

Biotic and Abiotic Drivers of Plant-Pollinator Interaction Rewiring

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PREVIEW

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Abstract

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In this dissertation, I examine variation in plant-pollinator interaction patterns. I present two observational studies exploring drivers of interaction variation, followed by an experiment in which I demonstrate the effect of changing plant-pollinator interactions. First, I use a structural equation modeling framework to demonstrate that temperature variation and plant community dissimilarity directly drive variation in plant-pollinator interaction patterns. Both variables also provide pathways for geographic distance to indirectly impact rewiring. Second, I use a multinomial logistic regression to show that pollinators prefer different flowers at different temperatures, even within a constant plant community. Third, I present an experimental manipulation that connects the removal of the most abundant bumble bee in a community to the production of fertilized seeds in a focal plant. In this experiment, I find that the composition of the plant and pollinator communities as well as the distribution of morphological traits both guilds influences the way in which pollinator removal influences pollination function. As a whole, this dissertation demonstrates that interspecific interactions cannot be considered static components of plant-pollinator communities. Rather, ecologists must consider how changes to biotic and abiotic conditions are likely to affect not only the organisms present in a community but also the interactions between them.

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PREVIEW

Chapter 1

Introduction

How and why do species interact? These questions, which form the basis of much of community ecology, continue to intrigue researchers. Despite a wide range of models describing community dynamics, the factors regulating interaction patterns remain obscured by non-linear and multi-dimensional drivers of interaction occurrence (Abrams, 2001). Though co-occurrence can be thought of as a minimum requirement for an interaction to occur, it is not the sole determinant of interaction patterns. Interaction turnover—the variation between interactions under different ecological conditions—can occur as a result of a change in the species present in the community (species turnover) or due to some behavioral change among species that co-occur under multiple contexts (rewiring) (Anderson et al., 2011; Poisot, Canard, Moullot, Mouquet, & Gravel, 2012). Studies have identified both species turnover and rewiring as significant sources of interaction turnover along spatial and temporal gradients (Burkle, Marlin, & Knight, 2013; CaraDonna et al., 2017; Carstensen, Sabatino, Trøjelsgaard, & Morellato, 2014; Trøjelsgaard, Jordano, Carstensen, & Olesen, 2015). However, while the processes underlying spatial and temporal patterns of species turnover have received substantial attention in ecological literature, the relationships between these gradients and rewiring remain poorly understood.

Rewiring is the term given to variation in interactions between species that co-occur under multiple ecological contexts. Since rewiring occurs despite the continued presence of both interaction partners, it often reflects a driver external to the interaction that alters the attractiveness or availability of resources in that community. In a recent review, Poisot,

Stouffer, and Gravel (2015) propose that such drivers of rewiring include environmental context, biological compatibility, and community composition. For instance, a bee may forage on different flowers at high and low temperatures depending on its metabolic needs even if the floral assemblage remains constant, but those metabolic concerns may become less important if trait-matching incentivizes a particular interaction or if strong competition from other pollinators disincentivizes another. While this framework represents a valuable way to conceptualize the drivers of rewiring, more empirical evidence is necessary to understand how interaction turnover relates to specific environmental and biological contexts. Further, research must connect changes in interaction patterns to the broader maintenance of biodiversity and ecological function in order to fully understand the multi-faceted ways in which global change pressures are likely to impact ecological communities.

Plant-pollinator communities are important biological systems with which we can expand scientific understanding of interaction turnover while also identifying specific functional implications associated with these ecological changes. Plant-pollinator interactions play an essential role in the maintenance of biodiversity: plant reproduction relies upon the consistent transfer of pollen between individuals, which is often vectored by mobile organisms like insects as they forage for floral resources. However, despite the ecological importance of plant-pollinator interactions, the mechanisms structuring these interactions and the variation therein remain poorly understood. We have very little insight into how interactions between species will change in a rapidly changing world, which limits our ability to predict how global environmental change will impact important ecological processes like pollination. For instance, what flowers will pollinators visit if temperatures increase? Will altered foraging patterns occur throughout a pollinator's entire range? What plant or pollinator characteristics might make species resistant—or susceptible—to interaction change? How will these changes influence pollination services? Answering such questions will help to determine how global environmental change will influence the persistence and maintenance of biodiversity and ecosystem function via pollination systems.

With this dissertation, I examine the causes and consequences of plant-pollinator interaction turnover in the Rocky Mountains of southern Colorado. I combine observational and experimental studies in an effort to understand how both the abiotic environments and biological contexts within which plants and pollinators interact affect the structure and function of these communities. In Chapter 2, I examine environmental and biological drivers of plant-pollinator interaction rewiring. I utilize a natural environmental gradient to explore the role of temperature in mediating spatial patterns of rewiring. I also discuss the niche and neutral processes that may underlie the effect of community composition on interactions between spatially persistent partners. In Chapter 3, I further explore the effects of temperature on pollinator foraging preferences. Specifically, I isolate the effects of temperature variation from variation in plant community composition in an effort to ascertain how pollinator foraging patterns vary within a consistent resource landscape. Finally in Chapter 4, I present experimental results that demonstrate the functional effects of single-pollinator-species losses. I show that the effect of these species losses on seed production in a focal plant species depends on the composition the remaining pollinator and plant communities as well as the distribution of key morphological traits within these communities.

Chapter 2

Temperature and community composition underlie geographic patterns of rewiring in plant-pollinator networks

2.1 Abstract

Plant-pollinator communities experience variation in the interactions between guilds that are unrelated to turnover in either the plant or pollinator community. This process, which is known as rewiring, often increases with the spatial separation of communities; however, any relationships between this spatial pattern and biologically meaningful drivers have not been identified. In this study, we find that both temperature difference and plant community dissimilarity provide pathways through which geographic distance drives rewiring. Geographic distance between sites does not have a direct effect on rewiring when these proximal drivers of rewiring are included in analyses, which further supports our hypothesis that spatial patterns in interaction variation reflect underlying ecological processes rather than inherent spatial structure. These results illustrate the importance of environmental and biological conditions to interaction variation in plant-pollinator communities and ultimately demonstrate key pathways through which global change dynamics may influence an important ecosystem function.

2.2 Introduction

Interspecific interactions, which are crucial components of biological communities, exhibit substantial variation over time and space (Burkle et al., 2013; CaraDonna et al., 2017; Carstensen et al., 2014; Simanonok & Burkle, 2014; Trøjelsgaard et al., 2015). The plant-animal interactions that facilitate pollination in over 85% of flowering plants (Ollerton, Winfree, & Tarrant, 2011) are susceptible to disruption via temporal (phenological) mismatches if pollinators are not actively foraging at times that flowers are producing pollen, to or spatial mismatches if the geographic ranges of plants and pollinators diverge due to environmental change (Burkle et al., 2013; CaraDonna et al., 2017). Since synchrony—both spatial and temporal—in the life histories of these organisms is essential to their ecological function, substantial work has been done to understand where and when plants and pollinators are likely to co-occur under shifting climatic and anthropogenic pressures (Dalsgaard, 2020; Gérard, Vanderplanck, Wood, & Michez, 2020; Miller-Struttmann et al., 2015). However, even if plants and pollinators achieve both spatial and temporal overlap, plant-pollinator interactions themselves experience turnover independent of species co-occurrence (Carstensen et al., 2014; Trøjelsgaard et al., 2015).

Rewiring—the name given to interaction turnover that is not explicitly driven by the loss of one or both interaction partners—can be partitioned into several distinct drivers (Poisot et al., 2015). Pollinators are likely to partition their interactions among plants in a way that maximizes the rewards obtained from each foraging interaction (Fontaine, Collin, & Dajoz, 2008; Valdovinos, Moisset de Espanés, Flores, & Ramos-Jiliberto, 2013). The type, amount, and quality of that reward may vary with environmental context (McCallum, McDougall, & Seymour, 2013); for instance at lower temperatures heat rewards might be more valuable than nectar (Rands & Whitney, 2008; Sapir, Shmida, & Ne’eman, 2006; Seymour, White, & Gibernau, 2003), while higher temperatures may affect the quality of nectar in terms of volume, sucrose concentration, and viscosity (Descamps, Quinet, Baijot, & Jacquemart, 2018;

McCombs, Debinski, Reinhardt, Germino, & Caragea, 2022; Nicolson, de Veer, Köhler, & Pirk, 2013; Russell & McFrederick, 2022; Tan et al., 2014). Pollinators also likely respond to the composition of the plant (resource) and pollinator (competitor) communities and partition their interactions in a way that minimizes interspecific competition while maximizing the rewards obtained from each foraging interaction (Valdovinos et al., 2016). Thus in order to effectively predict how rewiring may influence plant-pollinator communities experiencing global change, it is crucial to understand how these distinct environmental and biological drivers affect rewiring directly and in tandem with one another.

Spatial patterns of community dynamics are often used as proxies for environmental and biological drivers of ecological processes (McIntire & Fajardo, 2009). Environmental dissimilarity often covaries with geographic distance and predictable negative relationships exist between distance and community similarity (Dray et al., 2012; Nekola & White, 1999; Soininen, McDonald, & Hillebrand, 2007). Plant-pollinator interaction similarity also generally decreases with the distance between two communities, with parallel distance decay curves reported for species-driven and rewiring-driven interaction turnover (Carstensen et al., 2014; Trøjelsgaard et al., 2015). However, research to date has not explored whether these spatial patterns of rewiring can be considered proxies for more biologically meaningful variables like changes in temperature stress or altered competitive landscapes. Examining the biotic and abiotic drivers of rewiring across geographic space is therefore a valuable step in understanding how global change may impact the persistence of interaction-mediated ecosystem functions.

In this study, we explore potential spatial, environmental, and biological drivers of rewiring among plant-pollinator communities. We calculated the turnover in interactions among species that co-occurred between pairs of plant-pollinator networks from three years and 18 sites. We also calculated the difference in temperature (average and at the time of sampling), plant community composition, and pollinator community composition among these network pairs. These variables reflect a range of possible niche and neutral processes

that could affect pollinator foraging patterns, such as altered competitive dynamics and encounter probabilities. We then used a structural equation modeling framework to examine the pathways through which these potential drivers directly and indirectly affected rewiring in order to better understand what ecological processes underlie spatial patterns of plant-pollinator interaction turnover. Specifically, we examine whether geographic distance predicts rewiring independently of its effects on other environmental and biological factors as well as how geographic distance indirectly affects rewiring through these variables. We also examine three variables that we expected to have strong effects on the availability of floral resources—air temperature, plant community composition, and pollinator community composition—and determine whether differences in the environmental and biological contexts of plant-pollinator interactions affects their similarity between networks.

2.3 Methods

2.3.1 Study system

We conducted this study over three summers from 2020–2022. Each summer, we surveyed the plant-pollinator interactions at a subset of 18 subalpine wildflower meadows, all of which were within 20-km of the Rocky Mountain Biological Laboratory (Gunnison National Forest, Colorado, United States). During these visitation surveys, we observed plant-pollinator interactions for 45 minutes of active sampling, evenly distributed across three 1m x 10m transects. We caught any insect that touched the reproductive organs of a flower rooted within our transects. We identified all bumble bees to species level on the wing and released them once identified; all other insects were collected and subsequently identified to the genus level in the lab. We also surveyed the plant community on each sampling day, noting the identity and abundance of every plant rooted in our transects. We measured air temperature 10-cm above the ground every 30 minutes using a data logger (HOBO Pendant, UA-001-08) covered by a radiation shield that remained at each site for the duration of each summer.

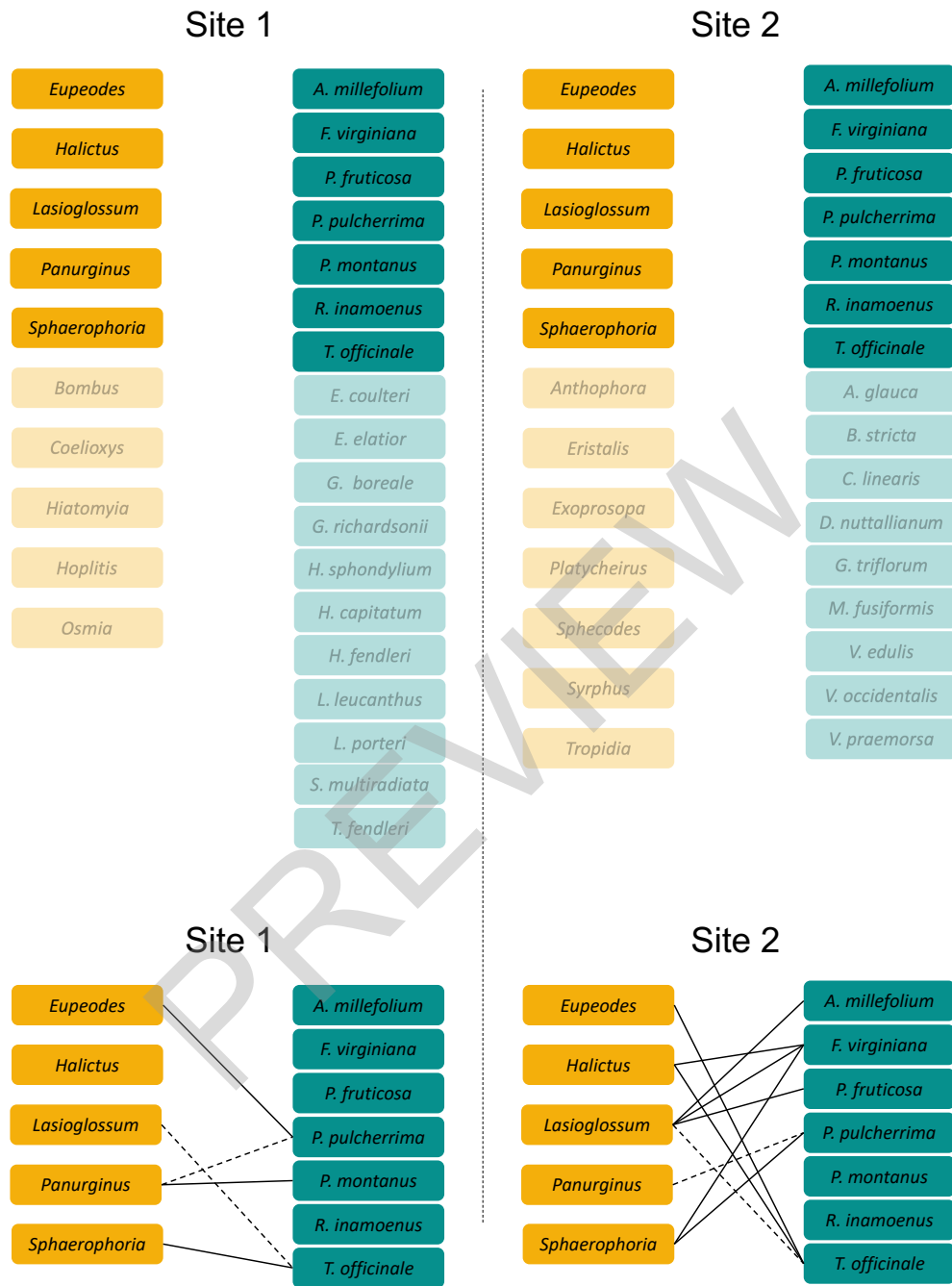


Figure 2.1: Visual depiction of rewiring between plant-pollinator networks at two sites. a) List of all pollinator genera (yellow) and plant species (teal) observed at two sites over the summer of 2020. Taxa shared between sites are indicated with dark colors and brackets and those that vary between sites are shown in light colors. b) Shared taxa with observed interactions indicated. Solid lines represent rewired interactions; dashed lines represent constant interactions.

2.3.2 Calculating rewiring

Since rewiring is a metric of interaction dissimilarity between two communities, all of our analyses involving rewiring comprise pairwise comparisons of every combination of sites. Rewiring is only possible if both partners are present in the two communities being compared. Thus, we began our rewiring calculations for each pair of sites by creating edge lists comprising just the plants and pollinators shared between both sites (Figure 2.1a). In order to ensure that our networks were not biased by uneven sampling effort, we performed this step for just a subset of five sampling rounds for each site/date combination (1SD below the mean) and then aggregated these possible and observed interactions from each site/date into single networks for the entire year. We then filled the edge lists with the number of times that we observed these possible shared interactions at each site (Figure 2.1b). This process yielded two numbers for each site pair—the number of interactions that occurred at one site but not the other (rewiring occurrence) and the number of interactions that occurred at both sites or neither site (no rewiring occurred).

2.3.3 Assessing drivers of rewiring

We used a structural equation modeling (SEM) framework (J. Grace, 2022) to understand how rewiring in our system was affected by geographic, ecological, and environmental differences between sites (Figure 2.2a). This SEM framework allowed us to test both direct and indirect relationships between predictor variables and rewiring that would be impossible to explore using a single regression model (J. B. Grace et al., 2012). Specifically, we examined (1) whether geographic distance and temperature difference had direct relationships with rewiring and (2) whether these two variables indirectly affected rewiring via changes to plant and pollinator community composition. We used the *piecewiseSEM* package (Lefcheck, 2016) to calculate standardized coefficients for the individual causal pathways in Figure 2.2a, with a linear model describing the relationship between geography and temperature and gen-