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Simultaneous niche expansion and contraction in plant–pollinator networks under drought

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Oikos

2022: e09265

doi: 10.1111/oik.09265

Subject Editor: Ignasi Bartomeus
Editor-in-Chief: Dries Bonte
Accepted 15 July 2022

Global climate change threatens to substantially rearrange species interactions, yet we lack clear predictions on how these changes will cascade through communities. Many perturbations associated with climate change, such as droughts, will change resource levels, with consequences for species interactions and thus ecological network structure. Diet theory predicts foraging niche expansion when preferred resources are scarce, yet under severe resource reduction interspecific competition could alternatively increase niche partitioning. Such niche expansion and/or contraction could profoundly shape ecological network structure following perturbations, but whether these predictions hold at the community level is unclear. We studied the impacts of drought on plant–pollinator networks in long-lived perennial plant communities in which drought affects flower and floral reward production. We assessed whether drought effects on available floral resources altered pollinator dietary niche breadth to drive higher network-level generalization. Accounting for interaction abundance and species turnover, we compared plant–pollinator networks in two drought years and three non-drought years. We found that drought restructured plant–pollinator networks, resulting in more generalization in terms of presence–absence of links, yet more specialization when accounting for quantitative network intensities. Our results support the application of diet theory to understanding how perturbations may impact ecological network structure.

Keywords: consumer–resource, diet breadth, foraging, mutualistic networks, niche partitioning, subalpine meadow

Introduction

In a rapidly changing world, it is critical that we understand how multispecies ecological communities respond to perturbation. Complex communities of interacting

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species form ecological networks whose overarching structures may be important for species persistence (Dunne et al. 2002, Bascompte et al. 2006) and ecosystem functioning (Stavert et al. 2019, Arceo-Gómez et al. 2020). Plant–pollinator networks are interactions of particular concern (Winfree et al. 2009), given their roles in agricultural production (Klein et al. 2007); the reproduction of 80–90% of wild angiosperms (Ollerton et al. 2011); and more broadly in the creation and maintenance of biodiversity (Bascompte et al. 2006). While some previous studies have examined how perturbations affect plant–pollinator network structure (Lu et al. 2016, Biella et al. 2020) for the most part this work has been descriptive in nature, rather than using ecological theory to contextualize or predict how networks will respond to perturbations. Even in theoretical work simulating perturbations, rules guiding how species connect or rewire after these changes have typically not been grounded in known ecological principles, but instead have followed somewhat arbitrary rules such as random rewiring with weighting by generalization (Zhang et al. 2011, Ramos-Jiliberto et al. 2012).

To mechanistically understand how perturbations will impact plant–pollinator networks, niche and diet theory offer a potentially powerful conceptual framework. Plant–pollinator interactions are labile through time (Alarcón et al. 2008) and can change rapidly with resource and competitor context (Fontaine et al. 2008, Brosi and Briggs 2013, Fründ et al. 2013, Brosi et al. 2017), allowing for the possibility of dietary niche dynamics in response to perturbation. Diet theory offers two general classes of predictions following resource perturbations in consumer–resource systems. First, when preferred resources are depressed, species will expand their foraging niches to compensate (i.e. increased generalization) (Stephens and Krebs 1987, Perry and Pianka 1997). Second, increased interspecific competition – arising from either depression of resources and/or increased pollinator densities – may lead to greater foraging niche partitioning (i.e. increased specialization). In turn, these changes in niche breadth and/or foraging intensity could have substantive impacts on ecological network structure. For example, increases in qualitative niche breadth of pollinators (which plant species are visited) would increase pollinator degree, network connectance and in the absence of other changes, nestedness (Blüthgen 2010) given its dependence on connectance.

Drought is a disturbance that may be particularly relevant for understanding how plant–pollinator networks will respond to perturbations. Particularly in systems with long-lived perennial plants, networks involving the very same plant individuals can be compared in both drought and non-drought states, with potentially dramatic differences in terms of composition of which plants bloom and overall number of flowers. This is in contrast to other disturbances like fire or invasion that have substantive effects on community composition, making it challenging to disentangle the effects of the disturbance from changes in community composition per se. Drought is also an increasing issue around the world given global environmental change (Trenberth et al. 2014). Many regions worldwide are experiencing increased severity and frequency of drought (Zhang et al. 2021), which may have large consequences for species interactions via changes in available resources.

Applying diet theory to plant–pollinator networks in the context of drought perturbations leads to at least three potentially contrasting predictions. First, if abiotic resources (especially water) are scarcer in a drought year and plants reduce floral reward production relative to non-drought conditions (i.e. per-capita resource levels are reduced), pollinators may expand the number of plant species they visit to meet their basic metabolic needs (Montero-Castaño and Vilà 2017, Endres et al. 2021). Thus, plant–pollinator networks becoming more general under drought would be consistent with resource reduction playing an important role in restructuring interactions. This prediction is particularly likely when intraspecific competition dominates consumer dynamics (Fontaine et al. 2008). Second, drought alternatively has the potential to put consumers in heightened competition with other species. Increased interspecific competition may be more likely if diverse consumer communities stay relatively fixed under drought perturbations, while resource levels are reduced. Increased interspecific competition can lead to niche contraction as each consumer focuses its efforts on the resources which it can feed upon most efficiently, given both exploitation and interference competition. This is possible in many temperate plant–pollinator systems since insect population dynamics are moderated to some extent by the resource conditions of the previous year (Boggs and Inouye 2012). Several studies on the diet breadth of birds (Smith 1991, León et al. 2014) as well as pollinators (Fründ et al. 2013) have shown niche contractions following increased interspecific competition. Thus, if we find overall niche contraction this would be consistent with competitive dynamics between species playing a more important role than resource reductions in restructuring interactions. Third, since drought can impact both floral resources as well as pollinator abundance and community composition (Ogilvie et al. 2017), it is possible that relatively balanced negative effects on both the resource and consumer sides could work in tandem to generate little or no impact on diet breadth and thus network structure. This outcome could also result if pollinator floral preferences remain relatively static even in the face of resource reductions and/or increases in competition, though we did not expect this, given that previous work shows substantial dietary flexibility of many pollinators (Inouye 1978, Fontaine et al. 2008, Brosi and Briggs 2013, Fründ et al. 2013).

To test how pollination networks respond to drought perturbations, we assessed plant–pollinator network structure in a montane system in Colorado, USA across two drought and three non-drought years. Because this system experiences major reductions in floral resources under drought conditions (e.g. with many plant species failing to bloom under drought conditions, Supporting information, Inouye and McGuire 1991, Ogilvie et al. 2017), we hypothesized that niche expansion of flower visitors (assumed to be pollinators) following resource reductions would be predominant, causing drought-year networks to become more generalized.

Methods

Study system

In the growing seasons of 2016–2020, we constructed plant–pollinator networks at three sites in and around the Rocky Mountain Biological Laboratory, Colorado, United States (RMBL, 38°57'5''N, 106°59'3''W, 2900 m a.s.l.). Sites were located in montane meadows > 2 km from one another to minimize spatial autocorrelation. Annual precipitation in this system occurs primarily in the form of snow, and thus drought conditions are generally a result of low snowfall/snowpack in the previous winter. Droughts are becoming more frequent at the site (barr unpubl.; D. Inouye, pers. comm.) and climate models for the region predict longer drought periods, less winter precipitation and potentially a weakened summer monsoon pattern (Wi et al. 2012, Pascale et al. 2017), which typically brings midsummer precipitation to these systems. Snowmelt timing represents the strongest determinant of the onset of the growing season (Inouye and Wielgolaski 2003) and the growing season is relatively short, approximately 4–5 months on average (30 year average snow free date: 16 May).

Plant communities in these sub-alpine meadows consist of approximately 50–60 flowering species (Langenheim 1955). Communities are primarily composed of native perennial species with a few annual species (1–2 total) and a small proportion of non-native species (less than 10 total). Most plant species in the system are long-lived and iteroparous. Pollinator diversity in the system consists of approximately 70–80 species (Gezon et al. 2015) including: bumble bees (Apidae*:* Bombus), solitary bees (Andrenidae*,* Halictidae and Megachilidae), hover flies (Syrphidae) and muscid flies (Muscidae). The system does not have exotic honey bees given the high elevation and long snow-covered winters. We never recorded non-insect floral visits in our sampling even though the system does have two species of hummingbirds.

Distinguishing drought and non-drought conditions

We used weather station data collected at RMBL to determine drought status for each year (data courtesy of billy barr, <www.gothicwx.org>). To statistically distinguish between drought and non-drought years, we used permutational multivariate analysis of variance (PERMANOVA) via the *adonis* function in the 'vegan' package (Oksanen et al. 2013), using the following drought variables: total annual precipitation (cm); date of first bare ground; total annual snowfall (cm); number of days above freezing; and number of days snow covered. We defined years based on winters, thus annual snowfall totals would include September–May of the following calendar year. Winters of 2016, 2017 and 2019 (non-drought) significantly differed from winters of 2018 and 2020 (drought) ($R^2 = 0.850$, $p = 0.012$, Supporting information). We also calculated deviations from 30-year averages annual snowfall and total annual precipitation for both drought years. Within the two drought years of 2018 and 2020 there was a 52 and 41 percent decrease in total snow from the 30-year average, respectively. Even more severely, total annual precipitation was decreased 76 and 71 percent in 2018 and 2020, respectively. We subsequently visualized the differences using non-metric multidimensional scaling (NMDS) (Oksanen et al. 2013) (Supporting information).

Interaction sampling

We recorded floral visitation to plants within four 1 × 20 m transects spaced 2 m apart. Transects were divided into sections 2 m in length and each section was observed for a total of 3 min of active observation time per week, for a total of 120 observation minutes per site during each sampling event. Each observation time was divided in half and the section was observed from both sides of the transect equally (90 seconds per side) to reduce visual perspective biases. We selected this method to address known issues of walking transects where observation time per species is unknown and more biased by floral abundance and flower and visitor observability (Gibson et al. 2011). We randomly assigned observers to transect sections to reduce observer biases. A team of observers (a mixture of consistent and different individuals each year) simultaneously sampled different transect sections at a given site (mean ± standard error of number of observers per year was 8 ± 1.54 observers). We strictly randomized the order of transect segment sampling as well as site order in a given week to reduce temporal sampling artefacts. We sampled each site six times per year mid-June to early August and separated sampling bouts by at least seven days.

When a pollinator visited the reproductive structures of a flower, we paused the observation time to catch and handle the pollinator. We identified pollinators in the field to 30 gross categories (Brosi et al. 2017), thus even if a pollinator was not successfully captured we still recorded the visitation event. If captured, pollinators were collected in vials with ethyl acetate for further identification. We identified and released bumble bees and butterflies in the field, because they have been historically oversampled at RMBL and have distinctive morphology. For bumble bees, we also individually marked each worker bee using permanent paint on their thorax and released them back into the site. If we saw the bee foraging in the transects again during the same sampling bout, we did not recount it, so as to avoid over-sampling bumble bee visits (as destructively sampled pollinators could not conduct subsequent flower visits). We excluded aphids, lygus bugs and ants as we did not consider them to be pollinators (Wardhaugh 2015).

All captured specimens were identified to family or generic level using the following resources: Diptera: McAlpine et al. (1981, 1987), Miranda et al. (2013); Hymenoptera: Stemkovski (unpubl.); Lepidoptera: Scott (1992). Whenever possible, the identification was then further refined to taxonomic categories or named species using Savage (2003), Savage and Sorokina (2021) and Stemkovski (unpubl.). The taxonomic resolution of pollinators for our study was uneven (i.e. ranging from named species to some uncaptured taxa only identified to family) as we opted to retain as much data as possible. To ensure that

this choice in uneven taxonomic resolution did not impact our results we additionally standardized to family-level identification. To do this, we created networks by only including insect specimens identified to family and lumping taxa into their family category if they were more finely identified. This did not heuristically change our results (Supporting information).

Network analysis

We performed all data analysis in R 4.1.0 (<www.r-project.org>). A fully reproducible RMarkdown report with all corresponding data is available at (<https://doi.org/10.5061/dryad.jwstqjqcs>). To understand if plant–pollinator niches expanded due to drought, plant–pollinator networks were constructed by pooling observations across samples and sites within non-drought years (2016, 2017 and 2019) and drought years (2018 and 2020). We pooled network data to allow for the most complete diet breadth information, which is a key predictor given our conceptual framework of diet and niche theory. To understand how diet breadth responses differed across sites and years, we split the data first by sites and then again by years and constructed null models bootstrapping to the site or year with the fewest total interactions. We were unable to repeat this process splitting data by site and year at the same time given the unreliability of network metrics of small networks.

Network metrics of generalism

We selected four network-level metrics related to generalism for both raw drought networks as well as for every downsampled non-drought network: 1) links per species (mean number of partners per taxa); 2) connectance (proportion of realized links among all the possible links); 3) H2′ (network-level specialization); and 4) NODF (nestedness metric based on overlap and decreasing fill). We calculated these metrics using the *networklevel* function in the 'bipartite' package (Dormann et al. 2008). Mean number of links, connectance and NODF are presence–absence metrics which assess the extent to which species are broadening their niches to include new resources. H2′ is a quantitative metric that assesses whether species are partitioning niches in terms of the interaction intensities (Blüthgen et al. 2006, 2008). Nestedness is thought to be important for network stability and persistence (Burgos et al. 2007, Zhang et al. 2011, James et al. 2012, though see Staniczenko et al. 2013) and also is sensitive to generalization where increased connectance tends to lead to more nestedness (James et al. 2012, Song et al. 2017).

Null models to account for interaction abundance

We used null models to construct networks in order to test for niche change. We relied on a null model approach because we tallied substantially fewer interactions in drought years relative to non-drought years. To isolate the effects of drought, as opposed to effects of interaction abundance alone, we created custom bootstrapping resampling techniques. We sampled (without replacement) the interactions present in non-drought years until the networks equaled the number of total interactions found in drought years (Supporting information). The process was repeated 999 times to create a null distribution of how networks in drought might look if they were solely a less abundant version of the non-drought network. We compared raw metric values in drought years for each of the four metrics to the null distribution for each downsampled non-drought network using non-parametric permutation tests. We tested statistical significance of the raw metric as the proportion of the permutation distribution more extreme than the raw value. We multiplied one-tailed p-values by 2 to make them two-tailed.

Site and year responses were similarly evaluated with null models. Here for each site or year we bootstrap resampled until the networks all equaled 85% of the number of total interactions within the site or year with the fewest total interactions. Differential responses by site and years were visualized with scatter plots and 95% confidence intervals. We did not statistically test differences between sites and/or years due to concerns of spurious statistical inference and instead present trends only.

Null models to account for interaction abundance and taxonomic turnover

Because we observed different pollinator taxa and plant species (in terms of which ones bloomed) in drought versus non-drought years, we also sought to assess if the differences in niche breadth we observed may have been due to community composition alone (e.g. species present in drought years could be constitutively more generalized relative to those present in non-drought years), as opposed to plastic behavioral pollinator diet changes. To account for this, we conducted a separate downsampling that constrained the non-drought web to taxa (both plant and pollinator taxa) that occurred in both the drought and non-drought years before using the bootstrapping techniques as explained above (Supporting information). Networks were constrained by both plant and pollinator taxa which caused plant richness to differ between drought and non-drought networks by one species (*Boechera stricta*). While this species bloomed in both drought and non-drought years, it interacted with only a single pollinator taxon that was not present in the drought years and thus was removed while constraining by taxonomic turnover.

Results

We observed 6652 interactions in networks pooled for non-drought years (2016, 2017 and 2019) and 1611 interactions in drought years (2018 and 2020). Networks in drought years were smaller in dimension with 42 plant species and 95 pollinator taxonomic categories compared to non-drought years where we observed 57 plant species and 124 pollinator categories. We observed 591 and 384 unique interactions in non-drought and drought years respectively.

Null models to account for interaction abundance

When comparing observed drought years to bootstrapped non-drought networks that accounted for abundance, drought years had significantly more links per species (mean number of partners per taxa, $p < 0.001$, Cohen's $d = 5.824$) and higher connectance ($p = 0.013$, Cohen's $d = 2.597$) than non-drought years (Fig. 1). Drought year networks were significantly more quantitatively specialized (higher H2′) relative to non-drought years ($p < 0.001$, Cohen's $d = 7.900$). Nestedness (NODF) did not differ between drought and non-drought years ($p = 0.693$, Cohen's $d = -0.560$).

Across all four metrics of interest, sites and years behaved similarly such that the effect of drought was greater than between site or between year variability (Fig. 2). There was more site-level separation in the drought years compared to the non-drought years (Fig. 2A). The non-drought year of 2019 appeared to have lower links per species and higher H2′ than the other two non-drought years though we did not statistically test for these differences and instead only present the trends (Fig. 2B).

Null model to account for interaction abundance and taxonomic turnover

Constraining non-drought networks to only include species that were observed in both non-drought and drought years reduced the non-drought networks from 57 plant species by 124 insect taxonomic categories to 37 plant species by 62 insect taxonomic categories and the pool of total interactions (later downsampled) from 6652 to 5940. Constraining the drought networks by the same species pool reduced the network from

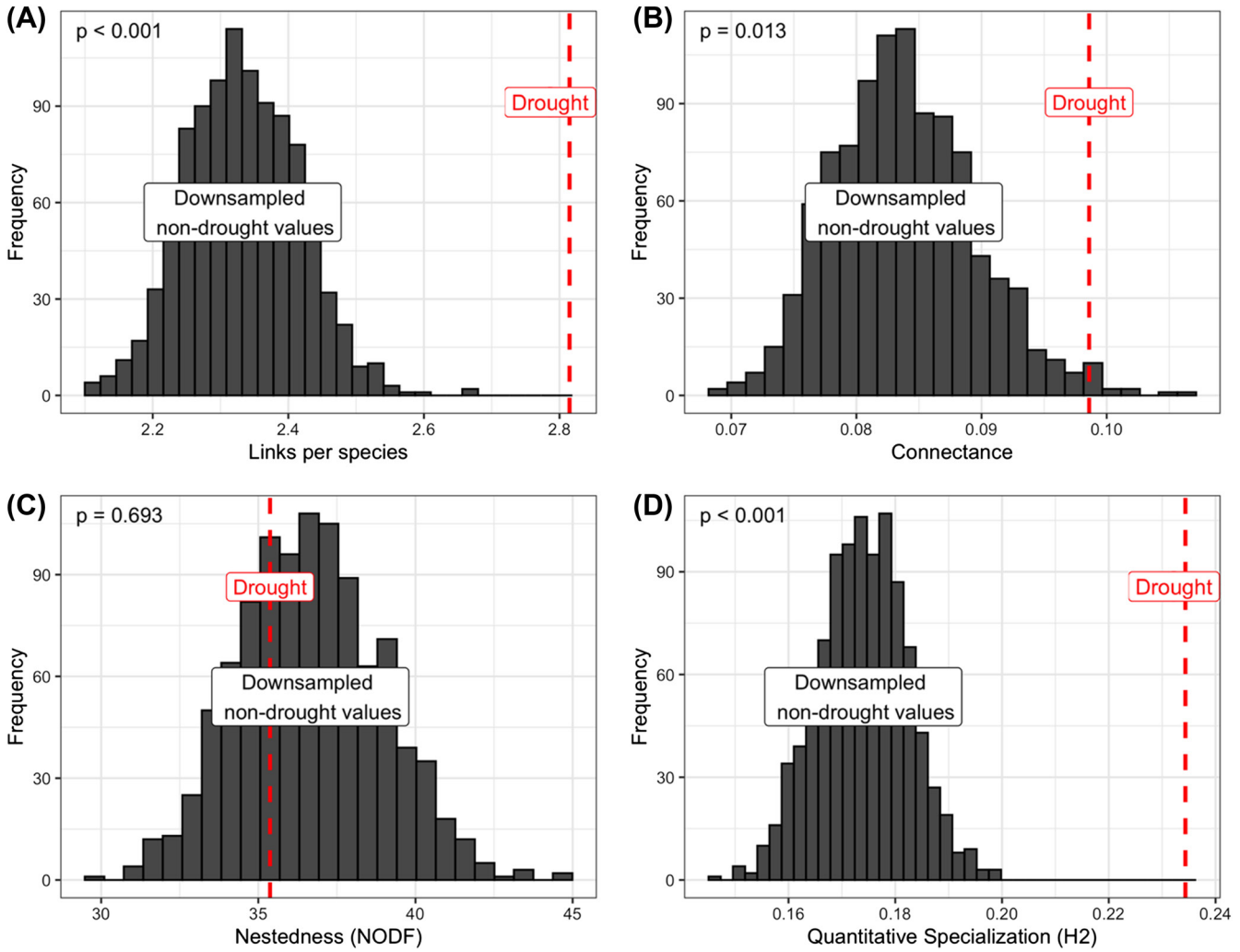


Figure 1. Distribution of network metrics calculated from null bootstraps (999 resamplings) for (A) links per species, (B) connectance, (C) NODF and (D) H2′. In each, the grey histogram bars represent metric values for each bootstrap where non-drought year networks have been sampled until the total number of interactions was the same as that found in the drought year (1788 interactions). The raw drought value for each metric is plotted in red. Significant divergences of this drought value from the distribution of null values is shown in the top corner. Significance was assessed non-parametrically where p-values less than 0.05 indicates the drought web is statistically different from the metrics found in the null bootstraps.

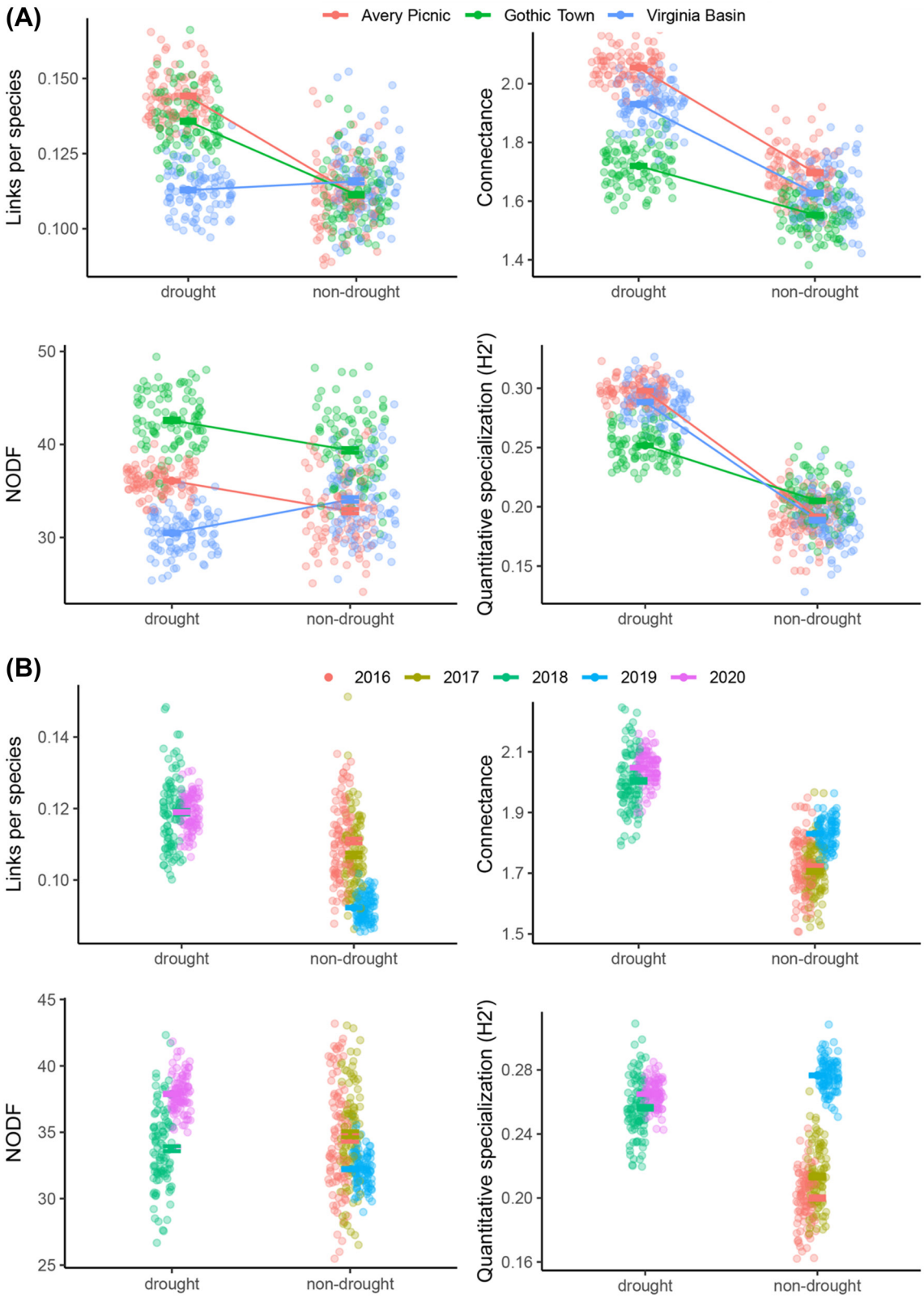


Figure 2. Site (A) and year (B) network metric variation for links per species, connectance, NODF and H2′ for drought and non-drought conditions. Means and 95% confidence intervals are plotted over 100 bootstrap samples per group.

42 plant species and 95 pollinators to 38 plant species by 62 pollinators and the total number of interactions to 1534. When corrected for both abundance and species composition, drought years still had significantly more links per species ($p < 0.001$, Cohen's $d = 6.380$) than non-drought years (Fig. 3), but connectance did not differ between drought and non-drought years ($p = 0.377$, Cohen's $d = 0.310$). Drought networks were significantly more quantitatively specialized ($H2'$, $p < 0.001$, Cohen's $d = 7.779$) than non-drought, but not less nested (NODF, $p = 0.054$, Cohen's $d = -1.650$).

Family-level analyses

Standardizing insect taxa to family-level reduced networks from 57 to 50 plant species, given that these seven plant species were only involved in interactions where the pollinator was not captured and identified to family, and reduced networks from 124 insect taxonomic categories to 24 pollinator families in non-drought years. In drought networks, 41 plant species were reduced to 39 plant species and 94 insect taxonomic categories was reduced to 24 pollinator families. Results using these family-level networks did not qualitatively differ from results based on the networks constructed with more finely identified pollinator taxa above (Supporting information).

Discussion

We found contrasting results for greater network generalization under drought conditions. In terms of the qualitative presence of links and connectance, drought networks were far more generalized than non-drought networks after

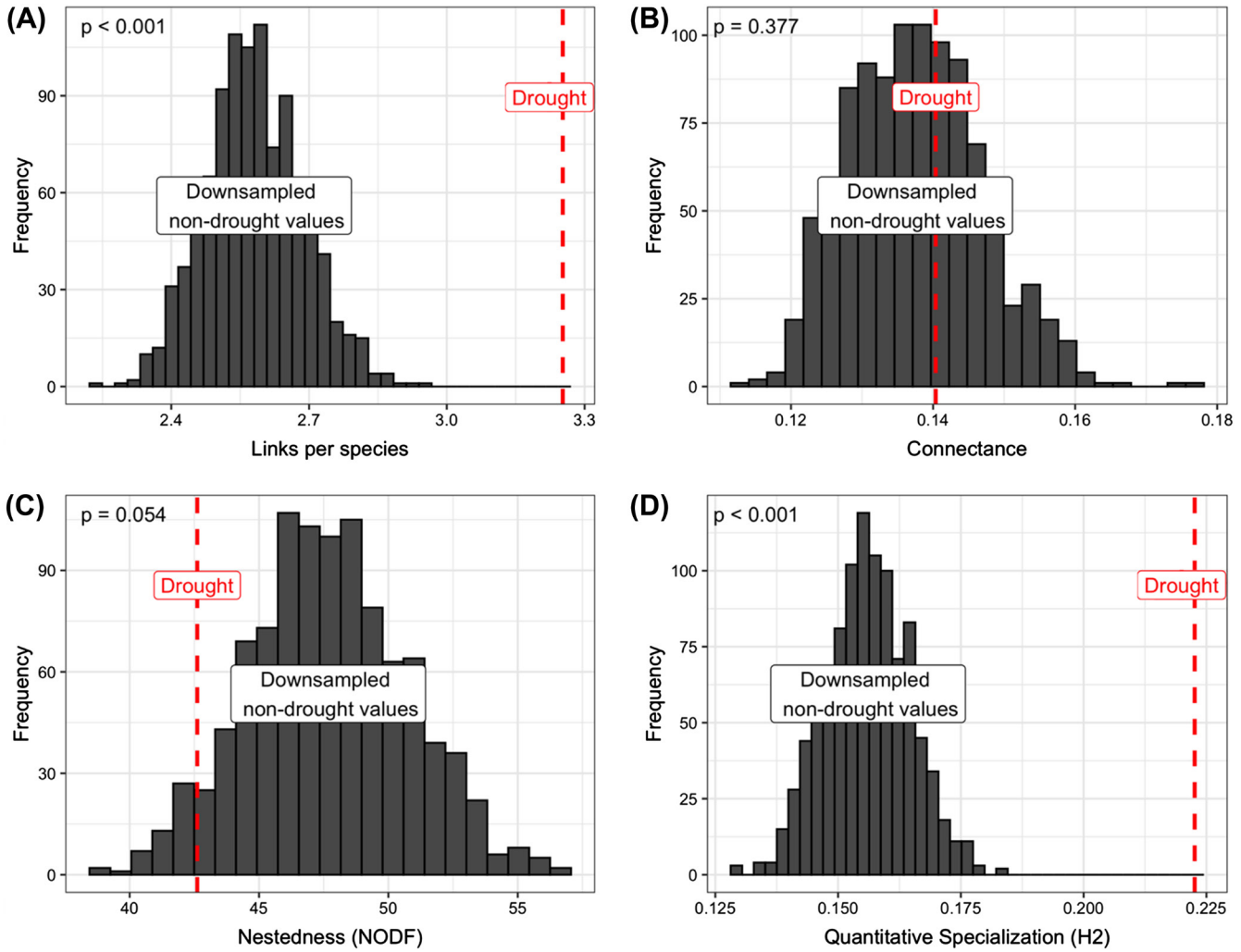


Figure 3. Distribution of network metrics calculated from null bootstraps (999 resamplings) after accounting for taxonomic turnover for (A) links per species, (B) connectance, (C) NODF and (D) $H2'$. Here, species were included in the resampled interaction networks only if they also existed in drought years. In each, the grey histogram bars represent metric values for each bootstrap where non-drought year networks constrained by species overlap have been sampled until the total number of interactions was the same as that found in the drought year (1551 interactions). The raw drought value for each metric is plotted in red. Significant divergences of this drought value from the distribution of null values is shown in the top corner.

accounting for interaction abundances. Conversely, drought networks were significantly more quantitatively specialized relative to non-drought years. Thus, in drought years pollinators appear to both visit a broader range of floral resources, but to also concentrate most of their foraging efforts on a smaller subset of those resources relative to non-drought years. This result is simultaneously consistent with ostensibly contrasting predictions from optimal foraging theory: greater generalization driven by resource reductions and greater specialization driven by increased interspecific competition. This result largely held after accounting for taxonomic turnover, consistent with the idea that behavioral changes in pollinators drove these patterns, instead of the selection of a subset of taxa in drought years that exhibit different foraging preferences than those present in non-drought years.

We predicted that resource reductions due to drought (e.g. substantially fewer flowers and likely less nectar per flower on average) would broaden foraging niches of pollinators in drought years. Our finding of more links per taxonomic category and connectance in drought years aligns with optimal foraging/diet theories which predict niche expansion during periods of food scarcity (Stephens and Krebs 1987, Perry and Pianka 1997). Several studies have found evidence supporting this prediction. Short term manipulations of floral density where key resources were removed by hand decreased quantitative specialization of the remaining species (Goldstein and Zych 2016). Likewise, Fontaine et al. (2008) increased conspecific density of bumble bees – thus increasing intraspecific competition in the absence of interspecific competition – within controlled glasshouse experiments and saw increased foraging niche breadth at higher bee density. They found both qualitative and quantitative foraging breadth increased as resources became more limited due to higher bee densities. Montero-Castaño and Vilà (2017) found that pollinator niche overlap increased following resource reduction (the removal of a highly rewarding and abundant plant). In the same study region as the present work, Endres et al. (2021) found niche broadening of a perennial monocarpic herb in terms of its interaction niche with pollinators in drought years, also in concordance with niche expansion diet theories.

Still, predictions of diet breath expansion in networks under reduced resources may be incomplete without also accounting for increased interspecific competition, which can enhance niche partitioning (Pianka 1974, 1976). Our finding of higher quantitative specialization is consistent with this prediction of niche partitioning with increased interspecific competition. Several studies have also found greater niche partitioning under resource reduction. Species with broadly overlapping diet niches in times of resource abundance often retreat to their specialized reserves when resources become more limited, such as in dry seasons in the tropics (Smith 1991, León et al. 2014). Hummingbirds experiencing similar resource scarcity due to prolonged dry season, yet very different interspecific competition regimes on two islands, broadened their dietary niche when few other species were present but contracted their niche when interspecific competition was greater (Feinsinger and Swarm 1982). Similarly, in manipulative cage experiments, bees faced with stronger interspecific competition (but concomitantly weaker intraspecific competition) contracted their foraging niches (Fründ et al. 2013). Simulation models including adaptive foraging also find that in network topologies with more qualitative resource overlap, pollinators become more quantitatively specialized (Valdovinos et al. 2016). These model predictions were consistent with data on bumble bee foraging (from the same study region as the current work), which showed greater quantitative specialization of foraging on the plant species they shared with the fewest other bee species (Valdovinos et al. 2016).

Several other facets of ecological theory, many focused on different considerations of scale, contribute to explaining how niches might simultaneously expand qualitatively while contracting quantitatively. For example, when habitat patches incur a cost to reach, it can lead to foragers that are habitat (spatial) specialists while simultaneously acting as resource generalists within their specialist habitats (MacArthur and Pianka 1966, Rosenzweig 1981). Even within the same species, scaling from individuals to an entire population can reveal contrasting niche breadth patterns in response to shifts in interspecific competition regimes (Bolnick et al. 2010). More work is needed to understand how foraging dynamics play out to shape ecological networks and their functioning as global change alters both resource and competitive regimes.

Our findings of increased connectance and unchanged nestedness in drought may also have important implications for ongoing network stability in the face of perturbation given that these metrics have been implicated in multiple theoretical studies assessing network stability (Dunne et al. 2002, Bascompte et al. 2006, Burgos et al. 2007, Okuyama and Holland 2008, Zhang et al. 2011, James et al. 2012, Vieira and Almeida-Neto 2015).

Speculations

Few studies have used ecological theory to ground predictions of how perturbations will affect network structure. Understanding the underlying mechanisms driving who interacts with whom and at what intensity will take long-term monitoring of sites to capture years with contrasting abiotic conditions and/or with perturbations such as severe weather events. Using consumer–resource and diet theories will be especially fruitful when perturbations involve changes to resource levels, as is often the case with drought or fire. Thus far, diet theory has largely been absent from discussions of how plant–pollinator interactions will respond to global change (e.g. responses reviewed by Descamps et al. 2021). Similarly, integrating optimal foraging theory within a network context (for food webs) has predicted diet breadth (Beckerman et al. 2006), yet such approaches have not to our knowledge been applied to understand changes following perturbations. We were unable to collect independent estimates of pollinator abundances which are crucially needed to mechanistically understand how foraging theory and competition are shaping plant–pollinator networks. Future work

should thus aim to assess pollinator populations toward this goal. Additionally, relating niche dynamics to temporal partitioning, which was outside the scope of this work, will be important to better understand how interspecific competition structures foraging patterns over the course of growing seasons (CaraDonna and Waser 2020). Recent models that allow for rewiring using mechanistic adaptive foraging processes (Glaum et al. 2021) could help determine interaction rules to test qualitative and quantitative niche dynamics in silico. Empirically, we need tests that manipulate both floral resources and forager species densities (both inter and intraspecific) and observe resulting niche breadth changes (Fontaine et al. 2008, Fründ et al. 2013). Lastly, understanding the functional consequences of changing pollinator niche is an area of active research (Brosi and Briggs 2013, Arceo-Gómez et al. 2016). For example, the increased qualitative generalization we observed may increase conspecific pollen loss and heterospecific pollen transfer, yet increased quantitative specialization might counteract this effect.

Conclusion

Our study shows the potential for perturbations such as droughts to alter foraging patterns and thus network structure, with potentially important – but unknown – consequences for network stability and functioning. Given how rapidly human-induced environmental change is altering both biodiversity and multiple dimensions of the abiotic environment, it is critical to understand how perturbations will directly and indirectly impact species interaction networks (Tylianakis et al. 2008, Ockendon et al. 2014) and the key ecosystem processes and functions they generate. To gain this understanding, it is imperative that mechanistic ecological theory – including, but not limited to diet theory – be developed and applied to this pressing challenge.

Acknowledgements – We thank J. Reithel and RMBL for research support during fieldwork. We thank B. Barr for weather data. We thank D. McDermott, L. Atalla, R. Kamakura, A. Miljanic, L. Gonzales, E. Dymit, K. Endres, S. Spaulding, B. Davis, A. Litz, A. Curtsdotter, A. Fife, D. MacArthur-Waltz, R. Brekke, S. Perrin, M. Caspary, C. Sowers, M. Sharer, H. Benkoski and K. Arrowsmith for field assistance. Insect pinning and laboratory processing was done by E. Dobbs, J. Bosch, C. Book, L. Kapel, B. Wang, B. Miller, D. Seo, T. Charlson, A. Liu, E. Nitze, A. Wassel, P. Grande, B. Brown, A. Lodise, N. Hidalgo, L. Hakkila, S. Boyd, S. Parker, E. Isaac, K. Woytek, D. Lahn and C. Johnson-Garrett. Permission to work on US Forest Service land provided through the RMBL Special Use Permit.
Funding – Funding was provided by NSF (DEB-1834497 to BB), ARCS Foundation (to CM), and a National Defense Science and Engineering Graduate Fellowship (to CM).

Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.jwstqjqcs> (Morozumi et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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