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Connor Morozumi Date

Perturbations in plant-pollinator networks: integrating theoretical and empirical approaches to understand responses to global change

By

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Doctor of Philosophy

Graduate Division of Biological and Biomedical Science
Population Biology, Ecology and Evolution

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M.Sc. Wildlife Ecology, Oregon State University, 2015

Advisor: Berry J. Brosi, Ph.D.

An abstract of a dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy
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Abstract

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Mutualisms—mutually beneficial ecological interactions— are critically important for sustaining life on this planet. Unfortunately, we know little about how these species interactions—including plant-pollinator relationships that are key for agricultural production as well as ongoing wild plant reproduction—will fare with rapid and ongoing anthropogenic change. When changes do perturb these enmeshed systems of multiple species and many interactions, we lack predictive understanding of how these perturbations will ripple through communities. Many studies of plant-pollinator interactions have depicted the relationships as networks, commonly with non-random structures which organize these interactions. Yet we do not understand how these structures influence how the networks will handle changes. Additionally, our understanding of these network structures needs to be better connected to the underlying ecological mechanisms such as resource competition and niche partitioning that are likely contributing to the overarching organization of plant-pollinator interactions across the network. This dissertation combines synthesis, theoretical, and empirical approaches to investigate how perturbation to plant-pollinator networks may alter these important partnerships. My thesis has three substantive chapters beyond the introduction (Chapter 1) and conclusion (Chapter 5). The first of these, Chapter 2, synthesizes and makes recommendations for how modeling and empirical approaches can be better integrated into network studies of plant-pollinator interactions. In Chapter 3, I use a modeling approach to examine how responses to perturbations, in this case robustness to sequential species extinctions, are driven by networks structure both in terms of who interacts with whom as well as their foraging intensities. I found that both topological and quantitative network structure were important in driving robustness, and amplified one another under certain extinction scenarios. In Chapter 4 I use an empirical approach to examine the effects of multiple drought events on restructuring networks within montane meadows in the Colorado Rocky Mountains. I found that under drought, networks simultaneously became more generalized in terms of the number of partnerships species were involved in, yet quantitatively more specialized in terms of their interaction intensities.

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Acknowledgments

It truly takes a village and I have many people to acknowledge who have assisted in getting me to this point in my scientific career and who have made it possible to complete this dissertation research. Thank you, Berry Brosi for pushing my scholarship to new levels. I am a better scientist and scientific communicator because I have been fortunate to work with you. I thank my dissertation committee for their helpful feedback: Katia Koelle (chair), Jaap de Roode, Dave Civitello, and Fernanda Valdovinos. I was incredibly fortunate to have an amazing cohort of friends and colleagues: Loy Xingwen, Daniel Desautels, Donna McDermott, Nicholas Johnson, Amanda Vicente and Brent Allman. You all are so bright, capable and kind. I know my time at Emory would not have been as rich as it was without the six of you. Similarly, the Population Biology, Ecology, and Evolution program has been such an important training ground for me. The small but mighty program has developed my quantitative skills and made me a more justice-focused scientist at the same time. I especially want to acknowledge the mentorship and teaching training I received from Nicole Gerardo. I also want to thank Sarah Emery and Natalie Christian for opening their labs to me in Louisville. Having a local support system towards the end of this PhD has been valuable. My sanity and serenity would have severely diminished without my communities and family who supported and cheered me on each step of the way. This work was financially supported by the National Defense Science and Engineering Graduate Fellowship and the ARCS Foundation Scholars program.

Chapter 2 acknowledgements— I thank Mark Novak, Daniel Stouffer and Fernanda Valdovinos, collaborators on this work who have provided excellent fodder for deeper thought on the ideas presented in this perspective.

Chapter 3 acknowledgements— This chapter is one piece of a much larger effort to understand antinested networks and I would be remiss not to acknowledge the principle architect of the code base for these efforts: Alva Karlsson Curtsdotter. Caleb Sowers and I worked jointly to develop and implement the robustness algorithms. Chris Anderson provided necessary code review and Fernanda Valdovinos provided manuscript review.

Chapter 4 acknowledgements— I wish to acknowledge my collaborators on this work: Loy Xingwen, Tori Reynolds, Beth Morrison, Annie Schiffer, Jade Savage, and Berry Brosi. This chapter could not have happened without a dedicated team who collected and processed these empirical data—especially during several seasons of crucial data collection in which I was not approved for out of state travel by the graduate school / university due to the COVID-19 pandemic. I benefited from fieldwork assistance from stellar individuals including leadership by: Kaysee Arrowsmith, Annie Schiffer, Melissa Caspary, Selena Perrin, and Tori Reynolds. I am indebted to the skilled and tireless field and lab work by: Donna McDermott, Laila Atalla, Renata Kamakura, Andriana Miljanic, Caleb Sowers, Kyra Woytek, Leandra Gonzales, Dylan MacArthur-Waltz, Shelby Spaulding, Kelly Endres, Ellen Dymit, Micah Sharer, Aidan Fife, Ben Davis, Amelia Litz, Erin Paulson, Adrienne Lodise, Eden Nitza, Lindsey Kapel, Albert Liu, Triston Charlson and Emily Isaac, Bijia Wang, Blake Miller, David Seo, Anna Wassel, Payton Grande, Belle Brown, Nycole Hidalgo, Leotie Hakkila, Jaime Bosch, David Lahn, Christy Johnson-Garrett, Therese Lamperty, Greta Gunning, Addison Keely, Madeleine Strait, Ashby Baker, Sabra Dewey, Manogya Chandar, Cristal Gomez. This work was supported by the National Science Foundation (DEB) and the Army Research Office (ARO MURI).

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Chapter 1: Introduction

1.1. Overview

My dissertation is focused on how multispecies plant-pollinator networks respond to perturbations. Plant-pollinator interactions play crucial roles in ecosystems and are threatened by anthropogenic change. Most species— including plants and their pollinators— interact with dozens or more other species. Ecologists have known for decades that perturbations that cause changes to even a single species can cascade through ecosystems (e.g., Paine 1966), and ignoring interactions or focusing on pairwise interactions may lead to a loss in predictive power. Complex, species-rich communities make it difficult to discern the mechanisms important in maintaining high diversity as well as supporting community stability and resilience. This is especially true for plant-pollinator interactions which play crucial roles in terrestrial ecosystems and communities globally. This gap in our understanding of these important biological relationships is particularly troubling in the face of concomitant ecosystem change and rapid species loss of pollinators.

1.2. Plant-pollinator systems

Plant-pollinator mutualisms are some of the most fundamental interactions within terrestrial ecosystems. Globally, the value of animal pollination is estimated at over $100 billion dollars and directly supports nearly a third of human nutritional needs (Klein et al. 2007, Gallai et al. 2009). These interactions directly support the reproductive success of >70% of plants and underpin terrestrial biomass (Ollerton et al. 2011). Unfortunately, across the globe, pollinator species are experiencing drastic population declines (Potts et al. 2010), as well as species losses.

For example, an estimated 25% of bumble bee species (*Bombus*) on the IUCN red list are declining and nearly one-quarter of the bumble bee species assessed in North America are considered vulnerable to critically endangered (Cameron and Sadd 2020). These rates of decline are likely underestimates due to the cryptic nature of insects, little to no monitoring efforts underway, as well as the paucity of basic natural history information for these species within diverse communities. Pollinator declines are thought to be driven by multifaceted threats such as land degradation and habitat loss, urbanization, pollution, disease, as well as indirect and direct impacts of climate change. Understanding how these systems of pollinators and the plants they visit is thus of pressing concern.

1.3. Ecological Networks

To understand changes to plant-pollinator interactions, my dissertation takes a network approach. Ecological networks are representations of species interactions where species are thought of as discrete "nodes" that are graphically connected to one another via "links" or "edges". For plant-pollinator interactions (as well as other two trophic interactions e.g., corals-symbiont, host-parasite, plant-seed disperser) we employ *bipartite* networks which assume all nodes within a trophic level (e.g., all the plants) interact only with species in the other trophic level. Bipartite networks in graph theory are those whose nodes can be divided into two disjoint and independent sets.

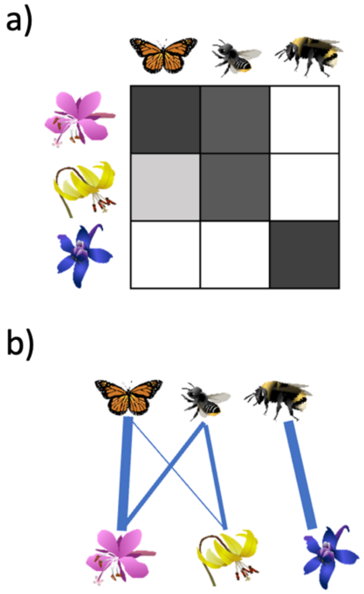


Figure 1. Example bipartite plant-pollinator network of three pollinators and three plants. Bipartite graphs can be depicted several ways. a) matrix format where nodes of the two disjoint set (e.g., pollinators and plants) are represented in rows and columns respectively. Filled cells show link interactions (shaded by intensity of interaction). b) the exact same interaction patterns can be visualized in a web where interaction intensities are depicted with line weight. Illustrations by X. Loy.

Within these networks, links between a plant and a pollinator indicate the presence and/or interaction intensity of a given interaction (Figure 1). Because many plant-pollinator interactions are diffuse, non-specific, and labile, the ability for networks to account for multispecies interactions, and for dynamism in link presence and/or intensity, is key.

Bipartite mutualistic networks have several features that are replicated across many mutualism types (e.g., corals-symbiont, plant-seed disperser, plant-pollinator) and ecosystems. Networks can be described via summarizations at three distinct levels: 1) node-level where each species gets scored based on items such as how many connections to other species it makes (*degree*), 2) guild-level where species within a trophic level are averaged into metrics that describe the entire guild, and 3) network-level where the entire network as an entity is summarized. At the node-level, surveys of bipartite networks have found that mutualistic species have large ranges in the specificity of their interaction partners but within networks these distributions of degree across the nodes are often quite similar across different systems (Montoya et al. 2006). At the whole network-level—by far the most commonly assessed level of networks in studies to date—several recurring structures have been described. One common structure in mutualistic networks is that of highly *nested* interactions. Nestedness is a property where specialists interact with a subset of the interactions that generalists interact with.

Overall, network ecology offers a way to encapsulate multiple interactions at once and, importantly, to understand changes to suites of species. While mutualistic networks have canonical overarching network structures thought to confer stability and species persistence, we still lack generalizable understanding about the consequences of perturbations to plant-pollinator systems broadly.

Roadmap to the dissertation

In order to create a more generalizable understanding about plant-pollinator interactions and how they will change under perturbation, my dissertation takes a few distinct approaches. I present three original studies using plant-pollinator network approaches to understand how multispecies communities of mutualists structure their interactions in the face of environmental change. First, I review and synthesize current efforts in plant-pollinator network models aiming to increase empirical-theory integration with concrete recommendations (Chapter 2, described briefly below in section 1.4). Next, I use simulation models to test how plant-pollinator network structure affects network response to a specific perturbation, species loss (Chapter 3, introduced briefly below in section 1.5). Lastly, I use a natural experiment of repeated seasonal droughts to empirically test predictions of network structural change to perturbation (Chapter 4, described briefly below in section 1.6)

1.4. Chapter 2: Integrating plant-pollinator theory and empiricism

As ecosystems face rapid anthropogenic change, ecological and environmental science research and management practitioners would benefit from predictive theory about how these changes will impact whole communities. Unfortunately, the theory on mutualisms such as plant-pollinator interactions lags behind theory developed for antagonistic interactions. In addition, this theory has increasingly become divorced from empirical findings. In an effort to close this gap, we propose ways to enhance research integration between theoreticians and empiricists, especially in terms of jointly identifying and testing general rules / functions that can be applied to entire systems or large subcomponents of systems (e.g. trophic levels or guilds). We term these generalizations *submodels* since they are relatively simple models in their own right that can slot interchangeably into larger dynamical models. We argue that these submodels can act as jumping off points for theory and empirical work and provide a roadmap for how submodels can be parameterized as well as validated with empirical data showcasing two tractable submodel examples.

The first plant-pollinator network submodel we focus on is that of functional and numerical responses. *Functional responses* are forms that constrain interaction rates between plants and pollinators given limitations such as search and handling times of pollinators. While these have been better described and tested in feeding relationships within food webs, functional responses have had little theoretical and empirical synthesis thus far applied to mutualistic interactions. Indeed, some of the first dynamical models for mutualisms found these systems rapidly spiral out of control, with population sizes exponentially increasing toward infinity (the so-called "orgy of mutualistic benefaction") because they neglected to constrain interaction rates (May 1976). Second, *numerical responses* establish how these interaction visit rates translate to population growth of the plants and pollinators. Likewise, the forms of these responses have been poorly investigated in plant-pollinator networks. We next scale these responses from pairwise to multi-species responses that take into account the effect of additional species in driving interaction rates and population growth. Interestingly, plant-pollinator systems offer several advantages to empirically derive these rates (relative to other interaction types such as predator-prey) since observing visitation and counting reproductive output (at least for plants) is relatively straightforward. Thus, we include multiple suggestions for both theoreticians and empiricists to allow for more integration towards accurately describing these responses.

The second submodel we focus on is capturing dietary niche dynamics. When species lose a key resource partner, how will they compensate? In plant-pollinator networks, interactions are frequently general and liable (Alarcón et al. 2008, Caradonna et al. 2017). And while we know that interactions are flexible, we lack overarching principles that can be applied to predict how something like a loss of species or a change in abiotic resources might affect whole networks. Applying diet theory may be useful to make clear and testable predictions of how networks will respond to perturbation. Experimental frameworks which modify floral resources and/or amounts of competition between pollinators (e.g., Fontaine et al. 2008) will be useful in spurring research in this submodel. To understand how resource levels drive niche breadth and intensity of interactions, we again close this section with concrete recommendations for advancement of theory and empirical work.

1.5. Chapter 3: Modeling robustness and network structure

In this chapter, I used a simulation modeling framework to test how structural aspects of plant-pollinator networks impact a key dimension of stability—robustness to coextinctions. Briefly, I isolated two potentially distinct impacts of nestedness (again, a nearly ubiquitous feature of mutualistic networks in nature) by independently varying both network topology (who interacts with whom) and quantitative interaction intensities, to study their effects on robustness.

Mutualistic networks have characteristic network structure observed in many empirical networks (e.g. Bascompte et al. 2003, Montoya et al. 2006) and implemented in theoretical models (such as those reviewed in 1.2 and later in Chapter 2). For example, nestedness is thought to act to increase redundancy to protect against a partner failing or performing poorly. Species losses can ripple through systems with some network structures and not as easily with others. Across the entire network, nestedness appears to be important for network stability and resilience (Bascompte et al. 2006, Okuyama and Holland 2008, Bastolla et al. 2009). Yet, increased redundancy also places species in direct competition with more species for mutualistic partners and resources. Thus, large unanswered questions remain: how do these systems support multiple overlapping generalists? How is nestedness maintained in the face of the need for species to partition niches?

Recent findings show that while plant-pollinator networks are nested in terms of topology (i.e., who partners with whom), this topology only tells part of the story. Pollinators are able to flexibly forage and several lines of evidence show that many are capable of "adaptive foraging"—tailoring their foraging effort to maximize returns (Inouye 1978, Fontaine et al. 2008, Valdovinos et al. 2013). When pollinators adaptively forage within theoretical models, they arrange their interactions such that species feed most intensely on plants with the least amount of competition from other pollinators. Thus, we see networks that are nested in terms of their topologies, yet *antinested* quantitatively—species are specialized in their interaction intensities (Valdovinos et al. 2016). Past work which has attempted to test the effect of nestedness on network stability and responses to perturbation has yet to independently test the effects of topology and intensity simultaneously.

Simulation models which sequentially remove species from networks, and then study how many species are left, are one canonical method for understanding how networks will respond to environmental change. These test a network's robustness to species losses, where networks that have high robustness maintain high species richness until many species have been removed, while networks with low robustness suffer high loss of additional species when species are sequentially removed. Robustness simulations have found topologically nested network structures to be important determinants of robustness to species loss (Dunne et al. 2002, Memmott et al. 2004). Importantly, however, these traditional approaches are unable to incorporate interaction intensities into their species loss algorithms. Therefore, independent tests of robustness in quantitative and topological network structures have not yet occurred. In this chapter, I use an approach called "stochastic coextinction modeling" which allows accounting for interaction intensity—and expand it by applying it to sequential extinctions— to understand the distinct roles of topological and quantitative nestedness on robustness.

I found that while topological structure was more important than quantitative structure for robustness to co-extinctions, quantitative structure acted to magnify the effects of topology. Thus, when networks faced sequential deletion of species which were ordered from least to most linked, quantitatively nested networks were more robust than antinested neworks with the same topology.

1.6. Chapter 4: Simultaneous niche expansion and contraction in plant-pollinator networks under drought

If we are to truly understand perturbations in plant-pollinator systems we must pair the aforementioned theoretical and simulation modeling approaches with empirical studies in the field. In this chapter of my dissertation, I collected plant-pollinator network data for multiple growing seasons within montane sites in the Colorado Rocky Mountains. I assessed how drought, which occurred multiple times in the chronoseries, affected the niche breadth of species across the network to understand how drought restructures interactions.

Large-scale experimental work and natural experiments caused by gradients and abiotic changes are important tools to assess how these networks will respond to rapid environmental change. Previous efforts have found plant-pollinator network structure responds to perturbations including invasive species (Bartomeus et al. 2008, Kaiser-Bunbury et al. 2011, 2017), grazing (Vanbergen et al. 2014), and nutrient addition (Burkle and Irwin 2009), among others. While these studies have been informative in describing network changes, the field rarely links these changes to their mechanistic underpinnings. This is an important gap to address as we face rapid and multi-stressor environmental change across the globe.

One perturbation of concern is increased frequency and severity of drought. Droughts are becoming more common in many places; in western North America droughts are predicted to increase in duration and severity (Williams et al. 2020, Zhang et al. 2021). How plant-pollinator networks change under drought should be understandable and, to a degree predictable, from already developed consumer-resource and niche ecological theory (see Chapter 2 and section

1.4). I predicted that mechanistically, drought would change networks via resource partitioning and competition. In the system drought causes depression of abiotic resources necessary for floral rewards yet pollinator populations—due to life cycles which include an overwintering period inducing a lag effect—may not be similarly reduced in the year of the drought. If the resource reduction in flowers is a dominant force then we might expect foragers to need to forage more broadly to make up for these reductions, if instead intraspecific competition is dominant then we would expect to see niche expansion. Here I test these predictions with plant-pollinator networks faced with multiple drought perturbations in the field. While these predictions are important endeavors as our world continues to change, this chapter also serves as a nice model for implementing some of the recommendations brought forth in Chapter 2 as I strove for understanding network changes in terms of the underlying mechanisms of niche and diet theories.

I found that drought causes plant-pollinator networks in the Rocky Mountains to change. Networks under drought were statistically more general in terms of the links species made yet statistically more specialized in terms of the interaction frequency of those links. Simultaneous niche expansion and contraction as I have found in response to this perturbation could have profound effects in understanding plant-pollinator interactions under future climate change. This chapter is currently under review at *Oikos*.

Chapter 2: Integrating plant-pollinator theory and empiricism

2.1. Introduction

Network perspectives and tools have become a powerful approach towards understanding multi-species plant-pollinator interactions (Ings et al., 2009), and have been employed fruitfully in both empirical and theoretical work. For plant-pollinator networks, modeling and empirical efforts rarely inform one another and instead have largely run on separate trajectories. Given that plant-pollinator interactions are vital in maintaining diversity and ecosystem function (Fontaine et al., 2005; Loreau et al., 2001), and that pollinators are likely to be greatly impacted by global change (Hegland et al., 2009), we need stronger conceptual integration between models and empirical findings to help us better understand what drives the community processes of these essential systems.

Compared to analogous efforts describing the dynamics of systems such as food webs or predator-prey interactions, there has to date been a disconnect between theoretical and empirical findings in plant-pollinator systems. For example, models describing antagonistic interactions have more rigorously grounded theory in empirical findings than they have for mutualistic interactions. This includes empirical work in predator prey systems that has validated functional responses, describing how foraging rates change across various predator and prey densities (e.g., Skalski & Gilliam, 2001). Likewise, optimal foraging theory (the idea that foragers are selecting resources to maximize energy gain and reduce energy expenditure) has been tested empirically across a range of predator-prey systems (Stephens & Krebs, 1987), which aids in appropriate application of this mechanism in models. Models for plant-pollinators must also make similar assumptions, but there has generally been less validation of these modeling choices with empirical findings. Instead, the choice of functional forms has typically not been made based on empirical evidence from plant-pollinator systems, but rather have been selected for convenience or following empirical findings in vastly different ecological systems, which may not be relevant to the underlying ecology of mutualisms or nuances of plant-pollinator interactions in particular. For example, much of the theoretical work for plant-pollinator networks has been largely adapted from first principles derived in antagonistic networks and for the most part has not taken empirical findings in plant-pollinator systems into consideration. For example, while first principles in antagonistic predator-prey systems assume the consumption of prey necessarily decreases the population of prey by one, a similar assumption (albeit in the mutualistic positive direction) cannot be applied to plant-pollinator interactions because a single floral resource can be shared by many pollinators and the resource use does not translate to immediate plant population gain. The consequences of this disconnect between theory and empirical findings are perhaps highlighted by the fact that plant-pollinator network models have come to vastly different (and opposing) conclusions regarding how network structure effects stability, arising from irreconcilable underlying model assumptions (Bascompte et al., 2006; James et al., 2012; Okuyama & Holland, 2008; Staniczenko et al., 2013; reviewed in Valdovinos, 2019; Zhang et al., 2011).

Altogether, this leaves plant-pollinator models falling behind their antagonistic siblings and possibly forsaking a rich cross-pollination whereby predator prey and food webs research could capitalize on plant-pollinator findings as well. To more accurately understand plant-pollinator systems and advance mutualistic network research, we need to develop tractable methods to include empirical findings in models and incorporate theoretical frameworks in empiricism.

We see two main ways to improve integration between empirical and theoretical work, with both approaches having differing outcomes on model output and inference. On the one hand, theoreticians could attempt to incorporate empirically independently measured pairwise parameters (direct parameterization) to increase biological realism. Unfortunately, this would quickly overburden models due to the sheer number of parameters and would also present an intractable challenge for empirical data collection. A contrasting approach—and the one we advocate for here— to include *system-level* generalizations to plant-pollinator network models. In this review we refer to these system-level generalizations as *submodels* given that they are, in themselves, models with underlying assumptions (Box 1). Submodels are broad mechanistic patterns that can tractably be applied across many networks. In predator-prey dynamics and food-web research, several multispecies modeling frameworks have connected theory with empirical research to describe the broad mechanistic patterns underlying submodels. Thus, efforts to understand mechanisms underpinning antagonistic relationships have been more thorough than those for plant-pollinator systems. Here, we point to patterns, mechanisms and processes from plant-pollinator research that either have substantial empirical backing or highlight areas where theoretical inquiry can help direct empirical research, allowing us to then feed these findings back into multispecies models.

We have structured this review into two sections. Within we lay out the empirical evidence for, and theoretical adoption of, two exemplar submodels: *functional responses* (Section 1) and *diet* *theory/niche dynamics* (Section 2). Both have relatively large empirical literature bases supporting them and can be tractably included in theoretical models via our submodel framework, but have not been readily adopted into plant-pollinator models. These two submodels serve as examples to showcase how the submodel framework can increase the interplay between empirical and theoretical research. In Section 1, we investigate submodels related to interaction rates as described by functional responses and translation of interaction rates to population dynamics via numerical responses. In section 2, we assess the submodels of niche breadth and how intraguild competition can be captured in dynamical models. In both examples, we offer tractable ways of incorporating empirical findings into theoretical models to achieve more biologically meaningful outputs, as well as ways to inform and drive empiricists towards collecting data that would aid theoretical frameworks. We present key empirical findings to justify the assumptions that structure submodels, and we highlight gaps in the literature that should be filled. We close with a call to more tightly couple empiricism and theory to increase the utility of models towards understanding the principles underlying plant-pollinator networks.

2.2. Box 1: The Submodel Approach

Dynamical models for populations of interacting species are comprised of multiple generalizations, which represent different assumptions, mathematically described with a series of functions. These functions we call *submodels* as they in turn are models describing and/or simplifying a more complicated relationship. Submodels are system-level dynamics that are applied to all or a set (e.g. one trophic level / guild) of species within a network, and are already used relatively broadly in plant-pollinator network models. For example, many population growth models, including those for plant-pollinator networks, use a system-level generalization of logistic growth, in which per-capita population growth declines as a linear function of conspecific density.

We note that our definition of *submodel,* which concerns the underlying assumptions of different components of a dynamical formulation, differs from that used in some fisheries and ecosystem models (eg. the Atlantis model, Audzijonyte et al., 2019). In these, a submodel is instead an entire dynamical equation (or system of equations) and is considered a sub component because these large ecosystem models consist of many groups of dynamical equations each related to socio-cultural factors, fisheries practices and harvest, and population recruitment to name a few of their "submodels." Our framework also differs from the "sub-module" approach of constraining multispecies models to a smaller subset of interacting players as has been suggested for food webs (McCann, 2011).

2.3. Section 1: Maturation of functional and numerical responses to improve plant-pollinator models

Here we discuss how functional and numerical responses—as exemplar submodels—could be better developed in plant-pollinator models. *Functional responses* are typically defined as functions describing how interaction rates (e.g. predation, flower visitation) change with resource density (DeAngelis et al., 1975; Holling, 1965). *Numerical responses*, by contrast, scale or convert interaction frequencies (described by the functional response) to increases in population size or other dynamics such as changes in somatic growth rates. Considerably less work has focused on numerical responses relative to functional responses, particularly in mutualistic systems. We provide an overview of these two related components of dynamical models of ecological interactions, paying especially close attention to how formulations in mutualistic systems compare to predator-prey responses from which they are originally derived. Functional and numerical responses can be modeled from the perspective of one resource (one species of flowering plant) and one consumer (one species of pollinator), or can incorporate multispecies assemblages. In this section, we discuss both approaches. Additionally, we look at the assumptions that have been made for applying both functional and numerical responses to plant-pollinator systems (e.g., non-saturating search and handling times, no interference between pollinators). We close the section outlining the empirical support for these generalizations as well as highlighting recommendations for more robust testing and validation of these mechanisms in empirical and modeling work.

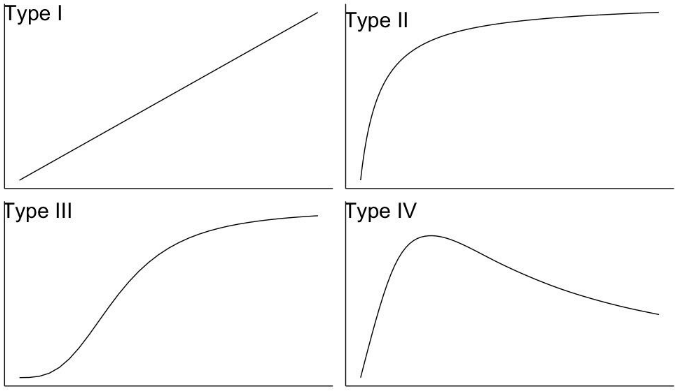
Functional responses

Functional responses have been included in species interaction models to account for the changes in consumer foraging rates that depend on consumer and/or prey densities (or the ratio of the two). In predator-prey systems these have been employed to account for various aspects of foraging such as the time it takes a predator to find and handle prey, predator learning, prey evasion, all of which can change rates of feeding (DeAngelis et al., 1975; Holling, 1965). For example, as prey density increases, predator foraging cannot continue to increase linearly since predators become satiated and prey handling is not instantaneous.

Two-species Responses

To date, plant-pollinator models have primarily employed two-species responses in network models. We note that these have alternatively been called single species or single resource functional responses elsewhere (Gentleman et al., 2003). Four proposed shapes or types have been proposed for functional responses (Box 2). Thus far, only two types of functional responses have been applied in plant-pollinator models.

2.4. Box 2: Functional Response Formulations



Two-species forms

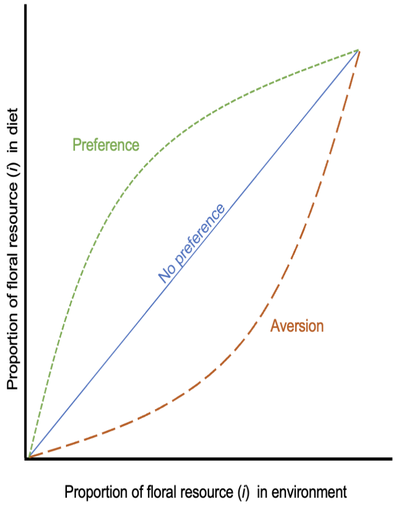
Type 1: Rate of interaction is a linear positive relationship across increasing resource density. This type of functional response would represent a scenario with instantaneous handling time. Holling's original formulation specified a linear response up to a maximum possible rate of interaction so that the Type 1 function saturated at some resource density (Holling, 1965). This 'broken-stick' formulation has not been adopted in models for mutualisms to our knowledge.

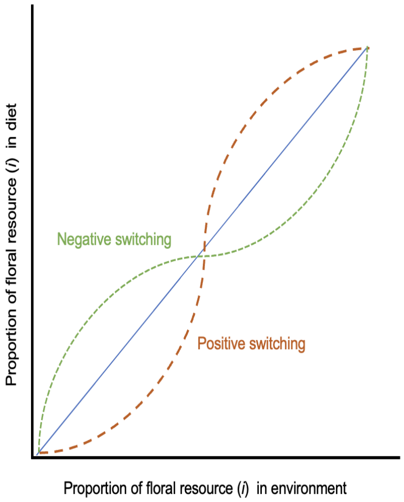
Type 2: A saturating curve represents the non-trivial handling times that limit the rate at which pollinators visit flowers, leading to consumption rates that increase non-linearly with increasing floral density.

Type 3: Type III curves have a sigmoidal shape whereby at low densities of resource the rates of consumption are low, followed by a rapid increase towards a saturation point. This could represent learning.

Type 4: Type IV responses are unimodal in shape, where a decrease in feeding rate occurs at very high densities of prey. This could occur with coordinated prey defenses that cannot occur at lower densities.

Multispecies forms





Deviations from two-species forms could take the form of a) either a preference or aversion to a certain interaction where an interaction is over- or under-represented compared to the number of interactions expected due to abundance of each species. b) Switching could occur whereby the shape of the preference and aversion curve inflects given the proportion of a given resources. This could occur if a resource that was preferred when a second resource was scarce becomes less attractive once the second resource is plentiful. Conversely, the opposite could occur where a resource that is avoided becomes more attractive once a second resource becomes more abundant. This could occur for a few reasons including direct interference or competitive dynamics leading to changed niche partitioning, aggregation of resources and spillover to name a few. Deviations from a two-species form might be driven by either ratios of pollinators, floral resources or some combination of both. To give a simple example, we could imagine a single pollinator species foraging on a single plant resource at a given rate, which follows some functional response curve as the density of that resource increases. When a second more highly-valued resource is added to the system, the foraging rate for the pollinator on the first resource might change because there is an alternate and preferred resource choice. Similarly, if a second pollinator is added and this new species is a good competitor for the available floral resources, this new pollinator might deplete the resources and thus change the foraging rate for the original pollinator. If floral resource densities are high, we might expect less impact from a second pollinator to foraging rates of the original pollinator. Figure adapted from Gentleman et al. 2003.

In one of the earliest mutualistic network models, Bascompte *et al.* (2006) utilized a linear functional response (Type I), using the assumption that handling times are sufficiently small enough in most generalized mutualisms that they can be ignored. The model did not include a saturating response so the interaction frequencies could increase infinitely driven by increases in one's partners. Functionally, this assumption translates to mutualistic benefits that are proportional to the densities at which partners encounter each other. Bascompte *et al.* (2006) found that model coefficients must thus be tightly bounded—i.e. interactions between the plants and the pollinators must be weak— so that positive benefits do not drive populations to infinity and community coexistence can occur.

Plant-pollinator interactions likely are limited by biological constraints of search and handling time, therefore necessitating a more complex functional response shape than the linear forms used in early models. Building on the prior work of Bascompte and others, but concerned that the necessity of weak interactions for coexistence was spurious Holland et al. (2006) and subsequently others have used a saturating response (Type II) within plant-pollinator network analyses (Okuyama & Holland, 2008; Rohr et al., 2014; Thébault & Fontaine, 2010; Zhang et al., 2011). To our knowledge, Type III functional responses have been rarely included in plant-pollinator systems (but see Feldman et al., 2004; Mesgaran et al., 2017) even though social learning—a possible driver of Type III dynamics—is common across some pollinator taxa (Avarguès-Weber et al., 2013). Similarly, there is empirical evidence of reduced visitation at high plant abundance in at least some circumstances (Benadi & Pauw, 2018; Ward et al., 2013) which might support the use of a Type IV functional response.

While two-species functional responses allow us to explore the underlying foraging biology between a single pollinator and a single floral resource, they likely do not adequately capture the complexities that can arise when multiple species become involved. These complexities include pollinator competition and/or facilitation, variation in preference for different floral resources, and time lags needed to learn to manipulate a new resource, among many others.

Multispecies Responses

Multispecies functional responses are those that describe interaction rates shaped by multiple species, typically multiple consumers and /or resources. The shape of the response curve defining interaction rates for a given pollinator species on a given plant is a function of the resource levels of all plants that pollinator interacts with and/or all other pollinator species it shares resources with (Box 2). In this way, a pollinator could compete with or be facilitated by other pollinators. Given the prevalence of multiple generalist species in plant-pollinator networks these dynamics are likely to be readily occurring.

A growing body of research describing and testing multispecies functional responses in predator-prey relationships has resulted in advances in both empirical (e.g., Soluk, 1993) and theoretical work (reviewed in Gentleman et al., 2003), and thus provides a framework for applying multispecies responses for plant-pollinator interactions. One potentially fruitful avenue is to evaluate the fit of several contrasting multispecies functional response models, assessing whether or not data support particular mechanisms such as consumer interference (e.g., Novak et al., 2017). In a plant-pollinator context, the rate of foraging on a plant might differ from purely abundance related expectations due to behavioral aspects like attractiveness of other plants, plant switching due to medicinal or nutritional needs, or direct pollinator interference. To our knowledge, multi-species functional responses have only been applied to pollinator visitation patterns once, by (Cervantes-Loreto et al., 2021), who used data on multiple pollinator species visiting multiple distinct types of artificial flowers in a computer-controlled foraging enclosure. Cervantes-Loreto et al. (2021) found strong support for their most complex model, which included pollinator interference. Interestingly, they found support for both positive and negative interference, with the presence of some competitor species increasing the foraging of a target species relative to intraspecific competition, while by contrast other species reduced foraging rates relative to conspecifics. While this work is a strong first step, to our knowledge there is no work that has fit multi-species functional response models to plant-pollinator data including multiple species of pollinators and actual plants (as opposed to artificial flowers).

An alternative to multispecies functional responses as formulated above is to instead use adaptive foraging theory to model interaction rates, which involves modeling resource competition more directly based on explicit resource accounting (e.g., Valdovinos et al. 2013). We discuss this approach further in Section 2 below.

On the whole, functional responses help increase understanding of how pollinator behavior and biological constraints shape foraging rates, yet interaction frequencies alone do not adequately reflect the fitness outcomes of these rates to both pollinators and plants. Additional submodels must also account for these fitness determinants in order to translate interaction intensities to population level outcomes.

Numerical responses

Numerical responses are defined as functions that translate interaction rates into organismal or population-level outcomes, such as converting predation rates into somatic growth or fecundity at the organismal level, or population growth at the species level. Numerical responses are alternatively named benefit accrual or net-benefit relationships, and in the context of plants the term "benefit accrual" is a logical term given that it describes the accrual of seed production arising from different numbers of pollinator visits conferring pollination. Similarly, for pollinators, numerical responses can scale floral visit number with reproduction, accounting for conversion efficiencies as well as other limiting factors in pollinator reproduction (e.g. related to nesting). As with functional responses, numerical responses can be focused on one interacting pair of species (two-species responses) or can involve multiple species.

Two-species responses

In plant-pollinator systems, most of the empirical and theoretical work on numerical responses has centered on two-species responses (but see Valdovinos et al. 2013, Valdovinos et al. 2016, Valdovinos et al. 2018, Valdovinos & Marsland 2021). Here, numerical responses typically take the form of a simple scalar of conversion efficiency applied across the network (multiplied by the interaction rate given by the functional response) to both plants and pollinators. Below we argue for separate treatment of plants and pollinators within plant-pollinator models due to differences in the underlying biology of each group.

For plants, numerical responses link the number of pollinator visits to new plants produced. Historically, numerical responses have often been assumed to be linear, with an increase in interaction frequency always resulting in an increased production of plants. However, empirical evidence and basic biological logic does not support this assumption; as with functional responses above, in nature numerical responses likely follow some saturating function. Biologically, there are inherent limits associated with plant reproduction, as each plant can only produce a given number of flowers that each have a set number of ovules that can be fertilized, thus, having a purely linear relationship between pollinator abundance and plant reproductive output is unrealistic. Beyond basic limits set by flower and ovule numbers, several empirical studies have found that very high pollinator visitation can actually damage flowers (Aizen et al., 2014; Rollin & Garibaldi, 2019), ultimately limiting reproductive success (seed set) even when pollen deposition is heightened (Sáez et al., 2014). For three species in an empirical test of numerical responses, Morris *et al.* (2010) found evidence for both saturating and unimodal curves, where very high visitation rates by pollinators again led to a decrease in reproductive success. Decreased seed set at higher visitation has been reported in other systems as well, due in part to stagnation of pollen tube growth caused by pollen oversaturation in pollen tubes (Young, 1988). These examples provide evidence for the inclusion of a unimodal numerical response (Type IV), at least for plants.

Recent extensions of numerical responses have updated these submodels, though more research is still needed. Ultimately, for plants a numerical response could perhaps start with a saturating response (Type II) representing the presumed upper limit in reproductive output for plants and then add parameters which account for other mechanistic and biologically relevant constraints that limit plant reproductive success (e.g. floral damage from pollinators). Models that investigate costs of mutualism for plants offer a nice way forward here. These usually use a consumer-resource framework where costs arise because of resource provisioning and depletion (Holland & DeAngelis, 2010). Some have modeled benefits and costs separately, both as Type II curves with opposing directions, that together allow for a unimodal response when costs are present (Peralta et al., 2020) . Others have further partitioned costs into decreases in reproductive and somatic growth as a function of the mutualistic interaction (Hale et al., 2020).

For pollinators, numerical responses may be considerably less involved than those for plants. These describe how captured floral resources numerically convert into new pollinator individuals. Still, exactly how interactions then translate into reproductive success of pollinators is unclear due to the paucity of empirical research (though see Vázquez et al., 2012). Nevertheless, concepts developed for predator-prey systems such as the substitutable or complementary nature of various resources (e.g., Tilman 1980) could be developed for floral resources that pollinators are visiting within plant-pollinator networks. Numerical formulations for pollinators might include other non-floral resources that could constrain population growth such as nest site or material limitations.

Applying formulations of numerical responses stemming from two-species responses will likely help improve model predictions (Valdovinos 2019) in their own right, yet we know that complex networks of interactions where additional resources or interactions can strongly shape interaction strengths in non-additive ways. Thus, we need to highlight and account for the importance of the multispecies numerical responses occurring in plant-pollinator networks.

Multispecies responses

Multispecies numerical responses describe how different combinations of interactions with different species determine conversion to somatic growth, reproduction, or population size (among other conversions, see above). For example, bees feeding on multiple plant species might produce more offspring because of access to greater nutritional diversity. For plants with multiple flower visitors, increased fruit set might result from pollinators that fill different pollination niches (reviewed in Loy & Brosi, 2022). To our knowledge, multispecies numerical responses have not been explored in plant-pollinator interactions.

Ways forward for functional and numerical responses in plant-pollinator networks

While previous efforts on functional response submodels represent important steps towards increasing realism in dynamical models of plant-pollinator networks, these simple formulations need to be updated based on current empirical and theoretical work, as has been done in predator-prey systems. Here we lay out recommendations for both theoreticians and empiricists (Box 3). Empirical evaluation of alternative functional response models in plant-pollinator systems are just beginning to be evaluated (Cervantes-Loreto et al., 2021). Empirical work should derive and test the fit for different curve shapes for foraging rates (Box 3). Importantly, careful empirical data collection, such as collecting network data for a consistent and measured amount of time and within a prescribed area where floral density is also measured, would more readily allow for calculation of foraging rates. While some empirical efforts are starting to include these measures more frequently, they are still quite rare.

Box 3: Moving Functional and Numerical Responses Forward

Recommendations for Theoreticians	Recommendations for Empiricists
Functional Responses ● Test sensitivity of plant-pollinator network model results (e.g., species persistence, population sizes, local stability, robustness to coextinction) to different functional response curve types. ● Develop multispecies predictions and hypotheses for when / under what conditions response surfaces will deviate from single-species responses *Numerical Responses* ● Extend theory derived from empirical work that captures maximum fitness (# ovules and # flowers) ● Assign numerical responses for each guild independently, based on their underlying biology; for example, pollinator populations could have a Type I numerical response, with reproduction scaling linearly from visitation frequencies, while plants	*Functional Responses* ● Estimate search and handling times for different guilds of pollinators on different groups of plants ● Fit contrasting basic shape(s) of functional response curves using cage, glasshouse, and/or foraging chamber experiments to manipulate density of pollinators and plants / flowers / artificial flowers and measure effect on foraging rates ● Repeat the above across distinct plant-pollinator communities, including a range of different species and functional groups ● Run multi-species foraging experiments (e.g., Cervantes-Loreto et al., 2021; Fontaine et al., 2008; Fründ et al., 2013) to assess multi-species functional responses (Cervantes-Loreto et al. 2021), including mechanisms such as pollinator interference

could have a Type IV response in which reproduction is highest at intermediate visitation frequencies and reduced when visitation is too high ● Test sensitivity of dynamical network model results (e.g., local stability, species persistence, robustness to coextinction) to different numerical response curve shapes. In particular, investigate the consequences of unimodal (Type IV) numerical responses of plant reproductive success	● In empirical pollination network studies, collect density-based measurements of plants and pollinator interactions (i.e. by sampling in a tightly-defined area, in which floral resources are sampled exhaustively, and for a tightly-specified amount of time). Such measurements work best when the area sampled is small enough to exhaustively assess every floral visitation interaction that occurs within the sampling time. ● Collect independent assessments of abundance of both plants and pollinators (separately from floral visitation); this is particularly challenging for pollinators *Numerical Responses* ● Use cage, glasshouse experiments to manipulate density of plants and pollinators and measure reproductive success to estimate numerical responses ● Repeat the above across distinct plant and pollinator species / functional groups

Greater integration of theory and empirical findings is necessary to make forward progress correctly applying numerical responses in plant-pollinator models. Therefore, we lay out some recommendations for empirical and theory work to address this gap (Box 3). Translating functional responses into population dynamics necessitates the use and development of separate numerical responses for plants and pollinators, which may have very different shapes and underlying assumptions. It should be noted that paradoxically numerical responses for pollinators are empirically more difficult to measure than they are for plants, while conceptually we find just the opposite: it is easier to consider simpler formulations for pollinators than for plants when linking number of visits into reproductive output. Food web and predator prey research can provide useful frameworks towards understanding the shape of numerical responses. For example, cage experiments have been used to track population dynamic consequences of exposure to different predation regimes (e.g., Meihls et al., 2010). For measuring the relationship between pollinator abundance and plant reproduction, we can utilize pollen limitation experiments (bagging virgin flowers) to directly test reproductive outcomes for plants, especially if paired with approaches like videography of single flowers to tightly estimate floral visitation. Measuring the relationship between plant abundance and pollinator fitness is a more difficult task, yet not impossible. Assessing reproduction is difficult for many pollinator taxa, including the majority of bees which are solitary and soil-nesting. It is also likely to be difficult for highly eusocial perennial bee colonies such as in honey bees (*Apis*) and social stingless bees (*Meliponini*), since stored resources (pollen, honey) are likely to blur the relationship between currently available floral resources and pollinator fecundity. Still, reproduction has been tractably assessed in some bee species, such as cavity nesting bees like *Osmia* (e.g., Williams & Kremen, 2007), and more primitively eusocial bees including bumble bees (e.g., Stanley et al., 2015). Pairing cage experiments (e.g., Fontaine et al., 2008; Fründ et al., 2013) with such pollinator species that are tractable to study in lab environments could be used to directly test reproductive outcomes for pollinators (Vazquez et al. 2012). Efforts should be made to leverage natural and manipulative experimental work in order to test these hypotheses and parameterize future models. Another gap is that numerical responses that take into account dynamics for multiple species are even less developed than multispecies functional responses, not only in the pollination literature, but also in the food-web world and ecological literature in general. Because plant reproductive success is so straightforward to assess, plant-pollinator interactions may be a useful system towards filling this gap and deriving new theory for multispecies responses more broadly.

Functional and numerical responses can have large consequences on network stability and major model findings (e.g. Bascompte et al., 2006; as opposed to Okuyama & Holland, 2008). These submodels are highly tractable, but more empirical and theoretical work is needed to determine which of these generalizable curve shapes are supported by data as well as determine the sensitivities changes in their form have on different model stability tests. We now turn to a second submodel regarding niche-dynamics, which also has potentially profound impacts on plant-pollinator network models.

2.5. Section 2: Niche-based predictions

In plant-pollinator network research, a key knowledge gap is understanding who interacts with whom, i.e. the identities of interactions. Network perturbations, increasingly common under anthropogenic change, often shift interaction identities, yet we lack predictive power to forecast how species will respond in the context of their individual interactions. Individual interactions within networks can restructure via “re-wiring”, i.e. new connection formation or loss, and “reweighting”, i.e. alteration of interaction strength and both are occurring readily across space and time (e.g., Brosi & Briggs, 2013; CaraDonna et al., 2017). Yet most currently-applied theory does not allow for this flexibility, assuming instead that observed connections represent “true” network structure and that these connections are static over time. While plant-pollinator network re-wiring has been investigated in a handful of studies (e.g., Ramos-Jiliberto et al., 2012; Zhang et al., 2011), it has been modeled phenomenologically and as an essentially minor process (see a recent review for more on this Valdovinos, 2019). For plant-pollinator systems, we still lack basic rules about which resource items a pollinator will feed on when faced with multiple floral resources. Empirical research on how interaction patterns change with inter- and intra-specific competition (Fontaine et al. 2008, Fründ et al. 2013), and how changes in food resources drive the reshuffling of interactions (e.g., Brosi et al. 2017, Endres et al. 2021) has just begun to be integrated into theoretical models of plant-pollinator networks (Glaum et al., 2021).

Combining diet and niche theories presents a tractable path forward toward this goal. Historically, diet theory has been largely focused on understanding diet choice for single species (reviewed in Sih & Christensen, 2001). Alternatively, niche theory has focused on understanding resource partitioning among multiple species, including a wide range of resources beyond dietary resources (e.g., including spatial niches as in MacArthur, 1958).

In this section, we cover two examples of this submodel which showcase how we can use niche and diet theory to better understand the dynamism of plant-pollinator networks. Importantly, these examples also do a good job integrating theory and empiricism. First, we look to use optimal diet theory to understand and predict niche breadth (and thus network degree) as has been done in food webs previously. Second, we examine the use of adaptive foraging concepts (extending optimal foraging theory) to understand and predict foraging intensities. We close this section with recommendations towards integrating these two parallel efforts together. These efforts will improve our predictions of network structural change following perturbation and widespread anthropogenic change to mutualistic interactions.

In food webs, stronger mechanistic ties have been made connecting foraging theory with niche breadth and rewiring than have been explored in plant-pollinator networks. Optimal foraging theory posits that individuals forage to maximize reward while minimizing costs. For example, Beckerman et al. (2006) built a model to test the extent to which optimal diet theory can predict the network property of connectance (realized links). They modeled the diet breadth of each predator species (i.e. network degree, the species richness of prey species that it would consume) in a network from three simple inputs: energy gained from a given species of prey, encounter rate, and handling time. Furthermore, they parameterized this model with empirical data including 1) handling times derived from hundreds of predator-prey studies on Type II functional responses (see Section 1 recommendations, Box 2), and 2) foraging trait data from empirical studies where energy content scales linearly with body mass. This approach has yet to be extended to plant-pollinator networks, perhaps in some part because the empirical evidence base is much smaller when compared to predator-prey systems. Doing so would integrate key empirical findings on interaction plasticity and could inform on how diet breadth of pollinators might change in response to floral resource availability. While drawing from diet theory alone will be beneficial for plant pollinator research, a primary limitation of this approach is that it does not take into account resource competition from other consumers.

A second example of a research effort that has tied diet and niche theory to empirical findings, this time in plant-pollinator interactions, is Valdovinos et al. (2016). This effort explored the consequences of adaptive foraging, a closely related, but distinct theoretical approach—also based on diet theory—where species maximize rewards by minimizing sharing of limited resources. This approach explicitly takes into account resource competition and species are able to reweight their foraging on different plant species in response to resource levels, again to maximize their overall energy intake via an optimization process (e.g. Kondoh 2003, Valdovinos et al. 2013). Adaptive foraging models generate predictions of foraging effort of a given consumer on a set of resources, which can be empirically validated. Valdovinos et al. (2016) used an adaptive foraging plant-pollinator model and the predictions it generated of foraging effort of pollinators on plants were mirrored in empirical data of bumble bee foraging.

Thus far, adaptive foraging models allow for species to reweight their foraging efforts to optimize resource acquisition, but to date few plant-pollinator models have allowed for rewiring and reweighting simultaneously (but see Glaum et al., 2021). Thus, these adaptive foraging models assume that any resource used, even those used extremely infrequently or minutely, are meaningful partnerships (ie. will not register as *zero* and force a change in network structure per se). As currently implemented, these models do not provide much of a lever to investigate the mechanisms driving rewiring. Given that rewiring is a common feature in plant-pollinator networks we need stronger theory to understand the outcomes of substantive changes in network topology. Currently we lack key theoretical grounding explaining high dynamism of network degree (or the number of partners), even though this is a fundamental feature found in plant-pollinator empirical networks and likely to become even more important in a changing world.

Suggestions to move these concepts forward

To implement this submodel, we require both theory development and more empirical work (Box 4). On the modeling side, niche theory lags behind functional and numerical response theory development both in plant-pollinator interactions as well as other interaction types.

Therefore, moving this submodel forward will take concerted effort to develop simple conceptual models. These should test the effects of mechanisms leading to rewiring and reweighting grounded in empirical and theoretical work on optimal foraging and dietary niche concepts. For example, above we outlined two tracks: diet breadth and adaptive foraging that independently touch on rewiring and reweighting, respectively. We suggest these tracks be merged and modelers aim to integrate optimal diet breadth into adaptive foraging approaches, so that we can understand the results of simultaneous rewiring and reweighting together (Glaum et al., 2021). These types of models would predict which plants a given pollinator is linked to (and how many), as well as the strength of each of those interactions as hypothesized by competition dynamics across the network.

Consumer-resource models are a good model choice for this endeavor as they can readily include submodels based on optimal foraging theory (Holland & DeAngelis, 2010; Valdovinos et al., 2013), in contrast to more canonical and phenomenological Lotka-Volterra models adapted from competition interaction studies. Consumer-resource models not only track the population abundances of the species within both guilds, but also explicitly keep track of resource levels at the heart of the species interaction. For example, in the case of plant-pollinator consumer-resource models, the resource of interest is floral nectar and pollen which pollinators draw down when they visit the plant. Thus, a consumer-resource model of plant-pollinator interactions tracks the dynamics of *three* populations (plant population size, pollinator population size, and resource levels). In contrast, Lotka-Volterra type models do not have a direct way to account for non-lethal foraging, and the phenomenological assignment of mutualistic benefits in these models implicitly allows multiple pollinator species to benefit equally from the same plant species.

Predator-prey Lotka-Volterra models do not suffer the same problem, because when a prey item is (lethally) consumed, that individual is removed from the prey population, and no other predator can benefit from it. In plant-pollinator and other mutualistic systems, however, there is no mechanism within the Lotka-Volterra modeling framework to "remove" the consumed resources, because a plant that is fed upon still exists after the interaction. Consumer-resource based approaches are critical tools for adaptive foraging models (Valdovinos et al., 2016) though for a diet-choice model like Beckerman (2006) they may be less strictly necessary. Nonetheless, we are excited at the prospect of more research using consumer-resource frameworks to generate rich theory for plant-pollinator networks.

One tension that exists at the modeling-empirical nexus within plant-pollinator networks is the treatment of all species within a trophic level as equivalent. Modelers make this choice for a suite of reasons, one of which being that understanding the fate of an exact species within a specific system is not generally the goal. Unfortunately, by treating all species as equivalent these plant-pollinator models do not allow one to understand what is structuring interaction identities. Instead, this abstraction leads to models attempting to predict interaction dynamics purely based on the abundance and number of links a species has (it should be noted that this abstraction can be incredibly useful. For example, with only varying species degree adaptive foraging models can predict foraging efforts supported by empirical data (Valdovinos et al., 2016)). On the other hand, abstracting all species-level information from networks may hamper integration of theory with relevant empirical findings on what structures interaction niches. Incorporating some variation such that individual species identities are included in the network models may go a long way towards improving our predictions of who interacts with whom. One feasible way to do this is to include a trait measure thought to be important for determining or constraining interactions that can occur in the network. In predator-prey models this has been achieved through the inclusion of a single trait measurement, body size (Beckerman et al., 2006; Petchey et al., 2008). In plant-pollinator interactions this is frequently done with flower corolla depth and pollinator proboscis length (Eklöf et al., 2013; Weinstein & Graham, 2017) or body size and floral area (Potts et al. 2003, Hicks et al 2016, Rowe et al. 2020). In order to understand general rules of what constrains interactions, deeper theory regarding the important sources of variability for plant-pollinator interactions needs to be developed. Currently models that attempt to use traits alone to predict interactions typically perform poorly. For example, using this kind of approach Eklöf et al. (2013) predicted only one-third of interactions correctly.

More empirical work on the mechanisms involved in this submodel are also necessary. For this, extensions of work in simplified systems could be used to test predictions. incorporating more highly manipulative work in this system will allow for more mechanistic understanding. For example, Nabors et al. (2018) effectively removed abundant honeybees from small plots using targeted smoke puffs which did not interfere with the foraging behaviors for other pollinator species. Manipulations along these lines could test how niches are shifted as resources become more plentiful and whether this is in line with foraging theory (e.g. competitive release Brosi & Briggs, 2013). These should include manipulations that vary inter and intraspecific competition (e.g., Fontaine et al., 2008; Fründ et al., 2013). More broadly, we need further tests of optimal foraging theory applied in plant-pollinator systems to validate assumptions as has been done more thoroughly in predation research. In order to test predictions of optimal foraging theory, empirical data collection must include data on densities of plants and pollinators, not just the number of times they interact.

Box 4: Moving Niche Dynamics Forward	
Recommendations for Theoreticians	Recommendations for Empiricists
● Extend diet breadth theory into plant-pollinator models (e.g., following Beckerman et al., 2006 for food webs). ● To do the above, establish simple allometric scaling rules (working with empirical data) for plant-pollinator feeding interactions, like those that have been established for many predator-prey interactions. ● Combine adaptive foraging with diet theory to jointly understand reweighting (Valdovinos et al. 2013, 2016) and rewiring consequences to network outcomes (e.g., local stability, species persistence, robustness to coextinction). Efforts to model rewiring and reweighting simultaneously are just beginning (Glaum et al., 2021). ● Integrate diet breadth models with adaptive foraging as an alternative means to constrain interaction occurrence. ● Extend consumer-resource models to make it easier to assess outcomes that are currently only straightforward in Lotka-Volterra models (including local stability and structural stability among other outcomes)	● Test predictions of how increased inter- and intra-specific competition affect diet breadth with simplified manipulative experiments. This could include laboratory trials within a foraging chamber (e.g., Cervantes-Loreto et al., 2021) and /or experimental treatments within glasshouse or field cages (e.g., Fontaine et al., 2008) where the densities of floral arrays as well as the densities of foragers can be carefully manipulated. A particular gap is understanding diet breadth responses when multiple factors (resource levels, competition) change simultaneously. ● Collect data on resource levels (floral rewards) to pair with interaction network data collection ● Work directly with theoreticians to build allometric relationships in plant-pollinator systems (e.g., floral display size and nectar quantity; handling time relationships between plant-pollinator pairs based on proboscis length and corolla depth), following efforts in predator-prey systems (e.g., as were implemented in Beckerman et al., 2006; Petchey et al., 2008) ● Collect plant-pollinator network data in temporally and spatially defined samples, that along with floral resource data allow for testing of optimal foraging-related submodels

	- include independent estimates of pollinator and plant (flower) abundance, along with measures of interaction frequency, to more clearly separate pollinator preference from mass-action foraging

2.6. Section 3: Conclusions

Theory inherently makes simplifications and approximations, yet in plant-pollinator networks we do not currently have a good sense of what is important and what can be abstracted away. Servedio (2020) provides a useful framework distinguishing between three categories of assumptions: critical, exploratory, and logistical. Critical assumptions are those directly being tested in a model akin to independent factors that an empiricist would vary in an experiment. Empiricists and modelers should work together to determine key critical assumptions, ensuring they rest on solid empirical and theoretical findings (or at least don’t seriously run counter to the body of literature). Exploratory assumptions, similarly, are factors that could be varied in a model but unlike critical assumptions are not central to the main thrust of the model. Again, empirical work in plant-pollinator systems can guide modelers in decisions about what exploratory assumptions to include. Lastly, logistical assumptions are those made primarily for tractability yet close collaboration between empiricists and theoreticians will ensure that these assumptions do not induce a critical misunderstanding of the available knowledge of the system. Empiricists and theoreticians should work jointly to build consensus on which submodels and simplifications in plant-pollinator models are critical and the context dependencies they may rely on.

Plant-pollinator interactions maintain terrestrial biodiversity and ecosystem functioning given that pollinators directly support wild plant populations (Bascompte et al. 2006) as well as human well-being through crop yields (Klein et al., 2007). Therefore, understanding how these relationships work is important for insight into how they will respond to climate change and other anthropogenic disturbances resulting in shifts between these interactions (Burkle et al., 2013). Network-based analyses have made great strides towards attaining a better grasp of how plant-pollinator communities may fare under perturbations, yet modeling and empirical efforts which are more integrated will be necessary to fully tackle this issue. Here we presented a framework for increasing biological realism in plant-pollinator models and more rapid evaluation of theoretical findings in empirical work. System-level approaches are a clear pathway to tractable unifying theory and empiricism in models of complex networks of interactions. Rigorously exploring, testing, and applying system-level generalizations in plant-pollinator network models will deepen our understanding of the principles of these systems.

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Chapter 3: Modeling robustness and network structure

3.1. Introduction

Predicting how highly interconnected species will respond to ecosystem change is an important goal in community ecology (Angert et al. 2013). Employing networks in ecology has made great strides towards describing highly complex suites of antagonistic (e.g. predator-prey, food webs, parasitic) and mutualistic (e.g. plant-pollinator, seed disperser) interactions. Networks of a given type often show characteristic network structure both across systems and organisms (Dunne et al. 2002, Bascompte et al. 2003). For example, mutualistic networks are usually highly nested whereby specialists interact with a subset of the species also interacting with generalists. Patterns of nestedness have been found in plant-pollinator, plant-seed disperser, coral-symbiont, and AM fungal-plant systems (Bascompte et al. 2003, Montesinos-Navarro et al. 2012, Fabina et al. 2012). Nestedness is thought to provide redundancy, buffering species from the negative effects if one partner goes extinct or suffers population declines. However, redundant interactions inherently increase competition for resources. It is unknown what maintains nestedness and how the benefits of redundancy in networks outweigh the costs. To this end, we need careful isolation of mechanisms underpinning structural components like nestedness to better understand the mechanisms driving network assembly.

Many network structural components such as nestedness consist of two intertwining components: topology and interaction strengths. Topology is the binary structure of who interacts with whom, while interaction strength is the intensity of interactions (e.g., the per-capita impact of one species on another). How nestedness promotes network stability is still unclear due, in part, to the confounding of interaction strengths with topological structure. Interactions may be nested *topologically* even while the strengths of these interactions are not (Staniczenko et al. 2013; Valdovinos et al. 2013, 2016). Previous theoretical work has evaluated the effect of nestedness on network stability by changing the identity of links or the topology but to our knowledge no study has systematically and independently altered the nestedness of interaction strengths.

Robustness to co-extinction assays are one approach to understand the effect of network structure on one aspect of stability. These assays subject networks to sequential species deletions and track the co-extinctions that result from loss of partner species. Networks with high robustness are defined as those that suffer fewer co-extinctions when a species is removed from the system while those with low robustness tend to suffer longer co-extinction cascades, ultimately leading to collapse. Robustness analyses have been used to test how different structural properties lead to greater network stability (Dunne et al. 2002) and have also tested different extinction orders based on node properties such as the generality of interactions (Solé and Montoya 2001, Memmott et al. 2004, Kaiser-Bunbury et al. 2010). Previous research has found that empirical networks with higher levels of topological nestedness are robust to co-extinctions (Memmott et al. 2004).

One criticism of classical robustness to co-extinction methods is that they have historically assumed that all individuals of each partner must go extinct before a co-extinction is recorded. Here we term these "deterministic" models. This assumption lacks biologically realism since mutualistic benefit to a partner can be lost before a species is extirpated. Stochastic coextinction models (SCMs) relax this assumption by giving a weighted chance that a species will be ‘unlucky’ and go extinct even if partners still exist (Vieira and Almeida-Neto 2015). This stochastic coextinction model uses interaction strengths to derive the chance of a species going extinct. Thus, in contrast to deterministic models, SCMs allow for incorporation of interaction strengths, not just topologies, into robustness assessments. Here we use this feature of SCMs— and extend this modeling framework— to investigate the separate effects of network structure and link intensities on stability.

In this work, we explored how different patterns of interaction intensities interact with network topology to affect robustness in mutualistic networks, using stochastic coextinction modeling. We assessed networks with nested, random, and anti-nested structures, in a full-factorial design considering both topology and interaction intensity (hereafter called quantitative nestedness). Second, we extended the SCM approach from Vieira & Almeida-Neto (2015) to allow for sequential species removals (in contrast to their original formulation, which was based on single extinctions) and then compared SCM with purely deterministic models in terms of robustness to co-extinction. Specifically, we test whether a) stochastic co-extinction cascades where sequential deletions were applied were less robust than deterministic models, and if b) nestedness confers robustness when underlying interaction strength is no longer coupled with topology. We hypothesized that topological nestedness would confer high robustness given that increased topological nestedness means higher redundancy of interaction partners. Alternatively, we hypothesized that increased quantitative nestedness would instead make networks more susceptible to co-extinctions. We predict this because empirical networks in nature are organized in anti-nested structures and models that allow for adaptive foraging will shift towards this configuration (Valdovinos et al. 2016). Thus, we hypothesized that highest robustness would be conferred when networks were topologically nested but quantitatively anti-nested. Additionally, we hypothesized that stochastisticity would make networks less robust relative to deterministic models, since cascading chains of coextinction are possible.

3.2. Methods

Generating mutualistic network structure

We tested robustness to co-extinctions within 43,200 bipartite mutualistic networks that varied in their distribution of links (topology) and interaction strengths across those links. We used a fully factorial design crossing topological and quantitative network structures that were either highly nested, intermediate-level nested, or highly anti-nested (n = 100 replicates per scenario). Topological network structures were generated in R (R Core Team 2021). We generated matrices with species richnesses, S = 50 and 100 and, for modeling simplicity, equally divided species into the two trophic levels that engage in the mutualism (thus all simulations had square matrices). For each network size we simulated networks with two levels of connectance or number of links (C= 0.08 and 0.25). These parameter values are summarized in Table 1.

We first created networks that initially only had topological structure (0s if no interaction occurred and 1 for the presence of an interaction). To achieve networks with varying topology, we simulated 1,000,000 random networks of each S and C combination. We then ranked these generated networks by their NODF value (nestedness metric based on overlap and decreasing fill). For the topologically antinested set, we selected the 100 networks with the lowest NODF values. Similarly, for the intermediate nested set, we randomly selected 100 networks between the 40th and 60th percentile NODF values. Lastly, to obtain highly topologically nested networks we selected the 100 networks with the highest NODF values and applied an algorithm to increase the nestedness of these networks. The algorithm initially shuffles interactions to make the most connected plant and pollinator species fully connected. Then it iteratively moves all of the links for a given column and row to the top and to the left respectively, ordered by degree and alternating between columns and rows. This procedure creates very highly nested networks, while maintaining some variation in topology across networks. We checked to ensure that no matrices within each scenario had the exact same topology.

Atop these topological structures, we assigned quantitative structure where the interaction strengths distributed across the topology were either highly nested, highly anti-nested, or random using rank order. We assigned ranks to cells with an interaction either 1) diagonally along the complementarity diagonal for those in the anti-nested or nested treatments, reversing the order of fill between the two treatments, or 2) via random assignment for those in the random treatment. We chose interaction strengths as absolute values of random draws from a normal distribution with $\mu = 0$ and $\sigma = 0.0884$ and 0.1767 (following Allesina and Tang 2012). Interaction strengths were assumed to be symmetrical among interacting species pairs for simplicity.

Table 1. Parameters values for species richness (S), connectance (C), interactions strengths (σ), as well as the topological and quantitative structures used in the experiment. All factorial combinations of each parameter level were modeled.

Parameters	**Notation**	**Values**
Species richness	S	50, 100
Connectance	C	0.08, 0.25
Interaction Strengths	σ	0.0884, 0.1767
Topological structure		tA topologically antinested tN topologically nested tI topologically intermediate
Quantitative structure		qA quantitative antinested qN quantitative nested qR quantitative random
Extinction order		Random, Most to least linked, Least to most linked
Extinction rules		deterministic, Stochastic

Sequential Extinction Simulations

Deterministic Base Model

All model simulations were performed in Matlab (MATLAB 2018). We ran a suite of simulations varying the extinction order where the order of primary extinctions were selected 1) randomly, 2) most to least general, and 3) least to most general as assessed by number of links given previous robustness analyses which assessed these deletion orders (Dunne et al. 2002, Memmott et al. 2004). At each extinction step we recorded secondary extinctions that resulted from the removal of the target species. For the deterministic models, species were considered secondarily extinct if they no longer had any partners due to the removal of the target species.

Stochastic Coextinction Model

We relaxed the assumption that all partners must be lost before a secondary extinction could occur by adopting a stochastic co-extinction model (Vieira and Almeida-Neto 2015). This model weights probabilities of extinction based on the dependencies of remaining partners, where d_{ij} is the dependency of species i on species j. This is calculated by dividing the quantitative strength of interaction between species i and j by the sum of all interaction strengths of partners to i, $d_{ij} = \frac{A_{ij}}{\sum A_i}$. We weighted extinction by d_{ij} where the probability of going extinct due to a loss of a partner at the previous step, $P_{ij} = d_{ij}$. These weighted stochastic chances of extinctions were drawn for every species connected to the primary extinct target. If a co-extinction occurred via this weighted chance, we recalculated dependencies for partners of the newly extinct species (now from the other trophic level as the first extinction). This process repeated until no new co-extinctions were recorded. Thus, this model allows for complex coextinction cascades to propagate through the network. Vieira and Almeida-Neto (2015) added a second term, intrinsic dependence on mutualism, R_i, so that probability of extinction was $P_{ij} = R_i d_{ij}$. Here we set $R_i = 1$ for all species in our networks indicating complete dependence on mutualisms. Additionally, we extended the original model of Vieira and Almeida-Neto (2015) so that after a cascade finished (i.e. there were no more co-extinction propagations), we then selected another primary extinction and allowed a new cascade to propagate. We continued to remove primary species until the entire network collapsed (e.g., following Dunne et al. 2002, Memmott et al. 2004). This extension allowed us to directly compare robustness to the base deterministic model.

Statistics

We performed all data analysis and visualization in the statistical language R (R Core Team 2018). To understand how our network formation algorithms performed, we calculated the network property of nestedness (NODF). We measured robustness (*R*) by calculating the proportion of species remaining in the non-target group as the proportion of remaining target guild species and calculated the area under the curve (termed attack tolerance curves elsewhere). Mean robustnesses, averaged for each simulation (*n* =100) per scenario, were visually compared by plotting 95% confidence intervals around the means across scenarios and among the deterministic and stochastic frameworks. We chose this over formal statistical tests because sample size, which drives many statistics, can be arbitrarily chosen in simulation-based work.

3.3. Results

Scenario overview

In total, we assessed robustness to species loss in simulated networks within nine scenario types that factorially varied three levels each of topological and quantitative nestedness (Figure 1). We assessed both deterministic and stochastic robustness (Figure 1, orange and blue respectively), and three extinction orders, random (Figure 1A), least-to-most connected (Fig 1B), and most-to-least connected (Fig 1C).

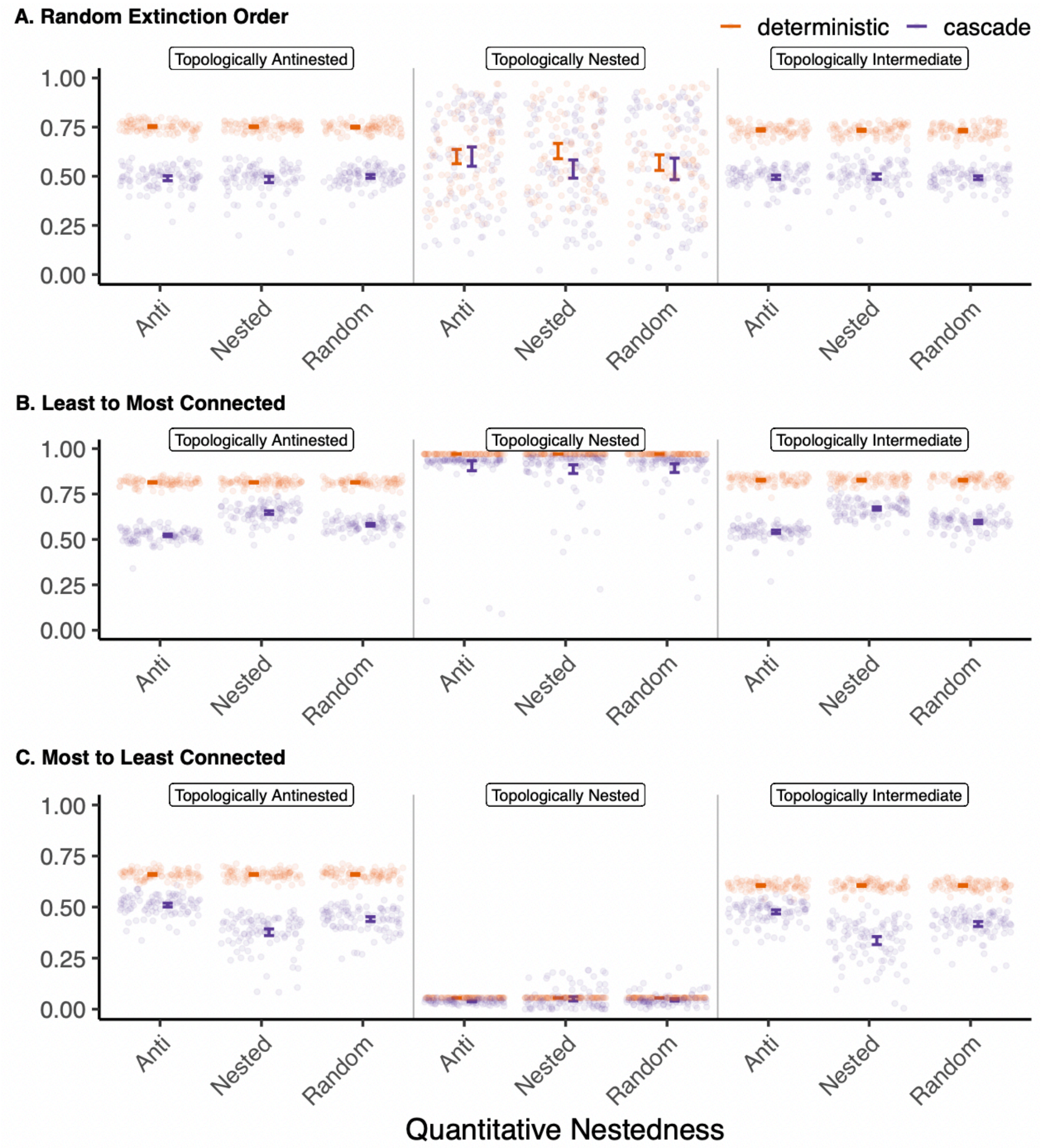

Figure 1. Mean robustness to co-extinction for each scenario. Error bars indicate 95% confidence intervals. Colors represent the deterministic (purple, dark) and stochastic cascade models (orange, light). The three levels of topological nestedness: Antinested, Nested, Intermediate are displayed in groups from left to right. For each topology their respective quantitative nestedness treatments are displayed. Simulations with varying extinction orders (A) random, (B) least to most connected and, (C) most to least connected. Results shown here are for $S = 100$, $C = 0.08$, and $\sigma = 0.0884$. Points are each of the 100 replicate networks we assessed per scenario.

whereas when primary species extinctions were instead ordered from most connected to least connected, topologically nested networks were not robust to species extinctions (Figure 1C).

Parameter variation

Across the combinations of species richness and connectances, as well as at the two interaction strengths we tested, combinations showed qualitatively similar patterns with respect to robustness (Appendix A). Figure 1 displays a representative combination of $S = 100$ and $C = 0.08$. One notable deviation is increased robustness in topologically nested scenarios when $S = 50$ and $C = 0.25$ (Figure S2). We found no differences in terms of how S or C interacted with interaction strength settings and therefore only present one here ($\sigma = 0.0884$).

Nestedness determination

Networks with topologically nested structure had mean NODF values of 66.05 +- 0.19 se, networks with topologically antinested structure had mean NODF values of 6.81 +-0.009 se, while the networks with topologically intermediate networks had mean NODF values of 8.73 +- 0.007 se.

Deterministic extinction model vs stochastic cascade model

Across most of the deterministic models, robustness to species extinctions was high (greater than 60% for the majority of scenarios). Because deterministic scenarios cannot take quantitative structures into account, we found very similar robustness values across the three quantitative levels for a given topology.

Across the majority of scenarios, stochastic cascades resulted in lower robustness to species extinctions as compared to analogous deterministic models. Stochastic cascades did not lead to reduced robustness relative to deterministic scenarios within topologically intermediate networks when extinction order was also random (Figure 1A).

Deletion sequence order

Consistent with previous studies (e.g., Dunne et al. 2002, Memmott et al. 2004), deletion order was important for robustness. When species extinction order was chosen randomly, all networks were highly robust (Figure 1A). When primary species extinctions were ordered from least connected to most connected, topologically nested networks were highly robust (Figure 1B). Lastly, when primary species extinctions were ordered from most to least connected, topologically nested networks were not robust (Figure 1C).

Robustness between quantitative network structure groups

Varying combinations of topological and quantitative nestedness structures yielded different robustness to simulated co-extinctions (Figure 1). Within the topologically antinested and topologically intermediate networks there were differences between the three quantitative nestedness structures when comparing least-to-most and most-to-least connected extinction scenarios. By contrast, within the topologically nested networks, we found smaller robustness differences across quantitative nested groups.

When extinctions were ordered from least connected to most connected, quantitatively nested networks were on the whole more robust than networks with antinested or random quantitative structure. Quantitative antinested networks in these cases were the least robust of the three quantitative structures tested. These patterns were reversed when extinctions were ordered from most-to-least connected: quantitatively nested networks were less robust than the networks with antinested or random quantitative structure. Quantitative antinested networks in these cases were the most robust of the three quantitative structures tested.

3.4. Discussion

Here we independently varied topological and quantitative nestedness within mutualistic networks to assess their effects on robustness to coextinction. We found three main results. First, we found that topological structure matters more than quantitative structure in driving robustness to coextinction. Second, we found that quantitative structure still plays an important role in determining robustness. Lastly, we found that quantitative structure served to magnify the effects of topological structure on robustness. We discuss the implications of each of these results below and close with some future directions spurred by this research.

Topological structure drove robustness to coextinction to a greater degree than did quantitative structure. That is to say, the changes in robustness between different topologies were substantially larger than the changes between different quantitative structures. Previous research has identified that nested topologies are highly robust to species co-extinctions when extinctions are ordered from least-to-most connected and, conversely not robust when ordered from most to least connected (Memmott et al. 2004, Burgos et al. 2007). Our results supported these findings where topologically nested networks collapsed readily when highly connected species were selected to go extinct first, but were highly robust when the ordering of extinctions was reversed.

While topology was the main determinant of robustness, we found that network robustness depended on both topology and interaction intensity. Within most topologies we found diverging robustness values between the three quantitative levels. We had hypothesized that the most robust networks would have topologically nested but quantitatively antinested structures. For the most part we did not find that quantitatively antinested networks were more robust than quantitatively nested or random networks. We also did not find there was one consistently best topological and/or quantitative structure, instead we found that the extinction order context was important, which we discuss below.

Importantly, quantitative structure acted to exacerbate topological patterns. For example, when extinction orders were from most connected to least connected— an extinction order in which topologically nested networks routinely do not perform well (Burgos et al. 2007) — networks that were quantitatively nested had lower robustness than quantitatively antinested or random networks. Similarly, for the opposite extinction order, least-to-most connected, nested networks outperform other topologies, and our results show that nested quantitative structures further enhance robustness in this scenario. Interestingly, the results related to quantitative structure were strongest for the anti-nested and random topologies; for nested topologies, the topology itself drove strong robustness responses with little variation among the quantitative structures.

In assessing the robustness consequences of different combinations of topological and quantitative nestedness, it is worth considering which combinations are common in nature. While many empirical mutualistic networks show high levels of topological nestedness (Bascompte et al. 2003), assuming that patterns of quantitative interaction intensities parallel this topology makes little sense from a resource competition standpoint. For example, in plant-pollinator interactions with this network structure, essentially every pollinator species is in strong competition with several other pollinators for the same floral resources. Analogously, nearly all plant species would be visited by pollinators that have visited other species of plants, therefore potentially encouraging heterospecific pollen transfer. Instead, specialization—i.e. niche partitioning—is predicted by niche and optimal foraging theories whereby species competing for resources will specialize to reduce interspecific competition (Brosi 2016).

Quantitative anti-nestedness may be one way we see this type of resource partitioning occur in multi-species networks (Loy and Brosi 2022). Our work shows that mutualistic networks may be buffeted to species loss when they are topologically nested yet quantitatively antinested—but only in extinction orders where specialists are most vulnerable. This is somewhat supported by what has been found in empirical networks where topological networks are nested yet quantitative structure based on preference is no different than random (Staniczenko *et al.* 2013). Additionally, quantitative antinestedness has been found in the bumble bee sub-module of pollination networks (Valdovinos *et al.* 2016) but has yet to be tested empirically in community-level networks when accounting for pollinator preference rather than solely interaction intensity, which is confounded with pollinator abundances (Staniczenko et al. 2013).

Here we report on a modeling framework where we extended previous coextinction analyses to examine the role quantitative interaction structure has in driving robustness to species loss. Coextinction assays are often criticized for their binary nature (i.e. interactions either exist or they do not). In nature we often observe the functional loss of an interaction due to low population abundances before complete local extinction of either partner (Tylianakis *et al.* 2008;

Säterberg *et al.* 2013; Valiente-Banuet *et al.* 2015). For example, loss of adequate pollination services may be due to low abundances of available pollinators, not the absence of pollinators entirely. Kaiser-Bunbury et al. (2010) did incorporate interaction intensities into a robustness analysis. They ordered species extinctions by targeting the most frequently visiting pollinator species within their networks and found stark differences between extinction scenarios ordered by presence-absence extinction order. Importantly, this effort was unable to disentangle quantitative and qualitative structure given that they used empirical networks as inputs. We employed a stochastic coextinction modeling framework to isolate the effects of quantitative structure from topology. By allowing species to have some weighted probability of going extinct even while available partners remain, the model also tried to include the loss of interactions that precede species extinctions themselves. We had hypothesized that robustness would be lower in the stochastic model compared to the deterministic model. This was largely the case, likely driven by the fact that the stochastic model allows for extinction cascades in ways that the deterministic model does not.

Future Directions

Our findings and approach highlight several important avenues for future work. First, we extended the stochastic coextinction model originally formulated by Vieira and Almeida-Neto (2015) so that primary extinctions were chosen sequentially. This allows their model to be directly compared to other robustness algorithms (e.g., Memmott et al. 2004), and in turn allows testing other quantitative network structures that may be of interest in the future. Second, in this effort, we chose—for the sake of isolating solely the effects of topological and quantitative network structure—to set the parameter of mutualism dependence so that all species relied completely on their mutualisms to survive. Yet within plant-pollinator networks there exist plant species that can self-fertilize and there are pollinators such as many fly species which do not require floral resources for reproductive success. Thus, a natural extension would be to relax this assumption of mutualism dependence. Third, our deterministic and stochastic models were based only on network structure. Applying these topological and quantitative structures instead within a more mechanistic model, such as dynamical Lotka-Volterra or consumer-resource framework that explicitly tracks species abundances could be useful in understanding how different forms of nestedness are related to robustness as well as other key network outcomes such as local stability, resilience, persistence, etc. In particular, previous work in food webs suggests that robustness results generated by topology-only processes can contrast strongly with results from dynamical models (Curtsdotter et al. 2011). Lastly, our model did not include the ability for species to rewire or reweight their foraging efforts. Applying our topological and quantitative networks to robustness models that do allow for this (e.g., Baumgartner et al. 2020) could be important for understanding realistic responses to co-extinctions.

3.5. Conclusion

Globally, we are in the midst of the sixth major extinction (Ceballos *et al.* 2015), losing species at an unprecedented rate. Several studies have indicated long-term declines in species richness and abundances of pollinators (Potts *et al.* 2010; Hallmann *et al.* 2017) driven by multiple stressors such as lack of floral resources, pesticide exposures, climate change, and habitat loss (Goulson *et al.* 2015). Due to their key functional role in maintaining many terrestrial ecosystems via plant reproduction (Bascompte et al. 2006, Ollerton et al. 2011) and providing trillions of dollars in ecosystem services to crop production (Klein et al. 2007), understanding the function of plant-pollinator communities after species loss is vital. Our findings here indicate that more work is necessary to disentangle the interacting structures of network topology and quantitative interaction intensities as these two components of mutualistic networks both contribute to robustness in the face of species extinctions.

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Chapter 4: Simultaneous niche expansion and contraction in plant-pollinator networks under drought

4.1. Introduction

In a rapidly changing world, it is critical that we understand how multispecies ecological communities respond to perturbation. Complex communities of interacting species form ecological networks whose overarching structures may be important for species persistence (e.g., 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 (e.g., 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 (e.g., Lu et al. 2016) 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 (e.g., 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 (e.g., Alarcón et al. 2008) and can change rapidly with resource and competitor context (Fontaine et al. 2008, Fründ et al. 2013, Brosi and Briggs 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 leads 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. 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 (e.g., 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 (e.g., 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 (e.g., 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 (e.g., Inouye 1978, Fontaine et al. 2008, Fründ et al. 2013, Brosi and Briggs 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), 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.

4.2. 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 above sea level). Sites were located in montane meadows > 2km 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 unpublished; 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: May 16).

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 precipitation; date of first bare ground; total snow pack; number of days above freezing; and number of days snow covered. 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 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 1m x 20m transects spaced 2m apart. Transects were divided into sections 2m in length and each section was observed for a total of 3 minutes 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 and strictly randomized the order of transect segment sampling to reduce temporal sampling artefacts. We 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 (see 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 (unpublished); Lepidoptera: Scott (1992). Whenever possible, the identification was then further refined to taxonomic categories or named species using Savage (2003) Savage & Sorokina (2021), Stemkovski (unpublished). The taxonomic resolution of pollinators for our study was uneven (i.e., ranging from named species to some uncaptured taxa groups that were visually distinguishable, including some categories that involve multiple insect families) 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 drought and non-drought networks to family-level identification (Supporting information).

Network Analysis

We performed all data analysis in R 4.1.0 (R Core Team 2021). A fully reproducible RMarkdown report with all corresponding data is available in [masked for review]. Plant-pollinator networks were constructed by pooling observations across samples and sites within non-drought years (2016, 2017 and 2019) and drought years (2018, 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.

Downsampling to account for abundance

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 used a bootstrapping resampling technique. We sampled (with 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.

Downsampling to account for abundance and taxonomic turnover

Because we observed different pollinator taxa and plant species (in terms of which ones bloomed) in drought vs. non-drought years, we also sought to assess if differences 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 that occurred in both the drought and non-drought years before using the bootstrapping technique as explained above.

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) degree (mean number of links per node); 2) connectance (proportion of realized links); 3) network-level specialization (H2'); and 4) nestedness (NODF). We calculated these metrics using the 'bipartite' package (Dormann et al. 2008). Mean number of links and connectance 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. Nestedness is thought to be important for network stability and persistence and also is sensitive to generalization where increased connectance tends to lead to more nestedness (James et al. 2012).

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.

4.3. Results

We observed 6,652 interactions in networks pooled for non-drought years (2016, 2017, and 2019) and 1,534 interactions in drought years (2018 and 2020). Networks in drought years were smaller in dimension with 41 plant species and 94 pollinator taxonomic categories compared to non-drought years where we observed 57 plant species and 128 pollinator categories. We observed 623 and 380 unique interactions in non-drought and drought years respectively.

Downsampling to account for abundance

When comparing observed drought years to bootstrapped non-drought networks that accounted for abundance, drought years had significantly more links per species ($P < 0.001$) and higher connectance ($P = 0.026$) than non-drought years (Figure 1, Figure S3). Drought year networks were significantly more quantitatively specialized (higher H2’) relative to non-drought years ($P < 0.001$). Nestedness (NODF) did not differ between drought and non-drought years ($P = 0.614$).

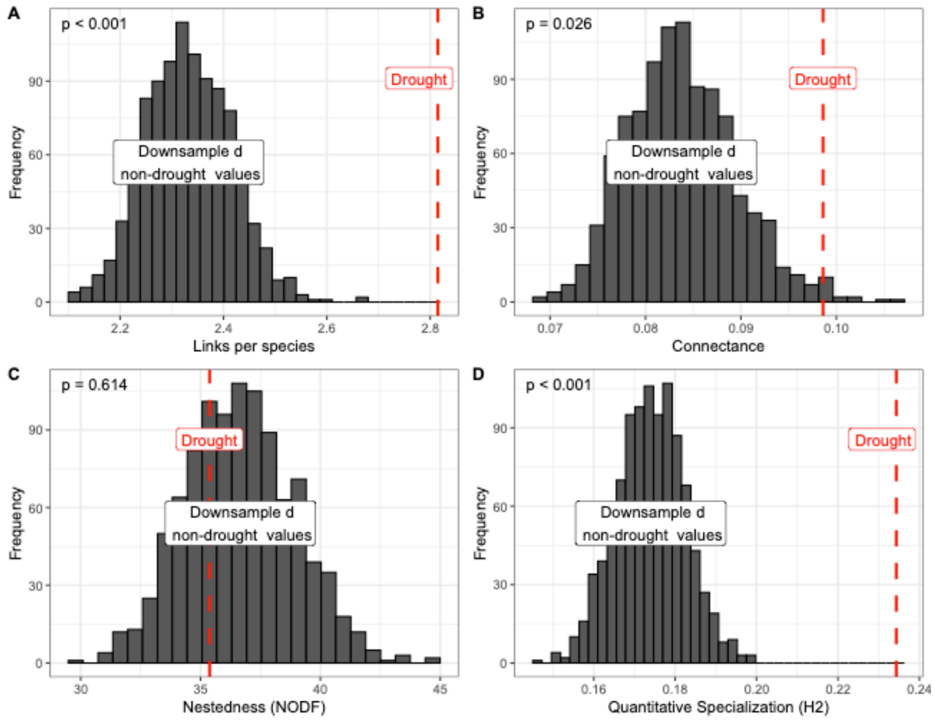

Figure 1 Distribution of network metrics calculated from downsampled bootstraps (999 resamplings) for (A) Links per species, (B) Connectance, (C) NODF, and (D) H2'. In each, the grey histogram bars represent metric values for each bootstrap where non-drought year networks have been sampled until the total number of interactions was the same as that found in the drought year (1,788 interactions). The raw drought value for each metric is plotted in red. Significant divergences of this drought value from the distribution of downsampled 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 downsamples.

Downsampling to account for 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 128 insect taxonomic categories to 36 plant species by 62 insect taxonomic categories and the pool of total interactions (later downsampled) from 6,652 to 5,940. Constraining the drought networks by the same species pool reduced the network from 41 plant species and 94 pollinators to 37 plant species by 62 pollinators and the total number of interactions to 1,534. When corrected for both abundance and species composition, plant and pollinators in drought years still had significantly more links per species (*P* <0.001) than non-drought years (Figure 2), but connectance did not differ between drought and non-drought years (*P* = 0.754). Drought networks were significantly more quantitatively specialized (H2', *P* < 0.001) than non-drought, but not less nested (NODF, *P* = 0.108).

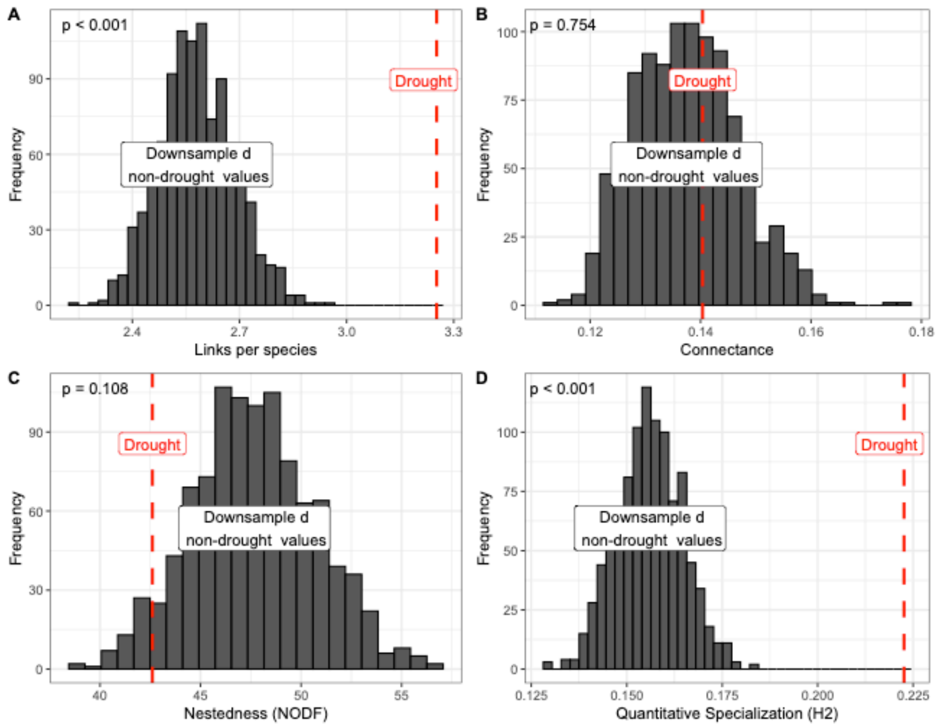

Figure 2 Distribution of network metrics calculated from downsampled bootstraps (999 resamplings) after accounting for taxonomic turnover for (A) Links per species, (B) Connectance, (C) NODF, and (D) H2'. Here, species were included in the resampled interaction networks only if they also existed in drought 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 (1,551 interactions). The raw drought value for each metric is plotted in red. Significant divergences of this drought value from the distribution of downsampled values is shown in the top corner.

Family-level analyses

Standardizing taxa to family-level reduced networks from 57 to 50 plants, due to only capturing specimens on those plants, and reduced networks from 128 insect taxonomic categories to 24 pollinator families in non-drought. In drought networks, 41 plant species were reduced to 39 plant species and 94 insect taxonomic categories was reduced to 24 pollinator families. Downsampled 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).

4.4. Discussion

We found contrasting results for greater network generalization under drought conditions. In terms of the qualitative presence of links, drought networks were far more generalized than non-drought networks after 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 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 in drought years aligns with optimal foraging / diet theories which predict niche expansion during periods of food scarcity (Stephens and Krebs 1986, Perry and Pianka 1997). Several studies have found evidence supporting this prediction. 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 (e.g., 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 (e.g. 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.

Future directions

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 in Descamps et al. 2021). Similarly, integrating optimal foraging theory within a network context (for food webs) has predicted diet breadth (e.g., Beckerman et al. 2006), yet such approaches have not to our knowledge been applied to understand changes following perturbations. 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 (e.g., CaraDonna and Waser 2020). Recent models that allow for rewiring using mechanistic adaptive foraging processes (Glaum et al. 2020) 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.

4.5. 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.

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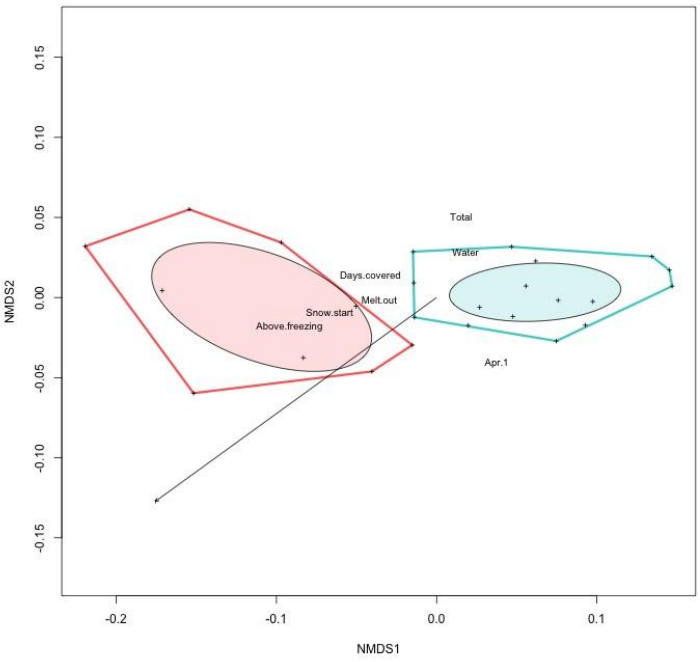
4.7. Supporting Information

Appendix S1: Figure S1

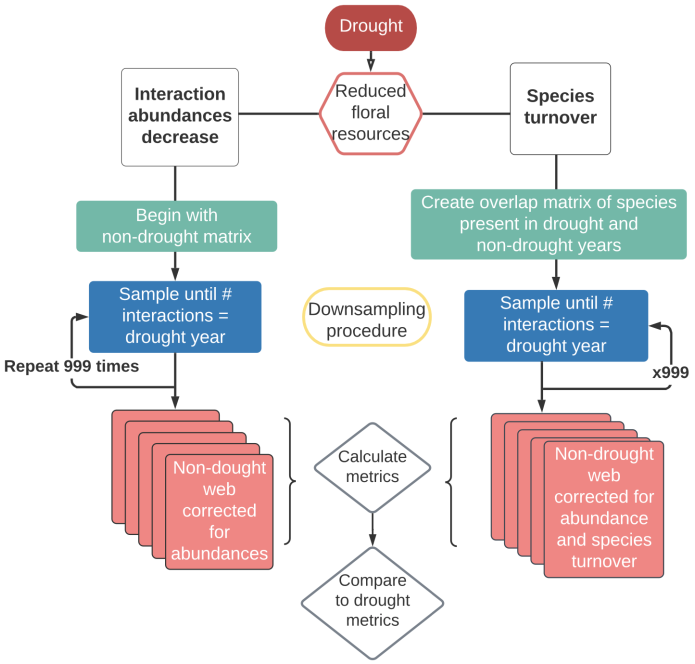
Two-dimensional NMDS of 8 weather variables collected at the RMBL weather station for winters between 1991-2020. Convex hulls encircle drought years (red) and non-drought years (blue). Drought status is plotted jointly in black. Stress= 0.046. Because the system receives 80% of its precipitation in the form of snow, we focused on weather variables for the preceding winter of each growing season. Weather variables that were included: total snow (cm), day of year of snow pack formation, day of year of melt out, water content (cm), number of days above freezing, number of days with snow cover, snow pack at April 1 and May 1 of each year. Data are collected and maintained by billy barr.



Appendix S1: Figure S2

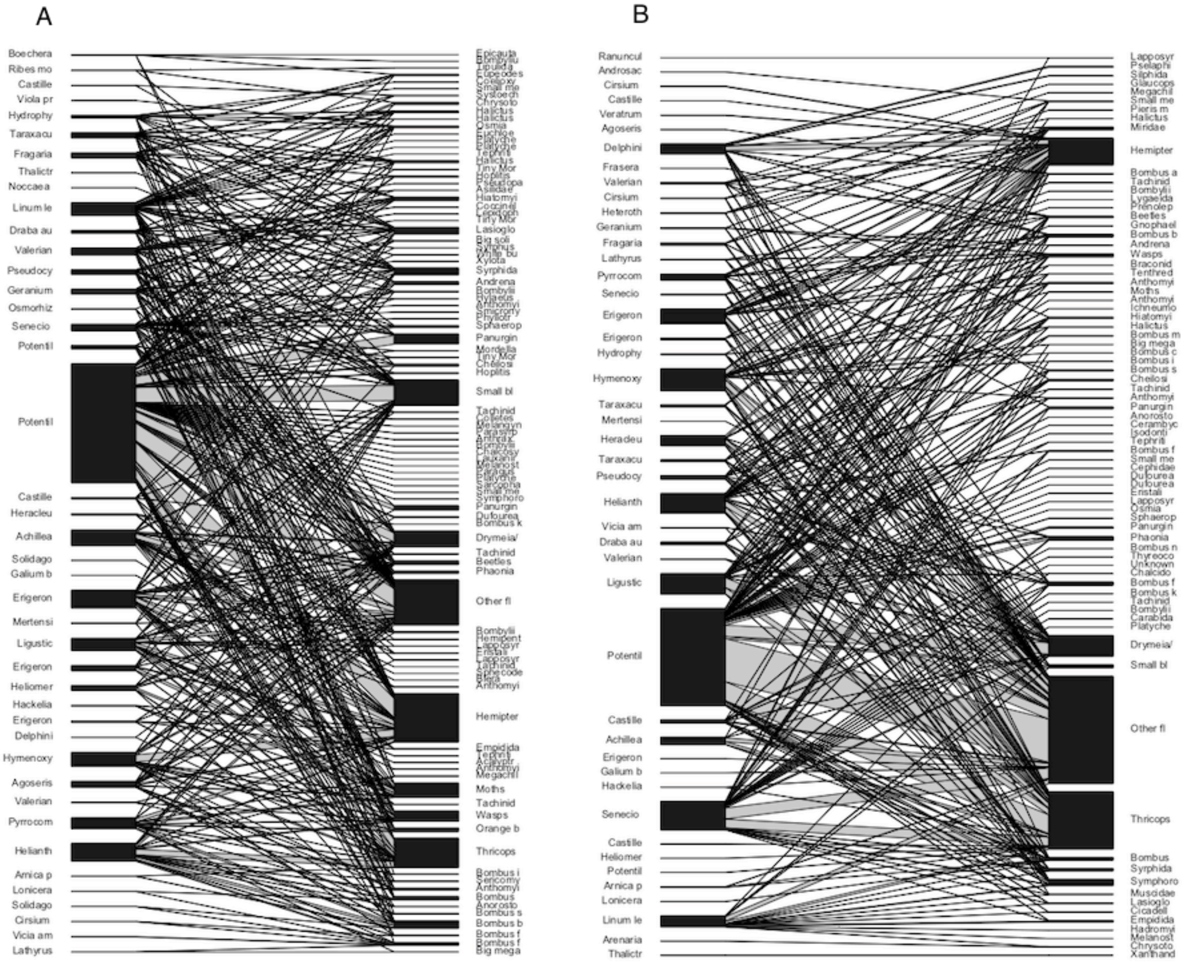
Downsampling procedure

In order to compare between drought and non-drought years we accounted for the total number of interactions. We saw nearly six times as many interactions in the non-drought years. It is not surprising that uncorrected non-drought networks were much larger and species had higher links per species. In part, this was due to sampling effects where we expect to see more unique interactions just as a result of observing more total interactions (Blüthgen 2010). While some metrics like H2` are robust to sampling effects, others such as connectance and links per species are sensitive to the amount of sampling (Blüthgen et al. 2006). Richness of interactions suffers from the same sampling effects as surveys for biodiversity do (arguably to even greater severity given that we fail to detect interactions at a higher rate than individual species, e.g., Bosch et al. 2009). This effect will impact both qualitative and quantitative measures of networks but tends to affect qualitative metrics to a far greater degree— these metrics rely more strongly on finding a true zero vs a false negative. Thus, to make a fair comparison between drought and non-drought years we employed a downsampling bootstrap type algorithm.



Appendix S1: Figure S3

Networks in drought (A) and one representative downsampled non-drought (B)



S3: Family-level analyses

When we only include specimens identified to family we observed 4,107 interactions in non-drought years and 1,315 interactions in drought years. In these networks we observed 142 and 156 unique interactions in drought and non-drought years respectively. Assessed at the family level, drought years also had significantly more links per species ($P < 0.001$) and were significantly more quantitatively specialized (higher H2') relative to non-drought years ($P < 0.001$). These networks were not more connected in drought years ($P = 0.698$) nor did they differ in terms of nestedness between drought and non-drought years ($P = 0.660$).

Controlling for taxonomic turnover networks assessed at the family-level resolution reduced the pool of total interactions decreased to 142 in drought years and to 161 in non-drought years. Constraining networks to the species overlap, family-level drought networks still had significantly more links per species ($P < 0.001$) and significantly more quantitatively specialized (H2', $P < 0.001$) than non-drought. Networks were not more statistically nested ($P = 0.862$) nor more connected ($P = 0.474$) in drought years as compared to non-drought years.

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Chapter 5: Conclusions and Future Directions

We still lack a strong understanding of how communities of mutualists, and the interactions between species, will shift due to anthropogenic change. In this dissertation I strove to pair synthesis work (Chapter 2) with simulation modeling (Chapter 3) and field-based empirical research (Chapter 4) to think holistically about perturbations to plant-pollinator interactions. My dissertation took a network approach acknowledging the reality of the 'tangled bank' in which species live (Darwin 1859). This approach makes sense for plant-pollinator mutualisms where most species are generalists, that is, most plant species are visited by many pollinator species, and most pollinator species in turn visit many different plant species (Waser et al. 1996). Much of the empirical work on mutualistic networks to date has been descriptive, despite the existence of ecological conceptual frameworks such as niche dynamics and diet theory, which could be helpful in determining interactions within a network and how they respond to perturbations. Past research findings show that these networks frequently have a characteristic structure of who interacts with whom. Yet open questions remain about how this network structure 1) will respond to perturbations to plant-pollinator systems and 2) whether these structures act to buffer mutualistic networks to these perturbations. Additionally, we do not understand how changes will ripple through these highly enmeshed communities. In the face of the reality of rapid environmental change, we do not understand if communities will be robust to this change. We require comprehensive studies that investigate the underlying ecological dynamics responsible for restructuring networks in response to anthropogenic change.

My dissertation aimed to address these knowledge gaps. In Chapter 2, I reviewed and synthesized the current disconnect between theoretical and empirical plant-pollinator network research. Next in Chapter 3, I carried out robustness to co-extinction modeling to understand how interaction topology and interaction strength act to make plant-pollinator networks susceptible or buffered from species extinction events. Lastly, in Chapter 4, I assessed empirical pollination network change in the Rocky Mountains of western Colorado—which are currently suffering the longest running drought recorded in the past 1200 years (Williams et al. 2022)—under multiple drought and non-drought years. I summarize the broader ideas and main findings of each chapter below.

5.1 Integrating theory and empiricism

Network approaches and tools are being increasingly applied to understand how perturbations impact plant-pollinator mutualisms. This has included both theoretical and empirical research approaches, but unfortunately to date those two classes of approaches have largely progressed independently, without informing or feeding back into one another. In chapter 2 I identify ways that these divergent lines of inquiry can be better integrated, with a focus on *submodels*, or stand-alone model components that describe the dynamics of multiple species. I walk through two major themes within plant-pollinator network research where integration of empirical work and theoretical approaches has a strong scientific value proposition. The first main theme is focused on functional and numerical responses. Functional responses describe interaction rates between consumer and resource species as a function of resource density, while numerical responses typically translate those interaction rates into individual or population growth rates. These responses have been poorly developed in plant-pollinator interaction research, especially in comparison to predator-prey research. First, I examined how functional and numerical responses can be formulated in two-species forms (i.e., a single resource species and a single consumer species; Holling 1965). I next turn to describing multispecies functional and numeric responses, which accommodate the effects of assemblages of species, including such processes as consumers interfering with one other. The second main topic I cover in this perspective is focused on using diet and niche theory to better predict who interacts with whom in pollination networks, and by how much. This is an area that has not been explored as much—relative to functional and numerical responses—in other ecological systems (including predator-prey systems), but which has substantial potential to improve understanding.

In this review I lay out several discrete steps for both theoreticians and empirical researchers collecting data on plant-pollinator networks. If we are to understand network responses to rapid anthropogenic change, several basic research lines about how interaction frequencies, resource densities, and subsequently the translation of pollinator visitation into mutualistic benefits within multispecies communities is needed. Because these communities are commonly comprised of hundreds of plants and pollinators and thousands of interactions, I call for increased research on fronts where generalizable forms and relationships can be applied across the entire network.

5.2 Understanding how perturbation responds to topological and quantitative network structure

Co-extinction simulations are a key modeling approach used to understand how multispecies networks respond to perturbations. Previous work has found that nested network topologies are an important driver of robustness (Burgos et al. 2007, Memmot et al. 2004), but to date nothing is known about how quantitative interaction structure impacts robustness. My collaborators and I performed a fully factorial experiment testing the interactive effects of topological and quantitative nestedness. We found that topological structure was more important in driving robustness to co-extinction, but that quantitative structure acted to amplify the effects of topology.

The model framework I developed is one of the first efforts to incorporate interaction intensity into robustness analyses, building on the stochastic coextinction modeling approach pioneered by Viera and Almeido-Neto (2015), but extending it to the loss of multiple species. The hope is that this framework is taken up by the field and used to test other quantitative structures thought to be important in mutualistic networks. Our key finding that quantitative structure acted to magnify weaknesses that certain nested topological structures have warrants further investigation into quantitative network structures in the future. While simulation models are necessarily simplistic depictions of one kind of perturbation, they are instructive in identifying extreme cases of sequential partner loss which may occur in response to ongoing anthropogenic climate change. In the last chapter I explored how real perturbations to empirical plant-pollinator networks changed partner generalization and foraging niche breadth in response to drought perturbations.

5.3 Drought perturbations in plant-pollinator networks

Plant-pollinator interactions are experiencing rapid abiotic change across the globe. Unfortunately, we have a poor understanding of how these perturbations will affect whole networks. As I have laid out in previous chapters, especially in Chapter 2, ecological theory exists to guide predictions of how networks may shift due to perturbations that act to change abiotic resource supplies. In this chapter I, along with several collaborators, compared plant-pollinator networks experiencing drought conditions. Following diet theory, there are two possible foraging responses that could lead to network structural change under drought. First, abiotic resources become scarcer, which in turn should lead to a lower overall base of plant resources for pollinators (nectar and pollen), in turn leading pollinators to expand which plants they visit, ultimately leading to more generalism with concomitant impacts on network structure. Alternatively, if this reduction in resources drives high levels of interspecific competition, each species should instead focus more on the resources that it has an advantage in exploiting, leading to increased specialization. I hypothesized that the overall reduction in the resource base would have a larger impact than interspecific competition, leading to increased generalization under drought conditions. Surprisingly, I found that these two contrasting mechanisms appear to be operating in parallel, leading to interactions that were broadened in terms of presence-absence of links, but simultaneously more specialized in terms of foraging effort.

The simultaneous changes to foraging niche I found have the potential to alter the quality of plant-pollinator interactions. Plants being visited by a greater number of pollinator visitors may experience reduced fitness and it is still unclear to what extent the quantitative specialization I also found will offset this potentially deleterious effect of drought perturbation in these systems.

5.4 Future directions

This dissertation aimed to examine perturbation to plant-pollinator systems from several different angles both theoretical and empirical. As systems face rapid anthropogenic change, we still do not understand how these changes will impact multispecies mutualistic networks. Here, I have highlighted some of the theoretical and empirical research needed to develop this field into a more predictive science.

To answer questions regarding perturbations to communities, there are several lines of research that are needed. First, a chapter of this dissertation, Chapter 4, could not have been done without ongoing monitoring of empirical plant-pollinator networks; there exists paucity in this type of longitudinal research. Second, we need more manipulative work on the scale of communities. This is inherently difficult within networks where plots must be large enough to capture the diverse assemblages of plant species necessary to build accurate networks. Some types of ecological manipulations may work well in this context. For example, Free Air Carbon Enrichment ("FACE") experiments explore the consequences of higher CO_2 concentrations at the plot level (McLeod and Long 1999). Manipulations of snowmelt via shadecloth (Steltzer et al. 2009) or inert black sand (Blankinship et al. 2014) can be applied on plots large enough to sample networks and thus should be applied in future studies. Additionally, I call for more coordinated efforts across scales (similar to NutNet, Borer 2014) that are necessary to understand the generalizability of findings about how networks will respond to anthropogenic change. Flavors of null model analyses exemplified in Chapter 4 should be employed and extended to compare network changes across these scales.

This dissertation calls for a deeper understanding of the mechanisms restructuring these interactions. I have mostly focused on consumer-resource based mechanisms as I think about the diverse assemblages of species within each of the guilds under resource competition with one another. This is not the only way to conceptualize plant-pollinator interactions. For example, while outside the scope of this dissertation, a large body of literature exists examining how foraging niches may be structured by trait morphology and from aspects like co-evolutionary dynamics within pairs of species in the networks. It remains unclear the relative contributions to overall network structure these and interspecific competition play and future work should try to bring these disparate research programs together. I believe this dissertation takes important steps in laying out a case for applying competition and niche processes investigated in predator-prey systems as a way to make plant-pollinator network science a more mechanistic endeavor.

Perturbations to plant-pollinator networks may have large consequences to wildland ecosystems, human agricultural production, and human health. Additionally, as we turn to restore degraded systems and conserve ecological communities in peril, we require a better handle on what structures plant-pollinator networks and how these structures may allow for these critical interactions to persist.

Introduction and Conclusion References

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