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The effects of anthropogenic change on pollination in plant-pollinator communities

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Doctor of Philosophy

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BSc Botany, University of Queensland, 2014

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An abstract of a dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
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Doctor of Philosophy
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Abstract

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Pollinators facilitate reproduction in ~80% of global plant species, making them integral to many agricultural and natural ecosystems. For over 200 years, western scientists have been fascinated by the intimate partnerships between pairs of plant and pollinator species. However, current pollinator declines and biodiversity loss have brought to attention the ecology of multi-species plant-pollinator communities. Now more than ever, we need to understand how diverse communities of plants and pollinators sustain one another, and how human activities threaten them. To this end, we must first have clarity on how pollinator diversity benefits plant pollination. Numerous studies have shown that increasing pollinator diversity improves pollination function. Yet this positive relationship is not always detectable, and even when it is, we are often unable to definitively explain why it manifests. In Chapter 2, I synthesized current empirical evidence of pollinator diversity-function relationships, highlighting problems, pitfalls and possibilities for advancing enquiry. Following this in-depth analysis of the value of pollinator diversity, I then examined two ways in which humans can impact natural pollination: i) through changes in pollinator diversity, and ii) through changes in plant-pollinator interactions. Chapter 3 examines how changes to land-use in the southeastern United States may affect the diversity of bees, a globally important insect pollinator. The U.S. government aims to convert the country's southeastern pine plantations from producing timber to bioenergy feedstock. I showed how changing the management of pine plantations from to bioenergy feedstock could have drastic effects on local bee communities. Nevertheless, results suggest that some methods of bioenergy pine production may be less detrimental. Furthermore, pine plantations collectively support more bee diversity than corn, an alternative bioenergy crop. I then focused on how human-induced changes to plant-pollinator interactions could affect plant community pollination. In Chapter 4, I examined how earlier flowering phenology (flowering time), a hallmark of climate change, impacted pollen limitation and plant fecundity. Using a field experiment conducted on montane meadow communities the Colorado Rocky Mountains, I showed that human-induced early blooming can change the pollination success and fecundity of different plant species, in ways that may affect future plant co-existence and diversity.

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Chapter 1: Introduction

1.1. Overview

Pollinators are vital to the sexual reproduction of ~90% of global plant species (Ollerton et al. 2011), making their ongoing worldwide decline a cause for great concern. As prominent examples of mutualism (Bronstein 2009), plant-pollinator interactions are usually reciprocally beneficial - in return for facilitating plant reproduction, most flowers provide their pollinators with food. It is thus unsurprising that diversity in plants and pollinators has been shown to decline in tandem (Biesmeijer et al. 2006). Plant-pollinator communities tend to be dominated by generalists (Martín González et al. 2010) – most pollinators that can visit many different plant species, and that can in turn be pollinated by a variety of pollinator species. This creates complex networks of multi-species interactions in natural communities, which can shape overall community function (e.g. the efficacy of pollination (Kaiser-Bunbury et al. 2017, Magrach et al. 2019, Arceo-Gómez et al. 2020)). Now more than ever, we need to understand how human-induced change affects the way in which diverse plant communities and pollinator communities sustain one another.

One way to examine how anthropogenic change impacts the mutualisms between the two communities, plants and pollinators, is as follows: First, we can ascertain how the diversity of one community benefits the other. How do diverse pollinators benefit plants? And likewise, how do diverse plants benefit pollinators? Second, having established how diversity in one community benefits the other, we can ask if and how anthropogenic change alters the diversity and structure of each of these communities. How do human activities affect pollinator diversity? Conversely, how do our activities change the diversity of animal-pollinated flowering plants? Finally, we can target human impacts on the interactions between the two communities that affect the mutualistic benefit received by either community. How do human-induced changes to plant-pollinator community interactions reduce the fitness and diversity of plant communities? How do similar changes affect the fitness and diversity of pollinator communities?

It is my hope that the following three chapters of this dissertation take us a step towards the above mentioned goals, by furthering our knowledge from at least one direction: anthropogenic effects on the benefit of pollinators to plants. To this end, we must first understand how and why diverse pollinator communities benefit plant pollination. I take on this challenge in a review and synthesis that integrates empirical pollination diversity-function research with the broader established diversity-function theory (Chapter 2, described briefly below in section 1.2), and recommended ways to expand on both. I then examine empirically two ways in which anthropogenic change can shape plant-pollinator communities to affect pollination: i) directly, through changes in pollinator community diversity (Chapter 3, described in section 1.3) and ii) indirectly, by altering plant-pollinator community interactions (Chapter 4, described in section 1.4).

1.2. Chapter 2: The effects of pollinator diversity on pollination function

Numerous studies show that having diverse pollinators enhances the pollination function received by plants. These pollinator diversity-function relationships have been found in agricultural (Hoehn et al. 2008, Albrecht et al. 2012, Miñarro and Twizell 2015, Winfree et al. 2018, Woodcock et al. 2019), natural (Dar et al. 2006, Muchhala et al. 2009, Prieto-Benítez et al. 2016) and experimental (Fontaine et al. 2006, Fründ et al. 2013, Ellis et al. 2017) settings. However, only a subset of these studies could infer the mechanisms behind these relationships with any certainty (e.g. Fontaine et al. 2006, Hoehn et al. 2008, Fründ et al. 2013, Ellis et al. 2017). Furthermore, other studies have been unable to detect pollinator diversity-function relationships at all (Pisanty et al. 2014, Pisanty et al. 2016). Our overall inability to reliably explain these equivocal findings suggests we do not have a firm grasp on the mechanisms that determine when and how pollinator diversity benefits pollination function.

Research on the relationship between biodiversity and ecosystem functioning has had a profound impact on the field of ecology in the last 25 years, in particular generating important insights into the functional consequences of diversity loss (Tilman et al. 1997). This has led to our current diversity-function framework (Hooper et al. 2005), which can be very useful if somewhat limited in scope, due to being largely based on single-trophic-level primary producers, usually plants. The current diversity-functioning framework tends to be much less effective at predicting functions that are driven by inter-trophic interactions (Sih et al. 1985, Cardinale et al. 2013), such as pollination (Blüthgen and Klein 2011). Among several limitations of the current framework is that it does not account for the rapid behavioral plasticity of animal pollinators (Morse 1977, Inouye 1978, Greenleaf and Kremen 2006, Klein et al. 2008, Carvalheiro et al. 2011, Brosi and Briggs 2013), which unlike plants can avoid or exploit changing environments instantaneously. In addition, the function of single-trophic primary producers for which the current framework is built upon can often be measured in standard units, ecosystem functions such as biomass or net ecosystem exchange that can be compared across study sites, regions, and species (Cardinale et al. 2013, Tilman et al. 2014). The function of pollinators lacks comparable units of measure across study systems, as it is usually measured in species-specific plant fecundity, such as seed number (Kearns and Inouye 1993). Seed numbers can have drastically different demographic consequences in different plant species depending on their life history (Silvertown et al. 1993). The current disconnect between pollination function and current diversity-function theory hinders collaboration and progress. It also makes it difficult to make sense of empirical research on pollinator diversity-function.

We need consensus on how the established diversity-function theory relates to pollination function. To this end, we need to first understand the context from which the current diversity-function was constructed (primarily single-trophic, primary-producer communities), so that we can establish its limits and where it may fall short in terms of predicting inter-trophic diversity-function. We can then examine historical and recent empirical research on pollinator diversity-function, and carefully assess whether and how findings fit within the current diversity-function framework. Given that this framework was not designed for the inter-trophic nature of pollination function, there will likely be examples of pollinator diversity-function that do not conform, and perhaps cases where the framework was applied to explain pollinator diversity-function in ways that overextend its limits. This will provide opportunities to clarify and expand on the established framework, to more precisely account for a wider range of diversity-function relationships. I have taken this approach to synthesizing current pollinator diversity-function research in Chapter 2. A manuscript by Berry Brosi and myself is current in revision for the journal *Ecology*.

1.3. Chapter 3: Anthropogenic effects on pollinator communities

Given how important pollinator diversity is to pollination function, a direct way in which anthropogenic change can affect the latter is by changing the former. Habitat degradation is of the greatest anthropogenic threats to pollinator diversity (Potts et al. 2010, Dicks et al. 2016), and biodiversity in general (Díaz et al. 2019). The destruction of pristine habitats for human land-use has clear impacts on biodiversity (Fletcher et al., 2011; Immerzeel, Verweij, Hilst, & Faaij, 2014). But some human-dominated landscapes also support rich wildlife, which may be sensitive to changes in land management (Klein et al. 2002, Bowen et al. 2007, Brockerhoff et al. 2008, Millan et al. 2015).

One such change may be on the horizon for huge swaths of the southeastern United States. The region's pine plantations are expected to provide feedstock to meet the nation's ambitious bioenergy production goals for 2022 (Sissine 2007). This represents a key example of the expansion of bioenergy cultivation worldwide. While pine plantations in southeast U.S. are typically managed for timber and pulp, intensifying feedstock production could entail widespread and dramatic changes to how the region's plantations are managed. Management differences between conventional and bioenergy feedstock pine plantations include a much more rapid cropping cycles that increase disturbance frequency (Klepac and Mitchell 2016), as well as the harvesting of fallen woody debris after clear-cutting that strips away potential ground-level habitat resources (Duden et al. 2018). These changes, applied across such a dominant agroecosystem in the southeast US, could have strong impacts on the region's pollinator diversity. Numerous studies show that how perennial plantations are managed impacts their capacity to support biodiversity (Bonham, Mesibov, & Bashford, 2002; Kerr, 1999; Mazurek & Zielinski, 2004), but how sensitive are pollinators to such differences? What is also unclear is whether variation in management across agricultural landscapes provides sufficient habitat heterogeneity to influence pollinator community turnover over larger spatial scales. Are agricultural landscapes dominated by one or few crop species necessarily homogeneous in terms of pollinator community composition?

We would like to be able to answer these questions before implementing landscape-wide changes that could impact pollinators across a significant geographical area. One way to achieve this is to study how bioenergy management practices influence pollinator diversity at small scales, so as to infer potential impacts at larger scales. However, only a fraction of pine plantations in the southeastern U.S. are currently dedicated to bioenergy production (Duden et al. 2018). Fortunately, stages in the growth and management for traditional timber products include stages in the growth and management of bioenergy feedstock. For example, conventional plantations are allowed to grow for up to 25 years, so that trees an achieve a greater bole diameter (Thompson and Pitt 2003) whereas bioenergy plantations may be harvested much earlier. Comparing pollinator diversity in young versus older plantations may offer foresight to future landscapes dominated by young plantations. Nevertheless, to infer the impacts of bioenergy cultivation on pollinator diversity in plantations across the southeastern U.S., we need data from plantations that span this immense geographic area. This will also allow us to assess the species turnover in plantations across the region, to evaluate whether land-use influences the heterogeneity of habitats for diverse pollinators.

Chapter 3 describes such a study on bee communities in pine plantations of the southeastern U.S.. Bees are a globally important group of pollinators (Patel et al. 2021) that have also seen declines in recent decades (Potts et al. 2010, Zattara and Aizen 2020). In this study, I worked with collaborators to examine how seemingly small changes in plantation management could shape bee community diversity and structure, using data from 83 sites across three states – Alabama, Florida, and Georgia. This study provides recommendations for how pine plantations can be managed to best conserve bee diversity. This work is published in *Journal of Applied Ecology* (Loy et al. 2020).

1.4. Chapter 4: Anthropogenic effects on plant community pollination

In addition to directly changing pollinator community composition, humans can also affect pollinator community function by interfering with the interactions between pollinators and plants

(Stout 2014). Measuring how community-level changes to plant-pollinator interactions affect pollination function is challenging for at least two major reasons.

First, it is difficult to evaluate whether observed interactions between a plant and floral visitor result in successful pollination (Ne'eman et al. 2010), much less whether changes to those interactions affect plant reproductive success. Some floral visitors do not pollinate flowers and yet others actually damage them (Irwin et al. 2010). Even among legitimate pollinators for a given plant species, it can be difficult to quantify the quality of interactions in a way that is meaningful to pollination function. Where this has been done, researchers typically attempt to identify and evaluate the efficacy of pollination between specific plant and pollinator species pairs (Ne'eman et al. 2010). One approach requires bagging flower buds before they bloom (so as to ensure zero pollinator visitation prior), allowing for a known pollinator to visit the flower when it blooms, bagging the flower again (to ensure only that pollinator species visited the target flower) and then counting the seeds produced by the flower, in order to determine the efficacy of a single visit from a given pollinator species. The per pollinator efficacy can then be multiplied by the natural number of floral visitations by this pollinator species, observed through weeks of visitation observations to unmanipulated flowers, to assess the natural contribution of the pollinator species to this individual plant or population. Needless to say, this process is extremely time and labor intensive, and impractical if we are to consider the pollination function in communities comprising numerous pollinator and plant species. An alternative is to manipulate community plant-pollinator interactions, and then measure corresponding changes to pollen limitation experience by plants. This is a standard technique used in studies examining the efficacy of available pollinators (Kearns and Inouye 1993). Briefly, this entails hand-pollinating a subset of flowers of a given species to saturate their pollen requirements, and then comparing the resulting seed set to adjacent flowers that received only natural pollination.

Hand-pollinated plants are assumed to be only limited by resources (and other non-pollinator factors), hence the difference in seedset between supplemented and naturally pollinated plants isolates the degree of pollen limitation experienced by the latter. This is also a labour intensive endeavour, and typically only done with one or a few plant species at a time.

Second, in real-world environments it can sometimes be challenging to separate the effects of change in community interactions from change in pollinator or plant community composition on pollination function. For example, land-use change described in the previous section resulted in changes in both pollinator and plant community composition (Loy et al. 2020), and it is not ecologically meaningful to make comparisons of pollination function between such compositionally dissimilar communities, especially in terms of seedset between plant species with different life history strategies (Silvertown et al. 1993). Research on anthropogenic impacts on plant-pollinator interactions tends to be focused on the introduction or removal of one or two species with disproportionately large influence on interactions in the remaining community. For example, exotic invasive plants have been shown to impact native plant pollination, either by drawing pollinators away from native plants (Waters et al. 2014) or reducing pollinator access by creating unfavorable habitats (Fiedler et al. 2012). On the other hand, experimental removal of pollinators - simulating single species extinction events - has been shown to change the interactions in the remaining plant-pollinator community with consequences to pollination function (Brosi and Briggs 2013). Both the addition and removal of pollinator (and plant) species have been studied in pollination networks, which are relatively novel modelling tools that attempt to capture patterns in the distribution and structure of interaction in plant-pollinator communities (Memmott et al. 2004, Ferrero et al. 2013, Albrecht et al. 2014, Valdovinos et al. 2018). It is worth noting that studies linking pollination networks to pollination functions are extremely few (Kaiser-Bunbury et al. 2017, Magrach et al.

2019, Arceo-Gómez et al. 2020). In addition to invasive species and species extinctions, anthropogenic climate change may also pose a significant threat to plant-pollinator community interactions, and has been a topic of active research in recent decades (Hegland et al. 2009). Climate change may alter the distribution of abiotically suitable habitat for both pollinators and plants, thereby changing spatial co-occurrence of plants and their pollinators (Gérard et al. 2020). However, climate change can also shape plant-pollinator communities by affecting community interactions without immediately changing local community composition by altering phenology.

Phenology is the timing of life history events, such as seasonal flowering time or pollinator activity periods. Changes in flowering phenology are a prominent feature of anthropogenic climate change (Thackeray et al. 2016, Zohner et al. 2020). Pollinators may not necessarily respond to earlier springtime blooming with earlier emergence (Hegland et al. 2009, Miller-Rushing et al. 2010, Olliff-Yang and Mesler 2018), perhaps due to differences in physiological constraints or environment triggers of phenology across taxa (Thackeray et al. 2016). This 'phenological mismatch' between plants and their pollinators has been shown to reduce pollination success and plant fecundity (Gordo and Sanz 2009). While not the focus of this dissertation, reciprocal impacts of phenological mismatch on pollinator fitness have also been found (Schenk et al. 2018). To have a clearer understanding of how anthropogenic climate change can affect pollination function by modifying species interactions, we need to consider changes in species interactions independent of changes in local community composition. Although a few studies have examined this phenomenon in isolated plant species, we do not know how common phenological change affects pollen limitation across different plant taxa, and whether it affects the relative fitness of co-occurring plants (but see Block et al. 2020). This is critical, as changes to species relative fitness can alter interspecific competitive outcomes, to shape long term coexistence and biodiversity (Ma et al. 2015, Wainwright et al. 2019, Descombes et al. 2020).

Chapter 4 details a study that examines how phenological change impacts pollen limitation and seedset in 14 co-occurring plant species. With my collaborators, I conducted an ambitious field experiment in the Colorado Rocky Mountains that manipulated flowering phenology in montane meadow study plots, potentiating changes in plant-pollinator interactions without changing local species diversity. I used pollen limitation experiments to measure differences in pollination function in phenology-manipulated plots relative to adjacent control plots. As a natural control for pollination-mediated changes in fecundity, I also measured the fecundity of co-occurring wind or self-pollinating plants. I then examined whether phenological shifts and potential plant-pollinator phenological mismatch altered the relative fitness of plants in these montane meadow communities.

Chapter 2: The effects of pollinator diversity on pollination function

2.1. Introduction

Concerns over pollinator declines have driven a resurgence in interest in the functional consequences of these declines for plant reproduction (Potts et al. 2010). Now more than ever, it is imperative that we understand how reduced pollinator diversity across both local and global scales impacts plant pollination and thus ultimately plant population dynamics. If research on pollination function is to address the salient consequences of pollinator decline, we need a clear understanding of the mechanisms by which pollinator diversity promotes plant reproductive functioning.

Biodiversity is known to play a key role in supporting a range of ecosystem and community functions (Tilman et al. 1997, Liang et al. 2016, Maynard et al. 2017) including pollination (Hoehn et al. 2008, Albrecht et al. 2012, Fründ et al. 2013, Winfree et al. 2018). One of the oldest biodiversity-functioning hypotheses is that a diverse community of primary producers (typically plants) benefits system-level productivity (often measured as biomass). This has been shown to be consistent across numerous controlled experiments (e.g. Tilman et al. 1996, Cardinale et al. 2013, Lange et al. 2015) and in the wild (Duffy et al. 2017).

While previous work on BEF relationships provides an invaluable foundation for understanding the effects of pollinator diversity on plant reproductive functioning, there are several important features that distinguish pollination function from the other types of ecosystem function commonly considered in the literature. First, while many studies on ecosystem function examine processes driven by multi-species communities, the bulk tend to focus on products or outcomes that can be meaningfully aggregated across multiple species independent of species identity (e.g. biomass accumulation, nutrient cycling, etc.). Pollinator-mediated plant reproduction, by contrast, can only be understood in the context of specific species identities: the successful transfer of, say, 10 pollen grains has different consequences for different plant species. Second, the vast majority of diversity-function literature focuses on organisms within a single trophic level (e.g. plant communities) whereas biotic pollination involves inter-trophic interactions between pollinators and plants. Third, animal pollinators are capable of rapid behavioral responses that can change the identity and frequency of their interactions, thereby affecting functional role and efficacy over very short timescales. Some biodiversity-function studies assume that species functional niches are static (e.g. Tilman et al. 1997), thus ignoring the potential role of plasticity of species functional roles in response to the presence of competitors in contributing to function. These features of pollination function are relevant to many other inter-trophic community functions as well, and we argue justify a distinction between "community function"—species-specific functions arising from and pertaining to species interactions—and "ecosystem function" that encompasses both biotic and abiotic elements and processes.

In this review we examine diversity-function mechanisms in pollination function, i.e. how pollinator diversity mediates plant reproductive success. Here we focus primarily on how pollinator communities enhance seed set in single plant taxa (i.e. 'community function' of pollinators on a plant species) but briefly discuss the dynamics of pollinator communities and plant communities in section 4.3.3 Complementarity in pollination networks. We specifically focus on empirical studies that identify specific pollinator diversity-function mechanisms over relatively small spatial and temporal scales. For concision, we do not cover theoretical studies on the function of inter-trophic interactions (e.g. Thébault and Loreau (2003)), the fascinating work showing positive diversity-function correlations in pollination at large spatial scales (e.g. Winfree et al. (2018)), or other work outside our stated scope. We begin with a brief overview of the three canonical diversity-function mechanisms that are well developed in the literature (Section 2). In Section 3, we consider how pollination function, as a type of community function, differs from general ecosystem functions more commonly considered in the diversity-function literature. With this understanding, we then examine in Section 4 how the three canonical diversity-function mechanisms act in pollination function. This allows us to identify and describe, in Section 5, a novel diversity-function mechanism—functional enhancement—that is not accounted for in the canonical BEF mechanisms. Finally, in Section 6 we discuss how future research can help disentangle different diversity-function mechanisms in pollination function and the relevance of these mechanisms to non-pollination community functions.

2.2. Canonical mechanisms of diversity-function relationships

The positive relationship often observed between species richness and ecosystem functioning, known as the diversity-function relationship, is thought to be driven by three primary mechanisms: 1. the sampling effect, 2. facilitation and 3. niche complementarity (Hooper et al. 2005). First, *the sampling effect* argues that increasing species richness also increases the probability that one or more highly functionally effective species will be included in a community. This emphasises species identity as a driver of function rather than species richness *per se*. In an Argentinian forest for example, monocultures of a single, highly successful invasive tree species had up to three times more biomass than species-rich, native forests (Flombaum et al. 2017). Second, *facilitation* (positive interactions between species in a community) can benefit the fitness of one or more species that in turn strongly contribute to overall community function. A classic example of this is how nitrogen-fixing leguminous plants enhance the growth of other plant species by increasing soil nitrogen, thereby indirectly increasing community biomass production (Spehn et al. 2002). Third, *niche* *complementarity* may occur when different species occupy niches that do not completely overlap, thus collectively providing better coverage of available niche space that enhances overall community function. For example, an experiment on tropical trees in Panama showed that species differences in leafing phenology and crown architecture enhanced light captured by the community to enhance biomass production in multi-species communities (Sapijanskas et al. 2014). Diversity in functional roles, rather than species richness *per se*, drives diversity-function relationships (Roscher et al. 2012). These three diversity-function mechanisms can also occur in tandem. For example, the sampling effect influences the likelihood that two species that exhibit high complementarity will be included in a community. These mechanisms have been extensively studied across a wide variety of ecosystem functions, laying the groundwork for understanding diversity-function relationships in pollination. Nevertheless, this framework—supported largely by studies on terrestrial plant communities—does not adequately describe all of the mechanisms that have been observed to drive diversity-function relationships in pollination.

2.3. Differentiating community and ecosystem function

The canonical mechanisms of biodiversity functioning are certainly relevant to pollination function and yet, as we will discuss in the following sections, do not capture important properties of inter-trophic ecological functions. We suggest that ecological functions that are defined by species identities be termed "community functions" to distinguish them from *ecosystem* functions that are independent of species identities. Many ecological functions track the flow or accumulation of material within an ecosystem and can be expressed in standard units but not all functions can be quantified this way. For example, productivity in an ecosystem can be measured in grams of biomass per area per year (g C m^{-2} $year^{-1}$), kilograms of soil nitrogen fixation per area per year (kg N m^{-2} $year^{-1}$) and hydrology in gallons per minute (gpm). Standard units allow direct comparison of the rates of these ecological processes between different communities or ecosystems. However, some ecological functions that are critical for the overall functioning of ecosystems are species-specific and do not have standard units of measurement. For example, pollination function—measured as the number of seeds produced by plants—cannot be summed across different plant species to assess function at the plant community level or (at least in terms of raw seed counts) be meaningfully compared across dissimilar plant communities. This is because per capita seed production can have vastly different demographic consequences in different species depending on their life history (Silvertown et al. 1993). Similarly, for other community functions, rates of prey consumption and seed dispersal are species-specific processes that make sense only in the context of species identities.

Community functions differ from ecosystem functions in several other ways. First, community functions involve species interactions that are typically inter-trophic, as is the case with plants and pollinators, predators and prey and plants and their seed dispersers. This stands in direct contrast to the bulk of work in the diversity-functioning realm, which is focused on single-trophic level systems. Second, changes in the composition or intensity of these inter-trophic species interactions can directly impact community function. The floral choices of pollinators, and the dietary choices of predators and frugivores, directly impact the function they provide. This underscores the importance of rapid behavioral plasticity in pollination systems, which we address later in this review. Third, community functions are bounded by population or community sizes and saturation is both plausible and meaningful. For example, pollination function can range from zero (no pollination) to the total number of ovules available for pollination, predator consumption of a given prey species ranges from zero to prey population size and frugivores may collect and move none or all available fruit from a plant community. By contrast, while ecosystem functions also have limits—e.g. biomass production in most ecosystems is limited by water and the energy received from sunlight—those limits are almost always hypothetical and complete saturation is typically physically impossible. For example, we seldom if ever consider whether all atmospheric nitrogen will be completely fixed by organisms or anticipate all terrestrial water in an ecosystem being exhausted through foliar transpiration. As processes that occur within ecosystems, community functions can indirectly influence ecosystem functions, potentially blurring the distinction between the two in some cases. We describe how pollination—a community function—can be driven by diversity in terms of both the canonical and novel diversity-function mechanisms.

2.4. Canonical diversity-function mechanisms in pollination function

2.4.1. Sampling Effect

The sampling effect posits that with increasing species richness, communities are more likely to include functionally superior species. While studies explicitly testing for the sampling effect in pollination function are few (but see Larsen et al. 2005), it is intuitive that larger subsets from a species pool of variably effective pollinators would more likely include the most effective pollinator species than smaller subsets. There is a wealth of evidence of substantial variation in the efficacy of pollinator species (even among generalists) that could allow for sampling effects (Moisan-Deserres et al. 2014 and others). However, sampling effects are simplistic in assuming that a highly effective pollinator species can remain constant in abundance and efficacy (Tilman et al. 1997). While this may be possible in some circumstances, under many conditions, plant and pollinator populations are heterogeneous through space and time (CaraDonna et al. 2014, Pisanty et al. 2016, Ellis et al. 2017, Miljanic et al. 2019), such that no one pollinator or pollinator-plant pairing will be consistently functionally superior or even realized (e.g. Alarcón et al. 2008, Petanidou et al. 2008). The sampling effect also fails to explain how pollinator community function frequently exceeds that expected by the most abundant or effective species, pointing to synergistic effects of species richness that are absent when functionally superior species operate in isolation. To understand the other emergent properties of species diversity in pollination function, we need to consider relationships in the roles and interactions among co-occurring pollinator species.

2.4.2. Facilitation

Facilitation occurs when one species benefits another, with no reciprocal harm to itself. Such relationships can thus be mutualisms or commensalisms but not antagonistic interactions, such as competition. Facilitation can enhance function if a species promotes the fitness of another species, which then contributes more to a focal ecosystem function than in the absence of the former. In thinking about how pollinator diversity affects pollination functioning, this requires that at least one pollinator species increases the fitness of another pollinator species, without fitness costs to itself, in ways that allow one or both pollinators to contribute greater pollination function. For facilitation to enhance pollination function, two criteria must be met. First, one pollinator species must benefit the fitness of another pollinator species (without being negatively affected itself by that interaction). This is the broad definition of facilitation. Second, the increase in fitness or population size of the benefiting species also must increase that species' contribution to pollination function. These criteria are rarely measured in nature but there are plausible cases. For example, Müllerian mimicry—whereby the fitness of multiple toxic species is enhanced by similar honest warning coloration—is well-studied in butterflies (Elias et al. 2008). This could theoretically benefit the pollination of butterfly-pollinated plants by increasing overall butterfly abundance. Similar benefits could arise from Batesian mimicry, such as in the case of bee-mimicking flies, provided that fly mimics remain rare enough to avoid diluting the benefit of true aposematism in the bees that they mimic. Pollinators may also facilitate one another by making additional resources available to them. For example, nectar robbing animals damage flowers to access nectar without pollinating them but the damage then creates opportunities for secondary nectar robbers. This does not always have negative impacts on plant fitness (Varma and Sinu 2019) but if this increases the fitness in secondary nectar robbers, then benefits to pollination function may be realized in other flower species for which the secondary nectar robber species are true pollinators. Facilitation among pollinators likely has real albeit indirect benefits to pollination function but more evidence will be needed to further this discussion.

2.4.3. Complementarity

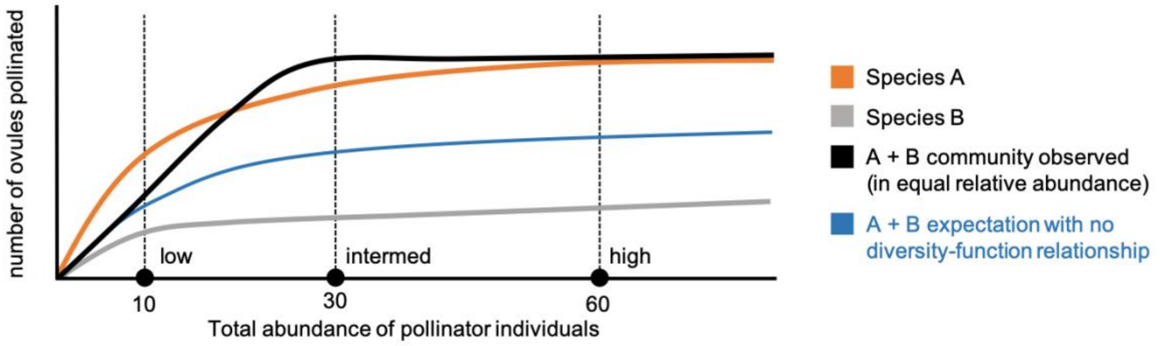
Niche complementarity occurs when two or more species utilize a common resource in distinctive ways, such that resource usage "complements" one another and reduces direct competition. Complementarity is considered a key driver of diversity-functioning relationships because when species differ in their use of a functionally important resource axis, having multiple species present in a community can increase the total amount of resource uptake. For example, consider two plant species, one of which uses ammonia as its nitrogen source while the other uses nitrate. If both species are present in a community, there is a larger pool of nitrogen available, likely increasing the overall biomass in the community. Complementarity is a central concept to both coexistence theory (Levine and HilleRisLambers 2009) and diversity-functioning relationships that is centered on non-overlapping niches. Here we focus on functional niche complementarity or differences in the way species fulfill a specific functional role, as opposed to general niche complementarity that is differences in the ecological niche of species that allow them to coexist.

2.4.3.1. Complementarity in pollination function

A pair of pollinator species are complementary in pollination function when they occupy non-identical pollination functional niches, and thus cover more functional niche space together than when in isolation. In theory, perfect complementarity maximizes function when all species in a community have no overlap in their functional niche (Blüthgen & Klein 2011), resulting in a linear increase in function with species richness. Conversely, zero complementarity occurs when all species in a community overlap completely in their functional niches and function does not change with diversity. Species that share the same functional niche exhibit 'redundancy', though they may still vary in their contribution to that niche due to differences in visitation frequency or per-visit effectiveness (Kremen et al. 2007). In nature, we typically see something between these two extremes: species do not have perfect / complete complementarity but instead have functional niches with some overlap.

Criteria have been laid out for establishing niche complementarity in pollinators foraging on a shared resource (Johnson and Hubbell 1975) but not for complementarity in pollination function received by plants (i.e., plant reproductive functioning). For two pollinator species to occupy complementary functional niches—pollinator "functional complementarity" (Blüthgen and Klein 2011)—we propose that three criteria must be met (latter two acknowledged by Pisanty et al. (2016)(Figure 1). We will illustrate these criteria with an example in the next paragraph. First, each pollinator species contributes to pollination and plant fitness by occupying realized functional niches that are substantially non-overlapping. Secondly, each of the pollinator species must surpass the function of others in its particular functional niche (Pisanty et al. 2016). If one or both pollinator species perform equally well in two alleged functional niches, then the two functional niches are either one and the same, or else one niche is a subset of the other. If one species is superior in function in both its niche as well as the niche of another species, then there is redundancy and not complementarity. Third, there must be some degree of independence between the differentiated functional niches, such that increased coverage in one niche cannot fully compensate for the reduced coverage in another (Pisanty et al. 2016).

Figure 1 Hypothetical scenario of diversity-function relationship when considering two pollinator species, A and B, in isolation and as well as in tandem, with increasing numbers of pollinator individuals (low, intermediate and high).



Total abundance of pollinators	Diversity-function relationship
LOW When considered in isolation, species A is more functionally effective than species B (10A > 10B). In the A + B community, the expected function of having two species is the sum of the function of 5 individuals of species A and B each (5A+5B).	**Not detectable / Sampling Effect**
INTERMEDIATE At a certain density of Species B (here about 10 individuals), the species begins to saturate its functional niche. If there is a diversity-function relationship (shown here), then the observed A + B community function will start to be greater than the expected, due to functional complementarity between A and B or functional enhancement of A by B. Within a certain range of abundances, the observed A + B community function is greater than that of having species A alone (30A), even though there are half the number of A individuals (15A+15B). This could occur if A and B occupy different functional niches, and 15 individuals of A are still well beyond the abundance needed to saturate the functional niche of A.	**Detectable** **Complementarity / Enhancement** i. Within range of abundances when community observed function exceeds function of Species A alone **OR** ii. With single-species treatments when compared to A + B expectation
HIGH Pollinators A and B are not able to further increase pollination as all ovules accessible to both Species have been pollinated.	**Detectable** **Complementarity / Enhancement** iWith single-species treatments when compared to A + B expectation

In a hypothetical example, let us suppose that two animal species, one nocturnal and one diurnal, aid in the pollination of a plant, with each species occupying a different temporal niche. If it does not matter whether an individual flower is visited by day or night, then day and night do not represent independent pollination functional niches. For functional complementarity, it must be evident that increases in the frequency of either night or day pollinators cannot compensate for decreases in the frequency of the other group. That is to say, if a surplus of night or day pollinators could potentially satisfy all of a plant's pollination needs, then both groups are functionally redundant and not complementary. In this example, functional complementarity could occur if the individual flowers on a pollen-limited plant bloom either at night or during the day and are only briefly receptive to pollen. In this scenario, diurnal pollinators cannot pollinate nocturnal flowers and vice versa, creating functional 'temporal complementarity' (Blüthgen and Klein 2011). Functional complementarity can only be definitively detected with experiments that manipulate pollinator abundance and diversity, though field observations of pollinator physical, physiological or behavioral traits may be necessary to reveal the precise mechanisms by which pollinators act in complementary ways. We highlight some known and putative mechanisms of pollinator complementarity in Table 1.

Table 1 Known and putative mechanisms of pollinator complementarity. Similar to Blüthgen and Klein (2011) we divide these into three categories: architectural, temporal and environmental complementarity. Delineation between the latter two categories can be arbitrary, as the abiotic environment can also vary with time. Within each category, we list examples sorted by increasing 'scale', describe in more detail the niche 'axis of complementarity', and the plant and pollinator taxa studied. Under 'diversity-function effect', we state whether research shows that plant seed or fruit set increases with additional pollinator species. In 'pollination functional complementarity' we assess, based on the ideas discussed in our paper, whether the study found evidence for pollinator functional complementarity (evidence supporting/not supporting or untested) and whether this evidence is correlational or shown to be causal through experimental manipulation.

Scale	Axis of complementarity	Plant(s), pollinators	Diversity-function	Pollination Functional Complementarity
Architectural - Complementarity in functional niche based on the structure or spatial arrangement of plants and their flowers or reproductive organs.				
Within flower	Placement of stigmas within flower	Strawberry, Bees (Chagnon et al. 1993)	yes	Evidence supporting, experiment
Inflorescence	Placement of florets within inflorescence	Sunflower, Bees (Pisanty et al. 2014)	no	Evidence not supporting
Plant	Height of flowers on tree (also *Abiotic environmental*)	Almond, Bees and flies (Brittain et al. 2013)	not shown	Not tested. Pollinator differences observed.
Population	Density of flowers on individual plants	*Cassia biflora*, Bees (Johnson and Hubbell 1975)	not shown	Not tested. Pollinator differences observed.
Plant / Population	Location of flowers on plant or within population	*Impatiens capensis*, Hummingbirds and bumble bees (Laverty and Plowright 1985)	not shown	Not tested. Pollinator differences observed.
Plant / Population	Height of flowers on plant (also *Temporal*)	Pumpkin, Insects (Hoehn et al. 2008)	yes	Evidence supporting, correlation
Plant / Population	Size of flowers	Watermelon, Bees (Pisanty et al. 2016)	no	Evidence not supporting. Pollinator differences observed.
Temporal - Complementarity in functional niche based on time of day, flowering period, seasons or years				
Plant / Population	Time of day (also *Abiotic environmental*)	*Justicea aurea,* Insects and hummingbirds (Willmer and Corbet 1981)	not shown	Not tested. Pollinator differences observed.
Plant / Population	Time of day	*Brassica rapa*, Insects (Rader et al. 2013)	not shown	Not tested. Pollinator differences observed.
Plant / Population	Time of day (also *Abiotic environmental*)	Kiwifruit, Insects (Miñarro and Twizell 2015)	not shown	Not tested. Pollinator differences observed.
Plant / Population	Time of day	*Silene colorata*, Insects (Prieto-Benítez et al. 2016)	not shown	Not tested. Pollinator differences observed.
Plant / Population	Time of day (Also *Architectural*)	Pumpkin, Insects (Hoehn *et al.* 2008)	yes	Evidence supporting, correlation
Plant / Population	Time of day	Radish, Insects (Albrecht et al. 2012)	yes	Not tested. Pollinator differences observed.
Plant / Population	Nocturnal-diurnal	Pipe organ cactus, Bats and hummingbirds (Dar et al. 2006)	not shown	Not tested. Pollinator differences observed.

Plant / Population	Nocturnal-diurnal	*Aphelandra acanthus*, Bats and hummingbirds (Muchhala et al. 2009)	not shown	Not tested. Pollinator differences observed.
Plant / Population	Nocturnal-diurnal, Seasonal	*Inga sessilis*, Bats, hummingbirds and hawkmoths (Amorim et al. 2013)	yes	Not tested. Pollinator differences observed.
Plant / Population	Seasonal (also *Abiotic environmental*)	Strawberry, Insects (Ellis et al. 2017)	yes	Evidence supporting, experiment

Abiotic environmental - Complementarity in functional niche based on pollinator tolerance for weather (prevailing, transient abiotic conditions) and microclimates.

Plant / Population	Weather - wind, rain, temperature (also *Temporal*)	Strawberry, Various insects (Ellis et al. 2017)	yes	Not tested. Pollinator differences observed.
Plant	Weather - wind (also A*rchitectural*)	Almond, Bees and flies (Brittain et al. 2013)	not shown	Not tested. Pollinator differences observed.
Population	Microclimate, edge effect	Watermelon, Various bees (Pisanty et al. 2016)	no	Evidence not supporting. Pollinator differences observed.

2.4.3.2. Competition and 'interactive functional complementarity'

While species niche differences can help reduce interspecific competition, competition can be necessary for niche complementarity to manifest. Early diversity-function models typically assumed that species niches are static (Tilman et al. 1997) and indeed many species functional traits are fixed. For example, most plants utilize only a single biochemical photosynthesis pathway (e.g. C3 or C4) making this an immutable trait in these species. Yet recent diversity-function models have begun to consider species interactions and plasticity in species traits (Soussana et al. 2012, Dooley et al. 2015), incorporating an important aspect of complementarity we have long known; it can be generated from real-time responses to contemporary interspecies competition (Morse 1974, Inouye 1978, Pimm et al. 1985) and not only through long-term, evolutionary divergence of species niches from historical competition (Futuyma and Moreno 1988). This type of 'interactive complementarity' (Fründ et al. 2013) has been readily observed in pollinators in the form of rapid and clear changes in foraging behaviour to avoid strong competition with heterospecifics. For example, in a study on hummingbird-pollinated *Justicea aurea* (Willmer and Corbet 1981), the largest hummingbird species commanded the most nectar-rich sunlit flowers, while the smaller species tend to be limited to shadier flowers, creating complementarity that would not occur if either pollinator occurred in isolation or did not compete. Similarly, in coffee pollination, wild bees were observed to move to lower sections of coffee trees to avoid competing with honey bees (Klein et al. 2008). Experiments with bumble bees foraging on goldenrod show that small bumble bee species foraged on the distal ends of goldenrod flowers to avoid competing with larger congeners (Morse 1977). However, it is important to note that changes and differences in functional niche do not necessarily imply that diversity has increased function. Ostensibly, one pollinator may simply preclude another from a subset of the latter's functional niche, with little increase in function of either niches. For interactive complementary to increase function, the occupant of the niche space that would otherwise be overlapping must be more effective at filling that niche than the species it excludes. While niche partitioning *per se* may not enhance function, it could enhance the activity or efficiency of a pollinator within a given niche ('functional enhancement', Section 5). For example, when we consider pollination function at plant community level, competition for flowers may encourage pollinator species to focus on individual plant species (Inouye 1978, Brosi and Briggs 2013, Fründ et al. 2013), improving conspecific pollen transfer. Here pollinators change their functional niche by narrowing it, but function is enhanced through improved efficiency within the narrowed niche.

We propose that the term 'interactive functional complementarity' be used to describe improvements to pollination function from competition between pollinators that change their functional niche, as opposed to inter-species interactions that simply increase the performance of a species within the same functional niche. The original definition of 'interactive complementarity' by Fründ et al. (2013) included a variety of interactions (e.g. facilitation, competition, predation etc.)

that changed a species' realized niche but not necessarily its functional niche. Interactive functional complementarity can arise when competition between two pollinator species creates realized functional niches that are sufficiently distinct (functional complementarity). The weaker competitor can potentially contribute to all functional niches but the superior competitor dominates only one of the functional niches by virtue of competition, allowing the weaker competitor to contribute to the remaining functional niche.

2.4.3.3. Complementarity in pollination networks

Interacting communities of plants and pollinators can form complex interaction networks, with pollinators tending to interact with non-random subsets of a plant community (Jordano et al. 2003). Pollinator species differ in their preferences for flower species, so we expect differences in pollinator species contribution to pollination function of various plant species, and that diverse pollinators promote greater seed set in plant communities.

Networks dominated by specialized or exclusive interactions between plants and pollinator species indicate high niche complementarity (denoted by H_2') while networks where most species share partners have redundancy (Blüthgen and Klein 2011). However, pollinators in a network may have redundancy in terms of presence-absence of interactions with plant species in the network but exhibit complementarity in the frequency at which they allocate visits to different species. This would occur if each pollinator species that visits multiple plant species allocates the majority of visits to the one or few plant species for which it experiences the least interspecies competition. This complementarity based on interaction frequency has sometimes been termed 'quantitative complementary' to distinguish it from 'topological complementarity' based on the presence-absence of species interactions. In theory, both types of network complementarity should increase the probability that pollen is transferred between conspecific plants, maximizing both male and female plant fitness (Blüthgen et al. 2007).

While the role of complementarity and redundancy in influencing the long-term stability of ecological networks has received much attention (Memmott et al. 2004, Blüthgen et al. 2007, Rooney and McCann 2012), very few studies link complementarity in pollinator communities to plant community reproductive success. This is likely because, as mentioned in Section 3, it is difficult to compare seed set between natural communities of varying species composition. Nevertheless, there are three notable studies that have attempted to measure the relationship between plant-pollinator network structure and pollination function. Using experimental mesocosms, Fründ et al. (2013) show that complementarity among pollinators increased plant community seed set. Here researchers created mesocosm plant communities by sowing the seeds of 16 plant species (nine pollinator-limited), ensuring identical species composition for direct comparison of pollination function between communities. In natural communities, Kaiser-Bunbury et al. (2017) and Magrach et al. (2019) also found evidence suggesting that complementarity between pollinators in terms of plant partners may translate to complementarity in pollination function. Kaiser-Bunbury et al. (2017) examined the fruitset of 10 native plant species on an island in the Seychelles, all of which rely on cross-pollination by pollinators due to natural barriers to self-pollination (i.e. dioecy, self-incompatibility). Researchers made use of this subset of island plant species that were strongly reliant on pollinators, and also widely distributed across the island. This makes for an unusual study system, not only because of the relatively confined and unusual biogeography, but also since natural plant assemblages tend to comprise species of varying pollinator dependence - up to 42% of plant species have mixed mating systems (Goodwillie et al. 2005), whereby plants are capable of some degree of autonomous seed set, and the influence of pollinators on fecundity varies with species.

The researchers measured differences in pollinator community function by considering all species in single mixed-effects model, analyzing changes in the correlation between pollinator visitation rate and the proportion of flowers that set fruit (with 'species' as a random effect). Magrach et al. (2019) also used a similar mixed-effects model approach to account for the 'species' effect on plant fecundity across different network sites. Magrach et al. (2019) conceded that average community seedset values can be skewed by one or a few species, and so also examined species equity in seedset. How pollinators mediate the equity of plant species seedset is a critical aspect of community function, as changes to species fitness differences may drive plant community coexistence and diversity (Ma et al. 2015, Wainwright et al. 2019).

Findings by Fründ et al. (2013), Kaiser-Bunbury et al. (2017) and Magrach et al. (2019) are consistent with expectations: network interaction diversity (conceptually analogous to community species diversity) is likely to improve function through niche complementarity (Tylianakis et al. 2010). Competition likely plays a role in driving network complementarity, by promoting interaction rewiring (switching of interaction partners, Montero-Castaño and Vilà 2017) or reweighing (changing interaction intensities, Valdovinos et al. 2016).

2.5. Functional enhancement: a novel diversity-function mechanism

There is a fourth way in which interacting pollinator species can enhance pollination that does not involve facilitation or niche complementarity. In fact, pollination function can be increased when pollinators remain overlapping in their niche-use and directly compete or interfere with one another's foraging. For example, antagonistic interactions between pollinators can spur one or more species to move between flowers more frequently to increase pollination rates (Greenleaf and Kremen 2006, Klein et al. 2008, Carvalheiro et al. 2011). The term 'functional facilitation' has sometimes been used to describe this effect (Klein et al. 2008) but is inconsistent with the common ecological definition of 'facilitation', which implies a positive relationship between two pollinator species (Brooker et al. 2008, Michalet and Pugnaire 2016). To avoid confusion, we propose the term '*functional enhancement*'.

Functional enhancement may be defined as the interspecific interactions that improve species function within an effect niche. Like interactive functional complementarity, it describes species interactions that improve functional effect beyond that expected when species are isolated but differs in that it does not involve niche shifts in the presence of other species. In theory, these interactions may be beneficial, antagonistic or neutral but antagonistic interactions appear to be more common in the case of pollination function. This is likely because pollination is enhanced by increased pollen movement between flowers and plant individuals, yet increased movement on the part of pollinators is at odds with optimizing their foraging efficiency (Pyke 1984), and may thus be avoided in the absence of competition or interference from other species. Functional enhancement in pollination can improve the quantity or quality of pollen transferred. Primary pollinator species may move more frequently between flowers because competing species make individual flowers less rewarding or to avoid harassment and confrontation (Greenleaf and Kremen 2006, Klein et al. 2008, Carvalheiro et al. 2011). This may increase the quantity of pollen moved, but may also lead to the second benefit: improvement in the quality of pollen, transferred from more genetically (and spatially) distant conspecific individuals (Brittain et al. 2013). Competition among pollinators may not necessarily change the range of plant species each visits, but may change their fidelity to plant species ("floral fidelity") thus altering patterns of conspecific pollen transfer (pollen quality)(Inouye 1978, Brosi and Briggs 2013, Fründ et al. 2013). Functional enhancement in pollination can occur in apparently neutral or 'null' interactions as well, when pollinators inadvertently 'cooperate' in the delivery and distribution of pollen within a flower or inflorescence due to differences in pollinator foraging habits or physical traits. For example, when one pollinator species aids in delivering large clumps of pollen to flowers, another pollinator species can subsequently contribute by spreading the pollen across stigmatic surfaces (Greenleaf and Kremen 2006, Hoehn et al. 2008).

2.6. Future research into diversity-function in inter-trophic interactions

2.6.1 Pollination function

To better understand pollinator diversity-function mechanisms, future studies need to experimentally manipulate both pollinator species richness and abundance, and measure pollination function in terms of pollination success. For example, in a two-species pollinator community, function must be measured with each species in isolation and also with both species combined. In addition to pollinator richness, three aspects of pollinator abundance should also be considered. The first two aspects of abundance are typical in "classical" plant studies of biodiversity-ecosystem functioning relationships but the third aspect needs to be included for community functions in which saturation is realistic and plausible, such as pollination. 1) The relative abundances of species must ideally be equal in combined-species treatments, so that the functional effect of either species is not overrepresented. 2) The total abundance of pollinators in combined versus single-species 'communities' must ideally be equal, as abundance may affect function independent of species identity. Function cannot be directly compared across communities with dissimilar total pollinator abundances. 3) Multiple levels of pollinator abundance should be considered, as pollinator diversity-function benefits may only be detectable at some pollinator abundances but not others, especially for pollination function within a single plant species (Figure 1).

Detecting pollinator diversity-function mechanisms within single plant species (as opposed to across a more diverse assemblage of plant species) is especially challenging for two reasons. First, distinct pollination functional niches within a single plant species, even if present, can be difficult to define. In a plant community, different plant species (or groups of functionally similar plant species) help define meaningful functional niches; pollinators of different plant species can be said to be complementary to one another at a community level. However, the mechanisms by which pollinator species partition pollination functioning within a plant species (as laid out in Table 1) are not usually obvious even with close observation, making it hard to assess if pollinators are fulfilling different functional roles. Second, we expect a saturating relationship between pollinator abundance and pollinator-mediated seed set but there is uncertainty around this upper limit. This is important because the functional benefits of pollinator diversity at or close to this limit will be undetectable, yet this does not indicate that diversity-function relationships are absent (Figure 1). We approach the upper limit of pollination function when having more members of a pollinator species or community does not further increase pollen-limited seed set. This occurs because there is always a finite number of flower ovules available for pollination and seed set can be limited by abiotic resources available to plants. In addition, the upper limit to pollination function is idiosyncratic to the plant and pollinator species involved. A given pollinator species or community can have a realistic upper limit of pollination function (that is lower than the theoretical upper limit) for a given plant species when there is imperfect trait matching (i.e. compatibility between pollinator and floral traits that affects pollination delivery) preventing pollinators from completely ameliorating pollen limitation even when receptive ovules remain available. In any case, the tendency for pollination function to saturate means that pollinator diversity-function relationships may only be detectable within a threshold of pollinator abundances. Uncertainty around this threshold means that most pollinator diversity-function experiments should ideally consider multiple levels of pollinator abundance to detect diversity-function effects (Figure 1).

2.6.2 Other inter-trophic community functions

In this review, we have largely discussed how diversity increases community function in a pollination context but the discussed mechanisms may be applicable to other vital community functions as well. Predation and animal seed dispersal are ecologically vital community functions with key similarities to pollination. They are inter-trophic, sensitive to changes in the composition and intensity of species interactions and are affected by animal behavior and movement. Two mechanisms highlighted in this review, which have received less attention in diversity-function research thus far, may be of special significance: interactive functional complementarity and functional enhancement. Like pollinators, animal predators and seed dispersers can change their foraging preferences to avoid competition (Araújo et al. 2011, Albrecht et al. 2013) and interactive functional complementarity could be common. For example, an apex predator might displace mesopredators into less favorable habitat, forcing them to tap into an otherwise unused prey source and increase overall prey consumption across the landscape (abiotic/environmental complementarity). Fruiting trees with greater, denser crops may draw larger frugivores that force smaller frugivores to trees with sparse yields. Functional enhancement within a niche is also possible. Competition amongst frugivores could force them to forage over wider areas and increase the seed dispersal distance for a given plant species. A predator that frequently experiences kleptoparasitism (stealing of prey) by other predators may need to increase its hunting frequency to make up for stolen prey. While functional enhancement in pollination tends to involve antagonistic interactions (see Section 5), in predation and seed dispersal they can be beneficial and even occur simultaneously with facilitation. For example, unusual cases of cooperative hunting have been reported (Bshary et al. 2006) or canopy frugivores may drop fruits that are eaten and dispersed by ground foragers. Here differences in foraging behavior drive increased activity within the same functional niche (assuming no functional difference in type of prey/seed dispersed) whilst benefiting one or both function providers.

Finally, like pollination, predation and animal seed dispersal also have the potential to saturate under realistic conditions. The number of prey to be consumed or seeds that can be dispersed both represent finite quantities, which at least in some cases can be completely consumed. The ability of predators or seed dispersal agents to acquire prey or seeds can also set an upper limit on function that is idiosyncratic to the species involved. This saturating relationship may require considering varying abundances of function providers because interactive functional complementarity may only manifest when species niches begin to saturate (Figure 1). The idea of varying abundances in diversity-functioning experiments has been supported by work on predation (Griffiths et al. 2008, Werling et al. 2012). Failure to account for saturating function could help explain—at least in part—why diversity-function relationships other than the sampling effect are sometimes not detected in experimental studies of predation and animal seed dispersal (Timóteo et al. 2016, Alhadidi et al. 2019) potentially contributing to the mixed evidence for diversity-function relationships in these fields.

2.7. Conclusion

To manage the functional benefits of community diversity, and predict the consequences of biodiversity decline, we need to better understand the mechanisms by which species richness drives community functions. More field studies are required to disentangle different mechanisms of diversity-function in pollination but special attention should be paid to understanding interactive functional complementarity and functional enhancement. Pollination, and other inter-trophic study systems that feature organisms capable of rapid behavioral responses, are ideal for studying niche changes and changes in functional rates, and may be the key to furthering our understanding of diversity-function relationships.

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Chapter 3: The impacts of bioenergy pine plantation management practices on bee communities

3.1. Introduction

Bioenergy production is a significant driver of land-use change in many parts of the world, and currently constitutes 2% (30–35 million hectares) of global cropland area (Popp et al., 2016). Bioenergy cultivation is predicted to increase substantially in the coming de- cades, given governmental mandates, tax exemptions and incentives (Sorda, Banse, & Kemfert, 2010), as well as the production of 'next-generation' or cellulosic bioenergy, which can potentially produce greater energy yields per unit area than traditional starch- or sugar-derived fuels. While the conversion of pristine habitats for the cultivation of perennial bioenergy crops poses a clear threat to biodiversity (Fletcher et al., 2011; Immerzeel, Verweij, Hilst, & Faaij, 2014), the ecological impact of introducing perennial bioenergy plantations to existing agricultural landscapes is less clear. How such perennial plantations are managed may significantly im- pact their capacity to support biodiversity (Bonham, Mesibov, & Bashford, 2002; Kerr, 1999; Mazurek & Zielinski, 2004).

Pine plantations in the United States represent a bioenergy feedstock system of key importance because these plantations — both modified from extensive existing plantations and also expansion of these areas — are expected to form the bulk of the nation's mandated bioenergy production goal of 36 billion gallons of liquid bioenergy to be produced annually by 2022 (Sissine, 2007). There have already been shifts in the use of these plantations from producing only conventional timber products to producing woody pellets that are currently used in bioenergy systems (Duden et al., 2018; Galik & Abt, 2016). Within the United States, the south- eastern coastal plain that extends from southeastern Virginia to southeastern Texas is expected to be the primary contributor to pine bioenergy feedstock. Three major bioenergy feedstock production methods have been proposed (Munsell & Fox, 2010): (a) converting conventional timber stands to short-rotation bioenergy plantations; (b) harvesting feedstock through thinning conventional plantations not primarily grown for bioenergy; and (c) harvesting of woody debris residues after plantations have been clear-cut. We need to understand the ecological impacts of changes in plantation management, especially relative to alternative bioenergy production systems such as annual crops like corn (Gonzalez et al., 2012), as well as how they compare to natural 'reference' habitats (Fletcher et al., 2011; Immerzeel et al., 2014), in this case naturally occurring stands of longleaf pine (e.g. Gottlieb et al., 2017).

The capacity for pine plantations to support wildlife is strongly dependent on management (Bonham et al., 2002; Kerr, 1999; Mazurek & Zielinski, 2004) and specific differences in bioenergy versus conventional timber plantation management may variably impact biodiversity. For example, in conventional timber plantations individual trees are allowed time to attain a critical bole diameter to maximize timber volume (Thompson & Pitt, 2003). In contrast, plantations managed for bioenergy feedstock are focused on efficiently amassing overall plantation biomass and so may benefit from more rapid crop turnover (Klepac & Mitchell, 2016). Resulting young plantations may have scant understorey vegetation and lack vertical structure, and thus lower habitat heterogeneity to support biodiversity (Riffell, Verschuyl, Miller, & Wigley, 2011b). A second means of obtaining biomass for bioenergy feedstock could involve little change from the status quo. Plantations managed for conventional timber products are usually thinned to reduce competition among trees and maximize growth in the remaining individuals (Thompson & Pitt, 2003). The biomass collected from thinning can be used as bioenergy feedstock. Pine plantations in the south- east United States managed for solid timber can be thinned after 10–15 years of growth, with landowners removing between 250 and 750 trees/ha (Stokes & Watson, 1996). Thinning may lead to in- creases in biodiversity. A study conducted in a U.S. national forest in Georgia observed greater bee species richness in thinned compared to dense pine forests (Hanula, Horn, & O'Brien, 2015; but see Breland, Turley, Gibbs, Isaacs, & Brudvig, 2018). Fallen woody debris is another by-product of timber production that may be harvested for biomass (Riffell, Verschuyl, Miller, & Wigley, 2011a). A meta-analysis of bioenergy harvest methods shows that removal of plantation ground debris differentially affects various taxa (Riffell et al., 2011b), as ground debris provides a valuable resource for a variety of organisms (Castro & Wise, 2010; Gottlieb et al., 2017; Mengak & Guynn Jr, 2003; Rodríguez & Kouki, 2015).

When considering the potential ecological impacts of bioenergy cultivation, it is particularly critical to examine taxonomic groups that provide vital ecosystem services. One such group is biotic pollinators, most notably bees (Hymenoptera: Apoidea), which provide pollination services that are vital to the productivity of both wild and cultivated plants. Habitat destruction and land-use change are thought to be the most important drivers of declines in pollinators such as bees (Dicks et al., 2016; Potts et al., 2010). Managed conifer forests can contribute significantly to the conservation of diverse species and ecosystem services, yet the extent to which they sup- port pollinators and pollination is poorly known (Rivers, Galbraith, et al., 2018). Given potentially significant impacts of bioenergy pro- duction on land-use change (Wright, Larson, Lark, & Gibbs, 2017), it is important to understand how management practices pertaining to bioenergy production could impact pollinator taxa.

Here we examine how managing pine plantations for bioenergy production in the southeastern United States may impact bee com- munities. Pine plantations grown for timber, paper and pulp (mainly *Pinus taeda* and *Pinus elliottii*) currently dominate large areas of the states of Georgia, Florida and Alabama. When cellulosic bioethanol technology becomes industrially viable, these plantations—after management changes—are expected to contribute a large portion of the United States' mandated bioenergy production goals, and are already contributing substantially to the global woody pellet biomass market (Dale et al., 2017). Examining biodiversity impacts of possible bioenergy management practices is necessary for policy makers and the bioenergy industry to make informed decisions that minimize potential ecological impacts. We examine how bee abundance and species diversity respond to three strategies for obtaining biomass for bioenergy: (a) a shift towards younger, denser plantations for more rapid biomass feedstock accumulation; (b) harvesting feedstock by thinning older plantations; (c) harvesting of woody debris after plantations have been clear-cut. We also examine bee communities in natural remnants, as a reference for unmanaged forest, and corn fields, which represent an alternative annual bioenergy crop type known to impact biodiversity (Fletcher et al., 2011; Immerzeel et al., 2014). We consider both bee richness and evenness, as the latter reflects the uniformity of species responses. We expect younger plantations to have developed less habitat heterogeneity than mature plantations, resulting in lower bee diversity. Thinning plantations should increase light and warmth in the understorey to encourage more flowering plants and greater bee diversity. As many bee species nest in woody de- bris and on the ground, debris removal should disturb nesting habitat to reduce bee diversity. Finally, we expected that managed pine stands would support greater bee diversity than corn fields.

3.2. Materials and Methods

3.2.1 Study sites and strata

We sampled bee communities from 83 sites, including 66 pine plantations, 10 natural reference-condition sites (longleaf pine forest remnants), and 7 corn production sites, distributed across the U.S. states of Florida, Georgia and Alabama, which are expected to be key bio- energy states. The sites were the same as those sampled for birds in prior work (Gottlieb et al., 2017) and clustered into three geographic 'strata' that did not follow state lines (Table 1). In pine plantations, we focus on three key attributes that reflect potential management changes for bioenergy feedstock production: (a) younger planta- tion age; (b) plantation thinning; and (c) harvesting of ground debris after plantations are clear-cut. We examined the effect of plantation age on bee communities by comparing young, unthinned plantations of about 8–12 years old (simulating harvest-ready bioenergy plantations) to more mature plantations that are 24–25 years old and have already been thinned. We also compared bee communities in plantations soon after thinning (simulating harvesting for bioenergy feedstock) to unthinned plantations of similar age (12–16 years). Finally, we examined the impact of harvesting plantation ground debris by comparing recently clear-cut plantations (felled within the last 2 years) with and without debris harvest. Each of the six 'plantation types' was represented in 9–12 sites (Table 1); all sites were >16 ha and spaced at least 2.5 km apart.

3.2.2 Measuring local bee and plant communities

We surveyed bee communities over the spring and summer seasons of 2013, 2014 and 2015. Sites were not sampled repeatedly across years. In each site, we marked out two 2 × 200 m sampling transects at least 50 m from the plantation edge and at least 100 m away from one another.

For each sampling day, we collected bees using pan traps and aerial netting, which work effectively in tandem (Westphal et al., 2008). Pan traps consisted of small, plastic cups (3.25 oz., model P325, SOLO Cup Company) painted with ultraviolet-bright blue, white or yellow paint, and filled with a dilute detergent-water solution that drowns the bees (Kearns & Inouye, 1993; Westphal et al., 2008). Fifteen pan traps were held approximately 40 cm above the ground on wire stakes (VIGORO plant props, model 611872, Spectrum Brands Holdings Inc., bent to better hold traps) so as to be visible above herbaceous vegetation, and positioned in alternating colours evenly along the centre 100 m of the sampled transect. Pan traps were set up in the morning and collected after 24 hr. During each sampling day, we also performed targeted aerial netting of bees along the entire length of a transect for 30 min, excluding handling time for every successful capture with a stopwatch. Bee surveys were postponed on cloudy or rainy days, and each transect was sampled up to four times on separate days, amounting to up to 8 sampling days per site. Due to unforeseen weather and logistical difficulties, however, 9 of the 66 sites are represented by only one transect or by fewer than three samples. These sites were spread across two of the three strata and across land-use categories. Still, we employed statistical methods robust to imbalances in sampling effort across our analyses. Collected bees were preserved in ethanol or pinned, brought back to the laboratory and identified to species or occasionally genus.

Table 1 Site replications per stratum for the six plantation types with and without potential management changes for bioenergy production, as well as natural longleaf pine stands and corn fields. Stratum S1 consisted of sites in Alabama; S2 in southern Georgia and the Florida panhandle; and S3 in north-central Florida.

Plantation Attributes	**Resembling bioenergy production**	**Total number of sites**	**Strata**	**No. of sites**	**Without Bioenergy production**	**Total number of sites**	**Strata**	**No. of sites**
Younger plantations	Young (8-12 years), unthinned	11	S1 S2 S3	4 3 4	Mature (24-25 years), thinned	12	S1 S2 S3	4 6 2
Harvesting feedstock by thinning	Thinned (12-16 years)	11	S1 S2 S3	4 3 4	Unthinned (12-16 years)	11	S1 S2 S3	4 3 4

Harvesting debris after clear-cut	Trees clear-cut, debris harvested	9	S1	2	Trees clear-cut, debris uncleared	12	S1	5
			S2	3			S2	3
			S3	4			S3	4
Non-plantation land-uses	Corn fields	7	S1	2	Natural longleaf pine stands	10	S1	3
			S2	3			S2	4
			S3	2			S3	3

We measured available floral resources at each site once during the study on a sampling day, within 1 m of the central 100 m of each transect, by counting and identifying to species all understorey non-grass plants that were in bloom. We surveyed floral resources among sites within a stratum as close together in time as possible to maximize comparability. A separate analysis of pollen loads present on some of the bee specimens from this work is covered in Bell et al. (2017), which describes interactions between bee and plant species.

3.2.3 Bee specimen preparation and identification

We usually pinned bee specimens on the day of sampling. We keyed out all specimens to genus, and 92% of taxa to species, using Discover Life online keys (https://www.discoverlife.org), in conjunction with Michener (2000) and Michener, McGinley, and Danforth (1994). Our identifications were verified by Ismael Hinojosa (Universidad Autonoma de Mexico) and Sam Droege (USGS); Sam Droege identified many specimens (particularly *Lasioglossum*) to species.

3.2.4 Data analysis

All statistical analyses were conducted in r (R Core Team, 2016).

3.2.4.1 Bee abundance

We analysed bee abundance per daily survey across plantation management types using generalized linear mixed-effects models implemented in the R package ‘glmmADMB’ (Skaug, Fournier, Bolker, Magnusson, & Nielsen, 2016) with negative binomial errors (count data, overdispersed relative to a Poisson distribution). In all cases we included ‘site’ nested within ‘strata’ (sites were clustered in three geographic strata) and as random effects, and examined two explanatory variables: (a) plantation management/land-use types; and (b) understorey plant richness. Understorey plant richness served as a single metric describing potentially available floral resources for bees for all 3 years of this study because flower abundance data from 2015 was of poor resolution. Based on 2013 and 2014 data, floral richness and flower abundance were strongly correlated (Pearson's product–moment correlation, $r = .73$, $p < .001$, $df = 37$, removing one outlier). We specified a priori pair-wise contrasts of plantation management types that simulate management practices with and without changes for bioenergy feedstock production, using general linear contrasts within our mixed-effects models with the R package ‘multcomp’ (Hothorn, Bretz, & Westfall, 2008). We also considered bee diversity in longleaf pine forest remnants (natural reference) and corn fields (alternative annual bioenergy crop type).

3.2.4.2 Bee species diversity

We analysed species diversity in each plantation type using both individual- and sample-based rarefaction to account for differences in bee individuals caught and sampling effort. Rarefaction allows for comparisons of the diversity between two sites as if they had the same number of sampled individuals or events (e.g. Chazdon, Colwell, & Denslow, 1998; Colwell et al., 2012). We constructed rarefied and extrapolated diversity estimates analyses with the R package ‘iNEXT’ (Hsieh, Ma, & Chao, 2016), which calculates boot- strapped diversity values with 95% confidence intervals (rep = 50) for 40 evenly spaced ‘knots’ between the first sample or individual. The extrapolation extends to double the minimum empirical sampling effort. These curves are plotted with ggiNEXt (Hsieh et al., 2016), an extension of the R package 'ggplot2' (Wickham, 2016). We examined species richness with sample-based rarefaction, and both species richness and inverse Simpson index (henceforth 'inverse Simpson') with individual-based rarefaction. The inverse Simpson is sensitive to dominance (Morris et al., 2014) and estimates 'effective richness' by penalizing true richness based on decreasing community evenness.

3.2.4.3 Beta diversity

To compare bee community composition among different plantation types, we created a Bray–Curtis dissimilarity matrix (R package 'vegan', Oksanen et al., 2016). We then plotted means and 95% confidence intervals of similarity of sites within a plantation type against its similarity to all other plantation types. This allows us to visualize the degree of species turnover among sites (beta diversity) of a given type relative to the global diversity of study sites.

3.2.4.4 Spatial autocorrelation

To test the assumption that sites in a stratum are independent, we used Mantel tests for spatial independence in community composition (R package 'vegan', Faith, Minchin, & Belbin, 1987; Oksanen et al., 2016) and Moran's I for abundance and species richness (R package 'ape', Paradis, Claude, & Strimmer, 2004). We tested for spatial autocorrelation within the three strata: S1, sites in Alabama; S2, sites in southern Georgia and the Florida panhandle; S3, sites in north- central Florida (Table 1).

3.3. Results

3.3.1 Sampling overview

We sampled a total of 5,737 bees representing 126 species or morphospecies, comprising 1,480 individuals, 82 species from Alabama; 976 individuals, 71 species from Florida; and 3,281 individuals, 78 species from Georgia. We caught 1,105 bees of 86 species by netting and 4,644 bees of 104 species from pan traps. Of the 126 morphospecies, we were able to identify all but nine to the species level. Those identified only at the genus level comprise just 48 of the 5,737 bee individuals in the study. Bee species and flower species recorded in this study can be found in the (Tables S1–S3). Flower richness at each site type is plotted in Figure S1. The most common flower species recorded were *Verbena brasiliensis*, *Justicia ovata*, *Callicarpa americana*, *Erigeron annuus* and *Rhexia virginica*. Results from spatial autocorrelation analyses are presented in Table S4. We proceeded with statistical analyses assuming spatial independence between sites, though we included site and stratum as random effects in our mixed-effects models to account for potential dependence in repeated measures within the strata and sites.

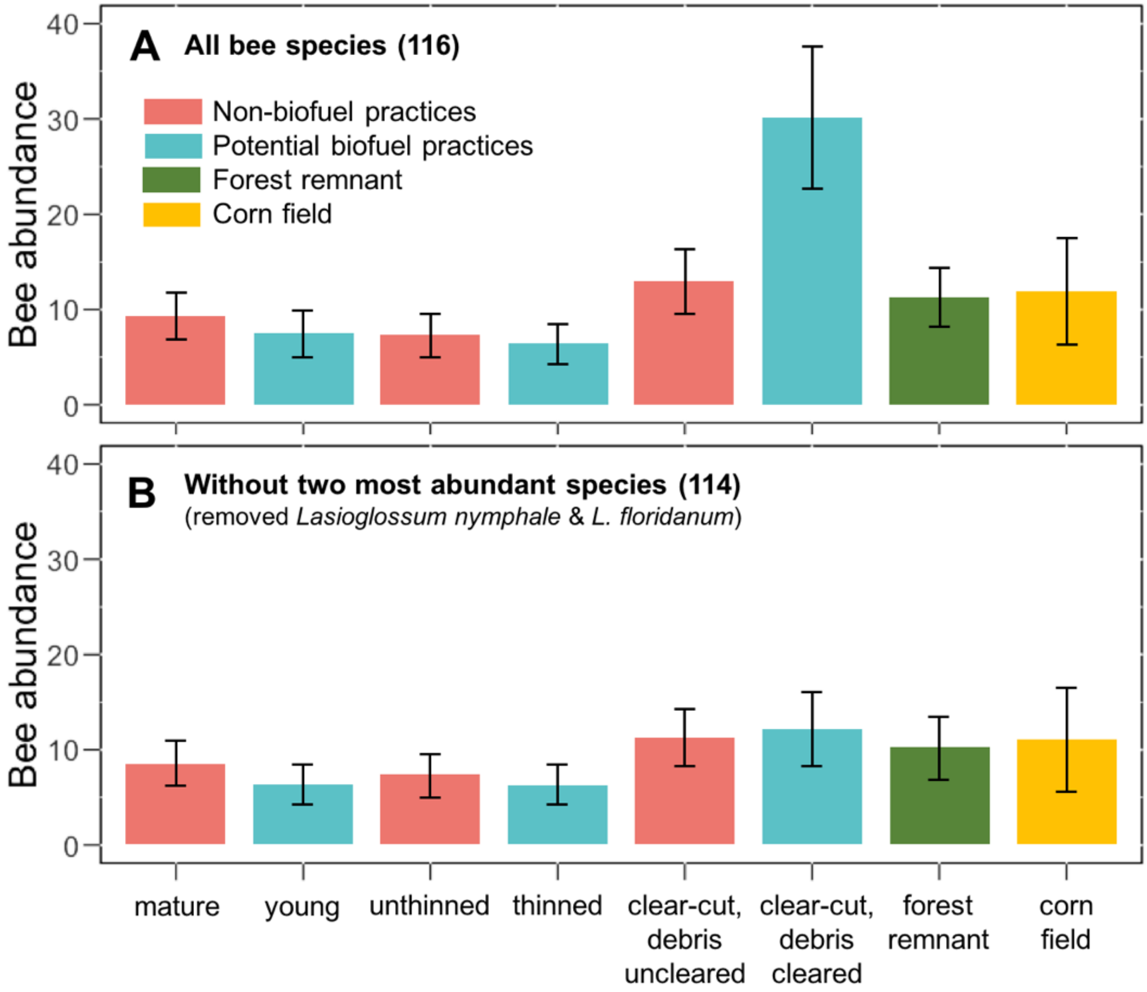

Figure 1 Mean number of bees sampled per day at a site in the six examined plantation types, natural longleaf pine stands and corn fields (an alternative, annual bioenergy crop). Error bars indicate 95% confidence intervals. Colors represent different plantation management practices or land-use types. Panels A and B show bee abundances including and excluding the two most dominant species in this study, *Lasioglossum nymphale* and *L. floridanum*.

3.3.2 Bee abundance

Management type but not understorey plant richness had significant effects on bee abundance. Bee abundance did not change with plantation age or thinning (Figure 1a) but was dramatically higher in clear-cut sites where plantation debris was harvested relative to where it was left in place (contrast: est. = 0.791, SE = 0.172, $p < 0.05$). In these debris-removal clear-cut sites, bee abundance was on average at least double that of any other site type. However, when the two most numerically dominant bee species, *Lasioglossum nymphale* and *L. floridanum*, were excluded from the dataset, abundances across all site types, including forest remnants and corn fields, were no longer significantly different (Figure 1).

3.3.3 Bee species diversity—Sample-based rarefaction

Bee species richness differed significantly among the managed plantation forests, forest remnants and corn fields. Forest remnants and cornfields had significantly lower richness curves than managed plantation forests but did not differ significantly from one another (Figure 2). When making comparisons only within managed plantation forests, however, sample-based rarefaction curves of species richness were not substantially different (i.e. overlapping confidence intervals) in our a priori pairwise contrasts (Figure 3).

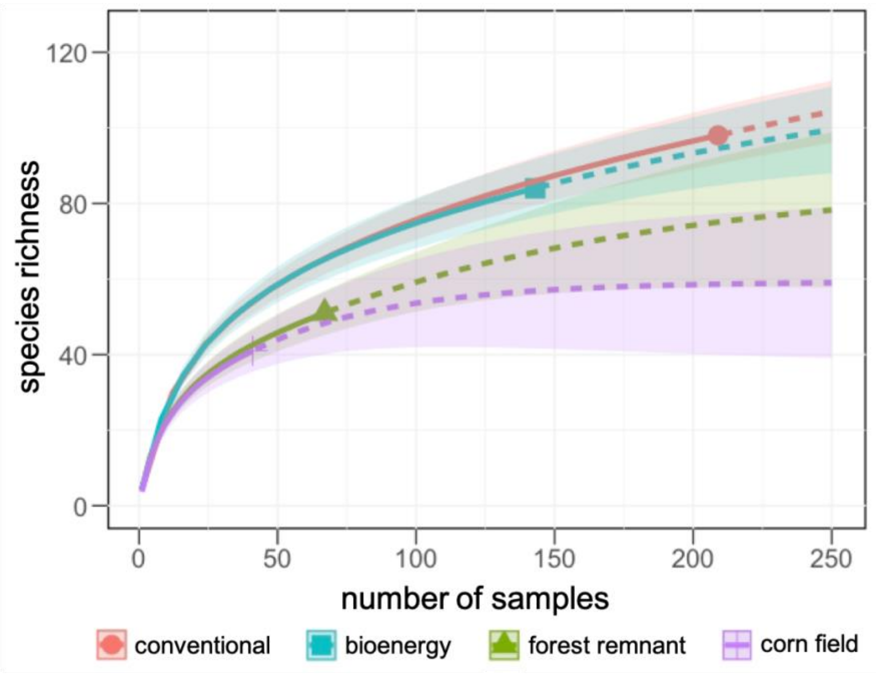

Figure 2 Bee richness in various habitat types rarefied by the number of sampling attempts. Curves represent 1. conventional timber product management practices, 2. bioenergy-like management practices, 3. corn fields (an alternative, annual biofuel crop type) and 4. longleaf pine forest remnants. Tinted areas show the bounds of bootstrapped 95% confidence intervals for each curve.

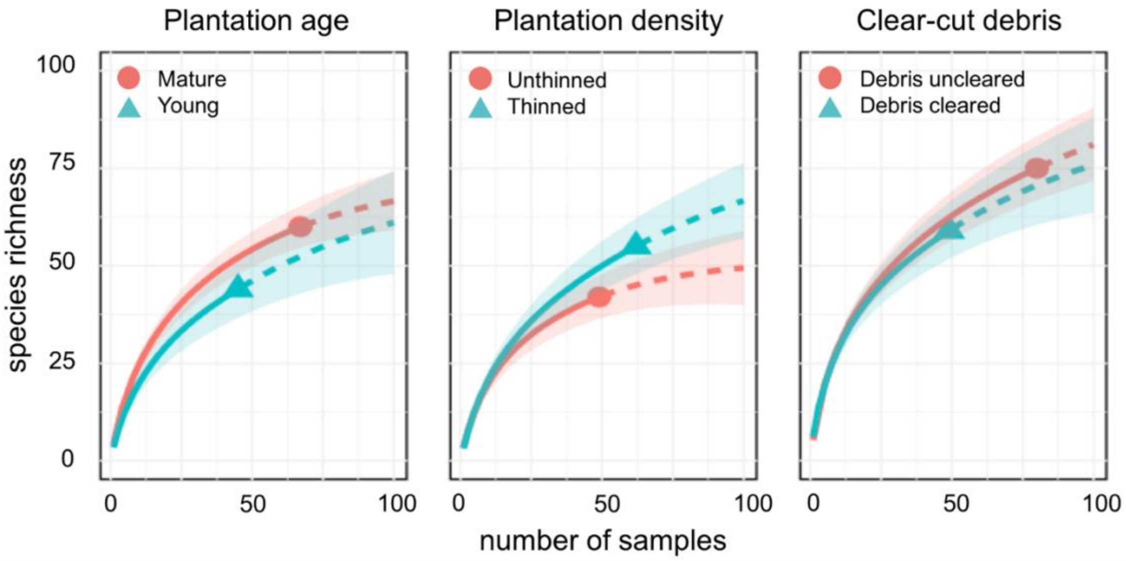

Figure 3 Sample-based rarefaction curves of bee species richness in the six examined plantation types. The x-axis shows the number of samples and the y-axis shows species richness values. Colors represent sites with non-bioenergy practices (orange) or potential bioenergy production practices (blue). Solid lines show bootstrapped interpolated richness values, ending in points that mark the highest observed species richness. Dashed lines are extrapolated richness values. Tinted areas indicate the bounds of 95% confidence intervals.

3.3.4 Bee species diversity—Individual-based rarefaction

We only detected significant differences in diversity between different plantation ages and treatment of debris after tree harvest (Figure 4). Younger plantations had similar richness accumulation curves to mature plantations but significantly lower inverse Simpson curves based on non-overlapping 95% confidence intervals. Clear-cut plantations with debris removed had much lower species richness and inverse Simpson curves compared to clear-cut plantations with debris left intact.

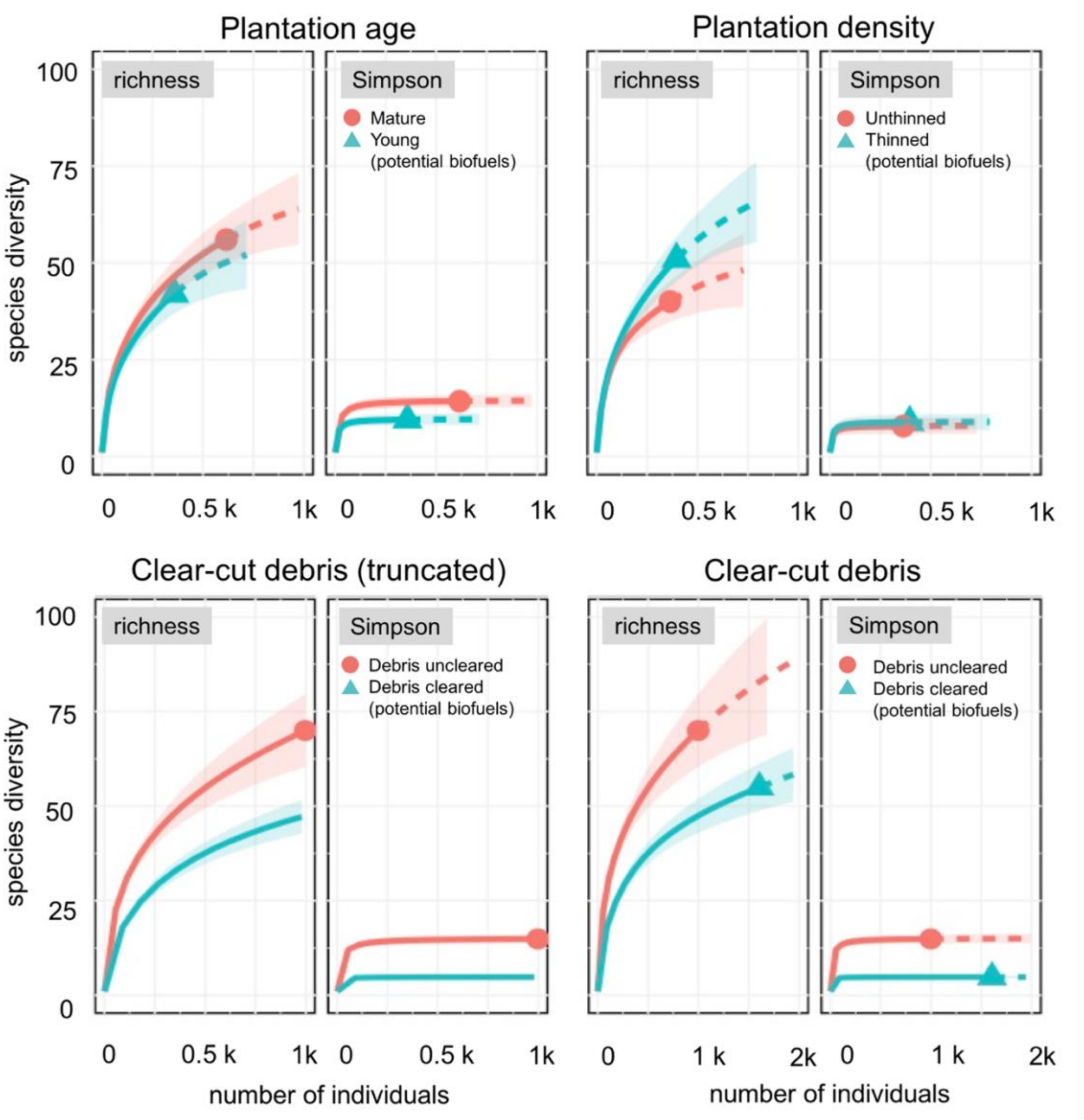

Figure 4 Individual-based rarefaction curves of species richness and inverse Simpson (measured in the same units as species richness) in the six examined plantation types. Clear-cut sites had drastically higher bee abundance than other sites, hence for easier visual comparison 'Treatment of debris' curves are also shown here truncated at 1000 individuals. The x-axis shows the number of sampled bee individuals and the y-axis shows species diversity values. Colors represent sites with non-bioenergy practices (orange) or potential bioenergy production practices (blue). Solid lines show bootstrapped interpolated diversity values, ending in points that mark the highest observed diversity.

Dashed lines are extrapolated diversity values. Tinted areas indicate the bounds of bootstrapped 95% confidence intervals.

3.3.5 Beta diversity

The bee communities among site were generally dissimilar (mean Bray–Curtis dissimilarity = 0.826; Figure 5, dashed line). Comparisons of mean pairwise community dissimilarity among our a priori contrasts did not show differences in beta diversity (non-overlapping 95% confidence intervals) in terms of young versus old or thinned versus unthinned plantations (Figure 5). By contrast, in clear-cut sites, debris removal treatments had substantially lower beta- diversity relative to sites without debris removal and across all land- use types we studied. Beta diversity was also significantly lower in pine forest remnants.

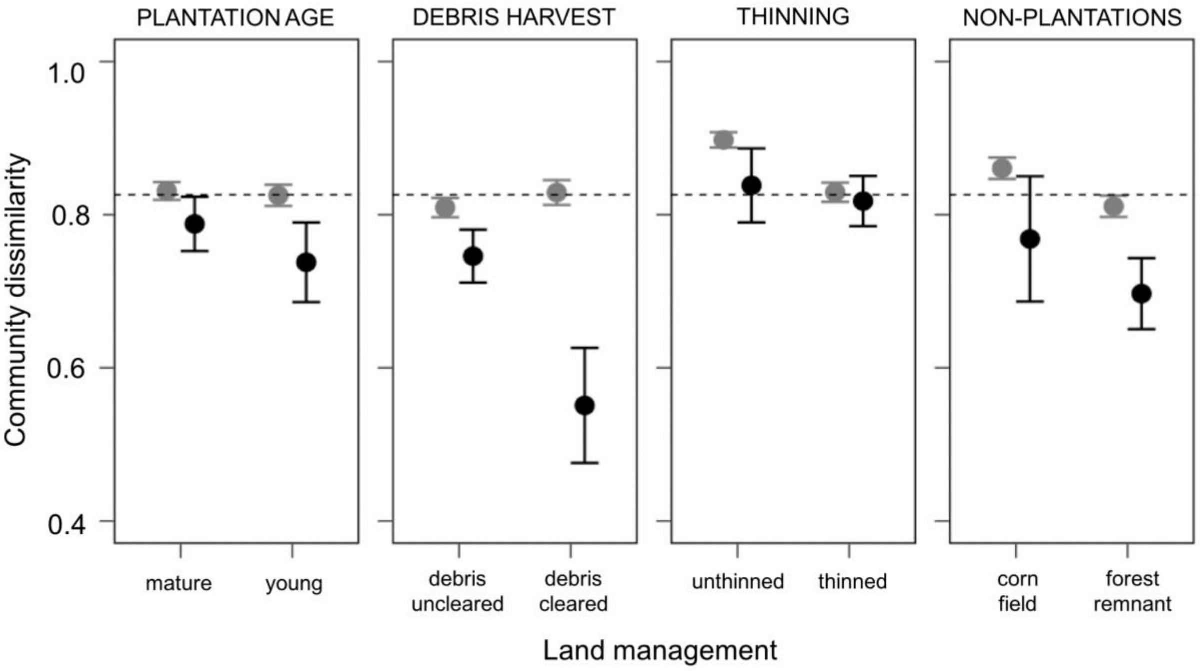

Figure 5 Bee beta diversity, shown as mean pairwise Bray-Curtis dissimilarity with 95% confidence intervals (y-axis) among land use types. Black dots show within-treatment pairwise mean

dissimilarity and grey dots show the pooled mean dissimilarity of the remaining site types. Dashed line depicts the mean pairwise similarity of all sites examined in this study.

3.4. Discussion

We examined how bee communities responded to three potential bioenergy production practices in pine plantations. We focused on: (a) stand age, (b) plantation thinning and (c) harvesting of woody debris after plantations are clear-cut. We found effects of plantation management on both bee abundance and diversity. Harvesting woody debris for bioenergy feedstock in clear-cut sites increased bee abundance, though this response is driven by just two hyper- abundant species. Indeed, while bee species richness was not markedly different when woody debris was harvested or in younger bioenergy plantations, both had lower inverse Simpson — lower 'effective richness' due to low community evenness. Decreases in community evenness suggest that the impact of plantation management varies among bee species. Beta diversity was also significantly lower in young and clear-cut plantations, suggesting that shorter har- vest rotations may drive convergence of local species assemblages towards more disturbance-tolerant or open habitat taxa. Plantations tended to be similar in bee species composition, with species such as *Melissodes communis*, *L. floridanum*, *L. reticulatum* and *L. puteulanum* being common. However, plantations collectively supported higher bee diversity than corn fields, an alternative bioenergy crop type. This is perhaps due to the variety of habitat conditions created through the different stages of plantation management and harvest. Thus, plantations may collectively also have greater habitat diversity than forest remnants, which may explain lower species diversity and community dissimilarity in the latter. Nevertheless, some bee species were more common in forest remnants, such as *L. imitatum*, *L. apopkense* and *Augochloropsis metallica*.

3.4.1 Plantation age

Appropriately managed plantations can over time develop diverse communities resembling those of native forests (Gallé, Torma, & Maák, 2016; Pawson, Brockerhoff, & Didham, 2009; Pawson, Brockerhoff, Meenken, & Didham, 2008) and can even include rare or endangered taxa (Berndt, Brockerhoff, & Jactel, 2008; Humphrey, Newton, Peace, & Holden, 2000). Longer harvest rotations, while less economically beneficial for timber production in many con- texts, often benefit conservation objectives (Brockerhoff, Jactel, Parrotta, Quine, & Sayer, 2008; Humphrey, 2005). We found that bee communities in older pine plantations had significantly higher inverse Simpson. However, that they did not support greater bee abundance or rarified species richness suggests greater community evenness. Alternatively, young stands may experience more invasion by open-habitat specialists (Koivula, Kukkonen, & Niemelä, 2002; Pawson et al., 2008, 2009) that could reduce their relative evenness. Community dissimilarity among young plantations was significantly lower than dissimilarity among other plantation types, indicating that younger plantations tended to share more similar species.

3.4.2 Plantation thinning

The biomass collected from thinning conventional timber plantations can be a source of bioenergy feedstock. Thinning creates canopy gaps, which changes understorey microclimate and vegetation (Ares, Neill, & Puettmann, 2010; Nunes, Oliveira, Cabral, Branquinho, & Correia, 2014; Son, Lee, Jun, & Kim, 2004) and has been known to in- crease abundance and/or diversity of bees in other forests (Proctor, Burke, & Crins, 2012; Taki et al., 2010). Furthermore, another study that thinned longleaf pine forests close to our study region saw increased bee abundance and richness (Breland et al., 2018). Surprisingly, we failed to find consistent impacts of tree thinning practices on bee abundance, alpha diversity or beta diversity. In theory, thinning encourages the growth of flowering plants in the understorey, though understorey plant richness did not correlate with bee communities in this study. It is plausible that benefits of thinning could be slow to accumulate for some taxa if (e.g.) time is needed for the understorey to develop floral resources for bees. Alternatively, tree thinning alone may not create quality bee habitat if understorey shrubs are not also removed to encourage proliferation of diverse, herbaceous plant communities (Proctor et al., 2012).

3.4.3 Treatment of woody debris

Woody residues from tree thinning and harvesting (e.g. branches, stumps etc.) can be collected for bioenergy feedstock in plantations grown primarily for timber (Riffell et al., 2011a). When left un-cleared, however, forest woody debris is utilized by a variety of wildlife and its absence has been linked to lower species diversity in a variety of taxa (Castro & Wise, 2010; Gottlieb et al., 2017; Mengak & Guynn Jr, 2003; Rodríguez & Kouki, 2015). We found that harvesting plantation woody debris correlated with higher bee abundances but on a per-individual basis, and species richness and community evenness were markedly lower. This is perhaps unsurprising, given that coarse woody debris has been associated with wood-nesting bee diversity in other managed forests (Rivers, Mathis, Moldenke, & Betts, 2018; Rodríguez & Kouki, 2017). Physical soil disturbance from the collection of debris may also impact ground nesters (Vázquez, Alvarez, Debandi, Aranibar, & Villagra, 2011). Even so, debris removal appeared to benefit two species: *L. floridanum* and *L. nymphale*, which accounted for approximately 60% (34.5% and 26.3% respectively) of the 1,666 individuals (out of 75 species) collected from debris- cleared sites. These two species accounted for <15% (14.2% and <1% respectively) of the 1,031 bees collected from sites where debris was left uncleared (out of 60 species). Many *Lasioglossum* species are widespread and highly tolerant of disturbed habitats, such as corn fields (Wheelock & O'Neal, 2016), so they may not be good indicators of habitat quality. When these two species were excluded from the analysis, the effect of debris removal on bee abundance became undiscernible. Given that clear-cut sites had significantly lower beta diversity, our findings may instead suggest a convergence in species assemblages in clear-cut sites, perhaps due to reduced habitat heterogeneity caused by disturbance (Karp et al., 2012; Maaß, Migliorini, Rillig, & Caruso, 2014; Myers, Chase, Crandall, & Jiménez, 2015).

3.5. Conclusions

We must weigh the relative gains of various land-use practices against their impacts on biodiversity. Debris removal in clear-cuts may generate the lowest biomass yields of any of the practices examined (Munsell & Fox, 2010, also see Gottlieb et al., 2017), as debris tends to be thinly dispersed per hectare and usually has a high bark content that makes for poor bioethanol feedstock (Kimbell, Maness, Brown, Bowyer, & Argow, 2009). Furthermore, debris is a valuable resource to bees and other taxa (Ulyshen, 2018), making debris harvest in clear-cut plantations least sustainable for biomass feedstock production. Relative to mature plantations, younger stands and clear-cut plantations have experienced relatively recent major disturbance during tree harvest and may thus favour bee species that are disturbance-tolerant or prefer open habitats, though potential negative impacts on late-succession specialists or wood- and ground-nesting species are currently unclear. Overall, sites tended to have high beta diversity, suggesting that maintaining landscape heterogeneity, including plantations in various stages of production, could benefit diversity of bees and other pollinators (Miljanic et al., 2019; Rodríguez & Kouki, 2017).

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3.7. Chapter 3 Supplementary Materials

Table S1. Species list of all bee species collected in this study and their abundances. Species are sorted alphabetically by family and then by genus.

	Mature plantations	Young plantations	Unthinned plantations	Thinned plantations	Clear-cut, debris intact	Clear-cut, debris cleared	Natural reference	Cornfield
TOTAL ABUNDANCE	**630**	**384**	**387**	**410**	**1031**	**1654**	**756**	**485**
ANDRENIDAE								
Andrena atlantica	0	0	1	0	0	0	0	0
Andrena barbara	0	0	0	0	4	0	0	0
Andrena confederata	0	0	0	0	0	1	0	0
Andrena cressonii	0	0	1	0	1	0	0	0
Andrena imitatrix	0	0	0	0	1	0	0	0
Andrena miserabilis	1	0	0	0	0	0	0	0
Andrena nasonii	1	0	0	0	0	0	0	0
Andrena perplexa	1	0	0	0	0	0	0	0
Andrena simplex	0	1	0	0	0	0	0	0
Perdita boltoniae	0	0	0	0	3	1	0	0
Perdita nubila	0	0	0	0	0	13	0	0
APIDAE								
Apis mellifera	16	12	13	10	39	67	6	3
Bombus bimaculatus	2	2	6	2	4	0	2	0
Bombus fervidus	0	0	0	0	1	0	0	0
Bombus fraternus	2	1	0	0	1	0	0	0
Bombus griseocolis	6	2	0	2	26	0	3	2
Bombus impatiens	21	8	11	8	21	11	11	4
Bombus pensylvanicus	2	1	2	1	16	0	1	0
Bombus sandersoni	0	0	0	0	1	0	0	0

Cemolobus impomoeae	5	0	0	1	1	2	3	0
Centris lanosa	0	0	0	0	0	1	0	0
Ceratina calcarata	0	2	1	1	0	0	0	0
Ceratina cockerelli	0	0	0	0	0	0	0	1
Ceratina dupla	4	3	4	1	0	0	0	0
Ceratina floridana	2	8	18	5	5	0	0	1
Ceratina mikmaqi	0	2	5	0	1	0	0	0
Ceratina sp. 1	1	0	0	0	0	0	0	0
Ceratina strenua	2	28	4	10	10	0	0	0
Eucera dubitata	0	0	0	1	5	0	0	0
Eucera rosae	0	0	0	0	1	0	0	0
Habropoda laboriosa	0	0	0	2	3	1	0	0
Melissodes apicata	0	1	3	0	0	2	1	0
Melissodes bimaculata	67	11	1	45	32	3	10	24
Melissodes communis	88	11	8	18	61	52	69	45
Melissodes comptoides	0	0	0	1	4	0	0	0
Melissodes mitchelli	0	0	0	0	0	1	0	0
Melissodes sp. 1	0	0	0	0	0	1	1	0
Melissodes tepaneca	0	0	0	0	0	1	1	0
Melissodes trinodis	29	2	2	3	73	50	5	8
Melitoma taurea	17	5	0	8	8	2	8	0
Peponapis pruinosa	0	0	0	0	0	1	0	0
Ptilothrix bombiformus	2	0	1	5	18	2	21	0
Svastra obliqua	0	0	0	0	6	0	1	0
Svastra petulca	0	0	0	0	3	0	0	0
Triepeolus sp. 1	0	0	0	1	0	0	0	0
Xenoglossa kansensis	1	0	0	0	0	0	0	0
Xylocopa micans	5	1	0	2	3	1	1	1
Xylocopa virginica	5	3	3	3	4	7	0	0

COLLETIDAE								
Colletes banksi	1	0	0	1	0	0	2	0
Colletes inaequalis	1	0	0	0	0	0	0	0
Colletes nudus	1	0	0	0	0	1	0	0
Colletes productus	0	0	1	0	0	0	0	0
Hylaeus confluens	0	0	1	0	0	0	0	0
HALICTIDAE								
Agapostemon splendens	18	4	0	1	25	17	6	9
Augochlora pura	0	3	5	7	1	0	0	3
Augochlorella aurata	2	10	116	113	12	0	8	10
Augochlorella gratiosa	1	28	19	18	0	0	1	6
Augochlorella persimilis	0	0	0	0	1	0	0	0
Augochloropsis metallica	3	2	8	5	7	1	23	0
Augochloropsis sumptuosa	1	0	0	0	1	3	17	0
Halictus parallelus	0	0	1	1	2	2	1	2
Halictus poeyi	9	10	0	13	32	38	9	23
Lasioglossum apopkense	8	8	1	1	5	30	84	0
Lasioglossum binghami	0	1	0	0	0	0	0	0
Lasioglossum birkmanni	1	0	10	7	1	0	0	0
Lasioglossum callidum	1	2	0	2	1	9	3	7
Lasioglossum cinctipes	0	0	0	0	1	0	0	0
Lasioglossum coreopsis	1	0	10	1	22	2	2	2
Lasioglossum creberrimum	4	0	13	0	0	0	1	2
Lasioglossum floridanum	37	78	0	17	146	575	80	25
Lasioglossum gotham	0	0	1	0	1	0	0	0
Lasioglossum hitchensi	4	0	0	1	2	0	2	2
Lasioglossum illinoense	0	0	0	1	2	0	0	1
Lasioglossum imitatum	0	0	1	2	8	1	20	6
Lasioglossum leucocomum	0	0	0	0	0	0	0	3

Lasioglossum leviense	40	1	25	2	4	10	41	1
Lasioglossum longifrons	6	1	5	8	33	60	7	20
Lasioglossum lustrans	0	0	0	0	2	4	0	1
Lasioglossum nelumbonis	0	0	0	0	5	0	0	3
Lasioglossum nymphale	6	6	0	1	20	433	18	1
Lasioglossum pectorale	21	30	3	16	49	10	6	10
Lasioglossum pilosum	0	0	3	0	3	8	0	87
Lasioglossum platyparium	0	0	0	0	0	0	1	0
Lasioglossum pruinosum	0	0	0	0	0	0	0	1
Lasioglossum puteulanum	70	15	16	4	144	114	18	66
Lasioglossum raleighense	1	0	0	0	0	0	0	0
Lasioglossum reticulatum	55	68	37	32	65	26	227	10
Lasioglossum sopinci	0	0	0	0	1	1	0	0
Lasioglossum sp. 1	3	0	0	3	2	4	0	2
Lasioglossum sp. 2	0	0	5	0	0	0	0	0
Lasioglossum sp. 3	0	0	0	0	0	1	0	0
Lasioglossum sp. 4	2	0	5	0	4	7	3	1
Lasioglossum tarponense	0	1	2	0	0	0	0	0
Lasioglossum tegulare	8	1	0	7	22	12	2	66
Lasioglossum trigeminum	5	1	10	1	10	10	9	21
Lasioglossum vierecki	1	1	0	0	0	5	2	0
Lasioglossum viridatum	3	0	1	0	0	1	7	0
Lasioglossum weemsi	2	0	0	1	2	0	1	0
Lithurgopsis gibbosa	0	0	0	0	0	5	0	0
Sphecodes atlantis	0	0	0	0	0	1	0	0
Sphecodes sp. 1	0	0	0	0	0	0	0	1
MEGACHILIDAE								
Coelioxys dolichos	0	0	0	2	0	0	0	0
Heriades leaviti	0	0	0	0	0	0	1	0

Hoplitis producta	2	1	0	0	1	0	1	1
Hoplitis truncata	0	2	0	1	0	0	0	0
Hoplitis truncatum	0	0	0	0	1	0	0	0
Megachile addenda	0	0	0	1	1	4	4	0
Megachile albitarsis	0	0	0	0	1	2	0	0
Megachile brevis	0	0	0	0	1	0	0	0
Megachile frugalis	0	1	0	0	0	0	0	0
Megachile gemula	0	0	0	0	1	0	0	0
Megachile georgica	0	0	0	0	0	0	2	1
Megachile mendica	18	2	1	2	11	14	0	2
Megachile parallela	1	0	0	0	0	0	0	0
Megachile petulans	6	2	1	3	15	5	1	0
Megachile pseudobrevis	2	0	0	0	3	5	0	0
Megachile rubi	1	0	0	0	0	1	0	0
Megachile sp. 1	0	0	0	0	0	1	0	0
Megachile texana	3	1	0	2	2	5	1	0
Megachile xylocopoides	0	0	0	0	1	1	0	0
Osmia atriventris	0	0	0	1	0	0	0	0
Osmia chalybea	0	0	1	1	0	0	0	0
Osmia inspergens	1	0	0	0	0	0	0	0
Osmia sandhouseae	0	0	1	1	1	5	0	0
MELITTIDAE								
Melitta americana	0	0	0	0	0	0	1	0

Table S2. The top 10 most common bee species collected from various land-use types in this study. Numbers in parentheses indicate the total number of individual bees collected from each site type. Percentages are of the percentage of individuals represented by a given species.

Mature plantations (630)		**Unthinned plantations (387)**		**Clear-cut, debris intact (1031)**		**Natural reference (756)**	
	%		%		%		%
Melissodes communis	14.0	*Augochlorella aurata*	30.0	*Lasioglossum floridanum*	14.2	*Lasioglossum reticulatum*	30.0
Lasioglossum puteulanum	11.1	*Lasioglossum reticulatum*	9.6	*Lasioglossum puteulanum*	14.0	*Lasioglossum apopkense*	11.1
Melissodes bimaculata	10.6	*Lasioglossum leviense*	6.5	*Melissodes trinodis*	7.1	*Lasioglossum floridanum*	10.6
Lasioglossum reticulatum	8.7	*Augochlorella gratiosa*	4.9	*Lasioglossum reticulatum*	6.3	*Melissodes communis*	9.1
Lasioglossum leviense	6.3	*Ceratina floridana*	4.7	*Melissodes communis*	5.9	*Lasioglossum leviense*	5.4
Lasioglossum floridanum	5.9	*Lasioglossum puteulanum*	4.1	*Lasioglossum pectorale*	4.8	*Augochloropsis metallica*	3.0
Melissodes trinodis	4.6	*Apis mellifera*	3.4	*Apis mellifera*	3.8	*Ptilothrix bombiformus*	2.8
Bombus impatiens	3.3	*Lasioglossum creberrimum*	3.4	*Lasioglossum longifrons*	3.2	*Lasioglossum imitatum*	2.6
Lasioglossum pectorale	3.3	*Bombus impatiens*	2.8	*Halictus poeyi*	3.1	*Lasioglossum nymphale*	2.4
Agapostemon splendens	2.9	*Lasioglossum birkmanni*	2.6	*Melissodes bimaculata*	3.1	*Lasioglossum puteulanum*	2.4

Young plantations (384)		**Thinned plantations (410)**		**Clear-cut, debris cleared (1654)**		**Cornfield (485)**	
	%		%		%		%
Lasioglossum floridanum	20.3	*Augochlorella aurata*	27.6	*Lasioglossum floridanum*	34.8	*Lasioglossum pilosum*	17.9
Lasioglossum reticulatum	17.7	*Melissodes bimaculata*	11.0	*Lasioglossum nymphale*	26.2	*Lasioglossum puteulanum*	13.6
Lasioglossum pectorale	7.8	*Lasioglossum reticulatum*	7.8	*Lasioglossum puteulanum*	6.9	*Lasioglossum tegulare*	13.6
Augochlorella gratiosa	7.3	*Augochlorella gratiosa*	4.4	*Apis mellifera*	4.1	*Melissodes communis*	9.3
Ceratina strenua	7.3	*Melissodes communis*	4.4	*Lasioglossum longifrons*	3.6	*Lasioglossum floridanum*	5.2
Lasioglossum puteulanum	3.9	*Lasioglossum floridanum*	4.1	*Melissodes communis*	3.1	*Melissodes bimaculata*	4.9
Apis mellifera	3.1	*Lasioglossum pectorale*	3.9	*Melissodes trinodis*	3.0	*Halictus poeyi*	4.7
Melissodes bimaculata	2.9	*Halictus poeyi*	3.2	*Halictus poeyi*	2.3	*Lasioglossum trigeminum*	4.3
Melissodes communis	2.9	*Apis mellifera*	2.4	*Lasioglossum apopkense*	1.8	*Lasioglossum longifrons*	4.1
Augochlorella aurata	2.6	*Ceratina strenua*	2.4	*Lasioglossum reticulatum*	1.6	*Augochlorella aurata*	2.1

Table S3. Species list of all plant species recording blooming during this study. Species are sorted alphabetically.

List of flowering plant species	
1	*Asclepias verticiliata*
2	*Asimina angustifolia*
3	*Bidens alba*
4	*Callicarpa americana*
5	*Campsis radicans*
6	*Centrosema virginianum*
7	*Chapmannia floridana*
8	*Cirsium nuttallii*
9	*Cnidoscolus urens*
10	*Commelina erecta*
11	*Convolvulus arvensis*
12	*Coreopsis major*
13	*Croton argyranthemus*
14	*Diodia teres*
15	*Doellingeria umbellata*
16	*Eclipta prostrata*
17	*Erechtites hieracifola*
18	*Erigeron annuus*
19	*Erigeron strigosus*
20	*Eriocaulon aquaticum*
21	*Eryngium baldwinii*
22	*Galium aparine*
23	*Galium pilosum*
24	*Hedyotis corymbosa*
25	*Helenium brevifolium*
26	*Helianthus strumosus*
27	*Hibiscus aculeatus*
28	*Hypericum perforatum*
29	*Ipomoea pandurata*
30	*Justicia ovata*
31	*Lespedeza repens*
32	*Lobelia canbyi*
33	*Ludwigia alternifolia*
34	*Ludwigia decurrens*
35	*Mentha spicata*
36	*Mimosa strigillosa*
37	*Oenothera laciniata*
38	*Oxalis stricta*
39	*Passiflora incarnata*
40	*Phytolacca americana*
41	*Polygala curtissii*
42	*Polypremum procumbens*
43	*Prunella vulgaris*
44	*Pyrrhopappus carolinianus*
45	*Rhexia mariana*
46	*Rhexia virginica*
47	*Richardia brasiliensis*
48	*Richardia scabra*
49	*Rubus fruticosus*
50	*Rudebeckia hirta*
51	*Ruellia humilis*
52	*Rumex acetosella*
53	*Scutellaria incana*
54	*Sisyrinchium californicum*
55	*Strophostyles* sp. 1
56	*Stylisma patens*
57	*Stylosanthes biflora*
58	*Symphyotrichum puniceum*
59	*Tephrosia spicata*
60	*Trachyspermum ammi*
61	*Tradescantia ohiensis*
62	*Tradescantia virginiana*
63	*Verbena brasiliensis*
64	*Yucca filamentosa*

Table S4. Results of Mantel test and Moran's *I* for spatial independence among sites (spatial autocorrelation). Mantel tests show significant spatial autocorrelation in community composition only in S2 (Mantel $r = 0.404$, $p < 0.001$, 50 000 permutations) but not in the other two strata (Table 2). None of the results for Moran's *I* were statistically significant.

		Mantel r: Community composition		**Moran's *I*: Abundance**				**Moran's *I*: Richness**			
Strata	**Location**	***r***	***p***	**Obs.**	***I***	***sd***	***p***	**Obs.**	***I***	***sd***	***p***
S1	Alabama sites	0.060	0.197	-0.050	-0.037	0.091	0.888	0.056	-0.037	0.104	0.374
S2	southern Georgia and Florida panhandle sites	0.404	<0.05*	0.133	-0.040	0.100	0.083	-0.073	-0.040	0.113	0.769
S3	north-central Florida sites	-0.076	0.749	-0.024	-0.036	0.070	0.871	0.058	-0.036	0.087	0.285

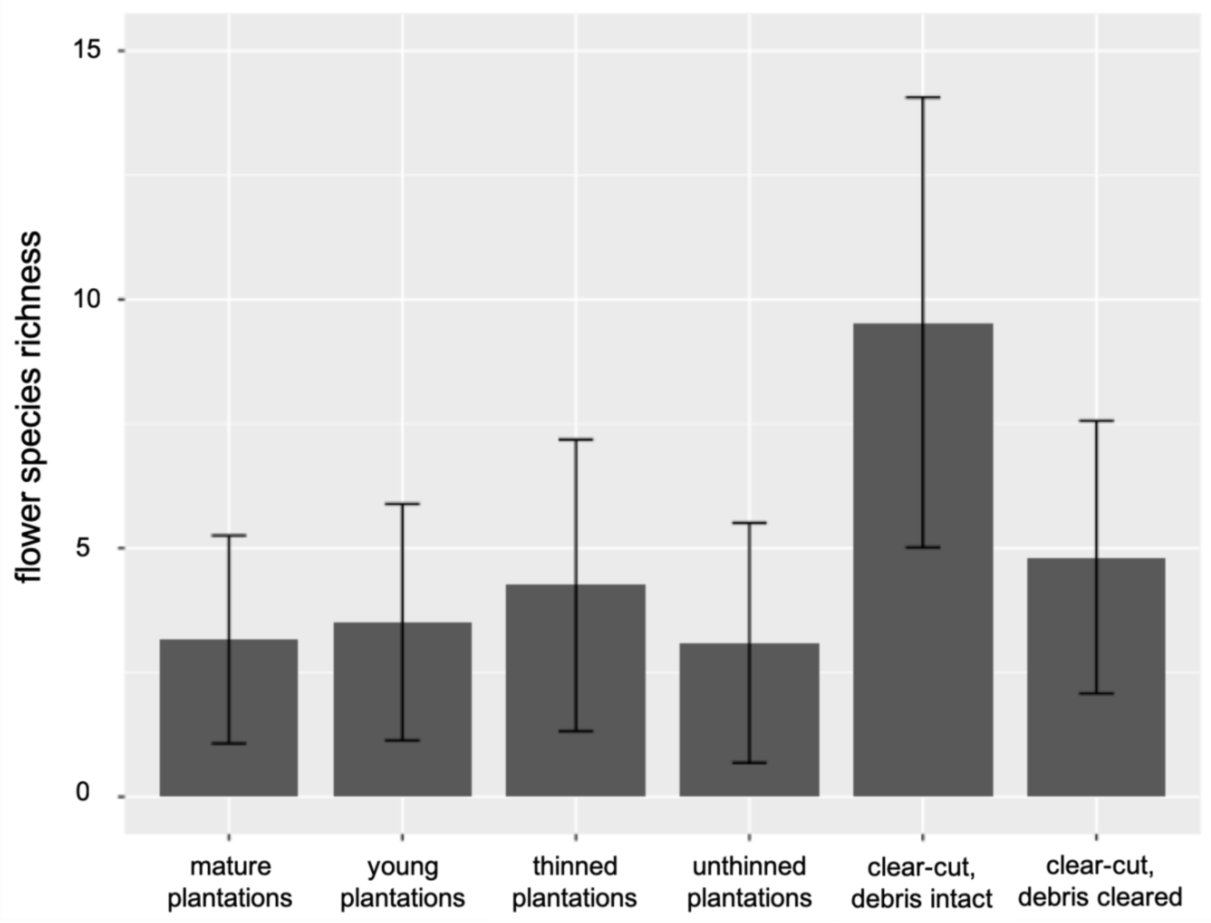

Figure S1. Mean flower species richness at the six plantation types examined in this study. Errors bars indicate standard deviations.

Chapter 4: Species-dependent effects on plant fecundity in a large-scale, community phenology manipulation experiment

4.1. Introduction

Changes in plant flowering time are prominent signs of global change (Wolf et al. 2017, Pearson 2019) but the impact of phenological change on plant fitness is poorly understood. Most flowering plant species experience periods in their life cycle during which the abiotic and biotic conditions are optimal for flowering and seed production. In seasonal temperate climates, this period is typically in spring and summer, for reasons such as favorable growing weather (Wheeler et al. 2015) or pollinator availability (Visser and Gienapp 2019). Various anthropogenic factors can trigger plant flowering times that deviate significantly from their seasonal optima (Wolf et al. 2017, Fisogni et al. 2020, Tadey 2020), with climate change being the most conspicuous (Inouye 2008, Bartomeus et al. 2011, Thackeray et al. 2016, Renner and Zohner 2018, Zohner et al. 2020). Recent studies suggest that phenological change can decrease fitness in some plant species (Thomson 2010, Kudo and Cooper 2019, Sritongchuay et al. 2021), but the generality of findings across plant taxa and systems is unclear. These studies tend to focus on one or few plant species independent of one another. Yet, we know that changes to the fitness of species relative to one another (relative fitness) caused by global change can shape coexistence and biodiversity (Ma et al. 2015, Wainwright et al. 2019, Descombes et al. 2020). To understand how phenological change could impact plant communities, we must consider its effect on the relative fitness of multiple, naturally co-occurring plant species.

Anthropogenically-driven phenological change typically advances and/or lengthens flowering time in affected species (CaraDonna et al. 2014, Wolf et al. 2017, Fisogni et al. 2020, Tadey 2020). This can affect plant fitness by numerous, non-exclusive abiotic and biotic ways. One of the most apparent abiotic stressors to early-blooming plants in seasonal temperate climates is exposure to freezing temperatures. Shifts towards earlier blooming may increase the risk of frost damage to flowers, reducing plant floral abundance and fitness (Inouye 2008, Wheeler et al. 2015, Pardee et al. 2019). Conversely, shifts to earlier blooming may benefit plants that are sensitive to late summer droughts (Franks 2011, Iler et al. 2019). Having an extended spring-summer growing season may also increase the duration of favourable conditions for some plants (Giménez-Benavides et al. 2011).

The effect of plant phenological change on biotic drivers of fitness is likewise context- and species-dependent. Differences in climate change sensitivity across taxa (Thackeray et al. 2016, Olliff-Yang and Mesler 2018, Kehrberger and Holzschuh 2019) can potentiate phenological mismatches between plant bloom time and the active period of their antagonists or mutualists, changing the frequency and intensity of such interactions. For example, in some cases earlier flowering increases the risk of herbivory (Brody 1997, Waterton and Cleland 2016). Alternatively, there is significant concern that earlier flowering might cause phenological mismatches between plant blooming and pollinator seasonal activity (Hegland et al. 2009, Miller-Rushing et al. 2010, Renner and Zohner 2018). The majority of global flowering plant species benefit from animal pollination (Ollerton et al. 2011), and some degree of temporal synchrony between seasonal flowering time and pollinator activity is required for efficient pollination. Nevertheless, empirical evidence that plant-pollinator phenological mismatches reduce plant seed set is limited (but see Thomson 2010, Kudo and Cooper 2019, Sritongchuay et al. 2021). This may be because imperfect synchrony with pollinators is adaptive for plants due to trade-offs with other aspects of life history (Bolmgren and Eriksson 2015), that plant-pollinator phenological relationships are robust to change in some generalist species (Bartomeus et al. 2011), or that the fitness losses from biotic phenological mismatch are overwhelmed by those caused by changes in the abiotic environment (Gezon et al. 2016). Despite apparent phenological mismatch in some plant-pollinator interactions (Hegland et al. 2009) we are uncertain of the impacts on plant fitness relative to phenologically driven abiotic change (Forrest 2015). The multitude of ways in which phenological change could impact plant fitness appears to be species-specific, and differences in species response to potential triggers of phenology and fitness change likely influence community dynamics.

Several challenges to examining the effects of phenological change on species relative fitness make it understudied. Field data that simulates or approximates the effects of future phenological change is difficult to obtain. Some studies have examined long-term interannual plant phenology (Gordo and Sanz 2009, CaraDonna et al. 2014), but complementary long-term data on interannual fitness is available for very few species (e.g. Thomson 2010). One alternative is to induce phenological change experimentally in wild plants and measure the immediate fitness effects. Some studies have manipulated flowering phenology in potted plants placed in the field (e.g. Waters et al. 2020), but manipulating the phenology of in-situ natural plant communities is extremely challenging, save for a few specific instances. In plant communities where flowering is triggered by snowmelt time, researchers have attempted to advance flowering phenology by using snow removal treatments in which snow is physically moved from study plots (Gezon et al. 2016, Sherwood et al. 2017). Due to the immense labor required to remove snow, snow removal studies have to date involved small plots (< 3 square meters) and have typically focused on one or a few plant species within those plots. We do not know the generality of these research findings across spatially-distant plant populations and communities. Also, small-plot snow-removal experiments may also create unrealistic microclimates around focal plants. The persistent snow banks that encircle small snow-free study plots reduce exposure and may modify soil moisture, either by potentially increasing the duration of moisture availability through the gradual melting snow banks, or directly reducing plot moisture by relocating snow that would otherwise melt directly onto the plot. Finally disentangling the abiotic stress of flowering early from the effects of pollen-limitation caused by potential plant-pollinator phenological mismatch is challenging. Detecting pollen-limitation requires laborious hand pollination treatment comparisons (Kearns and Inouye 1993). Measuring the relative fitness of multiple co-occurring species in replicated communities across a landscape requires an immense, coordinated effort.

In this study, we measured how experimentally induced early-flowering (henceforth ‘precocious flowering’) at a community level impacted the relative fitness of 14 subalpine plant species, ten of which require animal pollinators for maximum seed set (‘pollinator-limited’) and four capable of high seed set without animal pollinators (‘autonomous’). Autonomous species were included to evaluate any changes to fitness due to precocious flowering that are not mediated by animal pollinators (e.g., resource limitation, herbivory), and to incorporate diversity in species life-history strategies (e.g., parental investment) which may be associated with pollinator dependence. We accelerated snowmelt in eight 10 m x 14 m treatments plots across a mountain landscape - an endeavor unprecedented at this scale - and examined differences in plant seed set compared to eight paired adjacent control plots (16 plots total), measuring the fitness and relative fitness of co-occurring species in counts of seed. We used pollen limitation experiments (based on hand pollination) to measure pollen limitation in each study plot.

We hypothesized that the effects of precocious flowering on fecundity would be highly species-dependent, given the differences in species life histories and ecology (e.g., seasonal flowering time, dependence on pollinators, types of pollinators, frost tolerance). We also expect precocious flowering to reduce fecundity by increasing pollen limitation in pollinator-limited species (due to phenological mismatches with pollinators).

4.2. Methods

Study location

We manipulated snowmelt in montane meadows across two adjacent valleys around the Rocky Mountain Biological Laboratory located in Gunnison National Forest, Colorado, United States (38°57.5' N, 106°59.3' W, 2900 m above sea level). Snowfall in this system typically begins in September, and snowpack persist from November to late May. A short growing season commences once the ground is snow-free, lasting from May to September. There may be occasional frost events until June. Precipitation is minimal early in the growing season until the North American Monsoon arrives in July. Pollinator abundance and diversity increases with daily maximum temperature (Gezon et al. 2015), declining rapidly in mid-August to September. The vast majority of plant species in these montane meadows are long-lived perennials.

Experimental design and phenology manipulation

We established eight subalpine meadow study sites, spaced at least 800 m apart. In each site, we set up a pair of 10 m x 14 m plots at least 5 m apart (Figure 1), of similar slope, aspect and plant community composition (8 pairs, 16 plots). We randomly assigned one of the two plots to receive the accelerated snowmelt treatment, while the other was unmanipulated in terms of snowmelt and served as a control. We accelerated snowmelt using a tested solarization technique in order to advance plant phenology (Steltzer et al. 2009). Two to five weeks before the anticipated natural snowmelt date at every site, we spread a 10 m x 14 m sheet of woven black plastic 50% shade cloth over the designated snowmelt plot. We removed the shade cloth when we observed > 80% of the ground was snow-free.

We designated study areas in each plot once they were snow-free. Within each plot, we marked out with 12-inch wooden stakes and string, a meter-wide U-shaped region concentric to, but at least 1m away from, the plot edge (Figure 1). Here we tagged and tracked the fitness of focal species (detailed below). We marked three evenly spaced 1m x 10m transects in the centre of each plot, which we divided into 1m x 2m section to record community flowering phenology. Within each transect, we set up one random one-metre quadrat from which we surveyed plant community composition (3 quadrats in each plot, total of 6 at each site).

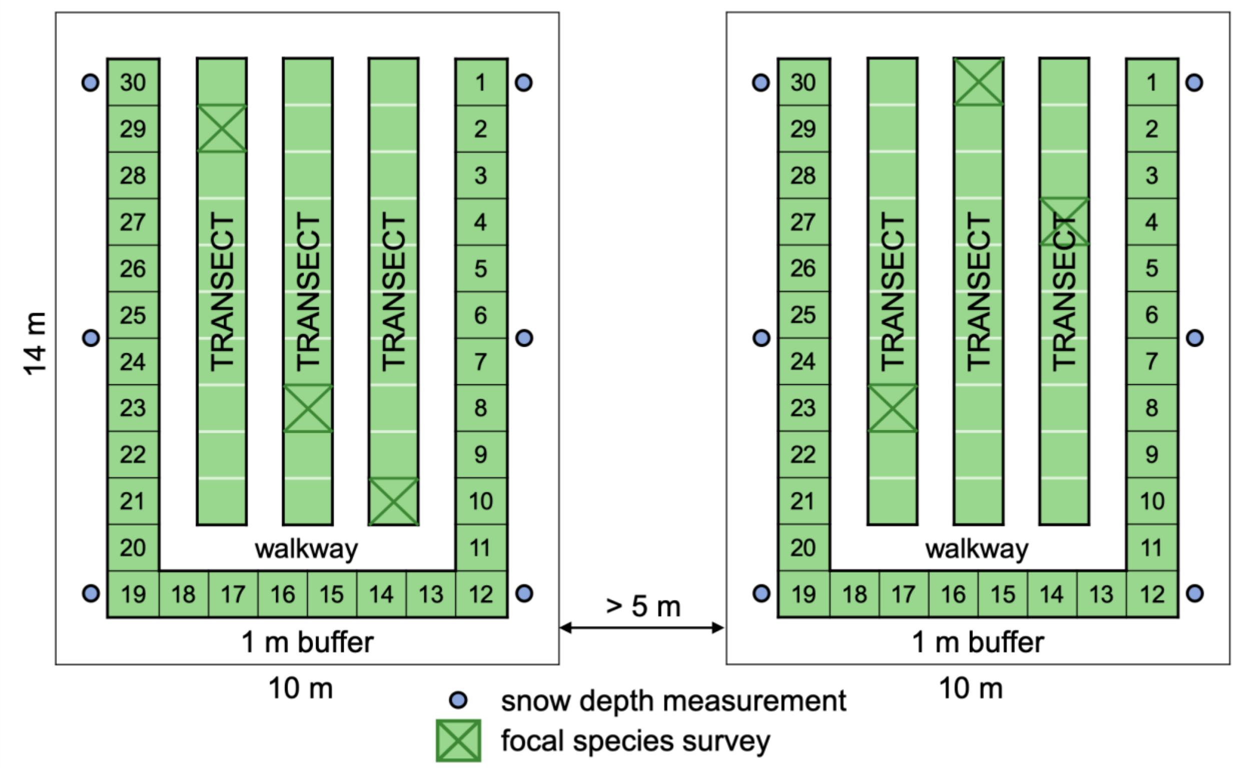

Figure 1. Experimental design showing paired plots within each of the eight sites (not to scale). At each plot, we measured seed production of focal species in the U-shaped region, comprising thirty 1m x 1m quadrats. At each plot, we tracked flowering phenology within 3

1m x 10m transects, each divided into 1m x 2m sections. Within each transect, we surveyed plant community composition from a randomly selected 1m x 1m quadrat. Blue circles show approximate points where we took weekly snow depth measurements from early May until plots were > 80% snow-free.

Measuring snowmelt date

We took weekly measurements of snow depth at all study plots. Starting in early May, we used an avalanche probe to determine snow depth at three points along the two longer sides of each study plot (6 points per plot, Figure 1). Because we were unable to visit plots daily due to time and logistic constraints, we estimated the precise snowmelt date by running linear regressions on the available snow depth data at each plot. We ground-truthed snowmelt date estimates with visual inspection of satellite images from the database Planet (Planet Team 2017) in five of our eight sites for which quality satellite data were available.

Tracking phenology

To measure precocious flowering caused by our snowmelt treatment, we tracked community flowering phenology in each plot. Once a week for the entire field season, we counted and recorded all open flowers of every non-graminoid species in the three transects of every plot.

Selection of focal species and individuals

We chose 14 focal species (Table 1), 10 known to be pollinator-limited and four capable of autonomous seed set (wind-pollination, selfing, apomixis). Pollinator-limited focal species represent all non-graminoid perennial species present in at least 4 of the 6 quadrats at any given site. Autonomous species were represented whenever we could find at least eight individuals in both plots at a site. This resulted in 3 - 7 focal species being represented at every site, with all sites containing both pollinator-limited and autonomous focal species. For every focal species at a site, we tagged 16 individuals, evenly divided between the accelerated snowmelt and control plots, by attaching colored plastic beads to stems using soft floral wire. To select individuals to tag, we first performed an exhaustive survey of focal species in each plot, then used a stratified random approach to ensure selected individuals were well-spaced so as to capture within-plot variation in microhabitats. This was achieved by dividing the U-shaped experiment area in each plot into quadrats labelled 1 - 30 (Figure 1) and identifying several well-spaced quadrats that contain the required focal species. Within each quadrat, we randomly selected individuals to tag. We counted the number of flowers each tagged individual produced during the studied season ('flower number'), and collected and counted seeds or fruits per individual ('per capita fecundity') at the end of the season.

Measuring pollen limitation

To understand the potential biotic cost to precocious flowering, such as mismatches between plants and their pollinators, we performed an experiment to test for pollen limitation in our focal species at the plot level. For eight of the focal species, we tagged an additional 16 individuals evenly divided between the accelerated snowmelt and control plots to receive hand pollination. Pollen supplementation by hand is a standard method used to isolate the effects of pollen limitation from other non-pollination limitations to plant fecundity (Kearns and Inouye 1993), most notably resource limitation, by saturating the pollen needs in a subset of a plant population. If pollen supplementation significantly increases the fecundity of plants relative to those receiving only natural pollination, then naturally received pollen quality or quantity is limiting population fecundity (i.e. pollen-limitation). We used a paintbrush to transfer pollen from 2-4 conspecific pollen donor individuals onto the stigmas of individuals tagged for the pollen limitation experiment. Pollen donors were untagged individuals from within the recipient's plot. Because many focal species produce a succession of flowers over several days, we revisited plots twice a week to hand-pollinate fresh flowers until the end of flowering. We counted the number of flowers each tagged individual produced during the studied season ('flower number') and collected and counted seeds or fruits per individual ('per capita fecundity') at the end of the season.

Table 1. List of focal species in this study, including their botanical family, pollinator requirement for seed set, number of study sites from which fecundity was collected (in addition to phenology), and whether we measured phenology-mediated pollen limitation in this study. *Erythronium grandiflorum* did not set seed at any of the sites (even outside of both study plots) and could not be included in the analysis. We did not include *Geum triflorum* in the pollen limitation experiment as we could not determine an appropriate method for hand pollinating this species.

	Species	**Family**	**Peak flowering in Control plots (Julian weeks)**							**No. of sites**	**Pollen limitation experiment**
			24	25	26	27	28	29	30		
1	*Delphinium nuttallianum*	Ranunculaceae			X	X	X			4	Yes
2	*Erythronium grandiflorum*	Liliaceae			X					2*	Yes*
3	*Fragaria virginiana*	Rosaceae				X	X			2	Yes
4	*Geum triflorum*	Rosaceae					X			1	No
5	*Hydrophyllum capitatum*	Boraginaceae				X				1	Yes
6	*Lathyrus lanzwertii*	Fabaceae					X	X		7	Yes
7	*Linum lewisii*	Linaceae						X		3	Yes

8	*Mertensia fusiformis*	Boraginaceae	X	X	X	X				4	Yes
9	*Potentilla pulcherrima*	Rosaceae					X	X	X	7	Yes
10	*Viola praemorsa*	Violaceae		X	X	X	X			2	Yes
11	*Boechera stricta*	Brassicaceae					X			4	-
12	*Ranunculus inamoenus*	Ranunculaceae			X	X	X			5	-
13	*Taraxacum officinalis*	Asteraceae		X	X	X	X			4	-
14	*Thalictrum fendleri*	Ranunculaceae						X		2	-

Data analysis

All statistical analyses were conducted in R (R Core Team 2016).

Accelerated snowmelt and phenological change

To quantify the bloom time for focal species at different locations, we calculated the weekly mean number of open flowers for every species in each 1 m x 2 m section of every transect. Based on these weekly means, we determined when each focal species reached its highest number of recorded flowers at every study plot. We chose to analyze peak flowering weeks, instead of the weeks when blooms were first observed, so as to capture plot-level bloom time (rather than the bloom time potentially biased by outlier individuals) – this approach performs well against other more complex phenology metrics (Taylor 2019). We calculated the peak flowering week for every focal species at every plot. To measure the effect of accelerated snowmelt on species flowering time at each site, we subtracted each species' peak flowering week in the snowmelt accelerated plot from the peak flowering week of its conspecifics in the adjacent control plot. The snowmelt acceleration only either advanced or did not change flowering time (the treatment never delayed peak flowering time in this study); hence, all values for phenological change were either negative (precocious flowering) or zero (no change). We then visualized the magnitude of precocious flowering in accelerated snowmelt plots by plotting 95% confidence intervals around the mean phenological change of all focal species relative to zero. We used the presence or absence of precocious flowering for each species at the plot level (phenological shift) in analyses of fecundity.

Phenological shift and community fecundity

To understand if precocious flowering changed community-level fecundity, we ran a model examining per capita fecundity of multiple focal species simultaneously. For this analysis, we excluded focal species that were represented in fewer than three sites, leaving eight focal species represented across all our sites. We used only data from naturally pollinated (no hand pollination) individuals. We were primarily interested in whether phenological change altered plant fecundity i.e. the presence/absence of precocious flowering for each species at the plot-level (phenological shift). We also wanted to know if the effect of phenological change on fecundity differed among species. Since plant fecundity can be strongly affected by the number of flowers an individual plant produces, we needed to account for natural variation in flower number if we were to isolate the effect of phenological change of per capita fecundity.

As such, we constructed generalized linear mixed-effects models of plant fecundity using the ‘glmmTMB’ package (Brooks et al. 2017), and included three factors: (a) phenological shift, (b) species identity and (c) flower number. Once again, these factors interact to influence plant fecundity in several ways that are critical to interpreting their effects. First, we were interested in whether the effect of precocious flowering on fecundity was species-dependent; hence, we needed to analyze the interaction between (a) phenological shift and (b) species identity. Second, our model had to consider the interaction between (b) species identity and (c) flower number. This was because species differ in the number of ovules per flower (e.g. *M. fusiformis* usually has < 5 ovules per flower while *B. stricta* can have up to 200), so the effect of an increase by a single flower unit on per capita fecundity is species-specific. As such, we designed our model to include a three-way interaction to evaluate whether (a) significantly changes the two-way interaction between (b) and (c). To maximize our statistical power, we prioritized maintaining the evaluation of these interactions, forgoing the estimation of main effects that interfered with model convergence. Our final model allowed the interpretation of 1. the main effect of phenological shift (a), 2. the isolated interaction (without main effects) between species identity and flower number (b : c) and 3. the isolated three-way interaction among all three main effects (a : b : c). We included 'plot' nested within 'site' as random effects, and specified negative binomial errors (count data overdispersed relative to a Poisson distribution). We evaluated statistical significance using the *Anova* function in the 'car' package (Fox and Weisberg 2019).

Phenological shift and pollen limitation

We used generalized linear mixed-effects models implemented with the "glmmTMB" package (Brooks et al. 2017). to assess whether precocious flowering mediated the effect of pollen limitation on per capita fecundity in pollinator-limited species. Here we were primarily interested in whether phenological change altered the effect of hand pollination on plant fecundity. The effect of hand pollination of plant fecundity will be largest when plants are severely pollen-limited and small or negligible when natural pollinators are sufficient. However, plant fecundity can be strongly affected by the number of flowers an individual plant produces. We thus needed to account for natural variation in flower number if we were to isolate the effect of phenological change on pollen limitation and fecundity.

As such, we analyzed how the per capita fecundity of each focal species changed with (a) phenological shift (presence/absence of precocious flowering for species at the plot-level), (b) presence/absence of supplemental hand pollination on the individual and (c) flower number (number of flowers produced by each individual). These factors interact to influence plant fecundity in several ways that are critical to interpreting their effects. Since we were primarily interested in whether precocious flowering changed pollen limitation, we needed to evaluate the interaction between (a) phenological shift and (b) hand pollination. However, our models also needed to consider the interaction between (b) hand pollination and (c) flower number. This was because while we expect both hand pollination and flower number to be positively correlated with seed set, the effect of flower number was likely much greater than that of hand pollination (in part due to high variance in flower number among conspecific individuals) and could thus obscure our ability to detect pollen limitation. We may also be more likely to detect the effect of hand pollination if its effect accumulates with increasing numbers of available flower ovules. As such, we designed our model to include a three-way interaction to evaluate whether (a) significantly changes the two-way interaction between (b) and (c). To maximize our statistical power, we prioritized assessing these interactions, forgoing the estimation of main effects that prevented with model convergence. Our final model of per capita fecundity allowed the interpretation of 1. the main effect of phenological shift (a); 2. the interaction (without main effects) between hand pollination and flower number (b : c), which indicates if fecundity was driven by the interactions between hand pollination and flower number without phenological shift; and 3. the three-way interaction among all three main effects (a : b : c), which indicates if the phenological manipulation affected pollen limitation depending on flower number for a plant species. We included 'plot' nested within 'site' as random effects (random intercepts) and specified negative binomial errors (count data overdispersed relative to a Poisson distribution). We evaluated statistical significance using the *Anova* function in the 'car' package (Fox and Weisberg 2019).

4.3. Results

Overview

Our snowmelt treatment advanced snowmelt in treatment plots relative to controls by a mean of 8.0 ± 1.76 days (± SE, Fig 2, A) and changed flowering phenology. The greatest effect of snowmelt acceleration was 17 days (site 'Pfeiler') and the smallest was one day ('BellviewBench'). Linear regressions and data used to estimate precise snowmelt dates are shown in Figure S1. Of the 14 focal species, one species, *E. grandiflorum*, did not set any seed regardless of plot, site or pollination treatment. This appeared to be due to late season frost that damaged flowers. This effect appeared to be landscape-wide, as seed set for this species was unusually rare even in individuals outside of study plots and sites (XL, personal observation). From the remaining 13 focal species, we collected and counted 96,260 seeds from a total of 1,101 individuals, 427 of which were hand pollinated twice weekly over their flowering duration.

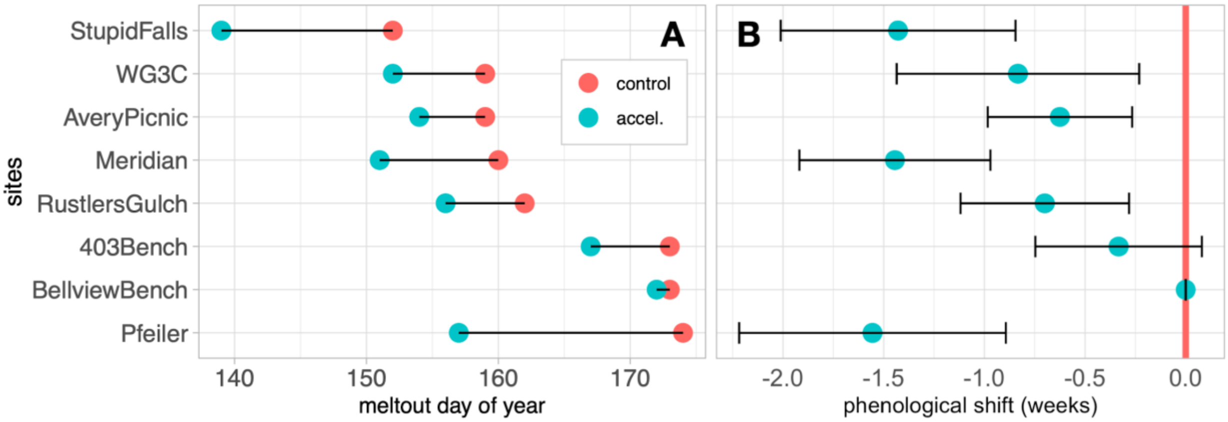

Figure 2. Snowmelt Julian day of accelerated snowmelt and control plot-pairs (A), alongside effect on focal species phenology (B), at all eight sites. Sites are sorted by meltout date of control plots. Panel A shows snowmelt dates of all plots based on linear regressions, with colors representing accelerated snowmelt and control plots. Panel B shows the mean change in flowering time for all focal species at each site's accelerated snowmelt plot relative to adjacent control plots (focal communities of paired plots within a site have identical composition). Error bars represent 95% confidence intervals. Flowering phenology was not changed for any species at the site 'BellviewBench'.

Accelerated snowmelt and phenological change

At most sites, focal species in the accelerated snowmelt plots bloomed significantly earlier than in control plots (precocious flowering, Figure 2, B) based on 95% confidence intervals largely not overlapping with zero. At a plot level, focal species did not always shift their phenology by more than a week, in which case we were unable to detect any phenology change during weekly phenology surveys. On average, the phenological shifts ranged from 0 - 3 weeks (Table S1), averaging - 0.93 ± 0.12 weeks (mean ± SE), i.e. the snowmelt acceleration plots bloomed approx. one week before the controls.

Phenological shift and community fecundity

In our model of the overall per-individual fecundity of plot-level focal communities, we found statistically significant three-way interactions between phenology shift, focal species identity, and flower number ($\alpha = 0.05$, $p < 0.001$). As such, linear correlations between any two main effects should be interpreted with caution. In general, fecundity was positively correlated with flower number (Figure 4). When species data were pooled their per capita fecundity was reduced under phenological shift, at least at higher flower numbers (Figure 4, A). However, this effect was significantly species-dependent (Figure 4, B), with phenological shift being beneficial or detrimental to per-capita fecundity in different species. For example, phenological shift tended to increase fecundity of *P. pulcherrima* but reduce fecundity in *B. stricta*, with flower number having a much stronger effect on the latter species ('Popu' and 'Bost', Figure 4, B). Six of the 14 focal species in this study were excluded from this analysis as they were represented in fewer than three sites: *E. grandiflorum*, *F. virginiana*, *G. triflorum*, *V. praemorsa*, *H. capitatum*, *T. fendleri*. This in turn excluded two sites from this analysis: 'BellviewBench' and '403Bench'.

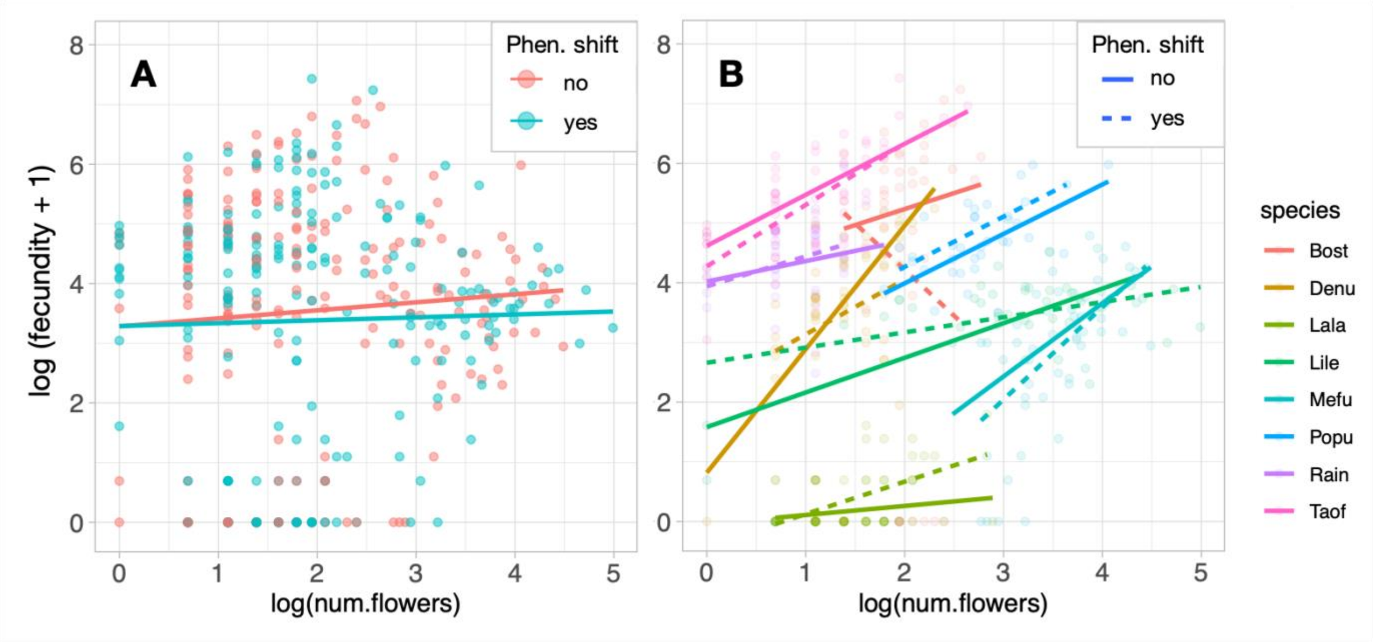

Figure 3. Linear relationships between per capita fecundity, flower number and phenological shift. This analysis includes just the individuals receiving only natural pollination. Panel A shows the linear relationship between log-transformed per capita fecundity and log-transformed flower number. Panel B shows the same relationship divided by the 10 focal species, with colors indicating species and line types indicating presence or absence of phenological response. Lines are best-fit linear relationships between per capita

fecundity and flower number. All lines were plotted using the *geom_smooth* function (method = lm) in the package *ggplot2*. Legend species abbreviations: Bost - *B. stricta*, Denu - *D. nuttallianum*, Frvi - *F. virginiana*, Lala - *L. lanzwertii*, Lile - *L. lewisii*, Mefu - *M. fusiformis*, Popu - *P. pulcherrima*, Rain - *R. inamoenus*, Taof - *T. offcinalis*, Vipr - *V. praemorsa*.

Phenological shift and pollen limitation

We examined phenology-mediated pollen limitation in seven pollen-limited focal species by examining interactions among the effect of hand pollination, phenological shift (presence/absence of precocious flowering for the species at plot-level), and flower number on per capita fecundity. Fecundity was measured in terms of seedset (number of developed seeds per individual) for all but one species, *Lathyrus lanzwertii*, in which fecundity was measured in fruitset (number of enlarged legume pods per individual).

i. Pollen limitation

We found significant two-way interactions between hand pollination and flower number in four species ($\alpha = 0.05$, $p < 0.01$): *D. nuttallianum*, *M. fusiformis*, *L. lanzwertii* and *P. pulcherrima*. In these species hand pollination appeared to increase per capita fecundity (Figure 3). The effect of hand pollination on *M. fusiformis* was almost imperceptible (Figure 3, E), though plotted log-transformed seed set data suggests the effect was positive (Figure 3, F). In *L. lewisii*, this two-way interaction approached statistical significance ($p = 0.054$) but here hand pollination seems to have decreased seedset (Figure 3, D), and we are thus unable to detect pollen limitation. Hand pollination may reduce seedset for several possible reasons (Kearns and Inouye 1993), including unintentional damage to flowers during handling, low pollen quality or viability (for consistency we only collected pollen from within study plots) or stigma clogging due to access pollen.

ii. Phenology-mediated pollen limitation

We detected significant three-way interactions involving phenological shift in *L. lanzwertii* but not any other focal species, i.e. we detected evidence of precocious flowering affecting pollen limitation only in *L. lanzwertii*. With significant three-way interactions, any linear correlations between two main effects should be interpreted with caution.

In *L. lanzwertii*, precocious blooming appeared to increase fruitset among individuals that did not receive hand pollination (comparison of the two solid lines in Figure 3, C. The removal of the potential outlier point in Figure 3, C - an individual that produced five fruits and 17 flowers, no hand pollination, with precocious flowering - resulted in minimal change to the plotted relationships and simply truncated the green solid line at 10 flowers). Hand pollinated individuals, regardless of plot-level phenological shift, also tended to produce more fruit than those from plots that bloomed at natural times, indicating natural pollen limitation (both dashed lines higher than solid red line in Figure 3, C). Among individuals from plots that shifted in phenology (comparing solid and dashed green lines in Figure 3, C), hand pollination appeared to increase fruitset in plants with < 5 flowers, possibly indicating pollen limitation in precocious individuals with fewer flowers, but we did not detect pollen limitation in individuals with more flowers, and hand pollination may have even reduced fruitset in these individuals.

In D. *nuttallianum,* three-way interactions involving phenological shift approached statistical significance (p = 0.085). Among the individuals of this species that produced numerous flowers, seedset may have been lowest in precocious individuals if they did not receive supplemental pollen by hand. (Fig 3, A).

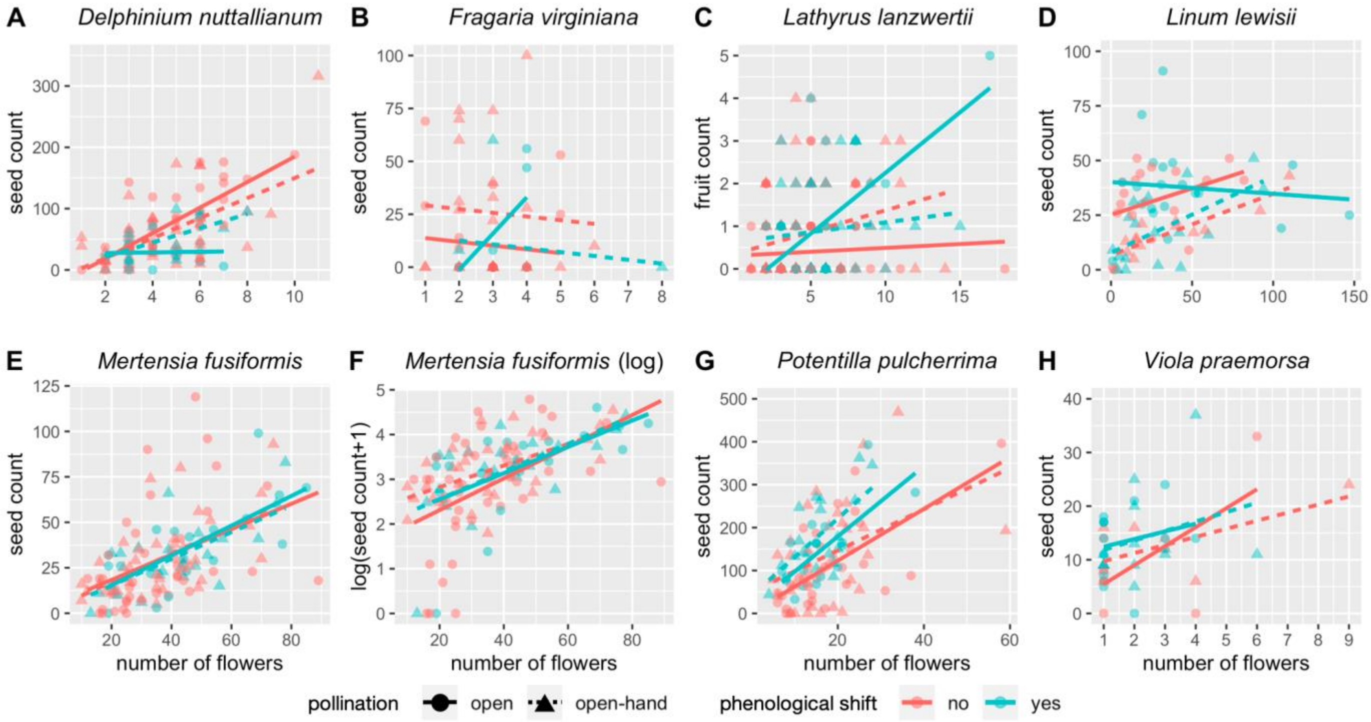

Figure 4. Pollen limitation experiment results showing per capita fecundity against flower number. Point shapes and line types represent individuals receiving the different pollination treatments: circle, solid line - open (natural pollination only) and triangle, dashed line - open-hand (natural + hand pollination). Lines are plotted using the *geom_smooth* function (method = lm) in the package *ggplot2*. Colors indicate whether or not the individual belonged to a plot where its species responded to accelerated snowmelt, by blooming at least one week earlier relative to the adjacent control plot.

4.4. Discussion

We need to determine whether human-induced phenological change has the potential to alter the relative fitness of co-occurring plant species, to shape community coexistence and diversity. In this study, we used a large-scale snowmelt acceleration treatment to induce precocious flowering in numerous co-occurring species from natural montane meadow communities. We examined how this phenological shift affected the fecundity of 14 focal species, of which 10 are at least partially reliant on animal pollinators for seedset while four can set seed autonomously. We first examined overall community fecundity, by focusing on eight focal species (five pollinator-dependent, three autonomous) that co-occurred in 3 - 6 communities. As hypothesized, phenological shift changed plant fecundity in species-specific ways. The overall effect of phenological shift appeared to be detrimental to fecundity (Figure 3, A) but some species may have benefitted (Figure 3, B). Among pollinator-dependent species, we found weak evidence for phenology-mediated pollen limitation in only one species, *D. nuttallianum* (Figure 4, A) but phenological shift may have enhanced the pollination of another species, *L. lanzwertii* (Figure 4, C).

Diverse effects of precocious flowering on species fecundity

Plants from temperate climates have evolved diverse strategies to cope with seasonal changes, so it is not surprising that the effects of phenological shift on fecundity are species-specific. Here we discuss a few of the possible reasons for this, namely species differences in: 1. phenological response to accelerated snowmelt, 2. natural seasonal flowering time, 3. ability to tolerate or exploit similar changes in the environment.

First, species vary in their phenological response to environmental cues. A study by CaraDonna et al. (2014) of 60 species from our study system showed that species are remarkably diverse in their flowering phenological response to interannual weather variation over 39 years. Our findings concur: while some focal species responded to accelerated snowmelt by blooming two or more weeks precociously (*B.stricta, L. lanzwertii*, *P. pulcherrimma*, *R. inamoenus, T. officinale,* Table S1), others never advanced their flowering by more than a week (*L. lewisii*, *M. fusiformis*, Table S1), and three focal species in this study (*G. triflorum*, *H. capitatum*, *T. fendleri*) showed no measurable phenological response to accelerated snowmelt at all (these were not included in the phenology-fecundity analyses). Snowmelt time is just one of many environmental cues known to trigger flowering (e.g. light duration (Bennie et al. 2016), temperature or rainfall (Rice et al. 2020)) and is not the only driver of flowering time in this study system (CaraDonna et al. 2014). Plants that are phenologically less sensitive to snowmelt time may not have experienced the same phenology-driven changes to fecundity. In this study, *M. fusiformis* phenological change was limited to about a week (Table S1) and this did not appear to change its fecundity significantly (Figure 3, B). By contrast, *B. stricta* experienced phenological shifts up to 3 weeks (Table S1), and this appeared to affect its fecundity more strongly (Figure 3, B).

Second, among individuals that responded phenologically to accelerated snowmelt, the challenges and opportunities they faced likely depended on their species' natural seasonal bloom time (i.e. differences between early- or late-season flowering species). In temperate and montane climates early-season species must frequently contend with frosts that can damage leaves and flowers (CaraDonna and Bain 2016, Zohner et al. 2020). This threat can be greatest for the earlier-blooming individuals of early-season flowering species, with negative consequences to fecundity (Thomson 2010). In contrast, species with late-season flowering species infrequently experience freezing temperatures. For such species, it is possible that blooming slightly earlier benefits fitness. In many seasonally snow-covered ecosystems, surface water is highest immediately after snowmelt and declines as the year progresses (McNamara et al. 2005, Blankinship et al. 2014). Blooming earlier in the season could give individuals of late-season species more time to exploit periods of higher soil moisture for flowering and reproduction. In this study, early-blooming *E. grandiflorum* produced no seed set all, potentially due to frost damage. However, in the latest flowering focal species *P. pulcherrima*, snowmelt appeared to uniformly increase seed set (Figure 3, B) potentially because it provided a longer growing season for this species.

Third, among focal species that bloomed precociously under accelerated snowmelt, there may be variation in the ability to tolerate the challenges and exploit the opportunities that come with advanced phenology in ways that change fecundity. For example, phenology-mediated pollen limitation affects some species more than others. Blooming earlier than usual could reduce the seedset of pollen-limited species due to phenological mismatch with suitable pollinators (Kudo and Cooper 2019) or low densities of co-flowering conspecifics (Sun et al. 2010, Ison and Wagenius 2014, Hall et al. 2018). In our study, we found weak evidence for pollen limitation in *D. nuttallianum* that bloomed precociously. Unlike *D. nuttallianum,* species that are capable of high autonomous seedset are probably more resilient to pollination-related changes in flowering time, so much so that flowering duration may have evolved to be comparatively brief in such species (Bucher and Römermann 2020). Phenological changes can also bring unexpected opportunities for pollinator-limited species, that likewise may not be relevant to autonomous species. We found that in *L. lanzwertii* precocious blooming seemed to reduce pollen limitation, in contrast to findings from studies focused on other species (Thomson 2010, Kudo and Cooper 2019, Sritongchuay et al. 2021). This could be due to a release from competition for pollinators, as changes in flowering time can alter co-flowering overlap and possible interactions between plant species (Gordo and Sanz 2009, Forrest et al. 2010, CaraDonna et al. 2014), highlighting the need for more studies that consider community-level changes in phenology. In our study system, pollinator diversity and abundance are highest in late summer but this is also when floral diversity and abundance peaks. Blooming precociously may have helped *L. lanzwertii* escape the intense interspecies competition for pollinators in late summer. This species can be pollinated by a variety of large-bodied bee species from three locally common genera (*Bombus*, *Megachile*, *Osmia* (Forrest et al. 2010); LX *personal observation*), and having generalized pollinator requirements may allow it to be more resilient to mismatches with any given pollinator species (Bartomeus et al. 2011).

In summary, the conditions that constitute the ideal temporal niche (niche in seasonal time) of each species are heterogenous over time (Catorci et al. 2017). These conditions do not necessarily improve or deteriorate as the season progresses and vary in their relative impact on fitness for any given species. A multi-year study on *Lathyrus vernus*, for example, showed early flowering individuals suffered greater herbivory but may also have had access to more resources, resulting in overall greater fitness (Johan Ehrlén and Zuzana Münzbergová 2009). As it is likely impossible for any species to optimally synchronize its phenology with all environmental variables, species likely tolerate some degree of 'optimal mismatching' (Visser and Gienapp 2019) that is idiosyncratic. Precocious phenology may put individuals out of sync with conditions generally optimal to their species, though under certain circumstances these individuals may avoid strong intraspecific competition and have greater fitness (Visser and Gienapp 2019). Nevertheless, the unique constraints of each species' temporal niche may be important to community assembly and facilitate coexistence by preventing any species from obtaining a universal competitive edge. For example, in a sub-Mediterranean grassland (Catorci et al. 2017), early flowering species showed a tendency for rapid growth but low competitive ability in terms of resource acquisition. This was in contrast to later flowering species, which had slower growth rates but more efficient water-use and resource acquisition. Thus, we may expect the effects of phenological change on reproductive success to not only vary with plant species, but potentially change plant community dynamics.

Relative importance of pollen limitation to phenology-mediated fecundity

A prominent question regarding how changes in flowering time affect plant fecundity is the relative importance of biotic versus abiotic factors (Forrest 2015). In this study, the biotic factor we focus on is pollination, as it is affected by flowering time and influences plant community assembly (Sargent and Ackerly 2008). We detected natural pollen limitation in several focal species but only found strong evidence that this was mediated by phenological shift in one. Plant-pollinator phenological mismatch as well as the flowering synchrony of conspecifics (Sun et al. 2010, Hall et al. 2018) can affect pollen limitation, but identifying specific mechanisms is beyond the scope of this study. While our hand pollination did not always result in greater fecundity than that of naturally pollinated plants, hand pollination tended to result in similar seedset regardless of phenology (with the exception of *F. virginiana*, Figure 3, B). These results may suggest that phenological shift did not significantly alter abiotic resource limitation in most of the pollinator-reliant focal species. Alternatively, the magnitude (effect size) of both pollen limitation and resource limitation could be similarly small across numerous species, and only significant and detectable when their combined effects are considered at the community-level in this study.

4.5. Conclusion

Several anthropogenic changes have been shown to shift plant flowering phenology, but the accelerated snowmelt treatment used in this study most closely resembles that which could be generated by climate change. Climate change can directly affect plant fitness through resource limitation (Franks 2011, Iler et al. 2019). Our study suggests that by changing flowering phenology, climate change may also change plant fitness, and pollen limitation may contribute to these changes. Several questions remain to be answered. First, it is as yet unclear if changes to pollen limitation in this study are due to changes in access to pollinators or the availability of conspecific pollen donors. Second, though our snowmelt acceleration treatments are the largest in terms of plot area that we know of, treatment plots are still microcosms within a larger, unmanipulated landscape and do not perfectly replicate the pervasive effects of climate-change. The precocious flowering individuals in this study may have experienced unnatural levels of pollen donor density or concentrated pollinator movement within accelerated snowmelt plots (Forrest 2015). Third, long-term, multi-year studies are required to understand how chronic phenological change affects the demographics of perennial species. While there are studies on the relationship between seedset or fruitset to the population demographics for a few species in our study system (e.g. Thomson 2010, Iler et al. 2019), we do not know how phenology will change interspecies competitive dynamics and coexistence. Fourth, this study does not address how intraspecific variation in phenological change affects the fitness of co-occurring species, which will have implications for population evolution and persistence. Finally, it is worth mentioning that one of our focal species, *E. grandiflorum*, failed to set seed at all during the study year, regardless of experimental treatment, and was not included in most of these analyses. This species is among the first to bloom in this study system, with individuals tending to produce at least some seeds every year if not damaged by frost (Thomson 2010). With ongoing rates of climate change, extreme weather events like late-spring frosts are becoming substantially more frequent across the Northern Hemisphere (Zohner et al. 2020). It is likely that in the future, the impacts of such events on plant species and communities may be exacerbated when occurring in tandem with anthropogenic phenological change.

4.6. References

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4.7. Chapter 4 Supplementary Materials

Figure S1. Linear regressions and data used to estimate precise snowmelt dates in accelerated snowmelt and control plots at RMBL 2019. We removed day 136 of snow depth measurements, which showed an unusual spike in snow depth inconsistent with the melt out rate of the underlying snowpack, due to a snowstorm the day before. The next measurement at this site was well below the snow depth prior to the snowstorm.

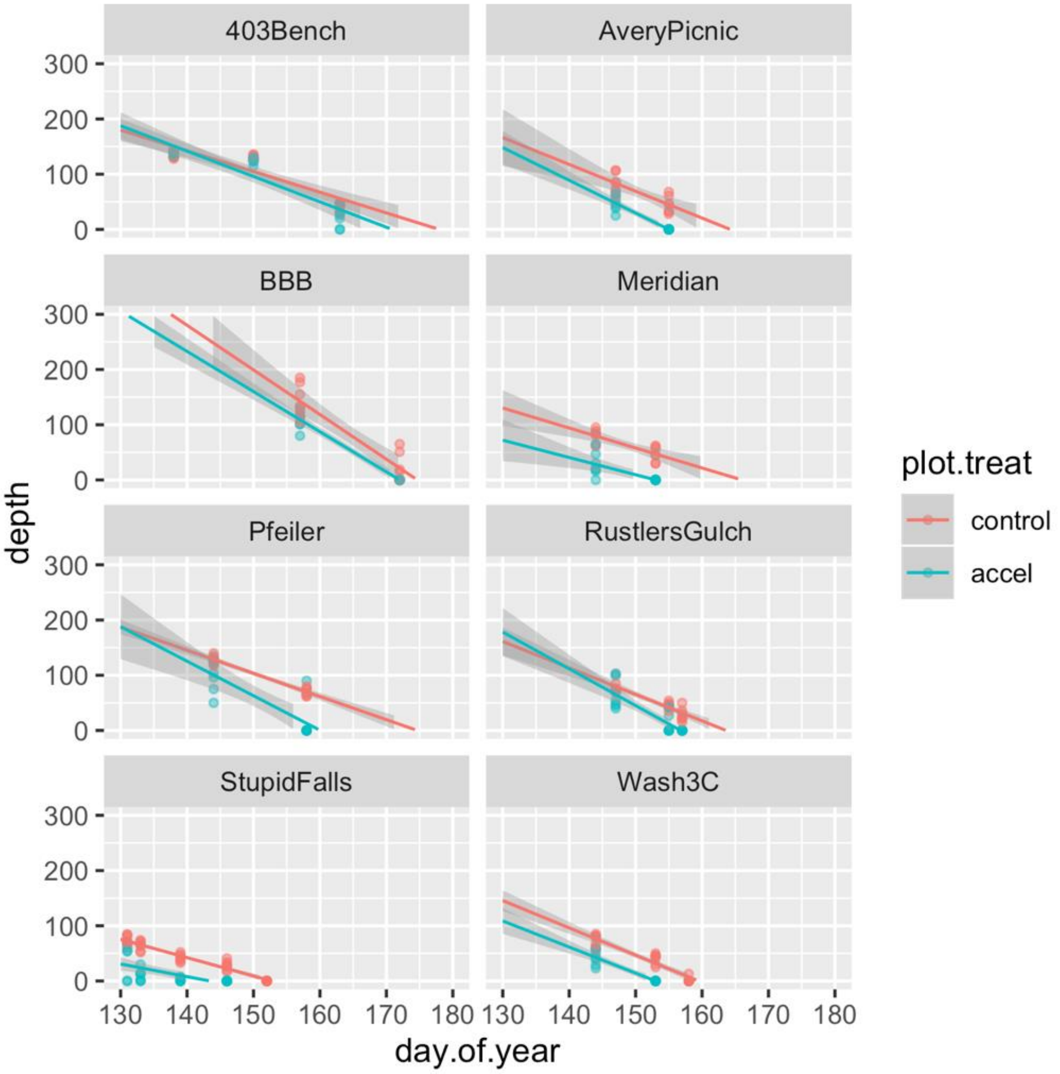

Table S1. Change in flowering time of each focus species at each accelerated snowmelt relative to their respective conspecifics in adjacent control plots within the same site. Note that species phenology was sometimes monitored in more sites than fecundity was measured in.

Focal species	**Snowmelt with no phenological change**	**Snowmelt with measurably earlier phenology and magnitude**			**Total no. of sites**
		1 week	**2 week**	**3 week**	
B. stricta	2		2	1	5
D. nuttallianum	2	1	1	1	5
E. grandiflorum		1	1		2
F. virginiana	1	1			2
G. triflorum	1				1
H. capitatum	1				1
L. lanzwertii	3	1	3		7
L. lewisii		3			3
M. fusiformis	1	5			6
P. pulcherima	2	5	1		8
R. inamoenus	1	3	1		5
T. fendleri	3				3
T. officinale	1	3	1		5
V. praemorsa	1	4		1	6

Chapter 5 : Conclusions & Future Directions

It is my hope that work presented in this dissertation takes us a step closer to understanding how human activities shape pollination at the community level. Here I have identified and contributed to filling three knowledge gaps, specifically:

1. How do diverse pollinator communities benefit plant pollination?
2. How does anthropogenic change shape pollinator diversity?
3. How does anthropogenic change shape pollination to affect plant diversity?

In this dissertation I have dedicated a chapter towards each of these three questions. I first reviewed and synthesized current research on pollinator diversity-function relationships in Chapter 2. Then, in Chapter 3 I use empirical field data to examine how ongoing shifts towards bioenergy cultivation in the southeastern United States could impact bee diversity. Finally, in Chapter 4 I describe a field experiment that I conducted to study how changes in flowering phenology, a prominent sign of global change, affects the pollination and fecundity of 14 co-occurring montane plant species. I summarize ideas and findings from these three chapters below.

5.1 The effects of pollinator diversity on pollination function

The benefit of biodiversity has been a focus of ecology research for over two decades (Tilman et al. 1997). Our current diversity-function framework (Hooper et al. 2005) has been invaluable to understanding diversity-function relationships, though being largely based on single-trophic communities (plants) it often falls short when applied to inter-trophic community functions like pollination. In this review, I attempted to integrate the current diversity-function framework with inter-trophic community function, focusing on empirical studies of the mechanisms that drive pollinator diversity-function relationships. First, I identified key features of inter-trophic community functions that have hampered reconciliation with current the diversity-function framework. Second, I examined how the current diversity-function framework is used to interpret findings from pollinator diversity-function experiments and observational studies and described ways in which these interpretations are sometimes inconsistent with established ecological concepts. Third, I proposed a revised diversity-function framework, and delved into two diversity-function mechanisms in particular that are applicable to pollination. The first of these, 'interactive functional complementarity', had been identified previously but was overlooked. The second is a novel diversity-function mechanism that I termed 'functional enhancement', which occurs when species richness increases within-niche activity. These two diversity-function mechanisms occur through species responses to the biotic environment, and are more obvious in animals (such as pollinators) that are capable of rapid behavioral change, possibly explaining why they may had received less attention in single-trophic plant diversity-function studies.

This review underscores that diversity in pollinator species is important to pollination function, in both natural and agricultural ecosystems. We are likely find even more evidence for pollinator diversity-function relationships moving forward, especially if we take into better consideration their inter-trophic nature and the role of animal behavioral response. To better preserve and manage pollination function, we need conserve pollinator community diversity but also understand the forces that shape species interactions in plant-pollinator communities.

5.2 Anthropogenic effects on pollinator communities

Global pollinator declines are driven by numerous anthropogenic factors (Potts et al. 2010). To avoid exacerbating the problem, we need to consider the impacts of ongoing and future large-scale environmental changes. The cultivation of bioenergy feedstocks is a growing land-use world-wide. Yet, we have a poor understanding of how bioenergy crop management practices affect pollinator diversity. This knowledge gap is particularly acute for cellulosic bioenergy feedstocks, such as tree plantations. In my second substantive dissertation chapter (now published; Loy et al. 2020), my collaborators and I examined bee communities in 83 sites across three states in the southeastern United States—Alabama, Florida and Georgia. We compared bee abundance and community diversity in 66 pine plantation sites that reflect management with and without potential bioenergy feedstock production. We found that bioenergy-associated management practices, such as having younger plantations (relative to older) reduced bee community diversity. In addition, harvesting fallen woody debris, which can be used as bioenergy feedstock, also reduced bee community diversity. This seemed to be at least partly driven by drastic increases in the abundance and dominance of just two bee species. We found that the different stages of plantation management collectively supported much higher bee diversity (beta-diversity) than corn fields (an alternative, annual bioenergy crop) or natural forest remnants alone. This suggests that even within the same crop species, spatial variation in management can generate enough habitat heterogeneity to have measurable impacts on pollinator diversity.

This study provides evidence that even in regions that have been heavily modified by humans, pollinator diversity may still be strongly affected by how the land is managed. Though the overall effect of bioenergy-associated management practices seemed detrimental to bee communities, the effects were clearly species-dependent, with at least two species increasing dramatically following the harvest of woody debris. Such dramatic changes in the relative abundance of pollinator species could ostensibly translate into changes in the relative fitness of plant species if, for example, the hyperabundant pollinators are more effective at pollinating some plant species than others. My last chapter explored whether changes to plant-pollinator interactions can alter in the relative fitness of plant species.

5.3 Anthropogenic effects on plant community pollination

A prominent feature of climate change in seasonal climates is shifts in plant flowering time (Thackeray et al. 2016, Zohner et al. 2020). Given that early flowering could cause pollen limitation in some plant species (Gezon et al. 2016, Olliff-Yang and Mesler 2018, Kudo and Cooper 2019), climate change has the potential to the relative fitness of plant species, with consequences plant community coexistence and diversity (Ma et al. 2015, Wainwright et al. 2019, Block et al. 2020). Together with numerous collaborators, I conducted a large-scale snowmelt acceleration experiment to advance flowering phenology in eight montane meadow communities spread across two valleys in Colorado. Each snowmelt acceleration plot was paired with an adjacent control plot without snowmelt manipulation. I measured how phenological change altered the fecundity of 14 plant species, separating out the contribution of pollen limitation to fecundity in eight species using hand pollination treatments. I found that early flowering may have enhanced pollination in one species but may have decreased pollination (i.e., increased pollen-limited seed production) in another. Similarly, when examining overall fecundity (not just limited by pollination), the effect of early flowering varied significantly with species identity but tended to be negative.

In this study, I showed that the effect of human-induced phenological change on plants can vary significantly across plant taxa, and that this may be at least partially mediated by changes in pollination. My results suggest that under anthropogenic change, pollination function may simultaneously increase, decrease or remain relatively unchanged in different species within a plant community, depending on their life-history strategies. Whether such effects can alter competitive dynamics within plant communities remain unclear and the long-term impact on plant diversity requires further investigation.

5.4 Future Directions

This dissertation provides a glimpse into how anthropogenic changes in land-use and climate may be affecting pollination in plant-pollinator communities. However, there is still much that we do not know about the dynamics of plant-pollinator communities, both within and beyond the systems I have examined. While Chapter 3 shows that land-use change in the southeastern U.S. could alter local bee communities, how this might affect plant-pollinator interactions and plant fitness is unknown. The southeastern U.S. is a biodiversity hotspot – a global region of exceptionally high endemism and biodiversity – where pollen limitation tends to be disproportionately high (Alonso et al. 2010). Yet research on plant-pollinator communities in this region is relatively limited. In contrast, plant-pollinator communities in the Colorado montane meadow ecosystems of Chapter 4 are well-studied. It is nevertheless important that we continue to conduct and support long-term research in such areas. Predicting the fate of plant-pollinator communities in a rapidly changing world requires understanding of chronic effects of human-induced change, and longitudinal research is critical in this regard. We should also continue to explore using modern analytical tools to extract new insights from historical data already available to us. For example, researchers have recently used DNA metabarcoding techniques to identify the pollen loads in museum specimens of the endangered bumble bee *Bombus affinis*, to determine historical changes in its floral diet (Simanonok et al. 2021). I am interested to take this a step further by using museum collections to understand historical plant-pollinator community interactions. Recent advances in ecological network theory now allow us to study the complex, multi-species interactions of plant-pollinator communities like never before, with a small but growing number of studies linking network properties to ecological function (Kaiser-Bunbury et al. 2017, Magrach et al. 2019, Arceo-Gómez et al. 2020). Understanding how past centuries of anthropogenic change have shaped historical and current plant-pollinator networks may help us better understand the changes to come.

This dissertation has focused on three knowledge gaps in plant-pollinator community ecology from the perspective of plant pollination. However, the reciprocal benefits of plant communities to pollinator communities also require more research attention. How does plant diversity benefit pollinator fitness? Studies linking wild pollinator diet breadth and fitness are rare (but see Spear et al. 2016). How does anthropogenic change shape plant communities to impact pollinator diversity? While bee declines continue to receive significant attention (e.g. Zattara and Aizen 2020), other diverse taxa also contribute significantly to crop and wild plant pollination (e.g. Walton et al. 2020) and require more consideration. Finally, we need to consider how anthropogenic change affects the benefit pollinators receive from facilitating pollination. For example, we need examine more closely at how plant-pollinator phenological mismatch impacts pollinator fitness and diversity (Schenk et al. 2018). This is admittedly challenging as even assessing fecundity for one pollinator population is typically much more difficult relative to plants. We also need to better understand how human-induced changes in plant diversity are altering the nutritional ecology of pollinators (Filipiak 2018).

While current rates of pollinator decline are unprecedented in human history, we have also never been better equipped to understand and mitigate our ecological impact on plant-pollinator communities. Given the wealth of evidence that pollinator diversity is critical to life as we know it, we must act now to mitigate anthropogenic impacts on plant-pollinator communities.

Introduction and Conclusion References

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