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HIGHLIGHTED STUDENT RESEARCH

Plant–pollinator interaction niche broadens in response to severe drought perturbations

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Abstract

The composition of plant–pollinator interactions—i.e., who interacts with whom in diverse communities—is highly dynamic, and we have a very limited understanding of how interaction identities change in response to perturbations in nature. One prediction from niche and diet theory is that resource niches will broaden to compensate for resource reductions driven by perturbations, yet this has not been empirically tested in plant–pollinator systems in response to real-world perturbations in the field. Here, we use a long-term dataset of floral visitation to *Ipomopsis aggregata*, a montane perennial herb, to test whether the breadth of its floral visitation niche (i.e., flower visitor richness) changed in response to naturally occurring drought perturbations. Fewer floral resources are available in drought years, which could drive pollinators to expand their foraging niches, thereby expanding plants' floral visitation niches. We compared two drought years to three non-drought years to analyze changes in niche breadth and community composition of floral visitors to *I. aggregata*, predicting broadened niche breadth and distinct visitor community composition in drought years compared to non-drought years. We found statistically significant increases in niche breadth in drought years as compared to non-drought conditions, but no statistically distinguishable changes in community composition of flower visitors. Our findings suggest that plants' floral visitation niches may exhibit considerable plasticity in response to disturbance. This may have widespread consequences for community-level stability as well as functional consequences if increased niche overlap affects pollination services.

Keywords Optimal foraging · Interspecific competition · Interaction plasticity · Floral visitation · Plant–pollinator · Foraging niche

Introduction

Understanding how species interactions respond to perturbations is key to improving our predictions for how disturbances will influence natural ecosystems. In particular, plasticity in interaction partner identity may be functionally important for how organisms respond to disturbance. For example, if a disturbance leads to the loss of one or more food resources from an animal's diet, plasticity in interaction partner (food resource) identity can allow for continuity in feeding, even if potentially at a lower resource intake level. In plant–pollinator communities, both sets of interacting species tend to show a high degree of interaction generalization, i.e., most plant species interact with many pollinator species, and most pollinator species in turn interact with multiple plant species (Waser et al. 1996). Moreover, the number of interaction partners for a target species can be strikingly dynamic

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Understanding how species change interaction partners following disturbance is key for managing ecosystems impacted by ongoing environmental change. This work supports the hypothesis—driven by diet theory—that the set of flower visitor interaction partners would increase to a focal plant in lower-resource (drought) conditions. This work is novel in its use of a predictive theoretical framework, its leveraging of long-term data on flower visitation, and its analytical framework that allows cohesive comparison of disparately collected data.

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both across and within years (e.g., Alarcón et al. 2008; CaraDonna et al. 2017; CaraDonna and Waser 2020), potentially varying based on resource availability and competition (e.g., Brosi 2016). Despite the recognition that plants and pollinators can change their interaction partners, many plant–pollinator network models assume stasis of interactions even with major disturbances such as the loss of many interaction partners (e.g., Memmott et al. 2004; Vieira and Almeida-Neto 2015). Given the central importance of pollinators in the reproduction of wild plants (Burd 1994; Knight et al. 2005; Ollerton et al. 2011) and the production of crops (Klein et al. 2008), it is imperative that we improve our understanding of how plant–pollinator interactions will respond to a range of disturbances, particularly given ongoing anthropogenic environmental change.

Niche theory and diet theory provide a conceptual basis for understanding and predicting conditions under which the number of interaction partners may expand or contract (e.g., Emlen 1966; MacArthur and Pianka 1966). Two counteracting forces are at play. Specifically, when overall per-capita resource levels decrease—either via a reduction in the resource base or an increase in the number of conspecific individuals (i.e., intraspecific competition)—consumers will typically broaden their dietary niche to include resources they may not utilize under ideal conditions (e.g., Schoener 1971; Svanbäck and Bolnick 2007; though see Weinstein and Graham 2017). By contrast, reductions in a resource base driven by an increase in *inter*specific competition will tend to decrease consumer niche breadth (i.e., increase specialization), if each species has an advantage in its consumption of one resource type (e.g., reduced handling time) (e.g., Bigger and Fox 1997; Bolnick et al. 2003, 2010).

These predictions have experimental support in plant–pollinator systems. Experiments with pollinators have found that manipulating interspecific competition influences the extent of generalization among the remaining pollinators as well as the resulting niche breadth (Morse 1977; Fründ et al. 2013). Such experimental work has manipulated interspecific competition in two ways. First, given that increasing pollinator densities in natural settings is logistically challenging, field experiments often take the opposite tack and instead reduce interspecific pollinator competition. Field experiments that reduced interspecific pollinator competition (removed a bumble bee species) showed that the dietary niches of remaining pollinator species broadened (Inouye 1978), and that short-term foraging specialization decreased (Brosi and Briggs 2013). A second approach is to use experimental enclosures where the density of pollinators can be controlled. For example, a greenhouse experiment that manipulated intraspecific bumble bee density while maintaining a constant floral resource base found that increased intraspecific competition increased diet breadth, in line with theoretical predictions (Fontaine et al. 2008).

Despite the numerous studies indicating that plant–pollinator interactions shift in response to controlled experimental resource manipulations, there are to our knowledge no studies of how the niche breadths of focal species respond to real disturbances in nature. This is important because experimental manipulations, while powerful for teasing out the effects of particular factors in isolation, may not reflect how organisms will respond when multiple factors change concurrently over relatively large spatial scales, as they typically do in natural disturbances. Some network-based studies have examined how plant–pollinator interactions respond to disturbances found in nature including among others grazing (Vázquez and Simberloff 2002; Vanbergen et al. 2014), invasive species (Baskett et al. 2011), and agricultural intensification over long timescales (Burkle et al. 2013). These studies, while highly informative, do not explicitly test the hypotheses generated by niche / diet theory and instead focus on structural changes to networks. Some focal-plant studies have assessed patterns of pollinator visitation after natural disturbances, such as hurricanes (e.g., Rathcke 2000), and droughts (Arroyo et al. 2020), although these studies did not focus on niche dynamics and instead only on the visitation rates by focal pollinators. The dearth of studies on this topic is perhaps unsurprising given the difficulties involved in such work. To have any kind of reasonable statistical replication requires not just one but multiple relatively similar natural perturbations, along with measurements of the same system in non-perturbed years. Thus, to be useful for this question a dataset must be not only long term, but also contain multiple occurrences of a focal disturbance. In addition, because measures of plant or pollinator niche breadth (which are ultimately measures of diversity) are sensitive to sampling intensity (Chazdon et al. 1998), any dataset used for this question must also utilize sampling methods that generate directly comparable data across years, even if sampling intensity varies.

In this study, we compiled a dataset with comparable sampling methods to examine pollinator floral niche breadth changes in response to a natural disturbance—severe drought, which in our study system is characterized by low snowpack in the preceding winter given that 80% of the precipitation comes in the form of snow. Our long-term dataset consists of five years of data collected intermittently over a 20-year span on floral visitation to one focal plant species, *Ipomopsis aggregata* (Pursh.) V.E. Grant (Polemoniaceae), in the Rocky Mountains (Colorado, USA), including two severe drought events. In our study system (composed almost completely of perennial herbs, CaraDonna et al. 2014), drought often decreases available floral resources at a community level. Some perennial species may not bloom at all in drought years (Thomson 2016) or decrease resources

on a per-plant (e.g., number of flowers) and per-flower (nectar volume) basis (Phillips et al. 2018). At our study site, plant communities in drought years have reduced floral resources (e.g., abundance; Online Resource Figure 1). By contrast, flower visitors in this system (mainly insects in Diptera and Hymenoptera) do not show such stark reductions in abundance in response to current-season drought, which could be in part because initial population values for some groups (e.g., bumble bees, solitary bees) each year may be determined by the favorability of resource conditions in the previous summer (Forrest et al. 2019). Because niche and diet theory predict that decreased resource abundance will broaden pollinator floral resource use, and because our knowledge of the system is consistent with drought-associated reduction in floral resources while consumer populations remain relatively constant, we predicted an increase in the richness and abundance of flower visitors to *I. aggregata* in drought conditions as compared to its visitors in non-drought years.

We used *I. aggregata* as a target species for several reasons. First, it blooms even under severe drought conditions (Levine and Paige 2004). Many other plant species in the long-lived montane perennial wildflower community in the Rocky Mountains will either substantially reduce flower production or skip flowering altogether when abiotic conditions are poor (e.g., Inouye 2008). Second, while *I. aggregata* is long-lived, it is also a monocarpic, pollinator-dependent species whose populations are seed-limited (Juenger and Bergelson 2000; Campbell and Waser 2007; Campbell 2019). As such, individuals that expend their sole reproductive opportunity to bloom under drought conditions will likely still allocate substantial resources to maximize pollination success and seed set. This is in contrast to other non-monocarpic plant species in our study community, which even if they bloom in drought years, may produce fewer flowers or have greatly reduced resource allocation to flowers relative to non-drought years (Inouye and McGuire 1991; Inouye 2008). Third, in typical years *I. aggregata* has a relatively limited niche breadth of floral visitors, in part due to its long corolla tube, and is typically visited primarily by hummingbirds, long-tongued bumble bees, and hawk moths (Waser 1978; Mayfield et al. 2001), though visits by other pollinator groups do occur (Price et al. 2005). Thus, niche breadth expansions in *I. aggregata* may be relatively easier to detect compared to more-generalized plant species.

We assessed how the suite of flower visitors to *I. aggregata* changes in drought versus non-drought years in terms of three specific responses: (1) floral visitor abundance; (2) pollinator niche breadth (i.e., richness of floral visitors); and (3) community composition of floral visitors. Due to a general reduction in floral resources of other plant species in drought conditions, we predicted: (1) an increase in the abundance of flower visitors to *I. aggregata*; (2) an increase in the richness of those visitors (i.e., niche breadth), even when controlling for any potential increase in floral visitor abundance; and (3) changes in community composition of floral visitors in drought relative to non-drought conditions, particularly reflecting an expansion in floral visitors beyond bumble bees and hummingbirds in drought years.

Materials and methods

Study system and data

This study was conducted in montane meadow habitats in and around the Rocky Mountain Biological Laboratory (RMBL) near Crested Butte, Colorado (38.9585° N, 106.9878° W) at ~ 2880 m elevation. The study area receives an annual average of 61 cm of water-equivalent precipitation (80% in the form of snow).

We compiled *Ipomopsis aggregata* visitation data collected between 1997 and 2018 in two separate collection efforts. We used a subset of data from the first collection effort, detailed by Price et al. (2005) with data collection from 1996 to 2002 (seven years of data). Here, we used data collected in three of those years (1997, 1998, and 2001) where the sampling allowed for statistical comparisons to our subsequent data collection. Data from the other four years were not used when they could not be transformed into consistent visitor categories with the same level of detail (See Online Resource 1 for additional information). We used all of the data from the second data collection effort (which was coordinated by the authors of this manuscript) in 2012 and 2018.

Drought classification

We used local weather records from the Gothic Weather database (http://www.gothicwx.org) collected on-site at RMBL to classify each year of our complied data into either drought or non-drought. We used a local weather dataset given that snowfall, accumulation, and spring melt-out dates can be particularly sensitive to microsite in mountainous regions. Indeed, even at and around RMBL date of snowmelt can vary by weeks depending on slope, aspect, and other microclimatic variability. The Gothic Weather database has collected these data in the exact same location across the study period, which limits any spatial biases in determining drought conditions at the site. Drought years were defined as those more than one standard deviation below the 30-year mean for both total snowfall and water equivalent. Using these standards, our drought years ranged from 490 to 640 cm total snowfall (42.16–42.39 cm water equivalent), with melt date (date of first bare ground at the RMBL weather station) 23 Apr to 05 May. Non-drought

years, by contrast, had considerably more total snowfall (928–1498 cm snow, 58.17 to 100.33 cm water equivalent), and melted out substantially later (dates 14 May to 01 June). To confirm the classification of drought years, we ran a permutational multivariate analysis of variance ("permanova"; conducted with the 'Adonis' function, 'vegan' package, Oksanen et al. 2013) to compare multivariate differences in a suite of relevant weather measurements. We included the following variables: total winter snowfall, days above freezing (Nov–May), total water (snow), total days of snow cover, snow cover on 01-Ap, and snow cover on 01-May (Online Resource Figure 2). We used weather data for all years since 1995 (note that our first historical sample was taken in 1997). The permanova analysis confirmed that drought years were significantly different from non-drought years for a multivariate suite of weather data ($F_{1,21} = 76.42$, $R^2 = 0.78$, $P < 0.01$, Online Resource Table 1).

Flower visitation

Data collection in the three non-drought years (1997, 1998, and 2001) consisted of hour-long observations of focal *I. aggregata* individuals. For the data we used here, the field team observed floral visitation at *I. aggregata* plants in three sites once per week over a six-week period (five weeks in 1997) covering the bulk of the blooming period of *I. aggregata* in our study area. Sampling in each week included three one-hour observations: morning, midday, and afternoon. One team member each year observed between 12 and 31 individual *I. aggregata* within a plot, with individual plants chosen haphazardly to allow for unobstructed observation from a fixed point outside of the plot. Each observation period consisted of one observer recording all visits to focal plants simultaneously, by scan-sampling all open flowers within the plot with aid from binoculars with a close (~ 2 m) minimum focal distance. When a flower visitation occurred, the observer noted the visitor identity and time of day, unique plant identification number, and the number of flowers that were visited at each plant. One visit consisted of an animal (hummingbird or insect) interacting with the reproductive parts of the *I. aggregata* flower. Each visitor was classified into one of seven categories: butterfly, bumble bee, hoverfly, hummingbird, other fly, solitary bee, or wasp.

In the second data collection effort, for the drought years 2012 and 2018, observers recorded visitation at several sites in the RMBL area. In 2012, the field team sampled 15 sites twice each and 11 once each during flowering period (26 sites total). In 2018, the field team resampled six sites established in 2012; five of them were resampled four times each and one of them three times. Resampled populations have almost certainly shifted somewhat within the general area of a site, as the species is monocarpic and does not reproduce vegetatively. Field teams selected circular 5 m radius plots that contained at least 20 flowering *I. aggregata* at the time of sampling (for consistency with Price et al. 2005). Observers performed pollinator surveys by conducting three 10-min observations of the 5 m plot at each site visit in 2012 and one 10-min observation performed per site visit in 2018. Observations entailed walking through the patch and nondestructively identifying each floral visitor according to 30 distinct categories (following Brosi et al. 2017). Because movement within the plot may have discouraged hummingbirds from visiting *I. aggregata* individuals, we supplemented within-plot observations with an additional 10-min observation at each patch prior to other sampling in both 2012 and 2018, during which observers stood stationary outside of the 5 m radius plot and recorded hummingbird and bumble bee visits. In 2012 one to three observers worked simultaneously for the hummingbird sampling period, while in 2018, two observers collected each sample.

We subsequently converted visitor identifications into seven visitor categories—bumble bee, butterfly, hummingbird, hoverfly, other fly, solitary bee, and wasp—similar to those used by Price et al. (2005) for comparison among sample years (see Table 1). Due to difficulties in determining consistency in counts during observation periods between

Table 1 Relative visitor category abundances of visits to *Ipomopsis aggregata* shown as percentages for each year

Year	Bumble bee	Butterfly	Hoverfly	Humming bird	Other fly	Solitary bee	Wasp	Total recorded visits
1997	26.18	0.43	30.9	36.48	0	6.01	0	233
1998	1.16	0	12.79	66.86	13.37	5.81	0	172
2001	2.29	0	43.79	44.77	4.58	1.31	3.27	306
2012[a]	2.72	1.77	14.27	59.38	10.05	5.57	6.25	736
2018[a]	6.12	2.04	24.49	38.78	8.16	0	20.41	49

Total recorded visits are provided for further context. Information on sampling effort per year detailed in methods

Bumble bee all *Bombus*, *Butterfly* all butterflies, *Hoverfly* Syrphidae, *Hummingbird* broad-tailed and Rufous Hummingbirds, *Other fly* Diptera, *Solitary bee* all solitary bees, *Wasp* all wasps

[a]Drought years

years, we excluded visits by ants, beetles, and other small insects, even though this may have reduced our power to detect niche expansion.

Data analysis

We used the statistical software R for all statistical analysis (R Core Team 2018). A fully reproducible Rmarkdown file of our analysis is included as a supplemental file (Online Resource 1), and the data are archived in the open-access repository Dryad.

Visitor abundance

Visitor abundance data consist of discrete counts, with repeated measures in the same sites within a summer growing season, and in some cases across years. Thus, we used generalized linear-mixed effect models (GLMMs) to analyze these data, allowing for both specification of a proper error model for discrete data, and also for correction of non-independence of sample data within sites and within years (via specification of a random-intercepts effect of site nested within year). The abundance data were over-dispersed relative to a Poisson distribution (as determined with the 'fitdist' function in the 'fitdistrplus' package, Delignette-Muller and Dutang 2015), therefore we used a GLMM with negative binomial errors via the 'glmmTMB' package (Brooks et al. 2017). To correct for differences in amount of observation time, we included as fixed effects 1) the number of observers for a given sample, and 2) the time spent observing (mins), in addition to our focal independent variable 3) drought. We assessed model assumptions of homogeneity of variance and normality of model residuals using the 'DHARMa' package (Hartig 2019).

Niche breadth: species richness

We assessed potential changes in niche breadth of flower visitors to *I. aggregata* by comparing the visitor category richness between drought and non-drought years. To assess whether visitor richness differed between drought and non-drought years we used two methods: individual-based rarefaction and a generalized linear mixed-effects model. We took a two-pronged approach to account for two separate but intertwined issues of: 1) unequal sampling effort across the years; and 2) repeated measures (multiple samples both within and across years in some of the same sites). Ideally, we would have used true visitor *species* richness—rather than the much coarser visitor *category* richness—but we were limited by the relatively taxonomically broad visitor identifications in the historical data.

First, individual-based rarefaction generates the rate of visitor richness accumulation with increasing number of individual flower visits sampled. This approach allowed us to compare sites and years with substantially different sampling effort, since sampling effort is known to have very strong effects on measured richness (Chazdon et al. 1998). In addition, conducting the rarefaction as individual-based was conservative because greater abundance of organisms alone can generate a greater species richness. For example, when secondary-growth rainforest plots are compared to primary-growth rainforest plots of equal area, the secondary-growth plots can appear to have higher tree species richness, purely because there are more tree stems on a per-area basis. When compared with individual-based rarefaction, however, primary-growth plots show a much higher per-individual species richness (Chazdon et al. 1998). This approach is particularly relevant for our dataset, because we expected to find higher abundance of flower visitors to *I. aggregata* in drought years (due to fewer floral resources overall). Thus, our individual-based rarefaction approach conservatively corrects for the potential of spuriously finding higher richness in drought years driven only by higher abundance of floral visitors. We conducted rarefaction analyses using the 'iNEXT' package in R (Hsieh et al. 2016), which generated rarefied richness estimates with confidence intervals for each year, using data for rarefied richness pooled across sites within each year. We also examined changes in species richness between drought versus non-drought years for data pooled across sites and years. Richness estimates were considered statistically different if there was no overlap in rarefied 95% confidence intervals.

Second, our dataset includes repeated samples within sites (including for some, repeated measures across years) that individual-based rarefaction cannot account for. Thus, we additionally modeled per-sample visitor richness using a GLMM, with random effects specified in the same manner as in the visitor abundance model above. As in the abundance model, because species richness is a discrete count-based metric, we used negative binomial errors in our GLMMs. Relative to our rarefaction analysis the GLMM has the strong advantage of taking random effects into account, but with that comes the disadvantages of 1) measuring only per-sample richness, in contrast to richness accumulated over many samples; and 2) not taking into account the potential for increased abundance to drive increased richness.

Niche breadth: community composition

To examine whether community composition of floral visitors to *I. aggregata* differed between drought and non-drought years, we calculated community dissimilarity indices between sites using the Morisita–Horn index (calculated with the 'vegdist' function in the 'vegan' package), due to

its insensitivity to differences in sampling effort relative to other indices relative to other indices (Horn 1966; Chao et al. 2006). We compared community composition using permutational multivariate analyses ('Adonis' function in the 'vegan' package). We further visualized these differences in community dissimilarity using non-metric multidimensional scaling (NMDS), an ordination technique appropriate for non-linear data (including species abundance counts) that represents the position of sample units in multidimensional space. In NMDS plots, sample units clustered closer together are more similar while sample units further apart are less similar. Here sample units (sites by year) clustered close together have more similar visitor category compositions. We used the function 'metaMDS' (from the 'vegan' package) to perform the ordination from Morista–Horn dissimilarity. We then fit our focal environmental vector (drought) onto the ordination to project correlation of drought and the ordination (function 'envfit').

Results

Overview

Across all five years of sampling, spread over a 21-year time frame, we observed 1,585 visits to *I. aggregata* over the course of over 200 h of observation time (Fig. 1). Of the seven visitor categories, only bumble bee, hoverfly, and hummingbird categories were observed in all five years (Table 1). As expected, hummingbirds made up the greatest percentage of visitation each year, ranging from 36 to 68% of total visits.

Visitor abundance

We found positive and statistically significant effects of drought on median visitor abundance, which was 4.31 times higher in drought years as compared to non-drought years after accounting for number of observers and time spent observing (z value = 2.12, $P = 0.03$, Fig. 1). Unsurprisingly, we also found a significant positive relationship with time spent observing (z value = 2.18, $P = 0.03$). In contrast to observation time, the number of observers did not significantly affect recorded visitor abundance (z value = 0.80, $P = 0.42$).

Niche breadth: measured as species richness

Both our individual-based rarefaction and GLMM approaches showed positive and statistically significant effects of drought on visitor category richness. This is shown for individual-based rarefaction based on non-overlapping confidence intervals when drought and non-drought years were pooled together (Fig. 2a), although this trend appears to be driven more strongly by 2012 where the number of visits observed was higher than 2018 (Fig. 2b). From the GLMM, median category visitor

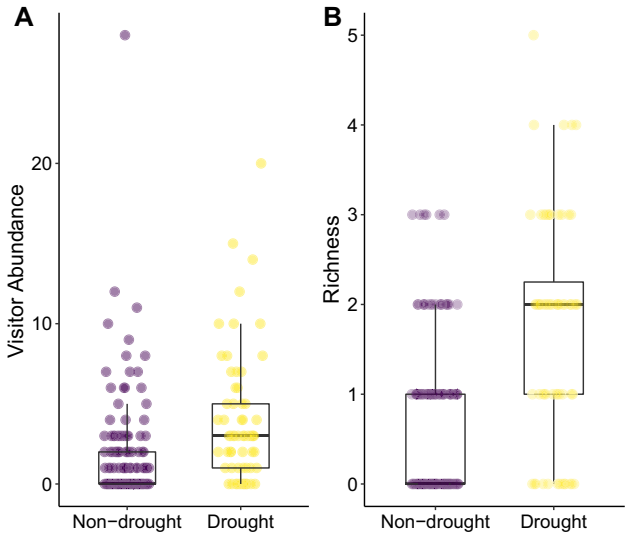

Fig. 1 **a** Abundance and **b** richness of visitation to I. *aggregata* in years of drought (2012 and 2018) and non-drought (1997, 1998, and 2001). Visitor abundance was pooled across seven visitor categories

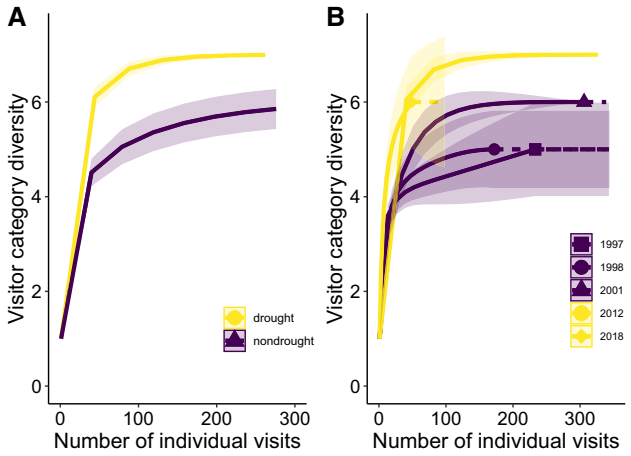

Fig. 2 Individual-based rarefaction analysis of *I. aggregata* visitor category richness for drought (yellow) and non-drought years (purple). Solid lines represent observed visitor category accumulation with the number of visits observed, and dashed lines represent extrapolated accumulation. Shaded bands are 95% confidence intervals obtained via bootstrapping methods with 200 replications. Symbol between solid and dashed lines indicates number of visits observed. **a** Rarefaction of drought (2012, 2018) and non-drought years (1997, 1998, 2001) combined for visitor category richness and **b** rarefaction of each sampled year (1997 = square; 1998 = circle; 2001 = triangle; 2012 = no symbol, presented without extrapolation; 2018 = diamond)

richness was 4.08 times higher in drought years as compared to non-drought years after accounting for number of observers and time spent observing (z value = 3.12, $P < 0.01$). Observation time was positively associated with higher richness (z value = 2.28, $P = 0.02$), while number of observers was not related to richness (z value = 0.65, $P = 0.51$), in parallel with our findings on abundance.

Niche breadth: community composition

We did not find statistically significant differences in floral visitor community composition between drought and non-drought years ($F_{1,39} = 1.85$, $R^2 = 0.05$, $P = 0.16$, Online Resource Table 2). Nevertheless, ordination of sites in species space suggested a marginally significant trend toward differentiation in community composition between drought and non-drought years (Fig. 3). Drought status explained much of the variation along axis 1 ($P = 0.07$, $R^2 = 0.14$), which in turn was the primary axis of separation between drought and non-drought sites. Notably, non-drought sites were more clustered than drought sites. Drought sites showed a large spread throughout the ordination, suggesting substantial variation in community composition across sites within drought years.

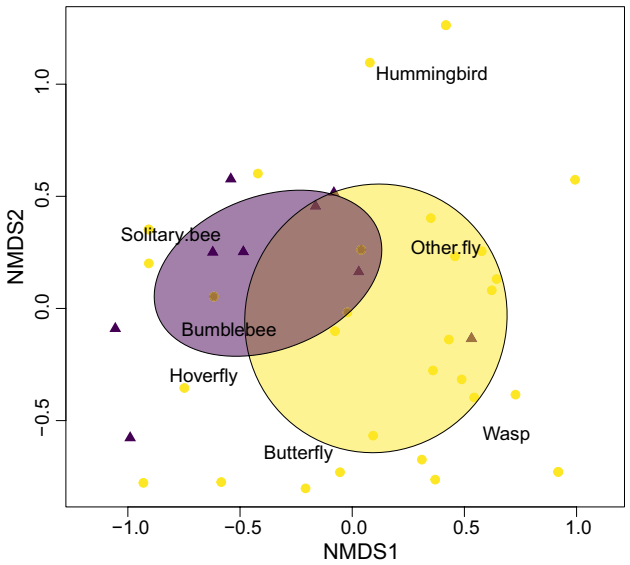

Fig. 3 Non-metric multidimensional scaling (NMDS) plot of *I. aggregata* visitor community composition at 41 sites in 5 years. We used Morisita–Horn as dissimilarly matrix. The NMDS plot with two axes resolved with a final stress of 0.17. Drought status acted as a driver of dissimilarity. To visualize groups' data collected in non-drought years are in purple triangles and data collected in drought years are in yellow circles. Visitor categories are graphed based on their mean value (plotted in black). Ellipsoids represent standard deviation of drought and non-drought site averages

Discussion

We examined how niche breadth and community composition of flower visitors to *Ipomopsis aggregata* changed in drought years compared to non-drought years. Following diet and niche theory, we hypothesized that flower visitors to *I. aggregata* would be more abundant and diverse in drought years due to pollinator diet breadth expansion to include *I. aggregata* when community-wide floral resource levels are low. We also hypothesized that these abundance and richness changes would be reflected in changes in the community composition of flower visitors in drought versus non-drought years. We found significantly higher visitor abundance and richness in drought years, consistent with the hypothesis that pollinator niche breadth increases in conditions of relative resource scarcity. By contrast, we did not find statistically significant differences in community composition of flower visitors between drought and non-drought years. Our findings suggest that plant–pollinator interaction identity can exhibit considerable plasticity in response to disturbance, in ways that are consistent with niche and diet theory. The functional consequences of niche expansion in flower visitors to *I. aggregata* in response to drought could be substantial—as we discuss in the subsequent paragraphs—but could be positive or negative and may impact plants and flower visitors differently.

Functional implications of pollinator flexibility for plants

Flexibility in flower visitor partner identity may help plants to maintain pollination services (and thus reproductive functioning and consistency in population size) in response to disturbance. A positive effect of visitor flexibility on plant reproduction is predicated on new visitors having at least some degree of pollination effectiveness. While flower visitor species can vary in their effectiveness (Mayfield et al. 2001), some studies suggest that floral visitor identity is not as important as the overall number of visitors (Vázquez et al. 2005; Hallett et al. 2017). For example, one study found that when a common bumble bee species was removed, pollination of *Asclepias verticillata* was offset by increased wasp visitation (Hallett et al. 2017). Similarly, there is evidence that the functional effect of generalist pollinators is driven primarily by their abundance relative to specialists, even if they are less effective as pollinators on a per-visit basis (Maldonado et al. 2013). In this study, we found both increased abundance and species richness of flower visitors in drought years, suggesting there is potential for flower visitor diversity to buffer fluctuations in pollination function due to

drought, assuming those visitors are indeed effective pollinators of *I. aggregata*.

Alternatively, increased partner flexibility could have deleterious implications for the reproductive success of *I. aggregata*, for two primary reasons. First, the expanded suite of flower visitors to *I. aggregata* in drought years likely consists of less-effective pollinators (e.g., syrphid flies) relative to its primary visitors in typical years (hummingbirds and bumble bees). These primary visitors have long proboscises and bills that match well with the long, tubular floral corolla of *I. aggregata* and likely facilitate efficient pollen transfer. In comparison, smaller flower visitors to *I.* aggregata—like most of those found in the expanded suite of visitors in drought years—may be less-effective pollinators due to relatively poor trait matching (Koski et al. 2018). These smaller flower visitors likely also have shorter flight distances which could limit how far pollen is dispersed (Greenleaf et al. 2007) and lead to increased rates of inbreeding for *I. aggregata* (Campbell and Dooley 1992). On the one hand, the inclusion of less-effective pollinators may not have functional consequences if the core set of more-effective visitors remains intact, as supported by overlap in visitor community composition between drought and non-drought years. On the other hand, the inclusion of less-effective pollinators could matter if less-effective pollinators (1) reduce visitation by more-effective pollinators by depleting floral resources (nectar or pollen); (2) reduce pollen levels—via pollen consumption or highly inefficient transfer—such that insufficient amounts are left for more-effective pollinators to deposit; (3) damage flowers while accessing floral rewards in ways that reduce pollinator attractiveness or affect seed development; or (4) fly shorter distances leading to genetic inbreeding. Indeed, we have observed syrphid flies, for example, consuming *I. aggregata* pollen and rarely coming into contact with the stigma, suggesting the potential for less-effective pollinators to affect pollination negatively.

Secondly, increased partner flexibility may negatively impact reproductive success by increasing hetero-specific pollen transfer (e.g., Morales and Traveset 2008). Whereas the work presented here focused on one target plant species, our findings are consistent with associated increases in the foraging niche breadth of flower visitors. "Floral fidelity" is the extent to which an individual flower visitor visits flowers of only a single plant species in a foraging bout (e.g., Brosi and Briggs 2013). When multiple plant species are visited in a foraging trip (i.e., low floral fidelity), hetero-specific pollen transfer can result, leading to negative effects on both the male and female components of plant fecundity (reviewed in Morales and Traveset 2008). From the perspective of male plant fitness, if pollen is transferred to a flower from a different plant species it is not able to fertilize ovules of flowers of its own species (i.e., conspecific pollen loss). Deposition of hetero-specific pollen on the stigmas of a target plant may reduce female plant fitness and seed production via several mechanisms, including stigmatic clogging and chemical allelopathy among others (Campbell and Motten 1985; Waser and Fugate 1986; Galen and Gregory 1989).

Functional implications of partner flexibility for flower visitors

The functional consequences of niche broadening for flower visitors are also likely mixed. On the one hand, if the widened visitor niche breadth of *I. aggregata* in drought years indicates that floral visitors exploit atypical rewards sources in drought years, this may provide them nutritional opportunities in the absence or reduction of preferred food resources (Waser et al. 2018). On the other hand, possible negative implications remain. For example, increased generalization might increase handling time if more types of flowers and/or more complex flowers are visited (Woodward and Laverty 1992; Laverty 1994; Gegear and Laverty 1995; Chittka and Thomson 1997), thus reducing overall foraging efficiency. This is exacerbated by the fact that variation in nectar production and concentration—which occurs in *I. aggregata* in drought conditions (Waser and Price 2016)—can additionally increase flower handling time by pollinators (Neff and Simpson 1990; Cresswell 1999). Finally, potential increases in niche overlap among flower visitors will likely affect competitive dynamics, for example drawing down average floral resource levels and necessitating more flower visits (and thus more energy expenditures) for any given flower visitor to maintain energy requirements.

Study limitations

This work, as in all field studies, has several limitations that could affect the interpretation of our results. A central limitation is that our analyses used multiple years of historical data that were not collected with identical protocols. Multi-year data sets are becoming increasingly important as ecologists seek to generalize results and understand trends over time, and the work we present here was possible only because of such long-term data collection. However, due to the large scale of data collection in this study—both temporally and spatially—sampling effort differed somewhat between years. Our analytical approach dealt directly with the differences in sampling effort among years, and also with differences in visitation among years, using individual-based rarefaction.

Still, there were other differences in sampling among years that could have affected our results, including variation in the number of observers, number of sites sampled, and time spent observing. Our GLMM models did find a positive relationship between observation time and both abundance and richness of flower visitors which could have biased our results. Additionally, the data for drought years included

many more sites (26 vs. 3), and typically more observers per sample, but substantially fewer repeated measures per site. We corrected for this by including observation time and observer number into our abundance and richness GLMMs, while including site as a random effect. Nonetheless, these differences could still have consequences for our results. One example is that observing more sites over a broader spatial range, as occurred in both of the drought years (relative to non-drought years), may have resulted in more varied floral-visitor communities relative to the sites used in non-drought years, which were much more geographically proximate. This probably reduced our statistical power to detect differences in visitor community composition between drought and non-drought years.

Another important set of limitations is that our sampling regime cannot account for changes across time not related to drought conditions. Some years are in sequence (e.g., 1997 and 1998) making it difficult to tease apart effects of drought and temporal autocorrelation. Additionally, we lacked temporal interspersion between drought and non-drought years, with drought-year observations occurring over a decade after those in non-drought years. This leaves open the possibility that changes in visitation occurred due to long-term temporal shifts in the visitor community, instead of drought effects. To address this issue, we conducted five sampling bouts at two sites in 2019, the non-drought year following our last drought-year data collection. Unfortunately, we abandoned sampling after recording only five individual flower visits in these 10 samples, i.e., a low enough detection rate such that the data (extrapolated across the entire season) would have been unlikely to have been useful in our individual-based rarefaction analyses. We suspect that the low detection rate was driven both by an unusually late onset of pollinator activity that year and a drastically lower abundance of flowering *I. aggregata* across all our sites, perhaps due to the depletion of reproductively mature individuals of this monocarpic species from the previous year's gregarious bloom event. Still, it is unlikely that our results are strongly driven by long-term changes in local pollinator communities. We found an increase in flower visitor richness in our drought years, which occurred in later years than our non-drought years. While Malaise trap data from the RMBL over the last 36 years show statistically significant declines in the abundance and biomass of both Diptera and Hymenoptera (D.W Inouye, *pers. comm.*), if that trend were driving our results, we would have expected a trend in the opposite direction (i.e., reduced flower visitor richness, rather than increased).

Future research directions

The potential for disturbances to impact plant and pollinator community stability via niche breadth expansion underscores a number of future research directions. A first key area for future research is to link niche breadth dynamics with functional implications. While we discussed the potential for such functional implications above, there remains a need for studies with this explicit focus. For example, can plants maintain seed production in the face of natural perturbations, because of the expanded breadth of floral visitors that we documented? And similarly, how does niche expansion impact flower visitor fecundity and population dynamics? Second, our study used a relatively specialist plant in terms of its flower visitors, and future research could investigate more-generalist species to test whether similar patterns are maintained. Third, our work investigated niche breadth of a single focal plant species. An interesting extension would instead look at a focal pollinator species across natural disturbance and perturbations. Fourth, expansion from a single species to networks of interacting plants and pollinators would also be fruitful. Fifth, plasticity in niche breadth is not only important for plants and pollinators but is also important in a range of other mutualistic interactions. All of these possible future research directions underscore the importance of long-term data collection, including high-quality records for weather and other abiotic data.

Conclusion

Anthropogenic environmental change is altering multiple dimensions of ecosystems around the world. This, in turn, may have substantial consequences on the species interactions that underpin the provisioning of a wide range of ecosystem services and functions. Much of the previous work on networks of ecological interactions has largely assumed either stasis or small changes in interactions following system changes or perturbations. In contrast, our results suggest that interaction niches in nature can display profound plasticity in response to perturbations. We also underscore that niche and diet theory provide a conceptual underpinning for characterizing changes in interaction niche breadth. We must embrace the dynamism and flexibility of organisms in nature—in concert with mechanistic ecological theory—to understand how ecological interactions, and the ecosystem dynamics and functions that are dependent upon them, will be altered in our rapidly changing world.

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Author contribution statement KLE and CNM contributed equally to this paper. HMB conceptualized the study. KLE, CNM, XL, and BB analyzed the data. KLE, CNM, and BB drafted the manuscript. All authors contributed to data collection. All authors contributed critically to editing the manuscript and gave final approval for publication.

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Declarations

Conflict of interest This article does not contain any studies with human participants or animals performed by any of the authors.

Ethics approval This article does not contain any studies with human participants or animals performed by any of the authors.

Consent to participate Not applicable.

Consent for publication Not applicable.

Availability of data and material The data was deposited in the repository Digital Dryad under the reference number [*ref number provided upon acceptance*].

Code availability Code developed during the current study is available from GitHub, access from the corresponding author on request.

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