict the influence of insect flower constancy on interspecific competition between insect pollinated plants. Journal of Theoretical Biology 168:309–314.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902–910.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432.

Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89:1510–1520.

Hillebrand, H., B. Blasius, E. T. Borer, J. M. Chase, J. Downing, B. K. Eriksson, C. T. Filstrup, W. S. Harpole, D. Hodapp, and S. Larsen. 2017. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. Journal of Applied Ecology 55:169–184.

Hooper, D., F. Chapin III, J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. Lawton, D. Lodge, M. Loreau, and S. Naeem. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Jiang, L., S. Wan, and L. Li. 2009. Species diversity and productivity: Why do results of diversity-manipulation experiments differ from natural patterns? Journal of Ecology 97:603–608.

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

Kephart, S. R., and C. B. Heiser. 1980. Reproductive isolation in Asclepias: lock and key hypothesis reconsidered. Evolution 34:738–746.

Kirwan, L., A. Lüscher, M. T. Sebastià, J. A. Finn, R. Collins, C. Porqueddu, A. Helgadottir, O. H. Baadshaug, C. Brophy, and C. Coran. 2007. Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. Journal of Ecology 95:530–539.

Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B 274:303–313.

Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences USA 99:16812–16816.

Lanuza, J. B., I. Bartomeus, and O. Godoy. 2018. Opposing effects of floral visitors and soil conditions on the determinants of competitive outcomes maintain species diversity in heterogeneous landscapes. Ecology Letters 21:865–874.

Larsen, T. H., N. M. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters 8:538–547.

Length, R. V. 2016. Least-squares means: the R package lsmeans. Journal of Statistical Software 69:1–33.

Levin, D. A., and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. American Naturalist 104:455–467.

Lewandowska, A. M., A. Biermann, E. T. Borer, M. A. Cebrian-Piqueras, S. A. Declerck, L. De Meester, E. Van Donk, L. Gamfeldt, D. S. Gruner, and N. Hagenah. 2016. The influence of balanced and imbalanced resource supply on biodiversity–functioning relationship across ecosystems. Philosophical Transactions of the Royal Society B 371:20150283.

Locey, K., and D. McGlinn. 2012. rpartitions: code for integer partitioning. Weecology, Logan, Utah, USA.

Locey, K. J., and E. P. White. 2013. How species richness and total abundance constrain the distribution of abundance. Ecology Letters 16:1177–1185.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Loreau, M., et al. 2001. Ecology: Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808.

Magrach, A., J. P. González-Varo, M. Boiffier, M. Vilà, and I. Bartomeus. 2017. Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. Nature Ecology & Evolution 1:1299–1307.

Mayfield, M. M., N. M. Waser, and M. V. Price. 2001. Exploring the 'most effective pollinator principle' with complex flowers: bumblebees and *Ipomopsis aggregata*. Annals of Botany 88:591–596.

McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Dornelas, B. J. Enquist, J. L. Green, and F. He. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters 10:995–1015.

Morales, C. L., and A. Traveset. 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. Critical Reviews in Plant Sciences 27:221–238.

Muchhala, N., Z. Brown, W. S. Armbruster, and M. D. Potts. 2010. Competition drives specialization in pollination systems through costs to male fitness. American Naturalist 176:732–743.

Muchhala, N., and J. D. Thomson. 2012. Interspecific competition in pollination systems: costs to male fitness via pollen misplacement. Functional Ecology 26:476–482.

Ne'eman, G., A. Jürgens, L. Newstrom-Lloyd, S. G. Potts, and A. Dafni. 2010. A framework for comparing pollinator performance: effectiveness and efficiency. Biological Reviews 85:435–451.

Nijs, I., and J. Roy. 2000. How important are species richness, species evenness and interspecific differences to productivity? A mathematical model Oikos 88:57–66.

Oksanen, J., et al. 2017. vegan: community ecology package. R package version 2.4-5. https://cran.r-project.org/web/packages/vegan/index.html

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos 120:321–326.

Pauw, A. 2013. Can pollination niches facilitate plant coexistence? Trends in Ecology & Evolution 28:30–37.

Penet, L., B. Marion, and A. Bonis. 2012. Impact of capitulum structure on reproductive success in the declining species *Centaurea cyanus* (Asteraceae): Small to self and big to flirt? Journal of Pollination Ecology 8:52–58.

Pielou, E. C. 1977. Mathematical ecology. Wiley, Hoboken, New Jersey, USA.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2017. nlme: linear and nonlinear mixed effects models. R package version 3.1-130. https://cran.r-project.org/web/packages/nlme/index.html

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rathcke, B. 1983. Competition and facilitation among plants for pollination. Pages 305–329 *in* L. Real, editor. Pollination Biology. Academic, New York, USA.

Reiss, J., J. R. Bridle, J. M. Montoya, and G. Woodward. 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends in Ecology & Evolution 24:505–514.

Schleuning, M., J. Fründ, and D. García. 2015. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions. Ecography 38:380–392.

Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. Ecology Letters 6:509–517.

Smith, B., and J. B. Wilson. 1996. A consumer's guide to evenness indices. Oikos 76:70–82.

Stavert, J. R., D. E. Pattemore, I. Bartomeus, A. C. Gaskett, and J. R. Beggs. 2018. Exotic flies maintain pollination services as native pollinators decline with agricultural expansion. Journal of Applied Ecology 55:1737–1746.

Stavert, J. R., D. E. Pattemore, A. C. Gaskett, J. R. Beggs, and I. Bartomeus. 2017. Exotic species enhance response diversity to land-use change but modify functional composition. Proceedings of the Royal Society B 284:20170788.

Symonds, M. R., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13–21.

Thompson, K., A. Askew, J. Grime, N. Dunnett, and A. Willis. 2005. Biodiversity, ecosystem function and plant traits in mature and immature plant communities. Functional Ecology 19:355–358.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Tilman, D. 2007. Interspecific competition and multispecies coexistence. Theoretical Ecology: Principles and Applications 3:84–97.

Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and ecosystem functioning. Annual Review of Ecology, Evolution, and Systematics 45:471.

Tucker, S. C. 2003. Floral development in legumes. Plant Physiology 131:911–926.

Valdovinos, F. S., B. J. Brosi, H. M. Briggs, P. Moisset de Espanés, R. Ramos-Jiliberto, and N. D. Martinez. 2016. Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. Ecology Letters 19:1277–1286.

Vázquez, D. P., W. F. Morris, and P. Jordano. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. Ecology Letters 8:1088–1094.

Verhoeven, K. J., K. L. Simonsen, and L. M. McIntyre. 2005. Implementing false discovery rate control: increasing your power. Oikos 108:643–647.

Wardle, D. A. 1999. Is "sampling effect" a problem for experiments investigating biodiversity-ecosystem function relationships? Oikos 87:403–407.

JAMIE R. STAVERT ET AL.

Whittaker, R. H. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30:279–338.

Wilcock, C., and R. Neiland. 2002. Pollination failure in plants: why it happens and when it matters. Trends in Plant Science 7:270–277.

Wilsey, B. J., and C. Potvin. 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. Ecology 81:887–892.

Winfree, R. 2013. Global change, biodiversity, and ecosystem services: What can we learn from studies of pollination? Basic and Applied Ecology 14:453–460.

Winfree, R., J. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology Letters 18:626–635.

Winfree, R., J. R. Reilly, I. Bartomeus, D. P. Cariveau, N. M. Williams, and J. Gibbs. 2018. Species turnover promotes the importance of bee diversity for crop pollination at regional scales. Science 359:791–793.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2749/suppinfo

DATA AVAILABILITY

Associated data and R code is available on Zenodo: https://doi.org/10.5281/zenodo.2633357