Biological Conservation 202 (2016) 110–118

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Comparing diversity to flower-bee interaction networks reveals unsuccessful foraging of native bees in disturbed habitats

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A R T I C L E I N F O

Article history:
Received 30 December 2015
Received in revised form 22 July 2016
Accepted 23 August 2016
Available online xxxx

Keywords:
Bipartite network
Community diversity
Ecological trap
Floral diversity
Land management
Plant-pollinator interactions

A B S T R A C T

As land is converted to agriculture (e.g., pastures), natural vegetation is repeatedly disturbed, creating various levels of habitat alteration in which flowering plants and pollinators (e.g., bees) interact. Community structure of flowering plants, bees, and flower-bee interactions may each respond to disturbance, but potentially in different ways or magnitudes. We studied flowering plants, bees, and their interactions across four mechanical disturbance levels in and near Archbold Biological Station, Florida (USA) for one year, using repeated sampling with standard techniques in replicated plots. Data were analyzed for community structure, flower-bee interactions and bipartite network structure. Over 7500 flowering plants (81 species) and almost 5000 bees (48 species) were sampled, representing >80% of estimated species richness. Disturbance altered available flower diversity and both shifted and simplified compositions of floral and bee communities. Importantly, the number of foraging bee species did not decrease with disturbance but fewer bee species interacted with flowers given greater disturbance, indicating that disturbance reduced successful foraging. Interaction networks became simpler with disturbance, and the non-native European honey bee (*Apis mellifera*) became more dominant as disturbance intensity increased. Flower-bee interactions were most sensitive to disturbance. For some native bees, anthropogenic disturbance may contribute to ecological trap conditions and drive long-term diversity patterns. Attention to interaction networks will help land managers identify plant species to conserve and restore flowering plants that are vital to native pollinator communities.

1. Introduction

Among factors affecting terrestrial ecological communities, human land management is globally pervasive and dominates at local and regional scales (Foley et al., 2005). Land management disturbs natural vegetation to suit human purposes, and biotic diversity is typically reduced from natural to managed systems (Marrero et al., 2014; Murphy and Romanuk, 2014; Valiente-Banuet et al., 2015). Compared to natural lands, managed lands (e.g., managed forests, agricultural lands) have altered plant composition and diversity and contribute to fragmentation of habitat (Foster et al., 2003; Fischer and Lindenmayer, 2007).

Land management includes practices such as logging and conversion of natural vegetation to agriculture. Here we focus on mechanical disturbance as a type of disturbance, specifically roller chopping. Roller-chopping is a common practice, in which large machinery breaks and crushes vegetation (Menges and Gordon, 2010). Conservation lands may also require mechanical disturbance, such as when fire-suppressed scrub vegetation is roller chopped once to reduce fuel loads before beginning a prescribed fire regime (Menges and Gordon, 2010). More intensive land management may include repeated roller chopping, clearing of woody debris, and seeding with grasses to convert natural vegetation to pasture (Boughton et al., 2010). Secondary succession may temporarily increase vegetation diversity and abundance in recently disturbed areas, but repeated and more intensive disturbance ultimately simplifies plant communities.

Pollinators also inhabit natural and managed lands and interact with flowering plants there. Pollinators (here we focus on bees) may be directly affected by land management (e.g., nest disruption) and/or indirectly by their interactions with flowering plants (Foley et al., 2005; Kremen et al., 2007; Winfree et al., 2009, 2011). Many people are most familiar with honey bees (*Apis mellifera* Linnaeus, 1758) because they are a widespread, generalist pollinator important to agriculture. While they contribute greatly to pollination, honey bees are not native to the US (Moritz et al., 2005). On the other hand, many native bee species are coevolved mutualists with native flowers, are often more specialized than honey bees, and can be diverse in natural lands and susceptible to land management (Wcislo and Cane, 1996; Schlaepfer et al., 2002; Fortuna and Bascompte, 2006; Greenleaf et al., 2007; Winfree et al., 2011). Also, honey bees are eusocial, whereas most native bees are solitary breeders, substantially smaller in body size, but often numerous and diverse (Batra, 1984). Smaller, solitary bees are more

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http://dx.doi.org/10.1016/j.biocon.2016.08.030

likely to nest near floral resources (Wcislo and Cane, 1996) and forage over shorter distances than larger bees (Greenleaf et al., 2007). As a result, native bee communities composed mostly of small, solitary species should be sensitive to land management that disturbs floral resources and habitat over large areas. Unfortunately, responses of flower-bee interactions and community compositional responses to land-use change are not sufficiently known (Winfree et al., 2011).

Bees may forage in managed lands (and thus contribute to observed pollinator diversity) but actually interact less with flowers when compared to undisturbed lands if flower composition has changed. If so, then bees should be expending substantial time and energy for this unsuccessful foraging without reward (e.g., pollen and nectar). This hypothesis - that vegetation disturbance by anthropogenic land management causes unsuccessful foraging by bees - is consistent with an ecological trap, which occurs when organisms choose to utilize altered habitat (that may have once been suitable) without success (Schlaepfer et al., 2002). To be clear, demonstrating fitness costs (i.e., survival and reproduction) would be a more complete demonstration of an ecological trap. Here we merely tested for general evidence of unsuccessful foraging among bee species given different levels of disturbance in managed lands, consistent with the need for more detailed research on native pollinators in anthropogenic habitats (Winfree et al., 2011).

Specifically, we hypothesized that vegetation changes may cause bees to respond in three ways, only one if which is consistent with an ecological trap (Fig. 1). First, bees closely co-evolved with flowering plants may track vegetation in both diversity and interactions (Fig. 1a) because they actively depend on specific floral resources (Kearns et al., 1998; Deyrup et al., 2002; Lennartsson, 2002; Van der Putten et al., 2004; Fontaine et al., 2005). If this is the case, we would expect to see declines in foraging *and* interacting bees with reduced flowering plant diversity (Fig. 1a). Alternatively, most foraging bees may act as generalists and forage at spatial scales beyond local vegetation disturbance, so that bee diversity and interactions are robust to local disturbance (Memmott et al., 2004; Fortuna and Bascompte, 2006; Nielsen and Totland, 2014). In that case (Fig. 1b), diversity of both foraging and interacting bees should change little with vegetation disturbance and bees should continue to interact with various flowering plants across disturbance regimes. Finally we hypothesized that most bees may forage unsuccessfully in disturbed lands because available flowers do not match coevolved adaptations (Fig. 1c), consistent with an ecological trap (Schlaepfer et al., 2002; Winfree et al., 2009). In that case, bees should be observed in the disturbed habitats but should not interact with flowers as often as in less-disturbed habitats.

To evaluate the above hypotheses (Fig. 1), we estimated diversity of available flowers and foraging bees as well as plant-bee interactions. We used bipartite networks to analyze interactions, where network complexity should contribute to ecosystem stability (Bascompte and Jordano, 2007). In principle, interaction networks in conservation lands should be more complex, whereas those in disturbed habitats should be simpler and more dominated by generalists, reflecting reduced diversity of each community (Moreira et al., 2015). We evaluated the hypotheses (Fig. 1) for a year in four habitats managed differently but located <8.5 km of each other. Disturbance levels studied here ranged from reference conditions to pastures; more extreme disturbance levels (e.g., row crops, suburban and urban areas, industrial lands) that may also contribute to expectations (Fig. 1) were not included here. In effect, this study evaluated relatively low-level disturbance effects on floral and bee diversity and their interactions.

We expected that regional bees may access all habitats throughout the year, though distance between habitats may exceed forage distances of individual bees (Zurbuchen et al., 2010). We predicted flowering plant communities would be affected by disturbance. We also expected a diverse bee community with various seasonal foraging and interaction behaviors, and thus a mixture of species' responses. We also anticipated annual, cumulative effects would be important to bees that forage through seasonal flowering events (Kremen et al., 2007). We therefore examined and compared both detailed (i.e., repeated measures analyses) and cumulative (e.g., annual richness) responses of flowers and bees to disturbance. We also expected native bees co-evolved with native flowers to more often demonstrate effects of land-use management than the non-native, generalist *A. mellifera*, which we predicted to be relatively insensitive to vegetation disturbance. The comparative approach used here (detailed and cumulative diversity and flower-bee networks) attempts to provide a more complete view of plant-pollinator responses to disturbance in our study system. This approach should be applicable in other study systems and help to inform conservation and restoration of community diversity and network structure.

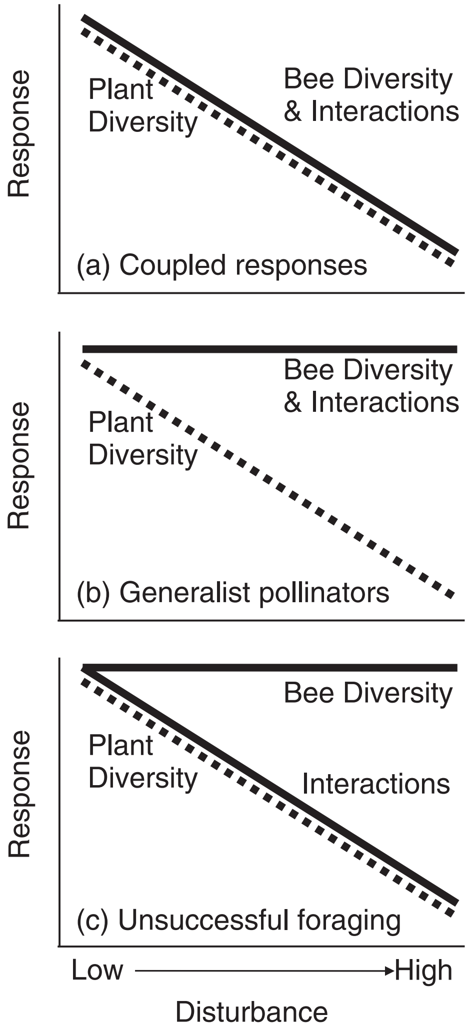

Fig. 1. Alternative hypotheses for the responses of plant and bee diversity (e.g., species richness) and plant-bee interactions to increasing levels of disturbance. Actual trends may differ from simple straight lines; relative positions among trends are most important. (a) Bees track vegetation responses in both diversity and interactions due to specialized, co-evolved foraging and feeding behaviors. (b) Bees are robust to local change in available flowers because they are mobile generalists. (c) Bee diversity does not track local disturbance of available flowers because bees continue to forage over disturbed habitats while flower-bee interactions are reduced with disturbance, indicating unsuccessful foraging.

2. Materials and methods

2.1. Study sites and sampling

This study was conducted in current and former scrub habitats on the Lake Wales Ridge of Florida (USA), which is a series of Pleistocene sand islands extending ~240 km along the center of the Florida peninsula. Scrub vegetation tends to be rich in flowering plants and is dominated by xeromorphic and fire-adapted shrubs and dwarf oaks (e.g., *Ceratiola ericoides* Michx., *Sabal etonia* Swingle ex Nash and *Quercus* spp.) and forbs (e.g., *Liatris* spp., *Polygonella* spp. and *Stipulicida setacea* Michx.). The sandy soils are nutrient-poor. The subtropical wet/dry seasonality plus sandy soils foster edaphic desert-like conditions in the dry season, despite heavy rains in the wet season (Myers and Ewel, 1990). Florida scrub vegetation is fire-adapted because lightning historically caused wildfires before fire suppression efforts (Abrahamson, 1984). The antiquity of the Lake Wales Ridge and its stringent environmental conditions have led to multiple endemic species, some of which are threatened or endangered (e.g., Evans et al. 2003 & 2004).

Study habitats were located in Archbold Biological Station (ABS) and adjacent lands (the Reserve and the McJunkin tract; Fig. A1). Archbold Biological Station consists of 2101 ha of pyrogenic scrub and pine flatwoods managed for conservation-related research since 1941 (Abrahamson et al., 1984). The Archbold Reserve is 1476 ha of land with remnant scrub and flatwood habitats immediately adjacent to ABS. Portions of the Reserve also include active cattle pastures which include exotic grass species (e.g., bahia grass (*Paspalum notatum* Flueggé), natal grass [*Melinis repens* (Willd.) Zizka]), but that also include flowering plants attractive to bees (i.e., pastures were not grass monocultures; Fig. A1, Table A.1). The Reserve has a varied history and spatial pattern of vegetation disturbance, including roller-chopped areas and heavily altered pasture lands. The McJunkin Tract (296 ha) is adjacent to ABS and had been roller-chopped repeatedly, and grazed by cattle until it was purchased in 2002 by the Florida Fish and Wildlife Conservation Commission (FFWCC).

In order of increasing disturbance, four disturbance categories in the three adjacent properties were: reference scrub, habitats roller-chopped once, habitats roller-chopped multiple times, and pastures. Reference scrub habitats (hereafter "reference" sites) were all located within ABS and had not received mechanical disturbance but had been burned based on recommended prescribed fire return intervals (Menges, 2007). Habitats roller-chopped once (hereafter "single" sites) were located in former scrub of the Archbold Reserve, adjacent to ABS. Habitats roller-chopped multiple times (hereafter "multi" sites) were located in the McJunkin Tract. Finally, pastures (also in the Archbold Reserve) had been repeatedly roller-chopped, cleared of woody debris, mowed, seeded with grass and formerly grazed. Distance between sites ranged from 0.2 km to 8.5 km (Fig. A1). Because actual historical land use (e.g., cattle ranching and conservation) cannot be arranged in an experimentally-ideal randomized grid, we handled potential effects of spatial autocorrelation among sites in analyses (described further in Section 2.2 below).

Four 100-m diameter plots with similar elevation and soil type were established in each of the four disturbance levels (16 total plots). Plots were selected randomly from a set of 28 possible sites (the use of 16 plots was sufficient based on preliminary power analyses). Plots were sampled in random order for four types of samples: flowering plants, foraging bees, interacting flowers, and interacting bees. Flowering plants (excluding grasses) were surveyed monthly from March 2013 through February 2014. Plants currently flowering (excluding grasses) and rooted within two 50 m × 2 m transects in each plot were recorded for species richness and abundance. Transects within plots incorporated habitat patchiness, a characteristic of Florida scrub, and were aligned on random compass directions from plot centers. Of course, flowering plants were not always in bloom in every plot during the course of this one-year study; multiple plots per disturbance category meant that each disturbance level had flowering plants each month (Table A.1). Plants were identified in the field using Taylor (1992).

Foraging bees were sampled in each plot using colored pan traps (blue, white, and yellow painted bowls filled with soapy water) and placed along transects in clear view (Droege, 2008). Pan traps very effectively capture many bees and other organisms, though some larger bees may escape (Droege, 2008). Pan trap sampling was constrained to seasonal collections (rather than monthly) to reduce mortality via sampling for potentially vulnerable populations. Thirty pan traps per plot were deployed for 24 h on days with optimal bee foraging weather (Droege, 2008). Bees were identified to species with a stereo microscope using Mitchell (1960) and Mitchell (1962), with identification verified by Stuart Fullerton (University of Central Florida) and/or compared to the Archbold Arthropod Collection, curated by Mark Deyrup (Archbold Biological Station). Voucher specimens are stored in the University of Central Florida Collection of Arthropods.

Interacting bees and flowers were sampled monthly along transects in each plot. Transects were scanned for flower-visiting bees for 20 min (using a stopwatch) in every site, excluding sample capture and handling time (Morandin and Kremen, 2012). If a site did not contain flowering plants during a sampling period, no bees were netted for interaction data. If few flowering plants were located along transects during sampling, the 20 min survey period was evenly distributed between available flowers. Bees observed visiting reproductive flower parts were collected with aerial nets. Interacting plant species were also recorded, and bees were identified as above. When monthly netting coincided with seasonal pan trapping, netting and trapping were scheduled a day apart to avoid collection bias.

2.2. Statistical analyses

Data were analyzed in four ways. Detailed data for bees and flowers (repeated measures) were analyzed with generalized linear mixed effects models. Cumulative (annual) data were analyzed by rarefaction (with boostrap randomization for confidence intervals) and by multivariate analyses. Finally, cumulative flower-bee interactions were analyzed as a bipartite network. The four sets of analyses complemented each other to fully reveal complex disturbance effects on plant and bee communities.

Monthly data for total abundance, species richness, and diversity (i.e., effective species richness; Jost, 2006) of flowers and bees were response variables in mixed effects models, where anthropogenic disturbance categories were fixed predictor variables. These analyses were conducted for four data sets: available flowers, interacting flowers, foraging bees, and interacting bees to result in 12 analyses (three metrics × four data sets). For each of the above 12 models, alternative distributions (i.e., Gaussian, Poisson, or negative binomial distributions) were evaluated, because we expected distributions to vary according to variables but tested that assumption. Finally, mixed effects models included time, spatial autocorrelation, or both time and space among plots as random intercept terms. Spatial autocorrelation was calculated using the *spdep* package in R (Bivand and Piras, 2015). Specifically, we used autocovariate regression (with neighborhood = 15 to evaluate all sample plots) because this method is appropriate for non-normal error distributions observed here for some analyses while other methods (e.g., simultaneous autoregressive models) require normal error distributions (Dormann et al., 2007). Temporal and spatial autocorrelation were included or excluded as random effects in alternative models to quantitatively test expectations of temporal autocorrelation in the year-long study and spatial autocorrelation among sites. Mixed effects models were computed using *glmmADMB* (Fournier et al., 2012) in R 3.1.2 (R Core Team, 2014). Alternative models (i.e., using alternative distributions and random effects) were compared using AICc weights (w_i; Burnham and Anderson, 2002), where we considered an evidence ratio ≥ 2 (i.e., $w_i \geq 2\, w_j$) to identify the most plausible model, using the *bbmle* package in R (Bolker, 2015) (Table A.2).

Cumulative species richness and composition were evaluated for flowering plants, passively-trapped bees, interacting flowering plants, and interacting bees in each management category to represent annual patterns. Cumulative species richness was estimated with rarefaction (Gotelli and Colwell, 2001), using *rich* in R (Rossi, 2011). Rarefaction used randomization (1000 iterations) with replacement so that estimated cumulative richness could be statistically compared with 95% confidence intervals. Cumulative composition (i.e., total annual species' abundances per plot) was evaluated with permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis distances and using adonis in the *vegan* package of R (Oksanen et al., 2015), with 9999 permutations. Nonmetric multidimensional scaling (NMDS) ordinations using Euclidean distances also helped visualize compositional outcomes. Because PERMANOVA and NMDS cannot readily account for spatial autocorrelation, spatial effects were not included in these analyses of cumulative patterns. Annual patterns in habitat-use were also informed by indicator species analysis, using the *labdsv* package (Roberts, 2015) (Table A.1). Indicator species are those that significantly correspond in their abundances to habitats (here disturbance levels). We also noted patterns among disturbance categories for listed (i.e., endangered or threatened according to FFWCC) plant species and non-native plant species (Table A.1).

Finally, cumulative flower-bee interactions among disturbance levels were analyzed as bipartite networks, using the *bipartite* package in R (Dormann et al., 2008). A bipartite network displays members of a trophic level (e.g., flowers) connected to members from another trophic level (e.g., bees). All flower-bee interactions recorded throughout the year were pooled per disturbance level for bipartite analyses. Network metrics (specialization, nestedness, and asymmetry; Dormann et al., 2008) were computed for each disturbance category with and without the non-native *A. mellifera* to evaluate its effects on results, given its dominance (Fig. A2). Network specialization scores the amount of specialist interactions in a network. Nestedness scores the degree to which specialist interactions are subsets of generalist interactions. Interaction strength asymmetry indicates the interdependence of the trophic levels (Dormann et al., 2008). Though useful and illustrative of details, network analyses may be sensitive to network size, rare species, and sampling intensity (Dormann et al., 2009). Thus we considered network analyses here as informative but secondary for inference compared to other analyses (above).

3. Results

A total of 7566 flowering plants (81 species, excluding grasses) and 4996 bees (48 species) were sampled (Table A.1). Of the 81 flowering plant species, 77 (95%) are described as animal-pollinated (Table A.1). Rarefaction indicated that an average of 86% (range = 81–91%) of plant species were observed, and an average of 83% (range = 79–86%) of bee species were observed (Fig. 2). Pan traps were expected to under-sample larger bees (>10 mm), which can escape (Droege, 2008). Consistent with that expectation, 47 *A. mellifera* (12–15 mm) were successfully caught in pan traps, but 12 other bee species were netted but never pan trapped, including large species, *Bombus impatiens* Cresson 1863 and *Xylocopa* Latreille 1802. We considered results to be a representative sample of plant and bee species diversity in the study area, though analyses of foraging bees likely under-represented large-bodied species.

3.1. Available flowering plants

Flowering plant abundance, species richness, diversity, and cumulative species richness were all significantly affected by anthropogenic disturbance (Table 1, Fig. 2a, Table A.2). Flowering plant abundance was most plausibly modeled with negative binomial distributions and temporal effects, but no spatial autocorrelation (Table A.2). Flower abundance increased with disturbance but decreased again in pastures to levels not significantly different from reference scrub (Table 1). Richness and diversity of available flowers were most plausibly modeled with Poisson distributions and temporal effects, but without spatial autocorrelation (Tables 1, A.2). Both richness and diversity increased with intermediate disturbance so that values for multi disturbance were significantly greater than for reference conditions, but decreased again for pasture sites to values similar to those for undisturbed reference conditions (Table 1).

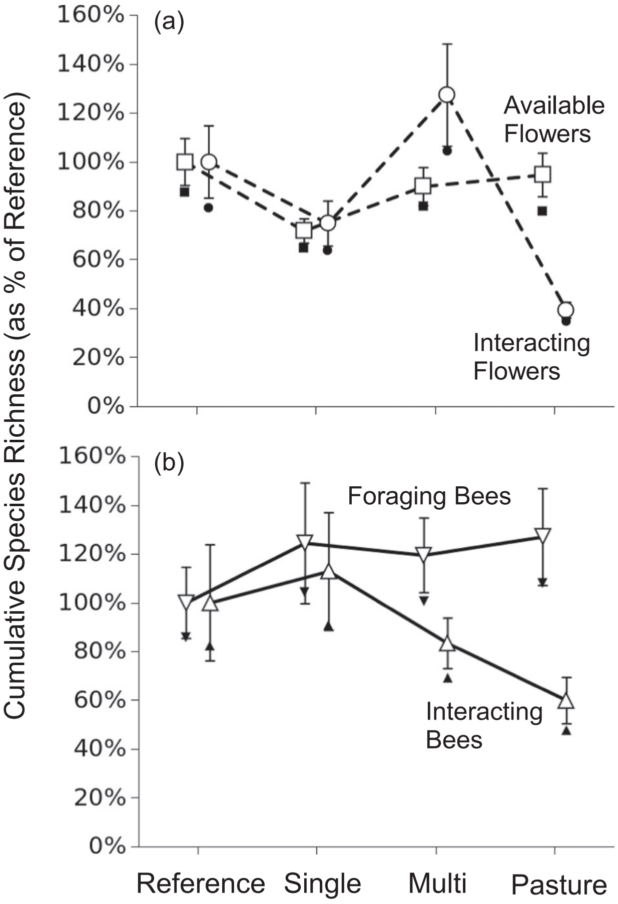

Fig. 2. Cumulative species richness, estimated by rarefaction (open symbols with 95% confidence intervals) and observed cumulative richness (filled symbols). (a) Available flower richness (squares) was less affected by disturbance than richness of flowers interacting with bees (circles). (b) Foraging bee richness (inverted triangles) maintained or even increased across disturbance levels but bees interacting with flowers declined (triangles), consistent with unsuccessful foraging (compare to Fig. 1c).

Cumulative flowering species richness was reduced in the single disturbance level compared to reference conditions, but multi and pasture habitats had values similar to reference habitats (Fig. 2a). Thus, the annual number of flower species available to bees was not clearly reduced by disturbance. However, abundance-based composition of that flower community was clearly affected by disturbance (PERMANOVA; $p < 0.001$). Reference scrub vegetation differed in composition from all disturbed habitats, which overlapped but became progressively constrained in NMDS (stress = 0.20) with more disturbance (Fig. 3a). Mean dissimilarities (Table 2) reflected compositional patterns shown in NMDS; variation *within* disturbance levels (i.e., heterogeneity among plots and through time) was greatest in reference habitats and generally reduced as disturbance levels increased, reflecting greater homogenization of the flowering plant community with disturbance. Compositional variation *among* disturbance levels was substantial and generally greater than variation *within* levels (Table 2).

Endangered and threatened plant species were found in all four disturbance levels, but were most common in reference habitat and decreased with disturbance (Table A.1). Non-native plant species were only found in pastures, which were the most altered sites studied here, but non-native *A. mellifera* were found in all disturbance levels (Table A.1). Significant plant indicator species were detected in each of the disturbance levels (Table A.1), though numbers of those indicators varied

Table 1
Model coefficients for most plausible models of abundance, species richness, and diversity (Jost, 2006) for all flowers, interacting flowers, foraging bees (trapped), and interacting bees (netted). Each response variable was analyzed with a mixed effects model, where potential temporal (T) and spatial (S) autocorrelation were evaluated as random effects. Alternative distributional assumptions (g = Gaussian, p = Poisson, n = negative binomial) were evaluated with information theoretic model comparison (Burnham and Anderson, 2002); listed assumptions (e.g., n) were most plausible (see Table A.2 for details). Reference significance denotes a difference from zero; other coefficients and significance values are relative to reference habitats (e.g., abundance of all flowering plants in pastures is slightly less than in reference habitats but not significantly different). Values in parentheses are standard errors. Significance: *<0.05; **<0.01; ***<0.001.

		Reference	Single	Multi	Pasture
All flowering plants	Abundance (T, n)	3.0 (0.3)***	0.4 (0.2)*	0.9 (0.2)***	−0.02 (0.2)
	Richness (T, p)	1.0 (0.2)***	0.06 (0.1)	0.5 (0.1)***	−0.06 (0.1)
	Diversity (T, p)	0.7 (0.1)***	0.04 (0.1)	0.4 (0.1)**	−0.03 (1.4)
Interacting flowering plants	Abundance (T, n)	0.4 (0.3)	0.2 (0.3)	0.3 (0.4)	−1.0 (0.4)*
	Richness (T, p)	−0.8 (0.2)**	0.4 (0.3)	0.5 (0.3)	−0.5 (0.3)
	Diversity (T, p)	−0.8 (0.2)***	0.4 (0.3)	0.4 (0.3)	−0.5 (0.3)
Foraging bees	Abundance (T, n)	4.5 (0.4)***	−0.3 (0.3)	−0.6 (0.3)*	−1.0 (0.3)***
	Richness (none, g)	5.1 (0.5)***	1.0 (0.7)	0.9 (0.7)	−0.2 (0.7)
	Diversity (T, g)	2.2 (0.3)***	0.1 (0.3)	−0.6 (0.3)*	0.4 (0.3)
Interacting bees	Abundance (S, p)	−2.5 (1.3)	−0.07 (0.2)	0.007 (0.1)	0.02 (0.2)
	Richness (S, p)	−2.4 (1.1)*	−0.03 (0.2)	−0.1 (0.2)	0.007 (0.3)
	Diversity (S, p)	−2.4 (1.1)*	0.1 (0.2)	0.01 (0.2)	0.07 (0.3)

among disturbance levels (reference = 10, single = 1, multi = 8, pasture = 14).

3.2. Flowering plants interacting with bees

The abundance of interacting flowers was most plausibly modeled with negative binomial distributions and temporal effects, but no spatial autocorrelation (Tables 1, A.2). Less than half of all flowering plants interacted with bees in every disturbance level, and that fraction was significantly reduced in pastures (Table 1). However, sites at intermediate disturbance levels did not have significantly altered abundances of flowering plants (Table 1). Species richness and effective diversity of interacting flowers were each most plausibly modeled with Poisson distributions and temporal effects, but no spatial autocorrelation (Tables 1, A.2). However, neither species richness nor diversity of interacting flowers were significantly affected by disturbance levels (Table 1).

Cumulative richness of interacting flowers varied among disturbance levels in a pattern mirroring all flowering plants, except for depressed values in pastures (Fig. 2b). As was true for all flowers (Section 3.1), multivariate analysis of interacting flower composition was more sensitive than univariate analysis for disturbance effects (PERMANOVA; $p < 0.001$). Effects on composition were supported by dissimilarity matrix values (Table 2) and NMDS ordination (stress = 0.16; Fig. 3b). Disturbance led to simplified and shifted subsets of flowers interacting with bees.

Of the 81 flowering plant species observed, 29 (36%) interacted with bees during the year-long study (Fig. 4, Table A.1). Five non-native flowering plant species were observed in pastures (*Crotalaria pallida* Aiton, *Desmodium incanum* DC., *Emilia fosbergii* Nicolson, *Macroptilium atropurpureum* (Moc. & Sessé ex DC.) Urb., and *Sida cordifolia* L.; Table A.1). None of those non-native plants were ever observed interacting with bees and are therefore not represented in the interaction data and unlikely to serve as floral resources for bees.

3.3. Foraging bees

A total of 4615 bees were collected in seasonal pan traps, representing 33 species (Table A.1). Total abundance of bees was most plausibly modeled using negative binomial distributions and seasons as random effects, but no spatial autocorrelation (Tables 1, A.2). Bee abundance progressively and significantly decreased with increased disturbance (Table 1), largely driven by declines in abundance of *Lasioglossum* Curtis 1833. Species richness of foraging bees fluctuated insignificantly with disturbance levels (Table 1), and neither temporal nor spatial effects were retained in the most plausible model (Tables 1, A.2). Effective species richness (i.e., $e^{H'}$) in multi habitats was significantly less than in reference habitats (Table 1), where the most plausible model used Gaussian distributions and temporal effects but no spatial autocorrelation (Tables 1, A.2).

Cumulative richness of foraging bees increased slightly with more disturbance (Fig. 2b). The difference between this result and repeated-measures analyses indicates more temporal species turnover of foraging bees with disturbance. As seen with flowers, disturbance strongly affected community composition of foraging bees (PERMANOVA; $p < 0.001$), which was supported by dissimilarity results (Table 2). Composition was quite heterogeneous among reference plots but more homogeneous among plots for any disturbed habitats (Fig. 3c). Ordination of bee abundances represented this contraction and dissimilarity of communities well (NMDS stress = 0.19; Fig. 3c); disturbed habitats had shifted subsets of the reference scrub bee community. The non-native *A. mellifera* roughly maintained abundance while native bees were less numerous in disturbed habitats, so honey bees became proportionally more dominant with greater habitat disturbance. Significant bee indicator species were detected in all disturbance levels except single sites (2 in reference, 2 in multi, 3 in pasture) (Table A.1).

3.4. Bees interacting with flowering plants

A total of 357 bees, representing 31 species, were netted while interacting with flowering plants during the study (Fig. 4; Table A.1). The most plausible mixed effects models of total abundance, mean species richness, and diversity for interacting bees were all based on Poisson distributions and included spatial autocovariates but no temporal effects (Tables 1, A.2). However, none detected significant effects of disturbance (Table 1). The most plausible models here included spatial autocovariates, unlike all other analyses above, which indicated a detail important to inference on hypotheses: foraging bees were more spatially dispersed than bees interacting with flowers. This detail was consistent with an ecological trap, which assumes that organisms, in this case bees, may forage unsuccessfully in low-quality habitat.

In contrast to slightly increased cumulative richness of foragers, cumulative species richness of interacting bees declined in multi habitats and in pastures (Fig. 2b). Given large bees were under-represented in foraging traps but represented in netted interactions, an even greater difference likely existed between foraging and interacting bee richness. Like all such analyses above, multivariate analysis of composition detected disturbance effects on interacting bees (PERMANOVA; $p < 0.001$), and ordination of those data indicated simplification and a shift of interacting bee composition with habitat disturbance (NMDS stress = 0.18; Table 2; Fig. 3d).

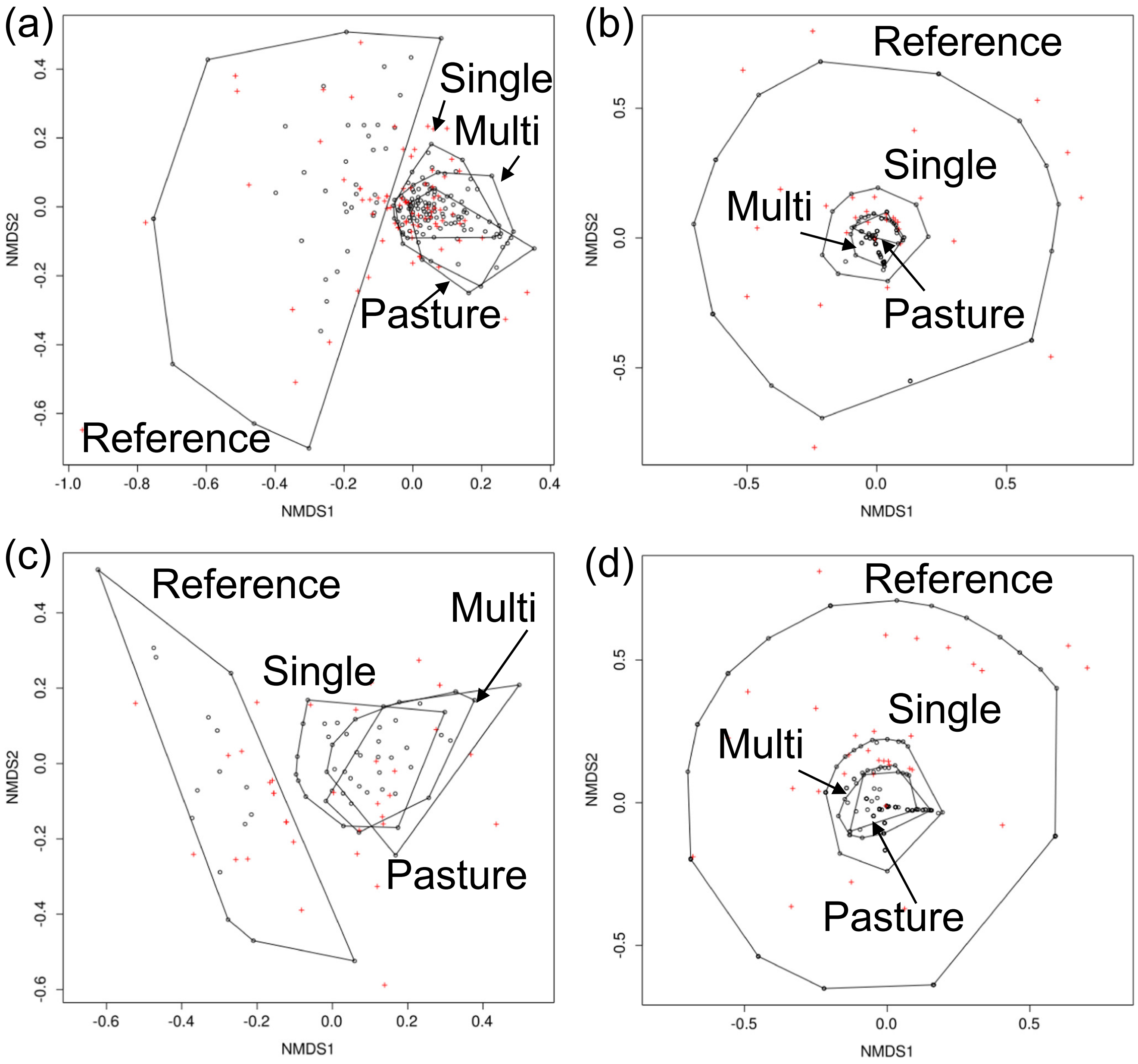

Fig. 3. Nonmetric multidimensional scaling (NMDS) ordinations of: (a) all flowering plants (stress = 0.20); (b) flowers interacting with bees (stress = 0.16); (c) foraging bees (stress = 0.19); and (d) bees interacting with flowers (stress = 0.18). Data include all samples collected during a year. Convex hulls denote disturbance levels, open circles denote samples and + symbols denote species.

3.5. Flower-bee interaction networks

Overall, habitat disturbance simplified plant-bee interaction networks (Fig. 4). Interaction networks had different memberships among disturbance levels, and the pasture network differed most from other disturbance levels. *A. mellifera* dominated plant-bee interactions in all four disturbance levels and especially in pastures (reference = 56% of interactions, single = 51%, multi = 61%, pasture = 71%) because fewer native bees interacted with available flower resources (Fig. 4, Table A.1). The number of different flower-bee interactions was markedly fewer in pastures (reference 38 interactions; single 32 interactions; multi 36 interactions; pasture 14 interactions). Only 5 of 17 bee species interacting with flowers in reference scrub also interacted in pastures, and an additional 5 bee species interacted in pastures that did not interact in reference scrub. The plant *Polygonella robusta* (Small) G.L. Nesom & V.M. Bates dominated interactions in single and multi disturbance levels but was replaced in pastures by *S. etonia*.

Some indicator species of disturbance levels were part of interaction networks (stars in Fig. 4, Table A.1), though interactions between indicator species were relatively rare. The multi network had the most interactions between indicators due to the role of the large *B. impatiens* (Fig. 4). The single indicator plant in pastures (*S. etonia*) did not interact with any indicator bees in that network but dominated interactions (Fig. 4). Network specialization increased with disturbance for native bees (Fig. A2) because the relatively few interacting bees were constrained to fewer flower sources (Fig. 4). The non-native *A. mellifera* reflects constraint in pastures due to its dominance and its heavy reliance on *S. etonia* and *Serenoa repens* (W. Bartram) Small (Fig. A2). Native bee nestedness varied across disturbance levels but was at least equal to reference scrub habitats (Fig. A2). Nestedness was accentuated with *A. mellifera* in reference and pasture habitats, where the generalist *A. mellifera* overlapped with other specialists in flower interactions (Fig. 4). Interaction strength asymmetry increased with disturbance, with or without *A. mellifera* (Fig. A2). Pastures were most positive for asymmetry,

Table 2
Annual mean Bray-Curtis dissimilarity matrices for plants, bees and interaction networks. Analyses were conducted on log-transformed abundances. Diagonal values = within a disturbance level, off-diagonals = among levels. Greater values indicate more dissimilarity.

		Reference	Single	Multi	Pasture
All flowering plants	Reference	0.92			
	Single	0.92	0.52		
	Multi	0.93	0.63	0.48	
	Pasture	0.98	0.73	0.58	0.35
Foraging bees	Reference	0.64			
	Single	0.63	0.61		
	Multi	0.62	0.60	0.49	
	Pasture	0.67	0.62	0.52	0.44
Interacting flowering plants	Reference	0.97			
	Single	0.96	0.54		
	Multi	0.97	0.65	0.49	
	Pasture	0.96	0.75	0.58	0.36
Interacting bees	Reference	0.92			
	Single	0.94	0.55		
	Multi	0.93	0.64	0.44	
	Pasture	0.93	0.68	0.48	0.31

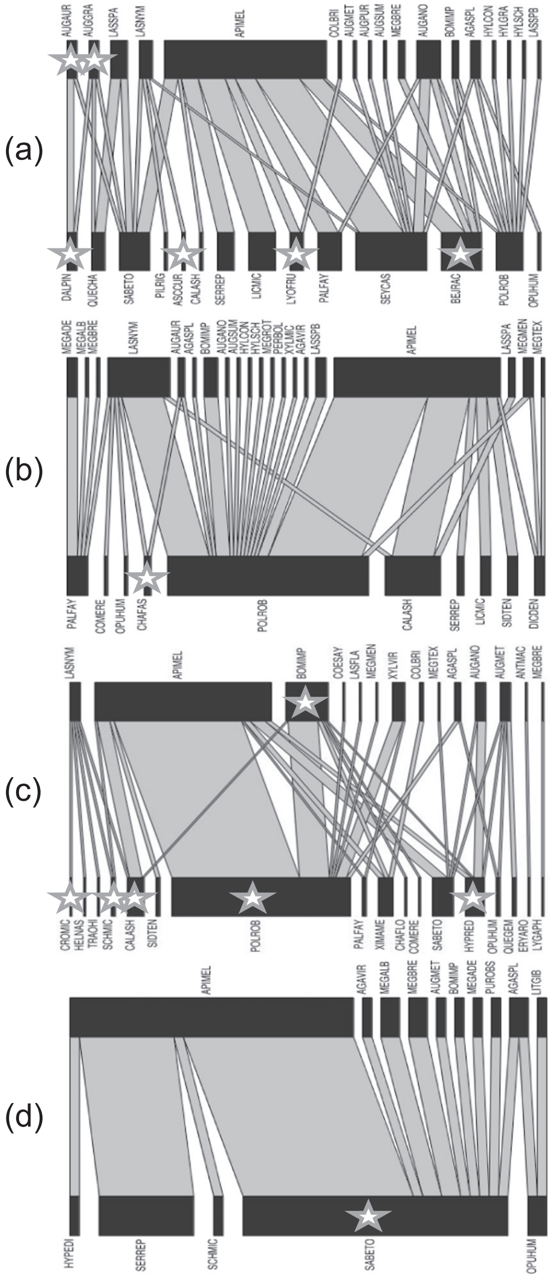

Fig. 4. Cumulative plant-bee interactions in each of the disturbance levels. (a) Reference sites (85 interactions). (b) Single sites (95 interactions). (c) Multi sites (135 interactions). (d) Pasture sites (42 interactions). In each bipartite network, bee species are on top, plant species are on the bottom. Width of the species and interaction bars are proportional to number of interactions. Stars denote significant indicator species of disturbance levels.

indicating greater dependence of bees on the fewer flowering plants there than in less-disturbed habitats.

In summary, univariate measures of means through time (i.e., total abundance, species richness, and diversity) for flowers and bees inconsistently detected habitat disturbance effects. Cumulative richness and multivariate analyses of composition detected significant disturbance effects for all analyzed components (available flowers, interacting flowers, foraging bees, and interacting bees) and indicated generally simpler and more homogeneous communities with more disturbance. Cumulative and multivariate results were generally consistent with the unsuccessful foraging hypothesis (Fig. 1c). Interaction networks indicated more specialization with disturbance for native bees and flowers, but *A. mellifera* negated that effect with its dominant role in the network. Interaction networks became simpler with disturbance, especially in pastures.

4. Discussion

Habitat disturbance increases extinction risk for both plants and pollinators but conservation and restoration can mitigate that risk (Kearns et al., 1998; Lennartsson, 2002; Fontaine et al., 2005; Forup et al., 2008; Vanbergen and the Insect Pollinators Initiative, 2013). Extinction risk for specialized and rare pollinators also affects certain endemic scrub plant species because pollen quantity or quality and reproductive output can be reduced in the absence of coevolved pollinators (Kearns et al., 1998; Deyrup et al., 2002; Lennartsson, 2002; Fontaine et al., 2005; Forup et al., 2008; Chi and Molano-Flores, 2015).

Our results are consistent with anthropogenic habitat disturbance impacts on community structure and interactions (Budria and Candolin, 2014; Courbin et al., 2014; Leal et al., 2014; Marrero et al., 2014; McCluney et al., 2014). Moreover, our results indicate that flower-bee interactions are sensitive to habitat disturbance, consistent with other recent plant-pollinator research (Winfree et al., 2009; Valiente-Banuet et al., 2015). Each analyzed component (flowering plants, interacting plants, foraging bees, and interacting bees) was significantly affected by disturbance, but in different ways. The spectrum of disturbance levels studied here ranged from reference habitats to pastures. Though other, more heavily disturbed habitats (e.g., urban) were not included, results here indicate that disturbance affects flower-bee interactions even at relatively low disturbance levels.

Repeated measures models of univariate response variables were less sensitive to disturbance effects than multivariate and cumulative richness estimates, as foreseen by Kremen et al. (2007). This outcome is consistent with temporally-variable floral and bee communities and suggests that conservation efforts for plant-pollinator interactions should include cumulative annual diversity in planning. Cumulative composition of foraging bees was affected by disturbance, and fewer bee species interacted with flowers in the highest disturbance categories (multi and pasture). The hypothesis that anthropogenic disturbance causes unsuccessful foraging by bees was supported, suggesting that anthropogenic habitat disturbance may contribute in part to an ecological trap for some bees (Schlaepfer et al., 2002; Winfree et al., 2009).

As expected, floral resources shifted across disturbance levels, especially in pasture habitats. Overall bee community composition also changed with disturbance. Beyond those changes, cumulative interactions between bees and flowers throughout the year were reduced with greater disturbance, consistent with the unsuccessful foraging hypothesis (compare Figs. 1c and 2b). Given bee mobility, patchy habitat in the study area, and many potential nest sites, bee community responses to disturbance recorded here were probably indirect effects (via floral changes) more often than direct effects (e.g., nest damage). Bee foraging should depend on resource availability and habitat quality (Hadley and Betts, 2012; Bennett et al., 2014). Nectar and pollen resources were available across disturbance levels, as evidenced by floral abundance, diversity, mean richness, and cumulative floral species richness among disturbance levels. However, floral quality (a matter of co-evolved adaptations) surely shifted for multiple bee species since floral composition shifted, and should have been most critical for specialist bees. Spatial autocorrelation components of analyses indicate that bees foraged more widely than their actual interactions with flowers, consistent with reduction of co-evolved resources due to disturbance and conditions for an ecological trap. Non-native flowering plants in pastures especially contributed to decreased floral quality for some bee species because no bees (including *A. mellifera*) were observed interacting with non-native flowers (consistent with Morandin and Kremen, 2012). Some bee species forage near nests but others forage at distances greater than maximal distance between experimental plots here (Pasquet et al., 2008; Zurbuchen et al., 2010). Comparative studies of select bee species expected to forage at different distances among different disturbance levels should tease apart community-level results such as those reported here.

Unsuccessful foraging among bee species in disturbed lands (especially pastures here) may be one proximal mechanism that contributes to reductions in bee diversity with greater disturbance. Anthropogenic disturbance of vegetation is widespread, spatially patchy, and more extensive and intensive in other areas (e.g., monocultures, urban lands). Assuming bees forage among disturbance levels (as indicated here), some populations may generally experience unsuccessful foraging with increased habitat alteration. This may especially happen if they specialize on nearby flowers that are vulnerable to disturbance, are solitary and thus do not receive information to actively adjust foraging trips that eusocial bees receive (Grüter and Ratnieks, 2011), and do not forage at great distances, as expected for smaller bees (Greenleaf et al., 2007). In this light, the relative success of *A. mellifera* across disturbance regimes in this study may be explained by their generalized foraging, eusociality, and moderate body size. Likewise, comparative foraging success across disturbance regimes may inform comparative behavioral ecology of pollinators (Jandt and Gordon, 2016). Unsuccessful foraging (e.g., by smaller solitary specialists) should contribute to reduced resources for their survival and reproduction, and thus affect fitness, in addition to matters of pollen supply (Műller et al., 2006). Further studies in a disturbance context on comparative foraging success across solitary and social systems may reveal much to explain relative responses of pollinators to anthropogenic disturbance and help to better understand selective mechanisms for sociality.

If any bee species benefited by disturbance of native vegetation, it was *A. mellifera*. More honey bees foraged in disturbed habitats and dominated interaction networks there. Honey bees are obviously well-adapted to human-modified landscapes. Among other bees in this study, species in the genus *Lasioglossum* were numerous foragers and potentially important to pollination but were reduced by disturbance. Though readily collected in traps in pastures, no *Lasioglossum* were observed interacting with flowering plants in pastures during the year. *Lasioglossum* are small-bodied, with a foraging range < 600 m (Gathmann and Tscharntke, 2002; Zurbuchen et al., 2010). It is likely that spatially-extensive conversion of scrub habitat to pasture has severely reduced pollination of native plants by *Lasioglossum* and other small, locally-foraging bees.

Beyond our study system, extensive conversion of natural vegetation to agriculture (e.g., pollinator-dependent row crops) has required greater dependence on honey bees, which in turn are increasingly at risk themselves to parasites, pesticides, and floral changes (Goulson et al., 2015). Greater bee diversity can reduce the risks associated with that sole-source pollination service, but will in turn require greater native floral diversity in agricultural lands (Goulson et al., 2015), restoration of natural vegetation patches among agricultural lands, and informed conservation of remaining natural lands.

Greater floral diversity for the purpose of promoting bee diversity in or around crops and in restoration projects could be accomplished by reintroducing native bee-preferred plants, because that is more practical than introducing native bees. To that end, studies on plant-pollinator networks (like this study) can be vital. In our study system, strong floral candidates for increasing bee diversity include *P. robusta*, *S. etonia*, *Calamintha ashei* (Weath.) Shinners and *Bejaria racemosa* (Vent.) all of which served as indicator species. Planting or encouraging growth conditions of those wildflowers in former pastures at or near our study sites should increase successful bee foraging in those areas, and thereby boost pollination and reproductive success of other flowers. After wildflowers are established, colonization by diverse native bees may require some time, depending on the spatial extent of agriculture and lands to be restored. Assuming bees can colonize restored lands and nest there (which we did not address), our results indicate that flower-bee interactions are sensitive to disturbance and thus may also rapidly respond to restoration (Valiente-Banuet et al., 2015).

Vegetation is often evaluated in conservation management, but pollinators can also inform that work and could be especially important if native plants reproduce poorly (Bakker et al., 1998; Seabloom et al., 2003). Protected conservation lands serve critical roles for maintaining diversity and interactions of co-evolved flowering plants and pollinators amidst anthropogenically disturbed lands (e.g., agriculture, urban areas; Kearns et al., 1998; Kremen et al., 2007). In addition to the effects of disturbance on vegetation, evidence here indicates that disturbance may also cause unsuccessful foraging by pollinators, contributing to ecological traps for those pollinators. We suggest that plant-pollinator interactions should be more highly valued as a measure of conservation and restoration success. Despite relatively high flowering species diversity, less than half of all available flowering plant species interacted with bees here. Other flower-visitors (dipterans, lepidopterans, coleopterans, etc.) are also important pollinators and may also be affected by disturbance (Kearns et al., 1998; Evans et al., 2004; Nielsen and Totland, 2014). All pollinators in anthropogenically disturbed habitats should be studied to develop a more complete understanding of plant-pollinator interactions. Restoring those local plant species that stand out as indicators in pollination networks may help reestablish community function and stability and serve as an endpoint measure for conservation and restoration.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.08.030.

Acknowledgments

We thank Bea Maas, Ross Hinkle, Josh King, and anonymous reviewers for helpful comments on previous drafts; Archbold Biological Station (especially Eric Menges, Stacy Smith, Sarah Haller and Mark Deyrup) and the University of Central Florida Department of Biology; North American Pollinator Protection Campaign, and the Ying Family Foundation for financial support.

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