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Widening Niche Breadth: Investigating the Plasticity of Plant-Pollinator Interactions

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Abstract

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Plant-pollinator interactions are one of the most ecologically important mutualisms and are a vital part of most terrestrial ecosystems. Despite the importance of these interactions, we still lack understanding of how plant-pollinator interactions fluctuate with changes in resource availability. Fluidity in interactions is important to understand as swiftly changing climates and global pollinator declines threaten stability of ecosystems and maintenance of biodiversity. I investigated the plasticity of plant-pollinator interactions in response to drought conditions and resulting decreases in floral resources. I examined floral visitation to *Ipomopsis aggregata* in the Rocky Mountains of Colorado over the course of two drought years and three non-drought years. I analyzed changes in niche breadth and community composition, predicting broadened niche breadth and varied community composition in drought years compared to non-drought years. My results confirmed broadened niche breadth of *I. aggregata* in drought compared to non-drought years, and visitor category diversity and richness trended higher in drought years. Results also revealed some variation in visitor community composition. Overall, my findings highlight that pollination niches may exhibit considerable plasticity in response to disturbance and that plant-pollinator interactions can be dynamic. This plasticity may serve to stabilize plant and pollinator communities. However, there are also potential negative implications for plants in terms of lower quality pollination service and for pollinators based on fitness costs.

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INTRODUCTION

Interactions between plants and pollinators are considered an immensely important ecological relationship. These interactions are critical to sexual reproduction in most flowering plant species (Ollerton et al. 2011) and are a vital part of most terrestrial ecosystems (Kearns et al. 1998, Ollerton et al. 2011, Bartomeus et al. 2013). Despite these close mutualisms, complex competition is occurring on both sides of the interaction. As plants compete for pollination service and pollinators compete for floral resources, niche partitioning among potential competitors influences the maintenance of biodiversity and ecosystem functioning (Hooper et al. 2005) by facilitating co-existence of species (Levine and HilleRisLambers 2009). Although there are several examples of strong co-dependence between individual plant and pollinator species (Pellmyr 2003, Cruaud et al. 2012), the vast majority of plants and their pollinators are generalists (meaning they can interact with a wide array of pollinators or plants) and have the ability to alter their range of interactions (Waser et al. 1996). Despite the significance of these relationships, we still lack a clear understanding of how interactions between plants and pollinators fluctuate in response to changes in resource availability (i.e. pollination service for plants and floral resources for pollinators). This is particularly important as factors such as climate change and global pollinator declines threaten to substantially disrupt natural environments. Greater understanding of generalization by plants and their pollinators is essential for predicting the impact of disturbance on the stability of plant-pollinator communities.

There are benefits to a wide fundamental niche, or niche breadth flexibility, in that individuals have access to a variety of resources as conditions change. Here, I discuss fundamental niche as the total interactions available to a species, i.e. all the pollinators that are able to visit a flower. For both plants and pollinators the benefits of a wide fundamental niche are largely based on the resulting ability to generalize or specialize interactions based on presence of competitors and the surrounding environment (Batstone et al. 2018). When competition increases, species may alter their resource use through specialization thereby decreasing competition between species or individuals (Hutchinson 1957). Since most plants can potentially be pollinated by various species, a plant species' relative pollinator interactions ('realized niche') can vary depending on the availability of suitable pollinators and the presence of other plant species that share in the pollinator species pool ('fundamental niche'). For example, experimentally removing a pollinator-attracting invasive plant from a plant-pollinator community increased visits to remaining plants and changed visitation frequency of common pollinator groups (Baskett et al. 2011). Similarly, it is also true that removing a single pollinator species can change pollinator foraging behavior to impact plant-pollinator interactions in the remaining community (Brosi et al. 2017, Hallett et al. 2017). Indeed, niche partitioning, whether among plants for pollinators or pollinators for different flowers, is likely driven mostly by the foraging choices of pollinators, at least in the short term. Like plants, pollinators may have very broad fundamental niches (Waser et al. 1996), which gives them latitude to alter the set of plants they interact with when disturbance (change in resource availability) occurs. Nevertheless, several aspects of plant anatomy and physiology drive pollinator choice. Different pollinators prefer certain floral traits (Grant and Grant 1965), and some floral configurations may exclude some types of pollinators (Olesen et al. 2007b). This trait compatibility may provide enhanced pollination effectiveness for plants and increased floral rewards for pollinators. However, even if plants and pollinators are compatible on the basis of traits, the quality of floral rewards remains important to pollinator foraging decisions (Konzmann and Lunau 2014, Fowler et al. 2016).

We continue to have a poor understanding of how perturbations which alter resource availability will affect interactions between species. While interaction changes between species can occur in the absence of perturbation (Rosenzweig 1991), environmental disturbances also have the potential to alter the way that species interact. Globally, the rate of severe climate-related events, including drought, is predicted to increase (Sheffield and Wood 2008, Dai 2012), underscoring the importance of understanding how disturbance impacts plant-pollinator systems compared to years of more amenable conditions (e.g higher rainfall). In particular, research has shown that drought poses a significant threat to both flowering plants and their pollinators (Brown et al. 2016), despite the fact that drought may often be a short-term disturbance. In pollination systems, water availability can drastically change the quality and quantity of floral resources for pollinators, which can in turn influence the dynamics of plant-pollinator interactions. For example, changes in floral resources due to drought can occur through phenological (timing) mismatches of flowering and pollinator emergence (Memmott et al. 2007, Hegland et al. 2009, Miller-Struttmann et al. 2015), decreased and more concentrated nectar (Waser and Price 2016), and decreased flowering per plant (Burkle and Runyon 2016, Phillips et al. 2018). In addition, drought conditions may alter floral plant community composition as well as floral resource abundance (Thomson 2016, Phillips et al. 2018). Decreased overall plant abundance may result in decreased competition between plants and increased availability of pollinators, thus allowing for more interaction generalization and broadened plant niche breadth. Thus, drought conditions can act as a natural experiment where niche breadth under average climate conditions can be compared to a perturbation that reduces resource availability for pollinators.

With this study, I answer the question: how plastic are plant-pollinator interactions in response to disturbance? It is not known how drought and resulting changes in resource availability impact plant niche breadth, and these shifts may provide important clues into how plants and pollinators respond to changes in resource availability. To assess the plasticity of plant-pollinator interactions, I examined visitation to *Ipomopsis aggregata*, an abundant drought-hardy plant, between drought and non-drought years in the Rocky Mountains of Colorado utilizing a long-term dataset collected over the past two decades. *I. aggregata* is known to be pollinated frequently by hummingbirds (Price et al. 2005). It is less commonly but most effectively visited by bumblebees (Mayfield et al. 2001), and occasionally visited by a wide range of other insects (Price et al. 2005). I hypothesized that niches within plant-pollinator systems are plastic, and interactions will change in response to changes in resource availability (i.e. floral abundance). I further hypothesized that niche breadth of floral visitors (i.e. visitor diversity) to *I. aggregata* will broaden in drought conditions, and community composition of floral visitors will be different than in normal precipitation years.

MATERIALS AND METHODS

Overview

For this study, I utilized *I. aggregata* visitation data from three non-drought years and two drought years, ranging from 1997 to 2018 collected in subalpine meadows in Colorado, USA. In each year field teams measured visitation to *Ipomopsis aggregata* by several categories of visitor over the course of several weeks within peak bloom for the species. I analyzed whether niche breadth broadened between drought and non-drought years, as well as if community composition changed.

Study System

Each year the field team collected field data at and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (38.9585° N, 106.9878° W). At ~9,500ft elevation, this ecosystem is comparable to subalpine meadows throughout the Western United States and experiences heavy winter snowfall. Total snowfall averages 1063.8 cm with 90cm of snow remains on the ground on May 1st (http://www.gothicwx.org). Vegetation relies on resulting snowmelt through the low-precipitation early summer until monsoons begin in early-mid July.

Ipomopsis aggregata (Pursh.) V.E. Grant (Polemoniaceae) is a flowering plant species common at the RMBL and found abundantly in montane regions from British Colombia to New Mexico and Arizona. The species grows well in drier and disturbed soils on slopes and hillsides. The floral morphology of *I. aggregata* (i.e. long, narrow corolla tubes, bright red coloring) suggests pollination predominantly by hummingbirds (Grant and Grant 1965, Crepet 1984), though visitation from several categories of insect, including solitary bees, wasps, and flies, also occurs (Price et al. 2005). Due in part to its use as a model organism, much is known about *I. aggregata* in this study location (Campbell 1996). *Ipomopsis aggregata* is monocarpic, meaning that individuals only flower once before dying, indicating the importance of pollination and seed set each year. Previous work demonstrates that despite its morphology and high hummingbird visitation, bumblebees are its most effective pollinator (Mayfield et al. 2001). Past research also indicates that the plant is pollen-limited (Hainsworth et al. 1985) and does not reproduce through self-pollination (Waser 1978), meaning that seed set is poor in absence of pollinators. Notably, *I. aggregata* flowers in drought years, when other flowering plant species may not (or may severely reduce the amount of flowers), and therefore represents a larger portion of floral resources in these years.

Visitation Measurements

This study uses historical visitation data collected in the years 1997, 1998, 2001, 2012, and 2018. Price et al. (2005) detail methods for observations in 1997, 1998, and 2001. In these years, the field team observed visitation at individual *I. aggregata* across three sites (P, T, and V). Observation for all sites occurred once per week over a six-week period (five weeks in 1997), with each week including three one-hour observations: morning, midday, and afternoon. One team member each year observed between 12 – 31 individual *I. aggregata* within a plot with individual plants chosen randomly. Each observation period consisted of one observer recording all visits to focal plants simultaneously, as well as marking the number of open flowers on each focal *I. aggregata* after data collection. One visit consists of a pollinator interacting with the reproductive parts of the *I. aggregata* flower. I utilized data from the years 1997, 1998, and 2001 due to their consistent sampling design comparable to data collection in recent years. Data from other years were not used because they could not be transformed into analogous visitor categories with the same level of detail.

In 2012 and 2018 observers recorded visitation at several sites chosen in the RMBL area; in 2012 the field team visited 15 sites twice during flowering period (11 were visited once) and in 2018 visited six sites four times (one was visited three times). Field teams only selected sites that contained at least 20 flowering *I. aggregata* at the time of sampling (for consistency with Price et al. 2005), with one 5m radius floral patch per site. The floral patch was randomly selected from total site area before the first sampling, marked with flags, and kept consistent for all sampling visits. At the beginning of each site visit the team conducted a floral survey of every *I. aggregata* and all co-flowering plants within the 5m radius patch. In each floral survey team members counted the number of flowers on each plant within the plot. Observers performed pollinator surveys by conducting three 10-minute observations of the 5m plot at each site visit in 2012, with one 10-minute observation preformed per site visit in 2018. Observations entailed walking through the patch and nondestructively identifying each floral visitor according to 30 distinct categories (see Brosi et al. (2017). To supplement within plot observations and account for observer movement biasing some pollinator groups such as hummingbirds more than others, observers recorded one additional 10-minute observation at each patch prior to other sampling. In 2012 one to three observers worked simultaneously, while in 2018, exactly two observers collected each sample.

I later converted visitor identifications into seven visitor categories – bumblebee, butterfly, hummingbird, hoverfly, other fly, solitary bee, and wasp – similar to those used by Price et al. (2005) for comparison (see Table 1). Due to difficulties in determining accurate counts during observation periods between years, I excluded visits by ants, beetles, and other small insects.

Data Analysis

I used the statistical software R for all statistical analysis (R Core Team 2018), evaluating changes in community composition and niche breadth (via changes in visitor category diversity) between the drought and non-drought years.

Drought Determination

To confirm the classification of 1997, 1998, and 2001 as non-drought years and 2012 and 2018 as drought years I used non-metric multidimensional scaling (NMDS) to compare multivariate differences in a suite of important weather measurements. I used historical weather information from the Gothic Weather database (http://www.gothicwx.org), which was originally sourced from data collected on site at the RMBL. I included the following variables in the NMDS: total winter snowfall, days above freezing (Nov – May), total water (snow), total days of snow cover, snow cover on April 1st, and snow cover on May 1st. NMDS was performed with the vegan package using the metaMDS function (Oksanen et al. 2019). I roughly classified years based on total snowfall, with >900cm of total snowfall classified as non-drought and <900cm of total snowfall classified as drought. I then fit an environmental vector (drought) onto the ordination to project correlation of drought and the ordination (function envfit).

Niche Breadth – Species Diversity

I assessed potential changes in niche breadth of flower visitors to *I. aggregata* by comparing the visitor category richness between drought and non-drought years using individual-based rarefaction. I used visitor category richness due to broader visitor identification in historical data. Individual-based rarefaction gives the rate of richness accumulation with increasing number of individual visits sampled. This approach allowed me to compare sites and years with substantially different sampling effort, which is known to have very strong effects on measured diversity (Chazdon et al. 1998). Rarefaction analyses were conducted using the iNEXT package in R (Hsieh et al. 2016), generating rarefied and extrapolated diversity estimates. I examined changes between years and between combined drought and non-drought groups, using both species richness and Shannon's diversity. I assessed differences between drought and non-drought years via overlap in 95% confidence intervals.

Community Composition

Community composition refers to the identity and abundance of species in a biotic community, in this case floral visitors to *I. aggregata*. To examine community composition differences between drought and non-drought years I calculated community dissimilarity indices between sites using the Morisita-Horn index for construction of dissimilarity matrices, due to its insensitivity to sampling effort differences (Horn 1966). I compared community composition via dissimilarity using permutational multivariate analyses (Adonis function, R vegan package). I further visualized these differences in community dissimilarity using non-metric multidimensional scaling (NMDS). NMDS is an ordination technique used for non-linear data (e.g. species abundance counts) that represents the position of sample units in multidimensional species space using distances between the composition of sample units for ordination. Therefore sample units clustered closer together have greater similarity while sample units far apart on the ordination have greater dissimilarity. I used the function metaMDS (vegan package) to perform the ordination from a dissimilarity matrix (function vegdist). I then fit the environmental vector (drought) onto the ordination to project correlation of drought and the ordination (function envfit).

RESULTS

Overview

Across all years, field teams observed 1,585 visits to *I. aggregata* over the course of over 200 hours of observation time. Of the seven visitor categories, only bumblebee, hoverfly, and hummingbird categories were observed in all five years (Table 1). As predicted, hummingbirds made up the greatest percentage of visitation each year, ranging from 36% to 68% of total visits.

Drought Determination

NMDS visualization of drought and non-drought years confirmed that years I grouped as non-drought (1997, 1998, 2001) and drought (2012, 2018) separated in multivariate space (Appendix A), based on total winter snowfall, days above freezing (Nov – May), total water (snow), total days of snow cover, snow cover on April 1st, and snow cover on May 1st. Stress was 0.075, indicating an excellent fit for the given ordination (McCune et al. 2002).

Niche Breath – Species Diversity

Using individual-based rarefaction, I found observable trends in differences in visitation diversity between drought and non-drought years (Fig 1). Drought years had a significantly higher species richness of visitor categories than non-drought years, while with Shannon's index visitor category diversity in drought years was higher than non-drought years with some overlap between 95% confidence intervals. When examining individual years, 2001 showed higher visitor category richness than the other non-drought years (Fig 1). For drought years, the 2012 trend displayed higher visitor category richness while the 2018 trends showed higher Shannon's diversity.

Community Composition

Ordination of sites in species space suggested some difference in average community composition between drought and non-drought years (Fig 2). Drought (black arrow) explained much of the variation along axis 1 ($p = 0.068$, $R^2 = 0.14$), with difference between drought and non-drought sites spread largely along the same axis. 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. In ordination space, the wasp category was visually particularly associated with drought, relative to other visitors. Stress (goodness-of-fit, reflecting how well the observed distances among samples is reflected in the ordination) as 0.17, which may indicate a good fit for the given ordination (McCune et al. 2002). When examined using permutational multivariate analysis (Adonis), I did not find statistically significant differences in community composition between drought and non-drought years ($p = 0.157$, Table 2), perhaps in part because of the broad variation in community composition in drought years.

DISCUSSION

In this study, I examined how niche breadth and community composition of flower visitors to *I. aggregata* changed in drought years compared to non-drought years. I hypothesized that pollinator niche breadth would widen to include more visitor categories in drought years and that flower visitor composition would vary between drought and non-drought years. I found significantly higher observed richness of visitor categories in drought years, consistent with the idea that pollinator niche breadth increases in conditions of relative resource scarcity. There was also a trend toward differences in the composition of the visitor community between drought and non-drought years, though there was no statistically significant difference.

My findings highlight that pollination niches may exhibit considerable plasticity in response to the environment and that plant-pollinator interactions can be dynamic. In generalist plant-pollinator interactions, fluidity in partnerships may help stabilize the long-term persistence of both pollinators and plants. However, there are also potential negative implications for plants in terms of lower quality pollination service (i.e. heterospecific pollen transfer) and for pollinators based on fitness costs. Fluidity in interactions is important to understand, as swiftly changing climate and global pollinator declines may threaten stability of systems and maintenance of biodiversity.

Changes in species visitation in response to drought may preserve community stability and ecosystem functioning (Olesen et al. 2007a, Ramos-Jiliberto et al. 2012, Valdovinos et al. 2013, Rohr et al. 2014), particularly for plants. Each drought season could have distinct impacts on community composition. My results suggest, however, that during drought years broadened niche breadth may allow for continued pollination service to *I. aggregata,* with the assumption that all visitors pollinate at some extent, therefore prompting continued community stability. Observed niche breadth broadening is important as the floral traits of *I. aggregata* suggest specialization towards hummingbird pollination (e.g. bright red petals, tubular shape, copious nectar) and hummingbirds are indeed its most frequent visitor in this study. Specialized species are thought to have greater risk of negative impacts with disturbance (Biesmeijer et al. 2006, Aizen et al. 2012). However, this study and others (Price et al. 2005) found that a variety of other pollinator types also visit *I. aggregata* flowers, and I further found that this variety increased in drought years. Diverse flower visitors may help to buffer fluctuations in the contribution of any one visitor category to *I. aggregata* pollination, but this is contingent on the relative effectiveness of different flower visitors at pollination. When examining plant-pollinator interaction effectiveness, one study found that when a common bumblebee species was removed, pollination was offset by increased and effective wasp pollination (Hallett et al. 2017). In this study I did not measure the effectiveness of different flower visitors at pollinating *I. aggregata*. Nevertheless, 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). There is evidence that the greatest impact of generalist pollinators is due in part to their abundance relative to specialists (Maldonado et al. 2013). Thus, even if visitation of some of *I. aggregata*'s pollinators is inconsistent in drought years, there may not be reduced pollination and seed production if other pollinators that do not usually visit *I. aggregata* do so with greater frequency.

Despite the compelling possibility of continued pollination service and maintenance of ecosystem functioning, my findings of broadened niche breadth and varied community composition in drought years could alternatively have deleterious implications for the reproductive success of *I. aggregata*. In particular, observations of varied community composition may indicate generalization on the part of pollinators potentially visiting a wider array of plant species. While having a diversity of generalized pollinators may be beneficial for maintaining reliable pollination services over time, specialization is preferable for ensuring effective conspecific pollen transfer. Movement of floral visitors between plant species can lead to interspecific pollen transfer (Kohn and Waser 1985, Feinsinger et al. 1988, Murcia and Feinsinger 1996, Bell et al. 2005). This heterospecific pollen deposition may prevent fertilization by additional pollen deposition on a stigma, ultimately decreasing plant reproductive success (Campbell and Motten 1985, Waser and Fugate 1986, Galen and Gregory 1989, Morales and

Traveset 2008). For hummingbirds, the most common visitor to *I. aggregata*, one study found that every intervening visit to a different flower species reduced conspecific pollen transfer to same species flowers by an average of 76% (Murcia and Feinsinger 1996). Further, a recent field study found that for *Delphinium barbeyi*, a similar and competing plant species to *I. aggregata*, heterospecific pollen deposition was common at low levels, and there was a clear positive relationship between conspecific pollen and seed production (Briggs et al. 2016). In drought years *I. aggregata* pollen production is reduced (Waser and Price 2016), likely making this relationship more pronounced. My findings indicate that loss of foraging specialization in drought years and greater variation in community composition combined with broadened niche breadth may result in higher heterospecifc pollen deposition, with negative consequences for reproduction even if effective pollinators are still present (Brosi and Briggs 2013). Ultimately, how niche breadth and community composition changes impact plant community stability and reproduction will depend on the net change in the quantity and quality of pollination services.

Just as changes in interaction patterns can have positive and negative effects on plants, they can also have varying impacts on pollinators. While plants continue to receive sufficient visitation for effective pollination, floral visitors may continue to access floral rewards of nectar and pollen based on the possibility of shifts in realized niche (Ramos-Jiliberto et al. 2012, Valdovinos et al. 2013). Here I found widened niche breadth of *I. aggregata* in drought years, suggesting the ability to pollinators to seek broadened floral rewards in years of drought. However, there remain possible negative implications of decreased specialization for floral visitors. For pollinators there is a trade-off between visiting flowers of the same species and visiting flowers of different species. Several hypotheses explain why pollinators often visits flowers of the same or similar species (Waser 1986, Chittka et al. 1999, Goulson 1999), but generally individual floral visitors must learn how to properly handle specific types of flowers to receive rewards (i.e. manipulate flowers to extract floral resources). Accordingly, initial handling time takes longer for more complex flowers (Laverty 1994, Gegear and Laverty 1995) such as those of *I. aggregata*. Decreased floral abundance may cause pollinators to seek alternate floral rewards, as suggested by my finding of widened niche breadth for *I. aggregata* in drought years, which may in turn cause initial handling time to increase if more types of flowers and more complex flowers are visited at once (Woodward and Laverty 1992, Laverty 1994, Gegear and Laverty 1995, Chittka and Thomson 1997). This may decrease foraging efficiency of individual pollinators with costs for individual fitness if floral constancy is not established. Further, drought substantially decreases *I. aggregata* nectar production (Waser and Price 2016), sometimes not producing enough nectar to be detectable with our methods (personal observation 2018). In addition, nectar concentration increased (personal observation 2018). Variation in nectar production and concentration can additionally affect flower handling time by pollinators (Neff and Simpson 1990, Cresswell 1999). Further, if visitation to *I. aggregata* increases due to decreased overall floral resource abundance, competition among floral visitors may increase. This increased competition may have negative effects on pollinator fitness, for example if flowers are already drained when a visitor arrives, making more visits necessary. Competition between visitors is often avoided through niche partitioning which facilitates coexistence of species (Levine and HilleRisLambers 2009). However, if alternative resources are not available, as may be the case in drought years, niche partitioning may not be possible to the necessary degree. Overall, similar to implications for *I. aggregata*, my findings suggest both positive and negative results for plant-pollinator community stability.

My findings indicate overall plasticity of interactions between plants and pollinators in responses to drought. While this may have both positive and negative results for plant-pollinator community stability, it is important to consider in the broader context of changing climates and global pollinator declines, both of which may be associated with changes in resource availability. Globally, climate change is predicted to have widespread consequences for precipitation, with a higher frequency of severe drought events in many ecosystems (Sheffield and Wood 2008, Dai 2012). If other plants experience similar interaction changes to *I. aggregata* in response to drought, there may be similar implications for plant-pollinator community stability as well. Further, changing climates, as well as several other environmental and human impacts, are implicated in global declines of pollinators (Potts et al. 2010). Decreases in number of pollinators may be considered a type of changing resource availability in plant-pollinator interactions. Together, changing climates and global pollinator declines present unique challenges for determining how interactions change in altered environments (Scheffers et al. 2016). The more we understand about how plant-pollinator interactions change in response to disturbance, the better our ability to predict change consequences and inform conservation efforts.

This work, as in all field studies, has several limitations that affect the interpretation of my results. A key limitation is that my analysis utilized multiple years of historical data, which were not collected consistently. Multi-year data sets are becoming increasingly important as ecologists seek to generalize results and understand trends over time. My study greatly benefits from this type of long-term data collection. However, due to the large scale of data collection in this study – temporally and spatially – sampling effort differed somewhat between years. My analysis plan dealt directly with the limitation of sampling differences among years by examining niche breadth and community composition changes as these do not depend on total abundance comparisons and can be preformed with techniques that account for sampling effort. Between years, sampling effort differed in the number of observers, number of sites sampled, and time spent observing. This could have consequences for my results; for example, observing sites over a broader spatial range, as occurred in both of the drought years, may result in more varied floral-visitor communities relative to the sites utilized in non-drought years, which were much more geographically proximate. Further, drought and non-drought observations varied temporally, with drought year observations occurring over a decade after those in non-drought years. This leaves the possibility that changes in visitation occurred due to long-term shifts in visitors instead of drought effects. However, the broadness of visitor categories used may help to account for these differences. Lastly, because of sampling effort differences I was not able to directly compare visitor abundance between years in this work. Visit abundance varied substantially between years (Table 1) with 2018, the year with the lowest sampling effort, showing the lowest visit abundance. Estimating how visitor abundances also differ between drought and non-drought years (or some other perturbation) would help strengthen hypotheses for how shifting niche breadth affects community resilience and should be addressed in future research.

From my findings it is clear that the potential for disturbance to impact plant and pollinator community stability underscores a number of future research directions. Future research should pursue investigation of interaction plasticity for other plants and other geographic areas to determine if my findings are consistent across species and systems. Further, plasticity in niche breadth is not only important for plants and pollinators but is important to investigate in other mutualistic interactions. Understanding interaction plasticity can help us make predictions for overall ecosystem stability and maintenance of biodiversity, which is necessary as we confront changes due to rapidly changing climates and human disturbance.

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TABLES

Table 1. Relative species visit abundances and total recorded floral visits per year. Relative visitor category abundances of visits to *Ipomopsis aggregata* shown as percentages for each year. 1997-2001 are normal precipitation years while 2012 and 2018 are drought years. Total recorded visits are provided for further context. Information on sampling effort per year detailed in methods. Bumblebee = all *Bombus*; Butterfly = all butterflies; Hoverfly = Syrphidae; Hummingbird = Broad-tailed and Rufous Hummingbirds; Other fly = Diptera; Solitary bee = all solitary bees, including halictidae, megachilidae; Wasp = all wasps.

Year	Bumblebee	Butterfly	Hoverfly	Hummingbird	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*	2.72	1.77	14.27	59.38	10.05	5.57	6.25	736
2018*	6.12	2.04	24.49	38.78	8.16	0	20.41	49

Table 2. Results of Permutational multivariate analysis of variance (Adonis function) of total observed visits between drought and non-drought years. Tests are based on Morisita - Horn dissimilarity with 100000 permutations.

Factor	Source	d.f.	SS	MS	F	R2	P
Drought	Drought	1	0.5351	0.53507	1.8477	0.04523	0.157
	Residuals	39	11.2937	0.28959		0.95477	
	Total	40	11.8288			1.00000	

FIGURES

Figure 1. Individual-based rarefaction analysis of visitor category indicating niche breadth changes. Observed rarefaction curves where solid lines represent observed species accumulation with the number of visits observed, and dashed lines represent extrapolated accumulation. Symbol between solid and dashed lines indicates # of visits actually observed. **(A)** Rarefaction of each sampled year (1997 = square; 1998 = circle; 2001 = triangle; 2012 = no symbol, presented without extrapolation; 2018 = diamond) for species richness and **(B)** Shannon's diversity index. **(C)** Rarefaction of drought (2012, 2018) and non-drought years (1997, 1998, 2001) combined with species richness index and **(D)** Shannon's index. **C** and **D** presented without extrapolation due to high # of individual visits observed.

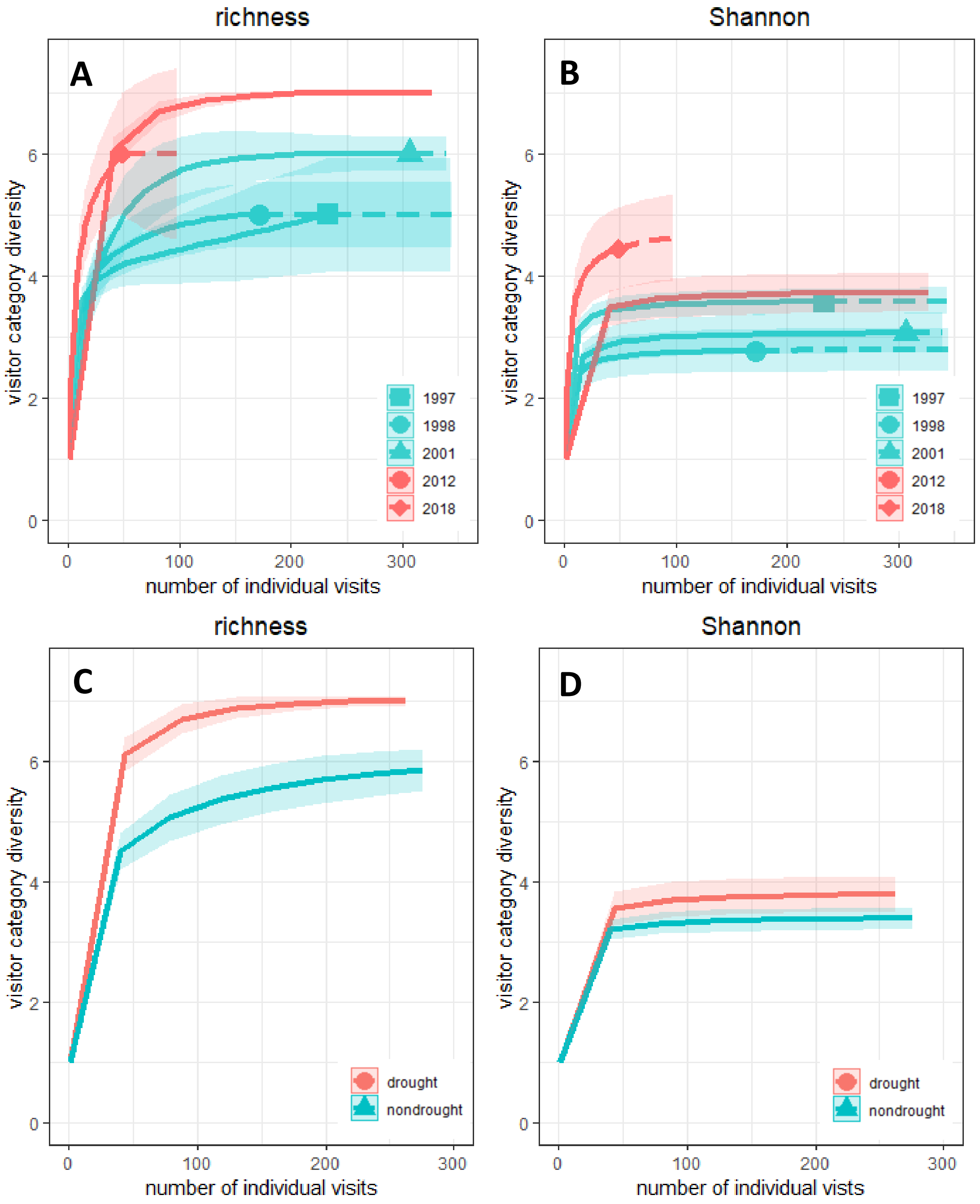
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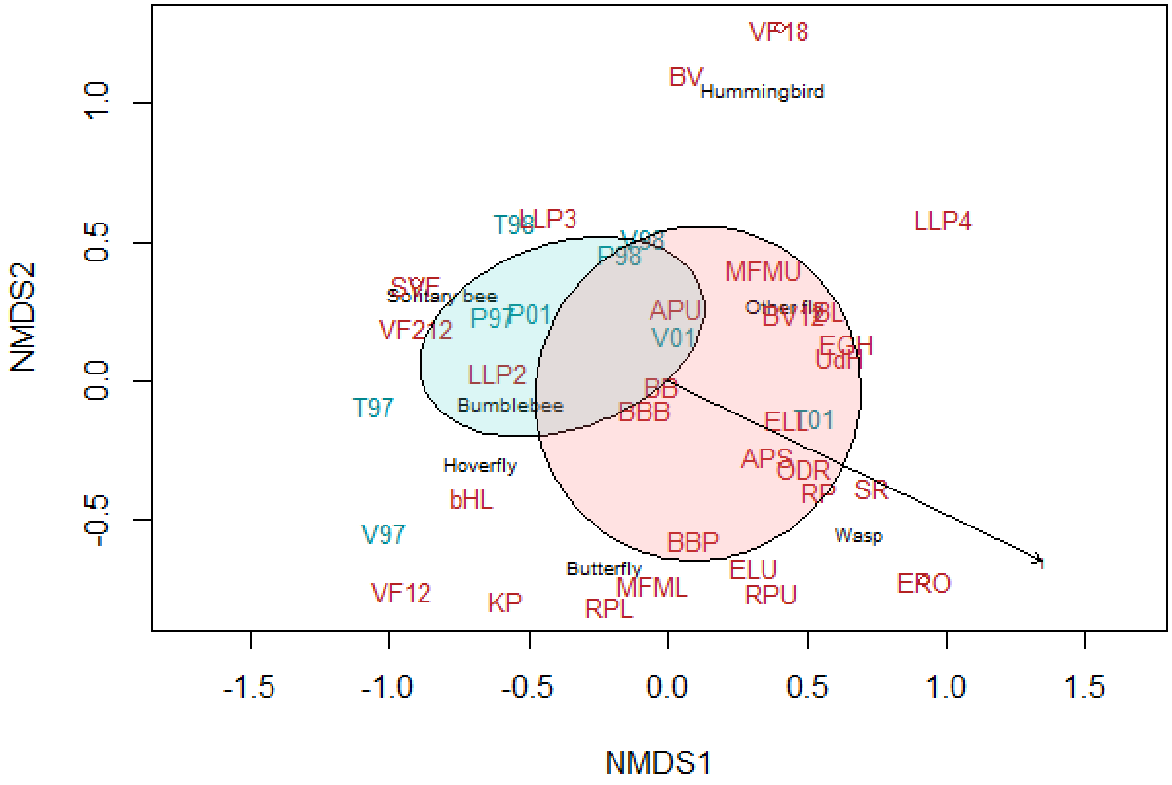
Figure 2. Morisita-Horn based non-metric multidimensional scaling (NMDS) plot of *I. aggregata* visitor community composition at 41 sites in 5 years. NMDS plot (stress = 0.17) shows drought as a driver of dissimilarity. The direction of drought obtained by fitting the abiotic factor in the ordination space of sites shown with the black arrow. Non-drought (blue) and drought sites (red) displayed in species space (species categories given in black). Ellipsoids represent standard deviation of drought and non-drought site averages.



APPENDIX

Appendix A. Non-metric multidimensional scaling (NMDS) plot of environmental variables. NMDS plot (stress = 0.075) shows years separate into drought and non-drought clusters. The direction of drought obtained by fitting the drought in the ordination space of environmental variables shown with the black arrow. Non-drought (blue) and drought sites (red) displayed. Ellipsoids represent standard deviation of drought and non-drought year averages.