RESEARCH ARTICLE

Benefits and limitations of isolated floral patches in a pollinator restoration project in Arizona

Molly L. McCormick^{1,2}, Clare E. Aslan¹, Todd A. Chaudhry³, Kristen A. Potter¹

This study examined invertebrate floral visitor responses to floral richness, floral abundance, and distance between floral patches within a newly planted pollinator restoration habitat in an arid ecosystem in central Arizona, United States. We created a pollinator habitat experiment consisting of a large central garden (11-m diameter) surrounded by concentric rings of smaller habitat patches (1-m diameter), separated from one another by 1, 8, 13, and 21 m, respectively, and including four flowering species. We observed plant and visitor interactions via structured 10-minute flower visitation observations over a 3-month period. Key findings included: (1) each plant species interacted with a variety of flower visitors, but flower visitor groups differed only marginally among the plant species; (2) floral patches outside the central garden exhibited reduced quantities of floral structures; and (3) number of floral structures per patch, but not isolation of floral patches within the habitat, affected the number of visitors and visitor taxa richness. For practitioners and land managers looking to restore pollination systems in arid ecosystems with low establishment via seeding, the results of this study suggest that installing species-rich and florally abundant patches of flowering plant species within a habitat could efficiently support plant-pollinator interactions.

Key words: floral visitor, foraging distance, habitat patches, pollinator, pollinator habitat, pollinator restoration

Implications for Practice

- Restoration plantings in support of pollinators must contain sufficient floral resources to support resident communities of pollinators over a season. This can be accomplished on a budget with the addition of flower patches within a habitat, instead of uniformly distributed flowers across an entire habitat.
- Isolated flowering patches may produce fewer flowers, perhaps as a result of edge effects. Flower visitation declined with decreasing flower density, but not with increasing isolation of flowering patches.

Introduction

A global decline in pollinator populations, termed the "pollinator crisis" (Kearns et al. 1998; Tylianakis 2013), has received broad attention because of its potential to impact ecosystem function, as well as food security and thus human welfare. Pollination is required for successful reproduction in 75% of flowering plant species (Ollerton et al. 2011) and 35% of food crops worldwide (Klein et al. 2007). Habitat loss is one of the main drivers of the pollinator crisis (Kearns et al. 1998; Potts et al. 2010). Restoration of flowering plant communities has been shown to improve pollination services and is therefore of broad management interest (Kaiser-Bunbury et al. 2017).

Understanding how to design habitats that best support diversity and abundance of pollinator communities is important for habitat management and restoration (Allen-Wardell et al. 1998). The Xerces Society for Invertebrate Conservation has produced regional guidelines for pollinator habitat initiatives (Vaughan et al. 2007; Lee-Mäder et al. 2013; Adamson et al. 2015). These guidelines discuss the importance of providing abundant and diverse season-long forage, protecting against exposure to chemicals, providing nesting habitat and water, and selecting a site based on growing conditions for plants (Lee-Mäder et al. 2013). Guidelines for pollinator habitat in natural areas often contain lists of pollinator plant species, but do not provide guidance on installation and spatial arrangement of these plants (e.g. Clark et al. 2017), and some also lack ecosystem-specific guidance. If land managers want to increase the efficacy of their efforts and support species-rich communities of pollinators with limited resources, especially in arid climates or where plant establishment is low (Jankju 2013), more specific planting guidance is needed.

Seeding a landscape with flowering plant species may not be sufficient to support rich and abundant pollinator communities, especially in arid or water-limited ecosystems in which recruitment success is highly dependent on rainfall (as reviewed by Bainbridge 2007) and plant establishment in desert ecosystems via seeding can fail (Abella et al. 2012). Furthermore, the

© 2019 Society for Ecological Restoration doi: 10.1111/rec.12995

Author contributions: MM, CA conceived and designed the research; MM performed the experiments; MM, CA analyzed the data; MM led the manuscript writing; CA, TC. KP contributed ideas and edits.

¹Landscape Conservation Initiative, Northern Arizona University, Flagstaff, AZ 86005, U.S.A.

²Address correspondence to M. L. McCormick, email mlm728@nau.edu
³National Park Service, Flagstaff, AZ 86011, U.S.A.

expense of installing a habitat that is sufficient for pollinators across multiple hectares can be prohibitive for many land managers (Banerjee et al. 2006). Land managers could instead consider creating a series of smaller-scale floral patches within the habitat to maximize species richness (Tscharntke et al. 2002; Hulvey et al. 2017). These floral patches should be separated by no more than the foraging range of the potential pollinator groups. However, the optimal flowering plant assemblage for these patches, as well as the effect of any degree of isolation on visitation to such patches, remain little understood.

In order to create best practices for designing pollinator habitat that contains high-quality floral patches, researchers need to examine the arrangement of floral patches within a habitat, and how these patches impact pollinator visitation. We explored how isolation of flower patches affects flower visitor community composition, flower visitation rate, visitor richness, and visitor community abundance in a single restored pollinator habitat in arid central Arizona. Our first hypothesis was that isolation would exert a negative effect on the number of floral visitors, visitor taxa richness, and visitation rate. Although three of the planted flowering species were in the family Asteraceae and therefore shared the same general flower structure, the species in this experiment did vary in flower color and size. Our second hypothesis was that diverse visitor communities would visit the four flowering plant species used in the restoration planting, such that a mix of flowers supports a higher richness of potential visitors than a monoculture would do.

Methods

Study Design

We designed and installed a set of restoration plantings consisting of a main central garden and smaller satellite habitat patches in an alfalfa field that had been abandoned for approximately 2 years. The experiment took place in the Verde Valley of central Arizona, United States. The Verde Valley is located in the transition zone between the Arizona/New Mexico Mountains and the Sonoran Basin and Range Ecoregions (Turner et al. 2005). The study site was located at the 124 ha Shield Ranch (34.517 N, -111.819 W), at the confluence of the Verde River and West Clear Creek. Habitats surrounding the study site consist of mostly Upper Sonoran Desert scrub with interspersed semi-desert grasslands (Turner et al. 2005), fallow and production agricultural fields, and mesquite (Prosopis velutina) bosques and cottonwood-willow (Populus fremontii, Salix spp., and Baccharis salicifolia) gallery forest near the waterways. The average precipitation at the site is 36.5 cm per year. Pollinator habitat projects, instigated by private landowners and farmers, have increased in the area following attention brought about by the pollinator crisis and the pollinator action plan (Pollinator Health Task Force 2015), and as mitigation following disturbance activities (e.g. roads, utility lines, fire) (pers. obs.).

Plant Production

We planted four species in a 2 ha field: Mexican hat (Ratibida columnifera, Asteraceae), blanket flower (Gaillardia *pulchella*, Asteraceae), desert marigold (*Baileya multiradiata*, Asteraceae), and desert globemallow (*Sphaeralcea ambigua*, Malvaceae). We chose these species because they are native, are commonly used in restoration projects across the region, are considered important species for pollinators (Natural Resource Conservation Service & The Xerces Society 2012), are commonly available from seed suppliers, and can grow and produce flowers in 1 year. Because they are also known to establish and persist at restoration sites, all four are known as "workhorse species" (Havens et al. 2015). Blooming for each of these species occurs continuously throughout the summer and early fall (July–November).

We acquired seeds from a variety of commercial and local sources so that each species had multiple source locations. We mixed these seed lots and then sowed seeds in the greenhouse 6 months before out-planting at the experimental site. This is a commonly used restoration practice in desert ecosystems and enhances the likelihood that plants will flower in the first year (e.g.Montalvo & Ellstrand 2014; Schlinkert et al. 2015; Smith et al. 2015).

Experimental Design

The planting design for this experiment consisted of a series of concentric rings around a densely planted central garden (Figs. 1 & 2). Each of the rings was an isolation treatment, within which plots were placed at fixed distances from the central garden. The ring design maximized the distances between treatments within the dimensions of the 2 ha field. Isolation distances between the rings were 1, 8, 13, and 21 m (Fig. 1). The distance between plots within a given ring was greater than the distances between rings. Previous studies that examined foraging by native bees informed these distances (Kunin 1997; Hegland & Boeke 2006; Blaauw & Isaacs 2014; Sardiñas et al. 2016). Bee foraging distance varies according to body size (Greenleaf et al. 2007), and our experimental design is well within the 150-600-m foraging distance recorded for many solitary bees (Gathmann & Tscharntke 2002). Native solitary bees were of particular interest as they are the most abundant pollinator group in arid land systems of Arizona (Minckley & Ascher 2013).

Each isolation ring consisted of eight equidistant replicate plots, each 1 m in diameter. Each plot contained 17 plants: 8 G. pulchella, 2 B. multiradiata, 5 R. columnifera, and 2 S. ambigua. We chose these densities to maximize the number of plants in a given plot and these abundances so that the biomass of each species in the plots was approximately equivalent. The central garden consisted of 27 individual 1-m-diameter plots (each planted in the same densities as were the plots in the isolation rings) placed immediately adjacent to one another (Fig. 2); thus, the diameter of the central garden as a whole was 11 m. Mulch, a cover crop of ryegrass (Lolium sp.) grass, and nonflowering vegetation separated the blocks to create distinct and isolated patches of flowering plants (Genung et al. 2010). We enclosed the plots with wire mesh cages to prevent grazing by wild deer and javelina. We removed the wire cages during observation. Throughout the study, if any weeds had colonized outside the focal plot and within 1 m of it and were in bloom, we removed



Figure 1. Experimental design. Center garden at 0 m consisted of 27 small 1-m plots planted adjacent to each other. Each of the concentric rings contained eight additional small plots, each also 1 m in diameter. The outer plots were spaced from the nearest ring by 1 (ring A), 8 (ring B), 13 (ring C), and 21 (ring D) m, respectively. The distance between replicate plots in a given ring was larger than that between plots in the adjacent rings. In the center garden, plots were nearly adjacent; in the 1-m ring, plots were 4.7 m apart; in the 8-m ring, plots were 11.0 m apart; in the 13-m ring, plots were 21.2 m apart; and in the 21-m ring, plots were 37.7 m apart. Plots were planted with a mixture of commonly used species in habitat restoration projects: Mexican hat (*Ratibida columnifera*), desert marigold (*Baileya multiradiata*), blanket flower (*Gaillardia pulchella*), and desert globemallow (*Sphaeralcea ambigua*). Mulch, cover crop, and nonflowering species separated the habitat patches.

flowers of those weeds before we observed visitors foraging in the plots.

Visitation and Plot Assessment

We sampled the plots for flower visitor activity weekly to biweekly from 4 August to 6 November, 2016. Observers stratified visits to plots in each treatment ring, so that we observed multiple rings at the same time. During each sampling event we recorded the number of floral structures of each species within each plot and the number and taxonomic group of flower visitors interacting with each plant species. We counted floral structures as number of individual open flowers for S. ambigua and number of individual open capitula for the Asteraceae. Each flower visitation observation consisted of a combined scan and focal survey in a 10-minute block (see Aslan et al. 2014). We observed only one plant species per plot at a time. On any given date, we observed a plant species only if it was blooming in all treatment rings. Observations occurred between 9:00 and 17:00 hours, when wind was less than 14 km/hour, and within a temperature range of 17-33°C, as suggested by Ward et al. (2014). We observed each of the focal plant species up to six times at each ring, depending on windspeed and temperature. Observation periods were randomized so that the 10-minute observation blocks occurred throughout the day. Since our goal was to examine the influence of ring isolation and flowering could be a confounding variable, we included only those dates with all plant species blooming in our analysis (16 September, 1 October, 14 October, 28 October, and 6 November). Across these dates combined, we monitored each plant species for 7.5 hours, totaling 30 observation hours during the course of the experiment.

We identified all visitors following citizen science taxonomic resolution protocols and categorized as follows: bees (Hymenoptera) to tribe, subfamily, or genus; butterflies (Lepidoptera) to species; and flies (Diptera) to family (after VanDyk 2013; Ward et al. 2014; Wilson & Messinger Carril 2016; Lotts et al. 2017). Because we were interested in visitation, we did not trap all visitors so as not to interfere with observation data, but accurate identification of bees and flies to the species level is not possible without specimen collection. Identifying visitors to broader taxonomic groups captures broad trends, but this does miss some more specialized and rare visitors (Kremen et al. 2011). At the end of each monitoring session, we calibrated our identification by forming consensus among observers regarding the identity and code used for each visitor for each date; this was done to reduce inter-observer variability in implementing the protocol. In addition, we collected one specimen of each observed visiting taxon after each monitoring date to ensure consistency in data. Insect voucher specimens will be deposited at the Museum of Northern Arizona.

We did not experimentally confirm transfer of pollen from floral visitors to the focal plant species, so for the purpose of this study we refer to known pollinator taxa as floral visitors that moved from flower to flower. If we observed an insect on the inflorescence, but it did not actively move from flower to flower (as was often the case for beetles, which were likely consuming pollen), we did not record it.

Statistical Analysis

To compare flower visitation among treatment rings, we employed generalized linear models in R (version 3.3.1; R Development Core Team 2012) using the *stats* package (R Core Team 2016). We included date, flower species, isolation distance (planting ring), and average number of flowers as predictor variables in the models. We tested each of the following response variables in turn: mean number of flower visitors per 10-minute observation period for each flower species-ring combination; total visitor taxa richness for each flower species-ring combination; and mean number of flower visitors per open flower for each flower species-ring combination.

To explore community composition in relation to each of the flowering species, we calculated visitor commonness values at the resolution of visitor taxon (adapted from Renne et al. 2000; Aslan et al. 2014). Visitor commonness distinguishes between rare and common visits of a given visitor taxon to the focal plant species, such that more common visitors are those that are present more often or visit more flowers of that species when they are present. For each plant species, we



Figure 2. Photos of the experiment at Shield Ranch in central Arizona. The photo on the left shows a portion of the large center garden, containing 27 small 1-m diameter plots. The photo on the right shows the most isolated plot, spaced 21 m from the nearest plot or 43 m from the center garden.

calculated scaled commonness using the following formula: commonness = $[(v^*i^*p)/m] * 100$, where v is the number of visits per minute for each plant-visitor taxon interaction at each ring (from focal survey); *i* is the average number of individuals seen on a plant species when in flower in a ring (from scan survey); *p* is the probability of that given visitor taxon visiting that focal plant; and *m* is minutes. We pooled the results for each visitor taxa-plant combination to calculate overall commonness. We then scaled the product so that the most common visitor had a value of 100, and the remaining visitors became percentages of the most common visitor.

To examine the degree of similarity among flower visitor communities by flower species and by isolation distance (planting ring), we calculated Bray–Curtis dissimilarity indices using the *vegan* package (R Core Team 2016). These calculations provided percent similarity of flower visitor communities among flower species and planting rings. We then used permutational multivariate analysis of variance (PERMANOVA) tests (also performed using the *vegan* package) to determine whether flower visitor communities were significantly different across flower species or planting rings. Environmental variables in the PERMANOVA tests included the average number of flowers, average temperature, and average windspeed recorded during each sampling event.

Results

Isolation Effects on Number of Individuals, Taxa Richness, and Visitation Rate

Contrary to our first hypothesis, the generalized linear models did not detect significant effects of isolation treatments (planting ring) on number of flower visitors per 10-minute observation period; total visitor taxon richness; or average number of flower visitors per open flower. Although the central garden exhibited a higher average number of flowers and number of visitor taxa, there was no clear pattern of declining visitation with increasing distance from the central garden (Table 1). The generalized linear models did detect significant relationships between the average number of open flowers per ring and the number of visitors per observation period (t = 5.23; p < 0.0001) and between the average number of open flowers per ring and total visitor taxon richness (t = 6.41; p < 0.0001).

Flower Visitor Community Composition

We identified 23 total visitor taxa (Table 2) to our experimental plants. A total of 22 visitor taxa were recorded for Ratibida columnifera, 24 for Gaillardia pulchella, 20 for Baileya multiradiata, and 18 for Sphaeralcea ambigua. Visitors were recorded during 67.3% of observation scan samples; remaining scans recorded no visitors (i.e. recorded zeros). Small long-horned bees (Melissodes spp.) were the most common visitor taxa for each of the flowering species. However, each of the flowering species interacted with a unique suite of visitor taxa (including multiple pollinator orders; Fig. 3). Bray-Curtis dissimilarity index values for flower species ranged from 28.18% dissimilarity between R. columnifera and B. multiradiata to 67.90% dissimilarity between G. pulchella and B. multiradiata (Table 3). By planting ring, dissimilarity ranged from 25.22% dissimilarity between rings A and C to 55.18% dissimilarity between ring B and the central garden (Table 3).

The results of the PERMANOVA tests indicated that flower visitor communities were only marginally different between flower species (F = 1.69; p = 0.09), providing only weak support for our second hypothesis. Flower visitor communities did not differ by isolation distance (F = 0.55; p = 0.817). Flower visitor community composition was

Table 1. Flower visitation metrics at each treatment ring across all dates. Number of visitors = average number of visitors per 1-minute scan in each plot.
Visitor taxon richness = total average number of visitor taxa per planting ring. Number of inflorescences = average number of flower heads in each plot.
Visitation rate = average number of visitors per 1-minute scan per open flower per ring. Metrics are averages over all observation dates (±SE).

Ring	Number of Visitors	Visitor Taxon Richness	Number of Inflorescences	Visitation Rate
Center	0.67 ± 0.17	5.00 ± 1.08	8.87 ± 2.12	0.08 ± 0.03
A (1 m)	0.49 ± 0.12	3.90 ± 0.95	4.14 ± 1.20	0.13 ± 0.04
B (8 m)	0.48 ± 0.11	2.95 ± 0.78	3.95 ± 1.25	0.22 ± 0.08
C (13 m)	0.54 ± 0.15	2.85 ± 0.72	4.10 ± 1.58	0.12 ± 0.07
D (21 m)	0.55 ± 0.15	3.45 ± 0.76	5.15 ± 1.33	0.07 ± 0.02

Table 2. L	ist of visitor taxa observed during th	e course of the study.	Taxon was id	entified on w	ing in the field.	Each time a vi	sitor was fi	rst observed, a
specimen w	as taken to the lab to be further identit	ied.						

Common Name	Family	Tribe, Subfamily, or Order	Genus/Species	Note
Hymenoptera				
Green sweat bee	Apidae	Agapostemon		
Longhorn bee (small)	Apidae	Eucerini	Melissodes	body 7-10 mm
Honeybee	Apidae		Apis mellifora	•
Longhorn bee (large)	Apidae	Eucerini	Melissodes	body 13-20 mm
Bumble bee	Apidae		Bombus	
Megachile bee	Megachilidae			
Cuckoo bee	Apidae	Epeolini	Triepeolus	
Sweat bee	Halictidae	Halictus	ĩ	
Metallic bee	Halictidae	Lasioglossum (Dialictus)		
Hairy belly bee	Megachilidae	Lithurginae	Lithurgopsis	
Lepidoptera	e	C		
Pacuvius duskywing	Hesperiidae	Pyrginae	Erynnis pacuvious	
Orange skipperling	Hesperiidae	Hesperiinae	Copaeodes aurantiaca	
Taxiles skipper	Hesperiidae	Hesperiinae	Poanes taxiles	
Cloudless sulfur	Pieridae	Coliadinae	Phoebis sennae	
Fiery skipper	Hesperiidae	Hesperiinae	Hylephila phyleus	
Western pygmy blue	Lycaenidae	Polyommatinae	Brephidium exilis	
Variegated fritillary	Nymphalidae	Heliconiinae	Euptoieta claudia	
White checkered skipper	Hesperiidae	Pyrginae	Pyrgus albescens	
Metalmark	Riodinidae	Riodininae	Calephelis sp.	
Diptera			1 1	
Syrphid fly	Syrphidae	Paragini	Paragus	
Beefly	Bombyliidae	5	0	
Small flies	-			Other small flies

significantly influenced by average temperature (F = 5.66; p = 0.001) and average windspeed (F = 2.34; p = 0.016) during observations.

Discussion

In this observational study in central Arizona, we examined how isolated patches within a single restored pollinator habitat were associated with number of visitors over time, visitor taxon richness, and number of visitors per open flower. We found that small plots of 1-m diameter spaced up to 21 m apart can receive frequent visits by potential flower visitors, at least as long as they are within dispersal distance of a larger floral patch. This implies that such restricted plantings of native flowering plants can attract likely pollinators, even when nested in a matrix of nonflowering vegetation. Although the central garden exhibited the highest average number of open flowers per plot and also the highest average total number of flower visitor taxa, there was no significant effect of isolation distance on any metric of flower visitation. Only the total number of flowers available in a plot was a significant predictor of number and richness of flower visitors. This finding complements other studies of habitat effects on visitation rate. Visitation rate has been shown to increase as abundance and richness of flowers increases (Carvalheiro et al. 2014; Ogilvie & Thomson 2016), and as density and richness of flowers increase with patch sizes at scales of $30-100 \text{ m}^2$ (Blaauw & Isaacs 2014) (the floral patches in this study were $1-95 \text{ m}^2$).

Plant species choice is an important consideration for pollinator management. This is particularly true in arid environments, where plant establishment can be challenging (Banerjee et al. 2006), and it is costly to purchase native forbs for plantings. In our study, although the four flowering species produce open, accessible, symmetrical flowers and three of these were in the family Asteraceae and thus produce composite flowers,



Figure 3. A graph showing the most common visitor taxa for each of the focal plant species. Commonness is a calculated mean visitation rate (number of visitors per minute) given the amount of pollinator taxa present at a site during the study period. The results are scaled so that the taxon that visited the flowering species most often was given a commonness value of 100, and subsequent taxa are some proportion thereof. Taxa shown here had commonness values of 10% or greater for each of the focal plant species, and the commonness number is listed beneath the name of each taxon.

Table 3. Percent dissimilarity in flower visitor community, by Bray–Curtis dissimilarity index. Planting rings were as follows: Center = central garden, A = 1-m planting distance from central ring, B = 8-m planting distance from ring A, C = 13-m planting distance from ring B, D = 21-m planting distance from ring C. Flower species were: GP = Gaillardia pulchella, BM = Baileya multiradiata, RC = Ratibida columnifera, SA = Sphaeralcea ambigua.

Planting Ring					
	Center	A (%)	B (%)	C (%)	D (%)
Center	_	41.84	55.18	44.00	39.41
А		_	30.61	25.22	28.27
В	_	_	_	40.22	34.67
С		_	_		30.67
D		—	_		
Flower species	;				
Flower species	GP	BM (%)	RC (%)	SA	A (%)
Flower species	GP —	BM (%) 67.90	RC (%) 58.54	SA 6	A (%) 2.98
Flower species GP BM	GP — —	BM (%) 67.90	RC (%) 58.54 28.18	SA 6: 3	x (%) 2.98 7.06
GP BM RC	GP — — —	BM (%) 67.90 	RC (%) 58.54 28.18	SA 6: 3: 3:	x (%) 2.98 7.06 4.20

the flowers do vary in size and color. Flower visitor community dissimilarity between these flower species ranged from 28.18 to 67.90%. There were only marginally significant differences between these communities, perhaps in part because the small longhorn bee dominated the visitor community for all four plants. However, the plant species differed in their subordinate visitor species (Fig. 3). Previous research has demonstrated that

species-rich pollinator communities are important because they are better able to respond to changing flowering phenology and plant species composition over time (Ferreira et al. 2013), they can reduce pollen limitation (Samnegård et al. 2011; Williams & Winfree 2012; Kennedy et al. 2013), and they can increase persistence of the pollinator community (Winfree et al. 2014). Our experiment was in line with the Xerces Society's goal of four to seven species in bloom at any given time for quality habitats (Vaughan et al. 2007; Lee-Mäder et al. 2013), and we recorded visitation by a total of 14 taxa over the course of flowering by those species.

To ensure that restored pollinator habitats provide adequate forage and persist over time, a restoration design must incorporate strategies that boost persistence of installed plant materials. These strategies could include use of greenhouse-grown plants installed at the restoration site (e.g. Bean et al. 2004; Abella et al. 2012), creating favorable microsites, increasing soil moisture, increasing seeding rate, and protecting plants from herbivory (Hulvey et al. 2017). Using floral patches such as in this experiment may reduce the amount of effort needed to prepare and maintain plantings and thus represent a strategy enabling managers to distribute limited pollinator resources across a broad landscape. If these plantings survive and reproduce, pollinator-friendly plants may spread across the landscape from each of these original foci. However, this process is likely to be most tenuous at the beginning: the small initial plantings may help to meet the needs of pollinators only if the patches are large enough that plants are able to establish, persist, and spread in an environment with harsh abiotic conditions (e.g. aridity or cold seasonality; Hulvey et al. 2017). Under ideal circumstances, this establishment and spread would occur without further assistance from managers, who face perennially limited time and money to invest in planting and maintenance.

Although the isolated flower patches in this experiment received flower visitation commensurate with their available flowers, they also contained fewer open flowers over the course of the experiment than did the large central garden. This occurred although the isolated patches and garden were initially planted with equal densities of experimental plants. Although we did not experimentally test possible sources of reduced flowering in the isolated patches, we speculate that edge effects may have affected plant performance. In particular, plants within each 1-m² isolation patch were in close proximity to herbivory cages (which were removed regularly for observation, representing potential physical disturbance) and the nonflowering matrix vegetation, which was short in stature and thus provided no windbreak or sun protection during the hottest and driest periods of the experiment. The matrix was also disturbed by removal of flowering weeds throughout the study. By contrast, the large majority of plants in the central garden were adjacent to other tall, flowering forbs and thus likely somewhat protected from disturbance, wind, and full sun. Our PERMANOVA results indicated that flower visitor community composition was significantly affected by windspeeds and temperature, which provides some evidence for the importance of abiotic environmental conditions in this study.

In spite of edge effects in this experiment, the $1-m^2$ plantings were large enough to produce flowers throughout the experiment and to attract flower visitors. We can therefore suggest that isolated plantings of this size could be used to "seed" a landscape with pollinator-friendly species, even if edge effects reduce total flower production. Edge effects might be decreased with the use of slightly larger patches, windbreaks, light shading, or supplemental watering, all of which could result in more hospitable abiotic conditions.

Landscape context also affects habitat for pollinators. In a meta-analysis of agroecosystems, Kennedy et al. (2013) discovered that visitors decrease foraging distance if the local habitat has diverse and abundant floral resources, but visitors increasingly rely on the broader landscape if the local habitat quality is poor (e.g. a monoculture of crops). Negative effects of fragmentation and habitat quality are compounded if nested within a larger degraded landscape, because pollinators may expend more energy per unit energy gained by foraging (Winfree et al. 2009; Kennedy et al. 2013). As a result, broadcast seeding with low or patchy plant establishment may not sufficiently support bees with small foraging distances, especially if the surrounding landscape is degraded or has gaps in seasonal forage availability, abundance, and/or richness, as occurred in our project site. In our experiment, it may have been crucial that the central garden was large enough to attract and sustain flower visitors and was also close enough to the smaller, isolated plantings that visitors could traverse between them. In restoration efforts employing small flowering patches, it is important to determine whether suitable habitat and pollinator forage materials occur near the restoration site and may thus supply pollinators to the new plantings. If not, installation of one or a few larger gardens could be an important additional component of a successful project. It is also important to consider that visitation in this system was dominated by a single taxonomic group (the small longhorn bee). The presence of such generalists, which may compensate for reductions in specialist pollinators, may be particularly important in such fragmented habitats (Xiao et al. 2016).

Implications for Future Research

Missing from this experiment was exploration of arrangement and size of "small" and "large" habitats. It may be that there is an ideal ratio of large to small habitat patches per area, and this would be useful for planning and design. There may also be an intermediate patch size and a target number of plant species that would better support pollinators and maximize the efficiency of resource expenditures for managers working across hundreds of acres.

This study is relevant to lower-elevation arid ecosystems where native bees comprise the majority of the pollinator community, and to ecosystems where broadcast seeding is less effective than direct planting. Our findings support the use of direct planting to ensure that plants are able to establish and flower in arid conditions. Such plantings are time- and work-intensive, requiring prior cultivation of seedlings as well as soil preparation and watering during and after transplant to enable establishment. Restoration resources can be targeted at small patches scattered across a site, ideally with one or a few larger source gardens, with no need to add flowering plants across the full matrix. Initial plantings should include diverse species with flowers of different shapes and sizes as well as blooming phenology spanning a wide time period, to ensure that the site contains diverse and long-lasting resources for pollinators. Different pollinator communities, like those in more mesic or higher-elevation locations, may require different approaches. In other studies, restoration planting isolation has been found to influence restoration success in grasslands, where, e.g. connectivity of habitat across the landscape was an important predictor of bee diversity (Winsa et al. 2017) and proximity to biodiverse habitat a predictor of both pollinator and forb diversity (Kohler et al. 2008; Helsen et al. 2013). In subtropical South Africa, pollination services for mango *Mangifera indica* declined with distance from natural areas (Carvalheiro et al. 2010). The importance of discrete patches of pollinator habitat within a landscape has also been examined in other contexts, but generally with larger patches than in our study. In agricultural areas

with larger patches than in our study. In agricultural areas, e.g. hedgerows of native plants boosted regional biodiversity across farmed sites in California (Morandin & Kremen 2013; Ponisio et al. 2016). Maintenance or reforestation of forested parcels interspersed with agricultural parcels in tropical Costa Rica enhanced pollinator communities, exhibiting a patch effect similar to ours but with patches much larger in scale (>20 ha) (Ricketts & Lonsdorf 2013). Understanding how the influences of patch size and isolation may vary under different temperature, precipitation, and regional biodiversity conditions will be important for guiding restoration across various habitat types in the future. There will be many opportunities to pursue these questions as the desire to support pollinators continues, and if land managers and scientists collaborate on pollinator restoration projects.

Acknowledgments

The authors would like to thank Thomas Whitham for advice on the project and editing the manuscript, Anabeth Avila Arenas, Dylan Ward, Peter Malmgren, and Sharon Marmaduke who helped install plots and collect data, Partners for Fish and Wildlife program and Friends of the Verde River who provided funding (USFWS grant number F13 AC00336), The Nature Conservancy who provided the project site, Lindsie McCabe for help identifying bees, Rob Hannawacker for help identifying butterflies, and the 100 volunteers who helped create and maintain the habitat in support of pollinators with this project.

LITERATURE CITED

- Abella SR, Craig DJ, Suazo AA (2012) Outplanting but not seeding establishes native desert perennials. Native Plants Journal 13:81–89
- Adamson NL, Borders B, Cruz JK, Jordan SF, Gill K, Goldenetz-Dollar J, et al. (2015) Pollinator habitat assessment form and guide: farms and agricultural landscapes. The Xerces Society for Invertebrate Conservation, Portland, Oregon
- Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, Cane J, et al. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of fruit crop yields. Conservation Biology 12:8–17
- Aslan CE, Zavaleta ES, Tershy B, Croll D, Robichaux RH (2014) Imperfect replacement of native species by non-native species as pollinators of endemic Hawaiian plants. Conservation Biology 28(2):478–488
- Bainbridge DA (2007) A guide for desert and dryland restoration: new hope for arid lands. Society for Ecological Restoration International, Washington D.C.

- Banerjee MJ, Gerhart VJ, Glenn EP (2006) Native plant regeneration on abandoned desert farmland: effects of irrigation, soil preparation, and amendments on seedling establishment. Restoration Ecology 14:339–348
- Bean TM, Smith SE, Karpisacak MM (2004) Intensive revegetation in Arizona's hot desert: the advantages of container stock. Native Plants Journal 5:173–180
- Blaauw BR, Isaacs R (2014) Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. Basic and Applied Ecology 15:701–711
- Carvalheiro LG, Seymour CL, Veldtman R, Nicolson SW (2010) Pollination services decline with distance from natural habitat even in biodiversity-rich areas. Journal of Applied Ecology 47:810–820
- Carvalheiro LG, Biesmeijer JC, Benadi G, Fründ J, Stang M, Bartomeus I, et al. (2014) The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. Ecology Letters 17:1389–1399
- Clark C, Cole E, Rankin D, Adams LD (eds) (2017) Maintaining and improving habitat for hummingbirds in California: a land manager's guide. U.S. Forest Service, Washington D.C.
- Ferreira PA, Boscolo D, Viana BF (2013) What do we know about the effects of landscape changes on plant-pollinator interaction networks? Ecological Indicators 31:35–40
- Gathmann A, Tscharntke T (2002) Foraging ranges of solitary bees. Journal of Animal Ecology 71:757–764
- Genung MA, Lessard JP, Brown CB, Bunn WA, Cregger MA, Reynolds WN, et al. (2010) Non-additive effects of genotypic diversity increase floral abundance and abundance of floral visitors. PLoS One 5:e8711
- Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589–596
- Havens K, Vitt P, Still S, Kramer AT, Fant JB, Schatz K (2015) Seed sourcing for restoration in an era of climate change. Natural Areas Journal 35:122–133
- Hegland S, Boeke L (2006) Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. Ecological Entomology 31:532–538
- Helsen K, Hermy M, Honnay O (2013) Spatial isolation slows down directional plant functional group assembly in restored semi-natural grasslands. Journal of Applied Ecology 50:404–413
- Hulvey KB, Leger EA, Porensky LM, Roche LM, Veblen KE, Fund A, Shaw J, Gornish ES (2017) Restoration islands: a tool for efficiently restoring dryland ecosystems? Restoration Ecology 25:124–134
- Jankju M (2013) Role of nurse shrubs in restoration of an arid rangeland: effects of microclimate on grass establishment. Journal of Arid Environments 89:103–109
- Kaiser-Bunbury CN, Mougal J, Whitington AE, Valentin T, Gabriel R, Olesen JM, Blüthgen N (2017) Ecosystem restoration strengthens pollination network resilience and function. Nature 542:223–227
- Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics 29:83–112
- Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, et al. (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecology Letters 16:584–599
- Klein AM, Vaissièrre BE, Cane JH, Steffan-Dewenter I, Cunnigham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences 274:303–313
- Kohler F, Verhulst J, Van Klink R, Kleijn D (2008) At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? Journal of Applied Ecology 45:753–762
- Kremen C, Ullmann KS, Thorp RW (2011) Evaluating the quality of citizen science data on pollinator communities. Conservation Biology 25:607–617
- Kunin WE (1997) Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of Brassica kaber. Journal of Ecology 85:225–234

- Lee-Mäder E, Borders B, Minnerath A (2013) Establishing pollinator meadows from seed. The Xerces Society for Invertebrate Conservation, Portland, Oregon
- Lotts K, Naberhaus T (coordinators) (2017) Butterflies and moths of North America. Version 01/19/2018. http://www.butterfliesandmoths.org/
- Lotts K, Naberhaus T, et al. (2017) Butterflies and moths of North America. Version 0/19/2018. http://www.butterfliesandmoths.org/
- Minckley RL, Ascher JS (2013) Preliminary survey of bee (hymenoptera: Anthophila) richness in the northwestern Chihuahuan Desert. Pages 138–143. In: USDA Forest Service Proceedings RMRS-P-36, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Coloraco
- Montalvo AM, Ellstrand NC (2014) Transplantation of the subshrub Lotus scoparius: testing the home-site advantage hypothesis. Conservation Biology 14:1034–1045
- Morandin LA, Kremen C (2013) Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecological Applications 23:829–839
- National Resource Conservation Service, The Xerces Society (2012) Plants for enhancing pollinator habitat in Arizona. U.S. Department of Agriculture, NRCS Technical Note, Plant Materials 12-1-Arizona, Tucson, Arizona
- Ogilvie JE, Thomson JD (2016) Site fidelity by bees drives pollination facilitation in sequentially blooming plant species. Ecology 97:1442-1451
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120:321–326
- Pollinator Health Task Force (2015) Pollinator research action plan. The White House, Washington D.C.
- Ponisio LC, M'gonigle LK, Kremen C (2016) On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. Global Change Biology 22:704–715
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25:345–353
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www/Rproject.org/
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Renne IJ, Gauthreaux SA, Gresham CA (2000) Seed dispersal of the Chinese tallow tree (*Sapium sebiferum* [L.] Roxb.) by birds in coastal South Carolina. The American Midland Naturalist 144:202–215
- Ricketts TH, Lonsdorf E (2013) Mapping the margin: comparing marginal values of tropical forest remnants for pollination services. Ecological Applications 23:1113–1123
- Samnegård U, Persson AS, Smith HG (2011) Gardens benefit bees and enhance pollination in intensively managed farmland. Biological Conservation 144:2602–2606

- Sardiñas HS, Tom K, Ponisio LC, Rominger A, Kremen C (2016) Sunflower (*Helianthus annuus*) pollination in California's Central Valley is limited by native bee nest site location. Ecological Applications 26: 438–447
- Schlinkert H, Westphal C, Clough Y, Lászió Z, Ludwig M, Tscharntke T (2015) Plant size as determinant of species richness of herbivores, natural enemies and pollinators across 21 Brassicaceae species. PLoS One 10:1–18
- Smith DS, Lau MK, Jacobs R, Monroy J, Shuster SM, Whitham TG (2015) Rapid plant evolution in the presence of an introduced species alters community composition. Oecologia 179:563–572
- Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: a mini review. Ecological Research 17:229–239
- Turner D, Marshall R, Enquist C, Gondor A, Gori D, Lopez E, Luna G, Aguilar RP, Watts C, Schwartz S (2005) Conservation priorities in the apache highlands ecoregion. Pages 375–379. In: USDA Forest Service Proceedings RMRS-P-36. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado
- Tylianakis JM (2013) The global plight of pollinators. Science 339: 1532-1533
- VanDyk J (editor) (2013). BugGuide, http://www.BugGuide.net (accessed 25 Nov 2018).
- Vaughan M, Hopwood J, Lee-Mäder E, Shepherd M, Kremen C, Stine A, Hoffman Black S (2007) Farming for bees: guidelines for providing native bee habitat on farms. The Xerces Society for Invertebrate Conservation, Portland, Oregon
- Ward K, Cariveau D, May E, Vaughan M, Williams N, Winfree R, Isaacs KG (2014) Streamlined bee monitoring protocol for assessing pollinator habitat. The Xerces Society, Portland, Oregon
- Williams NM, Winfree R (2012) Local habitat characteristics but not landscape urbanization drive pollinator visitation and native plant pollination in forest remnants. Biological Conservation 160:10–18
- Wilson JS, Messinger Carril O (2016) The bees in your backyard, a guide to North America's bees. Princeton University Press, Princeton, New Jersey
- Winfree R, Aguilar R, Vazquez DP, LeBuhn G, Aizen MA (2009) A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068–2076
- Winfree R, Williams NM, Dushoff J, Kremen C (2014) Species abundance, not diet breadth, drives the persistence of the most linked pollinators as plant-pollinator networks disassemble. The American Naturalist 183:600–611
- Winsa M, Öckinger E, Bommarco R, Lindborg R, Roberts SP, Wärnsberg J, Bartomeus I (2017) Sustained functional composition of pollinators in restored pastures despite slow functional restoration of plants. Ecology and Evolution 7:836–3846
- Xiao Y, Li X, Cao Y, Dong M (2016) The diverse effects of habitat fragmentation on plant–pollinator interactions. Plant Ecology 217:857–868

Coordinating Editor: Valter Amaral

Received: 27 November, 2018; First decision: 8 June, 2019; Revised: 7 June, 2019; Accepted: 10 February, 2019; First published online: 28 July, 2019