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UNIVERSITY OF CALGARY

Pollination Responses to Introduced Plants and an Elevation Gradient in Camas Dominated Wet Meadows

by

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Abstract

Global change is driving declines in insect biodiversity, with widespread consequences for ecosystem function. Climate change and invasive species are key global change factors, but the ways in which they alter pollination are poorly understood in many systems. Camas meadows occur in the southwestern-most areas of Canada, where they support high floral and pollinator diversity, yet we know little about the pollination ecology of these meadows, let alone how they are impacted by aspects of global change. My objectives in this thesis were to evaluate evidence that camas meadows are experiencing impacts related to climate change and plant invasions. I used a pollen limitation experiment conducted across an elevation gradient to evaluate whether variation in climate generates phenological asynchrony between camas and its pollinators, and used plant-pollinator network analysis to examine whether introduced plants were driving changes in pollination networks. I found that there was no evidence for phenological asynchrony, though camas reproduction was slightly limited by pollen at low elevations, while overall seed production declined as camas approached its elevational limit. Introduced species did not alter network structure, but when removed from networks they had come to dominate, networks were less able to resist further species loss. This suggests that if maintaining pollination is desired, invasive species management decisions should consider the risks associated with losing the floral resources they seek to control. My results describe a system which in its current state, appears robust to the aspects of global change examined (i.e., phenological disturbance and plant invasion) but may be sensitive to further disruption, particularly the removal of abundant introduced plants that pollinators have come to rely upon.

Key words: camas meadows, pollen limitation, environmental gradient, bipartite pollination network, biodiversity, pollination ecology, invasive species

Preface

Chapters two and three of this thesis are collaborative works with my supervisor, plus taxonomic contributions from Lincoln Best, and initial conceptualization plus funding/administrative contributions from Valerie Huff and Dr. Bren Beckwith. These chapters will be submitted for publication under the titles below:

Chapter two of this thesis will be submitted for publication as:

Rampton, R., Best, L.R., Huff, V., Beckwith, B., Galpern, P. Evaluating potential for phenological asynchrony through camas pollen limitation experiments across an elevation gradient.

Chapter three of this thesis will be submitted for publication as:

Rampton, R., Best, L.R., Huff, V., Beckwith, B., Galpern, P. Does removing introduced plants destabilize plant-pollinator networks? Evidence from camas dominated meadows.

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This project would not have been possible without the Kootenay Native Plant Society, in particular Valerie Huff with the support of Dr. Bren Beckwith, whose efforts to build local relationships and create the conditions for this project to succeed cannot be understated. I would like to thank Valerie and Bren for sharing their passion for camas, and also Valerie and Iraleigh Anderson for enabling my explorations of the plants of the Kootenays. I also thank Lincoln Best for providing me with the opportunity to learn all that I wanted and more about bees plus teaching me some tricks of the trade. I would like to thank all the members of the Galpern lab, past and present, as well as my friends at the University of Calgary, for their camaraderie, as well as Tannah Ernst and Tiffany Muncaster, whose efforts in the field helped make my data collection much more manageable and enjoyable. I am thankful to my family for supporting my choice of a career that is unlikely to benefit them in retirement, and to Nicola Rammell for supporting my pursuit of this degree and providing opinions at several steps along the way.

I am grateful to my committee members, Dr. Mindi Summers and Dr. Jana Vamosi for comments and advice throughout the process. I also want to acknowledge the landowners who provided access to their properties, including the Read & Leslie families, the city of Castlegar, the BC Ministry of Transportation and Infrastructure, BC Parks, and the Nature Trust of BC. I am thankful to have had the opportunity to complete this research on Sinixt, Syilx, and Secwépemc territory. Funding for this project came from a MITACS internship in partnership with the Kootenay Native Plant Society as part of a broader project funded by the Fish and Wildlife Compensation Program – Columbia Region and the Columbia Basin Trust.

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Chapter 1: Introduction

Global change, ecosystem services, and biodiversity decline

Human influence can be detected across a vast majority of the planet’s surface and continues to encroach upon even the most remote areas (Sanderson et al., 2002; Watson et al., 2016). The activities of humans are known to negatively impact biodiversity, with key factors including loss and degradation of habitat (i.e., land use change), the introduction of invasive species, and climate change (Newbold et al., 2015; Otero et al., 2020), all of which are suspected of driving high species extinction rates (Barnosky et al., 2011). The impacts of such factors are also likely to interact with one another to impact biodiversity, but may do so in a complex, difficult to predict manner (Didham et al., 2007).

Biodiversity is necessary to support ecosystem function, and when species are lost, the ecosystem services that humans rely on to sustain our population are likely to decline in concert (Hooper et al., 2012; Cardinale et al., 2012). Loss of insect biodiversity has been described by recent studies and meta-analyses, mostly in temperate regions of the northern hemisphere (Hallmann et al., 2017; Seibold et al., 2019; van Klink et al., 2020), though reports of similar declines are emerging in the tropics (Lewinsohn et al., 2022; see also the qualitative description by Janzen & Hallwachs, 2019). Despite an infamous minority of insects contributing ecosystem disservices, e.g., acting as crop pests (Asplen et al., 2015), and disease vectors (Juliano & Philip Lounibos, 2005), the vast majority of insect species play a variety of other crucial roles in ecosystem function, including control of pest populations, decomposition, and transfer of pollen that supports the reproduction of the majority of global plant diversity (Losey & Vaughan, 2006).

Pollination is particularly well studied due to its importance in ensuring global food production, with pollinators necessary for up to 40% of global crop production by mass (Klein et al., 2007), and higher proportions of certain essential nutrients (Eilers et al., 2011). Pollinators also prevent reproductive limitation of wild plant populations, which themselves provide important ecosystem services, such as maintenance of water quality, carbon sequestration, and air quality mediation (Potts et al., 2016). Pollinators are susceptible to the insect declines described above, and in fact represent some of the earliest examples (Biesmeijer et al., 2006; Burkle et al., 2013). There is mounting evidence that substantial changes in pollinator species richness (Burkle et al., 2013; Mathiasson & Rehan, 2019), plus abundance (Ulyshen & Horn, 2023) are occurring in a variety of temperate systems, but also globally (Zattara & Aizen, 2021).

The factors behind pollinator declines are as described above, with land use change, climate change, pesticides and introduced species thought to be contributing factors (Herrera, 2020; Ulyshen & Horn, 2023; Janousek et al., 2023). These declines are not necessarily universal, with agriculturally associated and generalist pollinators more likely to increase in abundance while their more specialized or rare counterparts decline (Burkle et al., 2013; Weiner et al., 2014; Powney et al., 2019). This loss of rare species is thought to lead to “ecological homogenization”, where previously distinct communities become similar to one another. This has been observed in floral resource and pollinator communities (Carvalheiro et al., 2013) as well as forest communities (Vellend et al., 2007).

Plant declines have also been shown to relate to pollinator declines (Biesmeijer et al., 2006; Baude et al., 2016), though it is unclear whether it is plants, pollinators or another underlying factor driving this association. Similarly to insects, plants are unlikely to decline in a uniform manner, with plants that rely on insects for pollination shown to be faring worse than those that can reproduce independently of insect visitation (Biesmeijer et al., 2006). Plant-pollinator interactions may be capable of stabilizing plant diversity, but only when plants are not competing strongly for pollinators, in which case the opposite (destabilization) occurs (Benadi et al., 2012). With pollinating insect declines, competition for the attention of fewer pollinators should increase (Benadi et al., 2012), potentially amplifying plant declines. Overall, plants and pollinators are strongly linked to one another, and understanding these linkages can increase our understanding of how pollination systems will be impacted by global change.

Pollination in relation to climate change and invasive species

Changes in climate are known to alter the timing of species activity, leading to concerns that the timing of plant flowering and pollinator foraging will no longer be synchronous, with loss of interactions resulting in pollinators going hungry, plants losing reproductive facilitation, and ecosystem function declining (Memmott et al., 2007; Hegland et al., 2009; Forrest, 2015). Some studies have observed this phenomenon (Gordo & Sanz, 2005; Kudo & Ida, 2013), but it is generally thought that timing of bee emergence and flowering are advancing at similar rates (Bartomeus et al. 2011; Bartomeus et al. 2013b; Forrest, 2015). These rates are not necessarily identical however, and there is a point where phenologies may diverge sufficiently to cause plant-pollinator asynchrony (Forrest, 2015). It remains unclear when (or if) such a phenomenon will occur in natural systems, especially since plants and pollinators are likely to undergo selection for synchrony of activity to avoid negative fitness outcomes (Hegland et al. 2009; Forrest, 2015). It is necessary to test for asynchrony in systems likely to experience it, i.e., those with temperature dependent, early spring bloom, involving pollinator dependent plants (Hegland et al., 2009). Doing so allows evaluation of the risk that changes in climate will alter phenology in a manner that leads to phenological asynchrony.

Changes in plant-pollinator interactions have also been documented in response to land-use change and invasive species. Networks, where links join plants and their pollinators, can be used to describe these interactions. Areas undisturbed by land-use change possess greater network complexity relative to those from impacted areas (Albrecht et al., 2007; Prendergast & Ollerton, 2021). Networks where introduced plants are present (Lopezaraiza–Mikel et al., 2007; Russo et al., 2014) or there is an introduced pollinator (Prendergast & Ollerton, 2022a) contained fewer observed connections between species relative to potential connections (i.e., connectance). However, a review by Parra-Tabla & Arceo-Gómez (2021) suggests that plant invasions generally do not significantly alter the properties of networks that impact network persistence. One property -- robustness -- the degree to which interaction networks are able to resist species loss, tends not to change despite introduced species becoming highly important in many networks examined. This suggests that while networks are noticeably altered in structure and species composition, they may not necessarily be less stable or functional. Evaluating whether this holds for new systems is useful, but it is also important to consider that under ecological restoration efforts (e.g., Weidlich et al. 2020) networks are likely to experience loss of introduced species. Exploring network responses to losses of introduced species (as in Kaiser-Bunbury et al. 2017; Parra-Tabla et al., 2019) is necessary to understand the broader impacts of invasion on pollination networks.

Overall, plant-pollinator interactions show clear responses to drivers of global change, suggesting risk of altered ecosystem function, but the negative consequences of alterations are so far not obvious (Forrest, 2015; Parra-Tabla & Arceo-Gómez, 2021). This thesis asks if there is evidence to the contrary. It does this in a new system that fits the criteria associated with sensitivity to phenological disruption (Hegland et al., 2009) and contains abundant pollinator-attracting introduced species that have invaded its pollination networks. I will assess the vulnerability of pollination to aspects of global change described above: first, the risk of climate mediated phenological changes disrupting seed production, and second, evidence for alteration of plant-pollinator network structure due to introduced plants integrating into pollination networks. I will also evaluate the sensitivity of such networks to the subsequent removal of introduced species. To evaluate phenological disruption, I will examine plant-pollinator interactions and resulting seed production across an eight-site elevation gradient. I will then use the same dataset to investigate plant-pollinator network responses to introduced plant integration, and finally assess whether removing introduced plants impacts network structure differently than removing equivalent quantities of native plants.

Study system

My study system involves wet meadows of the West Kootenay region of British Columbia (BC), located in southeastern BC, which includes the northern portion of the Columbia Basin. The West Kootenay contains the lower reaches of the Kootenay River, the upper reaches of the Columbia River, and their confluence (Irvine et al., 2015). The rivers have created deep river valleys, with the valley bottom or floodplain starting at around 400 metres in elevation, and mountains typically rising 1400 to 2000 metres above the valley floor. The high mountains collect snow in the winter, feeding rivers, creeks, streams, and seeps with snowmelt in the spring (Bottom et al., 2005). This moisture allows the formation of unique wet meadow plant communities amidst typically much drier habitat and associated plants. The meadows I studied generally face south, leading to relatively early spring onset. Snow melts early and spring arrives soon after due to high levels of solar radiation, most of which reaches the ground due to low tree cover. These traits combined with abundant water early in the season, but little to none later (as snowmelt runoff ceases) result in peak bloom occurring in early spring before many other habitats have begun to produce significant floral resources.

In terms of biodiversity, the region is known to support a provincially notable flora, and the broader Columbia Basin contains high bee diversity, with 647 bee species known from relatively little sampling (Tepedino & Griswold, 1995). If even a moderate fraction of these bee species reaches my study area, the diversity will be greater than most regions in western Canada, and there is evidence that this is the case. For example, another study in the area found high diversity, including many species not previously known from BC and Canada (Best, 2018). The previous study focused on dry south-facing meadows, leaving the pollinator community of wet meadows in the region unknown.

A characteristic plant of wet meadows in the West Kootenay region is *Camassia quamash,* or common camas, referred to hereafter as camas, since there is only one *Camassia* species present in the area. It provides a large quantity of floral resources, produced in early spring, which attract abundant, diverse pollinators that are required for camas seed production (Parachnowitsch & Elle, 2005; Gielens et al., 2014). While camas tends to become abundant in suitable meadows, it does not form monocultures, and the communities it occurs in are known to be rich in plant diversity (Parachnowitsch & Elle, 2005; Lilley & Vellend, 2009; Pätsch et al., 2022).

Camas is also of considerable cultural importance, and the persistence of camas meadows, especially floodplain meadows are likely related to Indigenous mediated disturbance regimes (Beckwith, 2004). Camas was harvested and represented a staple food for Indigenous peoples throughout its range across the northwestern United States and British Columbia (Turner & Kuhnlein, 1983; Beckwith, 2004). In certain areas, the tradition of camas harvest has persisted, though likely at reduced levels (Stucki, 2018). The Kootenay region of BC is not an area where this tradition has been retained, due to the displacement of the Indigenous people who coexisted and interacted with camas meadows. There have also been major ecological disturbances, including spread of invasive species, alterations to hydrology (Bottom et al., 2005; Naik & Jay, 2005), flooding of lowland habitat for dam reservoirs, and conversion of remaining non-flooded lowland camas habitat into housing and infrastructure.

Despite being known to support significant plant and pollinator diversity (Parachnowitsch & Elle, 2005; Lilley & Vellend, 2009), the presence of several camas meadows in the Kootenay region has only recently become widely known (Huff & Johansson, 2012), and pollinator data is lacking. The organization of pollinator diversity across different sites, times of the year, or elevations, as well as how plants and pollinators interact are all unknown. While not the primary purpose of this thesis, my work in this system also provides previously unavailable ecological data for a unique habitat type in a data poor, underappreciated region of high bee and floral diversity. My explorations of this data are summarized in two annual reports (Rampton et al. 2022, Rampton et al. 2023), and selected images are present in Appendix 5.

Research objectives

Several factors make camas meadows suitable to achieve my research objectives. In relation to phenological disruption, camas meadows are sensitive to the influence of climate, particularly to snowpack and spring onset. This reliance plus the dependence of camas seed production on pollinators and early spring flowering phenology puts camas at high risk of asynchrony occurring (Hegland et al., 2009). Within these meadows, the diverse, abundant bee and flowering plant communities provide an opportunity to study relatively complex pollinator networks, which contain a mixture of introduced and native floral resources. Variation in the abundances of introduced plants among sites provides an additional opportunity to explore the influence of species invasions on pollination network structure.

My objectives in this thesis were to document the pollination ecology of camas meadows across an elevation gradient, allowing me to assess the following research questions:

i) Is camas pollen limited, and if so, which environmental and biotic factors are associated with limitation?

ii) What are the impacts of introduced species on pollination network structure and ability to resist disturbance?

To assess question (i), Chapter Two describes the pollen limitation experiment I completed at eight camas meadows across an elevation gradient, and relates the results to the gradient, as well as the plant and pollinator communities present. To assess question (ii) I collected repeated samples of plant-pollinator interactions at eight camas meadows and used them to build plant-pollinator networks. Chapter Three describes how I used these pollinator networks to evaluate the extent to which introduced species alter network structure, then simulated removal of introduced species to see if their removal would disrupt network structure. These chapters each evaluate localized impacts of an aspect of global change upon pollination in camas meadows, adding to a growing body of literature documenting the impacts of global change upon pollinators and pollination systems. Chapter 4 summarizes the results and significance of chapters 2 and 3.

Statement of Contribution

Both chapters were primarily my own work, including study conceptualization, study design, data collection, thesis conceptualization, data analysis, data visualization, writing and editing. My supervisor (Dr. Paul Galpern) provided guidance in study design, study conceptualization, data analysis, data visualization, writing and editing, as well as providing funding and a lab to work out of. Both chapters benefitted from the assistance of skilled bee taxonomist, Lincoln Best, who provided species level bee identifications. This thesis was made possible through my Mitacs internship in collaboration with the Kootenay Native Plant Society (KNPS). Valerie Huff (VH) and Bren Beckwith (BB) of KNPS were involved in this collaboration. VH and BB both acquired funding, provided administrative support and study system expertise, plus guided the early conceptualization process.

Chapter 2 - Pollen limitation across an elevation gradient

Introduction

The ongoing global climate emergency has been shown to drive biological changes in animals and plants across both space and time (Petry et al., 2016; Walther et al., 2002). Phenological shifts have been widely documented in both plants and insects, with species blooming, emerging, or becoming active earlier in response to warmer and earlier springs (CaraDonna et al., 2014; Bartomeus et al., 2011). If interacting organisms do not respond to similar environmental cues, or if they respond differently to a single environmental cue, a lack of synchrony, or phenological mismatch in the timing of their activities may occur (Forrest, 2015).

Pollination is a key ecosystem function that relies on synchrony to maintain reproduction in most flowering plants, including a significant portion of global crop production (Klein et al., 2007; Potts et al., 2016). Pollination relies upon plant flowering and pollinator activity occurring synchronously during temporally limited flowering periods. If disruption to synchrony occurs, pollinators will lack food sources, while plant reproductive output (measured via seed set) is expected to decline with deficits in pollen deposition (Forrest, 2015).

A decrease in seed production due to a lack of pollination is called pollen limitation, which has been found in many plant species subjected to standard methods of evaluating limitation, i.e., pollen manipulation experiments (Burd, 1994; Ashman et al., 2004). Pollination can be limited through a variety of mechanisms, including inadequate diversity and abundance of pollinators, but also through the density of the focal plant and its relative abundance in the co-flowering plant community (Knight et al., 2006). In addition to these established factors, climate change induced mismatch between plant and pollinator phenology is expected to lead to declines in pollination and increases in pollen limitation (Forrest, 2015), which consequently impact the reproductive capacity of plant and pollinator populations (Ashman et al., 2004).

While phenological mismatch has been demonstrated in migratory birds (Mayor et al., 2017), it has not been observed consistently in pollination systems, and the reasons for this inconsistency are not well known (Forrest, 2015), though there is evidence that bee diversity can generate phenological complementarity, maintaining synchrony in the case of phenological disruption (Bartomeus et al., 2013b). There has been some evidence of early spring onset being associated with increased plant-pollinator asynchrony, increased pollen limitation, and low seed set (Kudo et al., 2004; Kudo & Ida, 2013), as well as indications that bees and plants are not responding to similar environmental cues (Olliff-Yang & Mesler, 2018; Kehrberger & Holzschuh, 2019; Weaver & Mallinger, 2022). Years in which plants flower early have also been associated with subsequent decreases in pollinator species richness, particularly in those that visit early season plant species (Petanidou et al., 2014). In contrast, an experimental study found that late-shifted flowering treatments were visited less and were reproductively limited by lack of pollen, while early-shifted flowering treatments were not pollen limited relative to controls (Gezon et al., 2016). Another study found that despite visitation rate decreasing in later flowering plants, pollinator quality compensated for changes in visitation rate, keeping pollination consistent (Gallagher & Campbell, 2020). Other studies have found no evidence for phenological mismatch, failing to detect asynchrony but suggesting future mismatch may be possible due to differential responses of plants and their pollinators to environmental cues (Bartomeus et al., 2011; Sevenello et al., 2020). Taken together, the varied results from different systems suggest that predicting the likelihood of phenological mismatch for any one plant-pollinator system or interaction may be difficult, although those occurring in systems where phenology is dependent on seasonal climatic milestones (e.g., snowmelt in sub-alpine and alpine meadows) are clearly at higher risk. As the mechanisms determining phenology vary in different systems, it is informative to examine new systems to establish their risk of phenological mismatch under changing climate.

Elevation gradients have been used to evaluate potential impacts of climate change (e.g., because spring timing is likely to vary across elevations; Rasmann et al., 2014; Petry et al., 2016). Responses to phenological cues vary; an individual species sometimes responds more strongly to cues at higher or lower elevations, and certain species or groups of taxa are also more responsive to cues than others (Crimmins et al., 2010; Cornelius et al., 2013). Studies that combine elevation gradients with evaluations of synchrony are few. Benadi et al., (2014), for example, found no evidence for mismatch between plants and pollinators at any elevation, while Mizunaga & Kudo (2017) found that seed set varied substantially at different elevations and was influenced by differences in phenology observed across a 400-metre elevation and snowmelt gradient. An additional study examined phenology of a single plant species over a snowmelt gradient and found plant phenology was explained by different environmental variables than pollinator phenology, with variables themselves dependent on local snow accumulation. These phenological differences between plants and pollinators were also associated with differences in seed set (Kudo, 2021). Existing evidence therefore suggests that phenological responses do differ across elevation gradients, but the impacts on fitness of plants and pollinators are poorly understood and need further evaluation (Forrest, 2015).

In the following study, we use an environmental gradient to generate variation in the timing of environmental cues across eight sites where peak bloom occurs early in spring. These sites occur in south facing openings in mixed forests, and receive snowmelt runoff that provides spring moisture, supporting a diverse community of forbs, with *C. quamash* as a dominant species.

We assess whether pollen limitation is present in this spring flowering study system, plus evaluate what best explains observed pollen limitation and seed production, focusing on phenological synchrony, but also other potential associated factors. We hypothesize that there will be differences in phenology-relevant environmental cues across the elevation gradient, and that these differences have the potential to disrupt synchrony, leading to pollen limitation across elevations. To test these hypotheses, we evaluate evidence for the following predictions:

a) The phenology of high elevation sites will be delayed relative to low elevation sites.
b) Pollen limitation will increase at high elevation sites because climate change is known to have greater impacts at higher elevations (Pepin et al., 2015; Fisogni et al., 2022), and asynchrony should increase where greater disruption to phenological cues has occurred.
c) Seed production will differ across sites with the number of seeds produced covarying with biotic and/or environmental factors.

d) If pollen limitation is present, there will be few or no pollinators available until after bloom has occurred, indicating asynchrony is driving pollen limitation.

Methods

Study system

Our study system involves eight wet meadows of the West Kootenay region of British Columbia (BC), located in southeastern BC (Figure 1). The mountains of the region collect snow in the winter, feeding rivers, creeks, and seeps with snowmelt in the spring (Bottom et al., 2005). The meadows studied are similar in that they face south to southeast, possess low tree cover, and are exposed to high solar radiation. This combination means the meadows are exposed to more warmth, which arrives earlier in spring, than many nearby habitats, leading to early spring onset.

Camassia quamash, or common camas, hereafter referred to as camas, is a characteristic plant of wet meadows in the study region. It produces a large quantity of floral resources in early spring, which attract abundant, diverse pollinators that are required for camas seed production (Parachnowitsch & Elle, 2005; Gielens et al., 2014). While camas tends to become abundant in suitable meadows, it does not form monocultures, and the communities it occurs in are known to be rich in plant diversity (Parachnowitsch & Elle, 2005; Lilley & Vellend, 2009).

Eight wet meadows were studied, all containing camas populations. These meadows represent an elevational gradient from 415 m to 1120 m above sea level, and each meadow was surrounded by forest or bordered by river. At several locations, there were other meadow patches nearby, separated by at least 25 m strips of forest. The largest meadow was approximately 70 m x 70 m in area, with the smallest 15 m x 50 m. This study examined only selected focal sites within meadows. Focal sites included the area bounded by three 25m long transects spaced up to 10m apart, plus up to 10m on each side of this area. Sites were visited 6 to 8 times between April 20th, 2022, and August 6th, 2022. Visit times varied based on phenology, but at each site, at least one visit occurred before peak camas bloom (most occurred before any camas bloom), and 2-3 visits occurred during peak camas bloom. The remaining visits occurred post camas bloom.

Field data collection

Two iButton Thermochron -24 – 70 C temperature loggers were installed within each focal site in May of 2021, one installed 10 cm below ground in a plastic sample tube and the other above ground at a height of approximately 1 m, in a sealed plastic sample bag installed on the northern facing side of a tree or shrub. The loggers recorded temperature every 84 minutes during the growing season (late April to August), and every 3 hours during fall and winter (September through April). Snowmelt date was determined by looking for the point in soil logger data where temperature was no longer stable (under insulating snow) and began to fluctuate in response to solar radiation, as in Forrest & Thomson (2011).

Environment & Climate Change Canada historical weather data (ECCC, 2022) for two weather stations in nearby communities were combined to estimate quantity of precipitation during bloom. Total precipitation during bloom time as well as the proportion of days with non-zero precipitation were calculated for each site.

Floral phenology

To assess bloom timing, we estimated the average phenological development of flowering plant species at each site visit, focusing on camas. After completing floral transect sampling (described below) we assigned a value for average sitewide phenology using the scale described in Hess et al., (1997), spanning inflorescence emergence (stage 5) through to seed maturity (stage 8).

Floral transects

Three parallel 25 m transects were established at each meadow, spread evenly throughout. For each transect at each site visit, we identified and counted all flowering plant inflorescences present within 1 m of the transect line on both sides. Most flowering plants were counted for inflorescences, but some plants were not feasible to count due to tiny, abundant inflorescences, and were instead assessed for presence or absence at 1 m intervals along the transect.

Pollinator interactions

All bees observed interacting with flowers were collected using hand nets for one person hour of searching time at each site visit, pausing timers during collection and processing of netted bees. Search time involved systematically walking through focal sites from patch to patch of floral resources, pausing at patches for approximately 30 seconds before moving to the next. Patches were treated equally, such that a given patch of floral resources would have been subject to a similar amount of sampling as all other patches. Sampling only occurred when weather conditions were conducive to bee activity, defined as having temperatures above 13 C, wind below 3 m/s, no precipitation, and cloud cover sparse enough that shadows were present. Floral transect sampling and bee sampling were usually completed on the same visit, but due to poor weather, bee sampling sometimes occurred during the next available weather window (usually the next day, but in one case, three days later).

Each collected bee had its floral interaction partner recorded. Sampling focused on bees, which were the dominant pollinators in previous sampling (Rampton et al., 2022). In addition to being dominant, bees typically contribute more to pollination than other insects (Bischoff et al., 2013; Földesi et al., 2021). This is supported by a past study in camas meadows that showed bees were more effective pollinators than other insects (Rammell et al., 2019).

To account for the expected effect of sample size on species richness, we used the iNEXT R package to perform extrapolation that estimates the species richness at each site using observed abundance and species richness (Hsieh et al., 2016). When including species richness in models, we tested both estimated and observed values to ensure that observed values were not themselves more important than estimated values in explaining variation.

Pollinator identification

Pinned specimens were used to identify bees to species (or morphospecies where current taxonomy was unable to distinguish species), by expert bee taxonomist Lincoln Best, utilizing the following revisions, books, and guides; Ascher and Pickering (2013), Bouseman and LaBerge (1978), de Silva (2012), Gibbs (2010), Hurd and Michener (1955), LaBerge (1969;

1973; 1980; 1985; 1986; 1989), LaBerge and Ribble (1975), McGinley (1986), Roberts (1973a), Roberts (1973b), Sheffield et al., (2011), Stephen (1954).

Hand pollination

To assess pollen limitation in camas, we conducted a pollen manipulation experiment using three standard treatments, an exclusion treatment (as in Gielens et al., 2014), plus a pollen addition treatment and an open-pollinated control treatment as described in Knight et al. (2006). The exclusion treatment aimed to confirm the pollinator dependence of camas, and the addition and control treatments untangle whether a lack of pollen or a lack of resources is limiting camas seed production. The no-pollination, or exclusion treatment involved enclosing unopened camas inflorescences within fine mesh bags, which remained in place until after flowering, excluding pollinators to obtain a no-pollination state. Open pollinated plants were the control treatment, being unmanipulated and representing pollination provided by the pollinator populations occurring naturally at a site. The final treatment group was pollen addition, where we brushed conspecific external pollen (from plants approximately 5m away from treatment plants) onto the stigma of each of the open flowers on treatment plants, which were also exposed to natural pollination. We selected pollen added and open treatment plants within focal sites, choosing twenty pairs of plants that were located near one another, had similar numbers of flowers, and shared phenology (similar bloom time), but were not necessarily similar in individual flower size. Each pair was typically located around 1m from any other pair. Due to camas flowers opening sequentially through time, several visits were necessary to pollinate a significant proportion of camas flowers. At each visit we recorded the number of flowers pollinated. After all flowers had senesced, inflorescences were left to develop seeds, and once they had nearly reached maturation, we collected all inflorescences and capsules.

After collection, we assessed the seed production of each inflorescence. Some inflorescences produced no seed capsules, while others were partially or completely lost, due to herbivory or other external factors. Any individuals that had uncertain seed production (e.g., missing inflorescences) were excluded from further analysis, as it is uncertain whether they would have produced seeds if they had not been damaged or lost. For plants that did produce seeds, we recorded the number produced per plant, along with the number of fruiting capsules containing at least one seed, and the total number of capsules (including failed or empty capsules).

Statistical analysis

Pollen limitation

To assess predictions (b) and (c). we used the dataset of seed counts, which had suspected overdispersion and zero inflation, where approximately 30% of observations were zeroes. We conducted a preliminary chi-squared test comparing the proportions of failed, missing, and successful inflorescences in the open and pollination groups to ensure that pollination treatment was not driving observed seed production failure and confounding results. To account for overdispersion and zero-inflation, we chose to fit Zero-Inflated Negative Binomial (ZINBI) location-scale models, using the GAMLSS package for R (Rigby & Stasinopoulos, 2005). This approach simultaneously modelled the process associated with the count of seeds produced and the process that yielded no seeds. We also modelled factors that may be driving count dispersion. There were, therefore, three parameters of the response distribution modelled (in contrast to typical regressions where only one parameter, the mean, is modelled). The parameters estimated were: a) the "location"; i.e., the mean count of seeds conditional on the predictor variables, b) the “scale”; i.e., the dispersion of the count of seeds conditional on the predictor variables; and c) a parameter governing the zero-inflation binary process; i.e., the success or failure of seed production conditional on the predictor variables.

Pollination treatment (i.e., open, no-pollination, and pollen added) and its interaction with elevation were the predictor variables of primary interest, and we used them to evaluate whether pollen limitation changed with elevation when modelling mean count of seeds (location) and zero-inflation (binary process) parameters. The number of flowers per inflorescence was included as a predictor for mean count of seeds, to control for the relationship between the number of flowers a plant can produce and the number of seeds it can produce. Number of flowers hand pollinated was also included as a predictor of mean count of seeds to control for increased hand pollination relating to increased seed production. For the count dispersion (scale parameter), we used a site categorical variable to model suspected differences in the dispersion in counts among sites.

Seed production

To evaluate whether other factors influenced seed production independently of pollen limitation, we considered variables related to pollinators and the surrounding floral community, including abundance and species richness of bees and co-flowering plants during camas bloom, as well as throughout the entire season. We standardized variables involving abundance and richness during camas bloom by dividing these variables by the number of visits, which varied among sites. We used the *iNEXT* package to generate sample-size independent extrapolated estimates of bee species richness for each site (Hsieh et al., 2016). We also considered whether the abundance of the most obvious invasive plant competitor of camas (*Vicia villosa)* was related either to the mean (location) of seed production, or zero inflation process. *V. villosa* was chosen as it was observed growing over camas plants during seed production, often smothering entire plants, at one site to the point where camas inflorescences found underneath had been snapped by the weight, resulting in failure to produce seeds.

Environmental variables that varied across the elevation gradient were also considered, including the elevation variable already in the model, but also precipitation during bloom, and percentage of rainy days during bloom, using values reported by nearby weather stations for dates between the start and end of hand pollination at each site (ECCC, 2022). Differences in bloom length between sites were accounted for by standardizing length dependent values (e.g., number of rainy days) by bloom length in days.

We evaluated a series of models with the final simple pollen limitation model as a starting point, first finding the variables for the zero-inflation process that yielded the lowest AIC, then for the scale parameter, and finally for the location parameter. We excluded variables from modelling that were correlated with elevation ($r > 0.6$). All analyses were completed using R 4.1.3 (R Core Team, 2022), with figures created using ggplot2 (Wickham, 2016). Post-hoc comparisons of seed production between the pollination treatments, including changes across elevation were completed using the R package *emmeans* (Lenth, 2023).

Assessing asynchrony

We also investigated the risk of pollination disruption due to phenological shifts. The abundances of bees and camas throughout the season were examined to identify potential gaps in bee availability where shifts could lead to mismatch between bees and camas. We also investigated whether bees throughout the growing season consist of known camas visitors.

Results

Phenology

We found that camas bloomed later as elevation increased, with peak bloom at the highest and lowest sites more than a month apart (Figure 2). Peak camas bloom occurred in late April and early May at low elevation sites, in mid-late May at middle elevation sites, and early June at the highest elevation site. Snowmelt date is clearly correlated with elevation, but not as strongly as flowering date, suggesting that there are better variables to explain observed patterns in bloom time, with growing degree days a prime candidate. Unfortunately, we were unable to evaluate the impact of growing degree days due to the failure of several loggers during mid-spring of 2022, though early spring, pre-failure data was adequate to estimate early spring snowmelt at seven of eight sites.

Pollen limitation

We found that camas depended on pollinators, had similar seed production success in both open and pollen added treatments, and experienced a small amount of pollen limitation (which was only marginally significant). There was relatively more pollen limitation at low elevation, which decreased as elevation increased (again only marginally significantly). A total of 383 inflorescences were examined; 35 had pollinators excluded and experienced no pollination, 175 were open pollinated, and 173 were hand pollinated. Pollinator-excluded (no pollination) inflorescences clearly failed to produce seeds at a higher rate than either pollination treatment, confirming the pollinator dependence of camas described elsewhere (Gielens et al., 2014).

Between the open and hand pollinated treatments, similar proportions failed or succeeded (Table 2). Within the individuals that failed, some did not produce any seeds, while others experienced partial or complete loss of inflorescences resulting from demographic events, such as herbivory, trampling, and overgrowth by invasive plants. For the open pollinated treatment, the number of inflorescences lost was the same as those that failed to set seed, while in the hand pollinated group more inflorescences were lost to demographic events than failed to set seed, though these differences were not statistically significant ($x^2 = 3.43$, $p = 0.18$). Together, these results suggest that differences in pollination between open and hand pollinated treatments do not alter the likelihood of failure, nor the likelihood of certain types of failure.

The pollen limitation model that produced the lowest AIC included an interaction between treatment and elevation, plus number of flowers per inflorescence, but not number of flowers pollinated (Table 3), which did not relate significantly to seeds produced.

Results of the final model are summarized in Table 4. For the location parameter, hand pollinated treatments produced marginally significantly more seeds than the open pollinated treatment, though the effect size was small (Figure 4). This suggests there was little, and potentially no pollen limitation.

The interaction between treatment and elevation was positive but again only marginally significant, meaning that higher elevation sites trend towards less pollen limitation than lower elevation sites, but we cannot be sure this is not simply due to chance. The trend can be seen in the raw data shown in Figure 3, with greater differences between seed production in low elevation sites relative to high elevation sites. The treatment by elevation interaction after controlling for other variables in the model is presented in a partial effects plot (Figure 5).

The number of flowers an inflorescence produced was significantly positively related to number of seeds produced, as expected (plants capable of producing more flowers are able to produce more seeds). Elevation was also negatively related to number of seeds produced, with higher elevation plants producing fewer seeds than lower elevation plants (Table 4).

For the binary process, we found that elevation was positively related to seed set success, but treatment was not, and for the dispersion (scale) parameter, some sites were significantly more variable than others, but variation did not correspond to treatment. Overall, there was weak evidence for pollen limitation, the degree of which was small. There was also only marginally significant evidence that pollen limitation decreased as elevation increased. Given the marginal significance and small effect sizes, camas seed production does not appear to be meaningfully limited by a lack of pollination.

Seed-production related variables

Several additional measures of pollination and environmental conditions varied across the environmental gradient. These variables were measured and investigated for their influence on seed production, and are described below, plus summarized in Table 5.

We counted a total of 110, 715 inflorescences, consisting of 69 flowering plant species. Floral abundance throughout the growing season can be seen in Figure 6, with camas contributing a relatively high proportion of the early spring peak in floral resources at all sites.

Camas was the most visited floral resource, both in terms of bee abundance, and bee species richness, with seventy-one distinct bee taxa detected visiting camas across all sites. Site level species richness extrapolations produced broad estimates that overlapped for most of the sites, with a slight trend toward higher estimates and observed values at higher elevation sites (Figure 7). The number of bees collected visiting flowers during samples that took place within camas bloom varied among sites, ranging from 15 to 69 individual bees, and 8 to 22 bee species per sample. These values represent hour long snapshots of bee visitation to camas and co-flowering plants during camas bloom.

Seed production

We found that most of the variables measured were strongly correlated with elevation, limiting our ability to distinguish their relative contributions to seed production. These variables were in addition to those from the simple pollen limitation model described above (treatment, site, elevation, and number of flowers per inflorescence), and include bee abundance and species richness during bloom, abundance of camas flowers, abundance and species richness of non-camas flowering plants, abundance of the invasive plant *V. villosa*, proportion of rainy days, and amount of precipitation (Table 5). Several of these variables were found to be strongly correlated with elevation, including extrapolated bee species richness, abundance of bees during bloom, and total precipitation, and were excluded from consideration in models to avoid multicollinearity. Despite only moderate correlations between the remaining variables, several predictors for the location term were nearly perfectly correlated with elevation in model covariance matrices ($r > 0.8$), plus camas abundance with the number of flowers per inflorescence ($r > 0.7$). The variables impacted include the following: proportion of rainy days, camas abundance, non-camas floral abundance, bee species richness, and *V. villosa* abundance. A similar problem involving total precipitation during bloom and elevation occurred when trying to determine a formula for the binary process that explained the most variation in success/failure and produced the lowest AIC.

The above terms were excluded from the final model, and elevation was retained, as it is likely to influence many of the more specific terms (e.g., bee abundance and precipitation). It is unlikely that swapping highly correlated variables to obtain the lowest AIC would result in a model that would generalize well to other datasets, especially since such variables represent conditions or phenomena that are themselves influenced by elevation. In addition to the correlated variables, a variable for non-camas floral species richness was not significantly related to seed production and was also excluded. As a result of the observed multicollinearity, the final model is identical to the simple pollen limitation model (Table 4), and the relationships modeled are as described above in the pollen limitation section (Figures 4, 5).

Are pollinators available and is asynchrony present?

At most sites, bees were consistently available throughout the season, though their abundance at several sites was low initially (Figure 7). There are also some mid-season minima in bee abundance, but these occur after camas bloom has finished.

Across the eight sites, 40 bee taxa were detected before camas bloom began. From the 2022 floral interaction data, 26 of these taxa were known camas visitors, the other 14 were not known camas visitors. The most abundant non-camas visitor was *Andrena angustitarsata,* which in this study was only collected from *Lomatium* species. In general, the non-camas visitors were rarer taxa, collectively representing 63 observations in the 2022 data, relative to 627 observations involving the 26 known camas visiting taxa. There were undetected camas-bee interactions present (Figure 9), which are likely to have included some of the rare non-camas visitors. Another observation with implications for bee populations is that we observed a greater proportion of male bees in the first round of sampling, with 45%, compared to the average for the rest of the season, at 21%.

Discussion

Despite the timing of indicators of spring varying by over a month across the elevation gradient, we found no compelling evidence that camas seed production is limited by pollination at any elevation, though there was a trend towards pollen limitation at low elevation. Seed production was better explained by elevation than pollination, with some evidence that seed production decreases at the elevational (and latitudinal) range limit of camas. At our study sites in the year this study occurred, camas demonstrated little risk of plant-bee asynchrony, as suitable bees were available before and after bloom time. These findings are consistent with a resilient pollination system that is not sensitive to the timing of trophic interactions, but instead may be sensitive to environmental factors, such as precipitation, that are likely to be highly variable under climate change scenarios (Gehne et al., 2016).

Phenology

We predicted that bloom would be delayed at higher elevations. This was the case, with camas at the highest elevation site blooming approximately one month later than the lowest elevation site (Figure 2). This is consistent with evaluations of phenology over elevation gradients at moderate elevations (Forrest & Thomson, 2011; Benadi et al., 2014), but stands in contrast to an alpine study that showed snow melt was more important than elevation (Kudo, 2021). With logger failures at some sites before camas bloom, it was not possible to quantify which variables best explained phenology across the gradient, though snowmelt data was available for most sites, and had a weak relationship with bloom time. This follows the mechanism in Forrest & Thomson (2011), where snowmelt exposes the previously insulated ground to solar radiation, warming the bees and plants that overwinter there, although in our study system, snowmelt did not explain all the variation in bloom time. Growing degree days or other mechanisms are likely to explain the remaining variation. We have anecdotal evidence for this, as one of our meadows experiencing forest ingrowth had camas plants flowering in shady, cool areas on the same day that plants in our study area were reaching full fruit development. This was nearly equivalent to the variation present across the entire elevation gradient (Figure 2), suggesting that local heterogeneity can drive large changes in phenology. Future studies should aim to either establish a greater number of sites at locations that vary in phenological cues or use high local variability to understand the relative importance of environmental factors in determining phenology. Evaluating such factors should allow insights into the sensitivity of camas phenology to known or modelled changes in climate.

Pollen limitation

We predicted that camas would experience greater pollen limitation at high elevation. There was marginally significant, low level pollen limitation in the present study (Table 4), as well as a marginally significant interaction between pollen limitation and elevation, in the opposite direction to our predictions. The weak evidence for a small amount of pollen limitation agrees with past studies of pollen limitation in camas in other habitats, with little to no limitation present (Parachnowitsch & Elle, 2005; Gielens et al., 2014). This is also in agreement with a metanalysis of pollen limitation (Knight et al., 2006) that suggests for most plants, pollen limitation is low when considering limitation over the lifetime of a whole plant. The fact that perennials can reproduce across multiple years has been suggested as a potential issue with pollen limitation studies, the reason being that most studies (including this one) do not span the lifespan of perennial species, so pollen limitation in an individual growing season may be compensated for in subsequent seasons via complex resource management strategies (Ashman et al., 2004; Knight et al., 2006). Such studies advise against concluding that pollen limitation is high using data from a single year, but in camas, we have the opposite scenario, where we did not observe significant limitation. Given the typical pattern of low lifetime pollen limitation, it is unlikely that our observed results represent an exceptional year, and likely that camas typically experiences little to no pollen limitation.

We also found that inflorescences with more flowers produced significantly more seeds, but that the number of flowers hand pollinated did not relate to the number of seeds produced (Table 4). The relationship between plant size and seed production is well known, as larger plants have more resources to produce more flowers and more seeds from those flowers (Willis & Hulme, 2004; Trader et al., 2006). Failing to observe a relationship between seed production and the number of flowers hand pollinated suggests that our hand pollination treatment was consistent across sites and individuals. Given the low pollen limitation we observed, our pollination efforts may have simply been consistent in providing no additional benefit to plants already adequately pollinated by the naturally available pollinators.

Elevation was inversely related to seed production, with low elevation plants producing more seeds per inflorescence than high elevation plants (Table 4). Considering that the sites studied are at the latitudinal range limit of camas in the region, and the highest elevation site studied is one of the highest known in the area, it appears that instead of pollen being the limiting factor, seed production is limited by growing conditions. Other plants have been found to produce fewer seeds near their range limits (Jump & Woodward, 2003; Vaupel & Matthies, 2012), but this may be species specific, as other studies have not found obvious declines (Theobald et al., 2016), or that declines in seed production at range limits vary by year and species (Rivest & Vellend, 2018). Camas appears to fall into the first group, though the present study did not include enough replication across elevation (n = 8) or years (n = 1) to be confident that the relationship we observed was not due to chance.

Seed production

We predicted that seed production would vary with biotic and abiotic factors across sites. We found that elevation, which negatively influenced seed production, was strongly correlated with several other measured variables. This plus limited site replication across the elevation gradient limited our ability to untangle the specific factors that influence seed production.

Many of the variables that were correlated with elevation have established relationships with pollination and seed production. Some are clear; bee abundance and diversity are known to positively influence seed or fruit production (Garibaldi et al., 2013; Winfree et al., 2018). Others are more complex, with precipitation typically thought to negatively impact pollination by suppressing bee activity (Totland, 1994; Tuell & Isaacs, 2010), though in wet meadows which depend on continued spring runoff (particularly from snowmelt) spring precipitation may extend suitable growing conditions and matter more than pollination in ensuring seed production. Floral diversity, which camas meadows are relatively rich in, is associated with greater productivity (Isbell et al., 2017) but may come at the cost of increased pollen limitation (Vamosi et al., 2006; Vamosi et al., 2013). Finally, camas meadows contain an abundance of introduced plants, which are known to outcompete and decrease biomass of native plants (less biomass means fewer seeds, e.g., our result that inflorescences with more flowers produce more seeds) (Flory & Clay, 2009; Bennett et al., 2011). In camas meadows, we did not have sufficient variation in these variables across elevation to evaluate whether their relationships with pollination and seed production hold.

Despite lacking site replication and the ability to resolve seed production relationships, our pollen limitation experiment was not limited by sample size. Replication at the plant level was high (n = 219), lending credibility to our conclusion that camas experienced only limited pollen limitation. To better understand the factors that limit camas reproduction, we recommend that further studies examine a broader area with greater replication to untangle which environmental variables drive the changes we observed in camas seed production across elevation.

Is plant-pollinator asynchrony likely?

In the absence of meaningful pollen limitation, we were unable to evaluate our final prediction that a lack of active bees during bloom would be responsible for pollen limitation, indicating asynchrony. We are, however, able to make some evaluation of the risk that this will occur. Bees that visit camas were available before, during, and after camas bloom, suggesting that the risk of asynchrony occurring in this study system is low. If camas bloom shifts earlier while bee phenology does not, camas has a low chance of reaching a point where there are no bees available. Bee abundance and species richness were lower before camas bloom, though a noted issue in phenological research is that pollinators are usually collected from the flowers of interest, making it difficult to conclude whether pollinators are emerging at the same time flowers bloom, whether they have emerged earlier and are foraging elsewhere, or have emerged with no food sources (Forrest & Thomson, 2011). In my study, early season bee abundance and species richness appeared to reflect floral resource availability. Evaluating true bee emergence would likely require nest emergence monitoring.

One reason to explain why we did not find asynchrony is that while camas represented the earliest major floral resource, it was not the first one available. The species *Montia linearis,* *Collinsia parviflora, Ranunculus glaberrimus*, *Claytonia lanceolata*, and *Erythronium grandiflorum* all preceded camas bloom, mostly at low abundance, or at least producing only small flowers*.* This was also documented in one other study that examined timing of bloom in camas meadows, with several less abundant species available before camas (Parachnowitsch & Elle, 2005). These species attracted few, though abundant (on a per flower basis) bee species compared to the camas bloom that occurred one to two weeks later, and it is possible that these are the plants at highest risk of asynchrony in this system, as they depend on relatively few pollinator species and flower as early as possible in spring.

This study used an elevation gradient to investigate whether environmental conditions drive plant-pollinator asynchrony, and thus pollen limitation. We did not find clear evidence that pollen limitation related to elevation. Our ability to detect asynchrony was likely limited by the cold, late spring experienced in the year of study, which is the opposite of the conditions that past research has shown are likely to generate asynchrony (Kudo & Ida, 2013). In fact, the observed (marginally significant) trend of greater pollen limitation at low elevation could have been due to low pollinator activity induced by regionally cool and wet April/May weather (Totland, 1994; Tuell & Isaacs, 2010), which was lacking by the time high elevation sites bloomed in June.

Our study does not have a method to evaluate the reproductive success of bees, which would be necessary to evaluate from a bee perspective whether phenological shifts have resulted in asynchrony and are having impacts on fitness (Forrest, 2015). Despite experiencing similar cues, limited initial evidence suggests that bees and plants are not shifting their phenologies synchronously, though evidence that shifts have had fitness impacts is lacking (Olliff-Yang & Mesler, 2018; Kehrberger & Holzschuh, 2019; Weaver & Mallinger, 2022). There does appear to be a risk of asynchrony in some bees resulting from responses to environmental cues that differ from those of plants, but this will require long term monitoring that can link disruption of synchrony to declines in reproductive success of bee populations over time.

Are plant-pollinator systems intrinsically resistant to asynchrony?

Because we did not find evidence for asynchrony, we considered potential reasons that it was not observed, including local variation in conditions, protandry in bees, and the influence of selection pressure.

Local, and yearly variation in snow melt, aspect, and albedo influence the conditions experienced at any individual location, with the magnitude of their impacts potentially equal or greater than those observed so far under climate change (compare Bartomeus et al., 2013a with Kudo & Ida, 2013). This can lead to phenomena such as mountaintop plants blooming before those on the slopes below them (e.g., in Totland, 1994 & Kudo, 2021), or in our study system, where camas bloom in the vicinity of one site spanned nearly the same length as bloom over the entire elevation gradient. This type of local variation will spread floral availability through time, buffering the impacts of any unequal shifts in timing between plants and pollinators, though the earliest individuals or species may still be at risk.

Male bees were observed in greater abundance early in the season relative to later. This is a known life history trait in some (particularly solitary) bees, called protandry, meaning that the earliest emerging bees in spring will not be females that are crucial for reproduction, but instead males, which are less crucial to population persistence, some of which may already be near sacrificial early emergers with low chances of reproductive success (Alcock, 2013). While protandry likely evolved for other reasons (Alcock, 2013), it may provide an unexpected buffering effect in early spring solitary bees by making early emergence less risky and providing pollination for the earliest flowering plants.

Much of this discussion assumes that there is no selection pressure acting on either plants or pollinators, yet because the consequences of potential mismatch involve reproductive failure or fitness declines for both plants and pollinators, there is likely to be strong selection pressure acting to keep phenologies linked (Forrest, 2015). Selection may enable the maintenance of synchrony for the time being, but it is possible climate change will reach a point where physiological limits cannot be evolved out of, and asynchrony will be inevitable (Forrest, 2015). It is also possible that asynchrony will not be the mechanism that leads to pollination decline, and instead that as physiological limits are reached, bees will fail to emerge all together, as suggested by a transplant experiment of high elevation bees to lower, warmer elevations (McCabe et al., 2022).

Conclusion

This study assessed pollen limitation and the potential for phenological asynchrony in a spring flowering plant that requires pollinators to reproduce. Pollen manipulation experiments were used to evaluate the contribution of pollinators to seed set relative to environmental limitations, and were performed across an eight site, 700-metre elevation gradient that served to generate variation in phenology-determining environmental cues. There was no evidence for significant pollen limitation across the gradient, instead elevation and associated variables had a greater influence on seed production, including a decline in seed production at the elevational range limit of camas. Bees were present before and after bloom time in our study system, so even if phenological shifts occur in only bees or only plants, phenological mismatch is unlikely, and pollination should remain stable. Changes in biotic and abiotic factors associated with elevation have greater potential to disrupt camas reproduction.

Figures & Tables

Figures

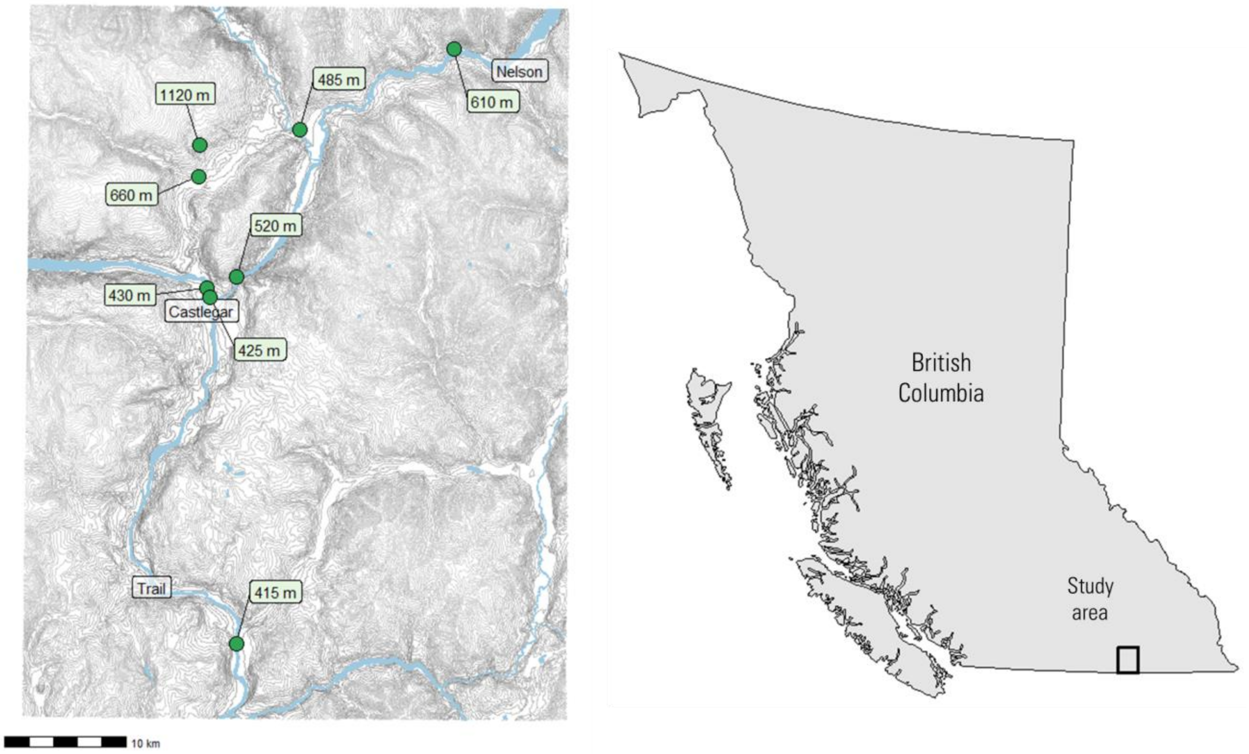

Figure 1. Locations and elevations of the eight camas meadows sampled in the West Kootenay, British Columbia, Canada.

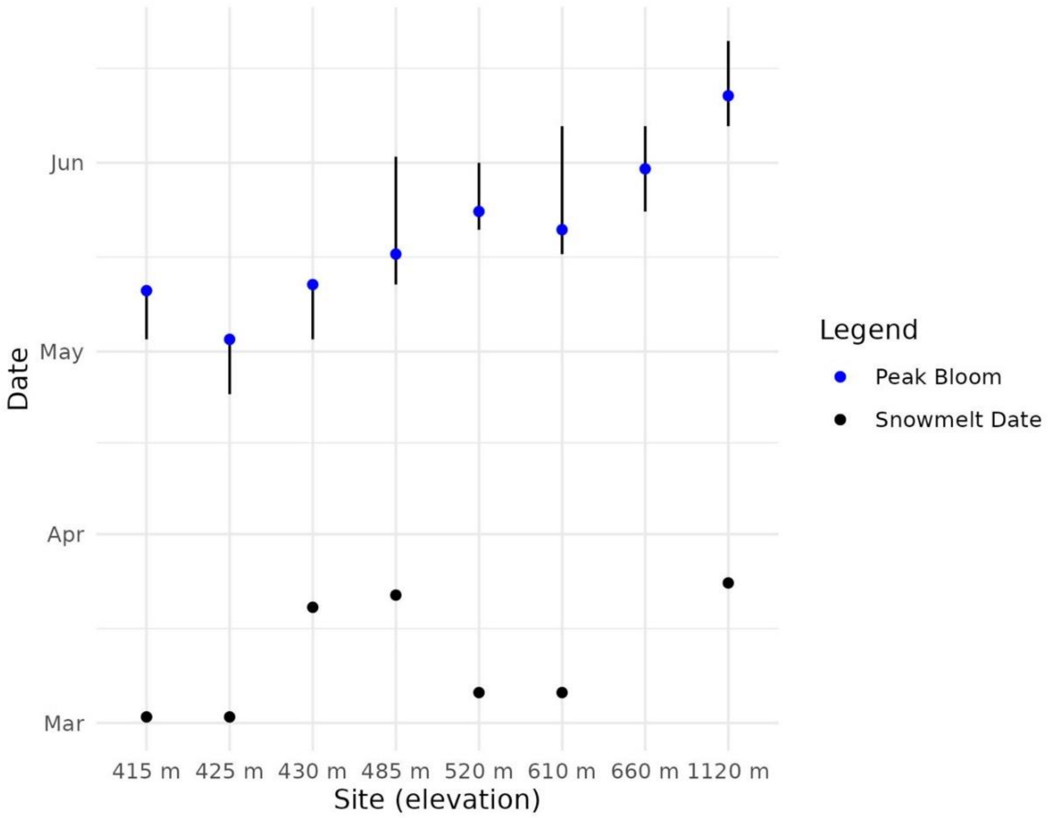

Figure 2. Peak bloom is delayed as elevation increases, while snowmelt is slightly delayed, but not matching the magnitude of shifts in bloom time. Lines represent phenological stages between 10% of flowers open and 70% of flowers opened (including senesced flowers). Blue dots represent peak bloom, or stage 65, where at least 50% of flowers have opened (Hess et al., 1997), while black dots represent estimated snowmelt date. Note the categorical site axis.

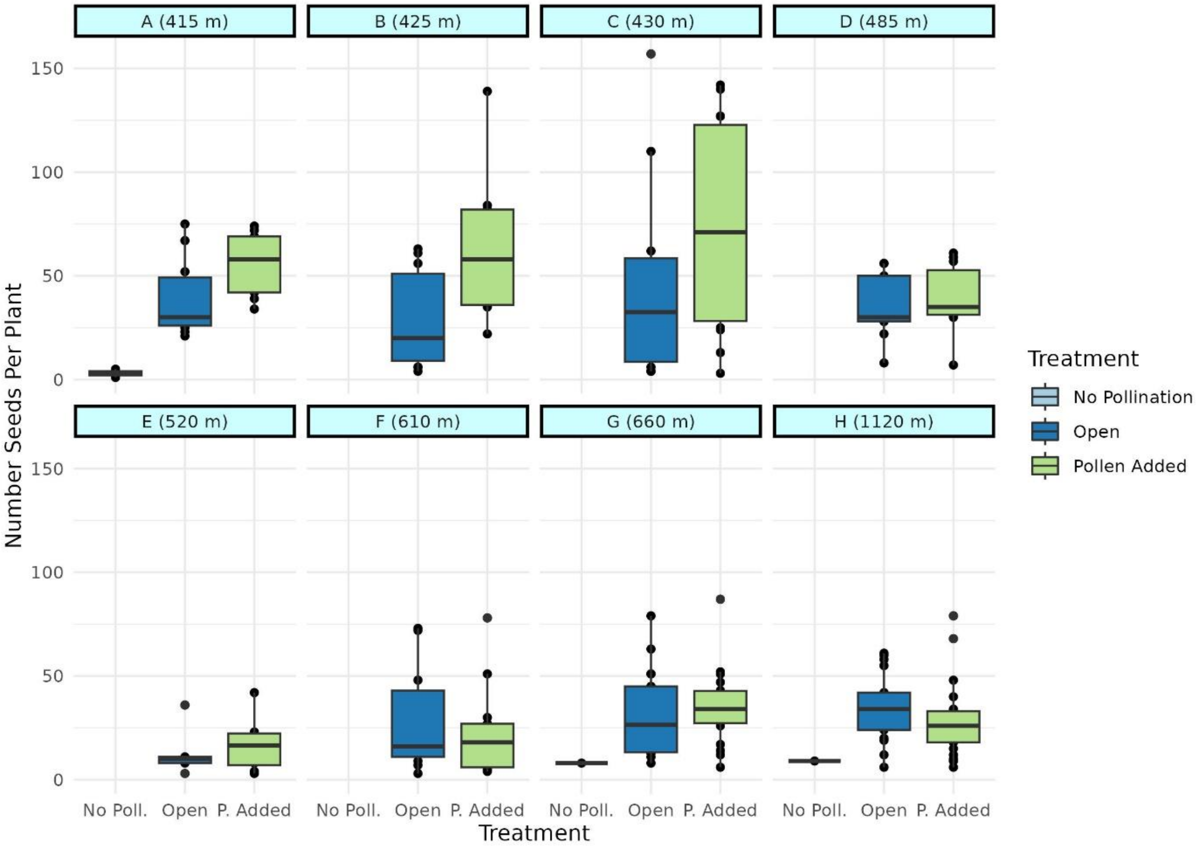

Figure 3. Seed production of each of the pollination experiment treatments. Blank columns in the "No Pollination" treatment indicate that no pollinator exclusion plants at that site produced seeds. Boxes summarize the data for each site-treatment combination. The horizontal bars within each box represent the median, while lower and upper margins of the boxes represent the 1st and 3rd quartiles, respectively, the lines represent data up to 1.5x the interquartile ranges (IQR), and dots represent data that fall outside 1.5x IQR (McGill et al., 1978).

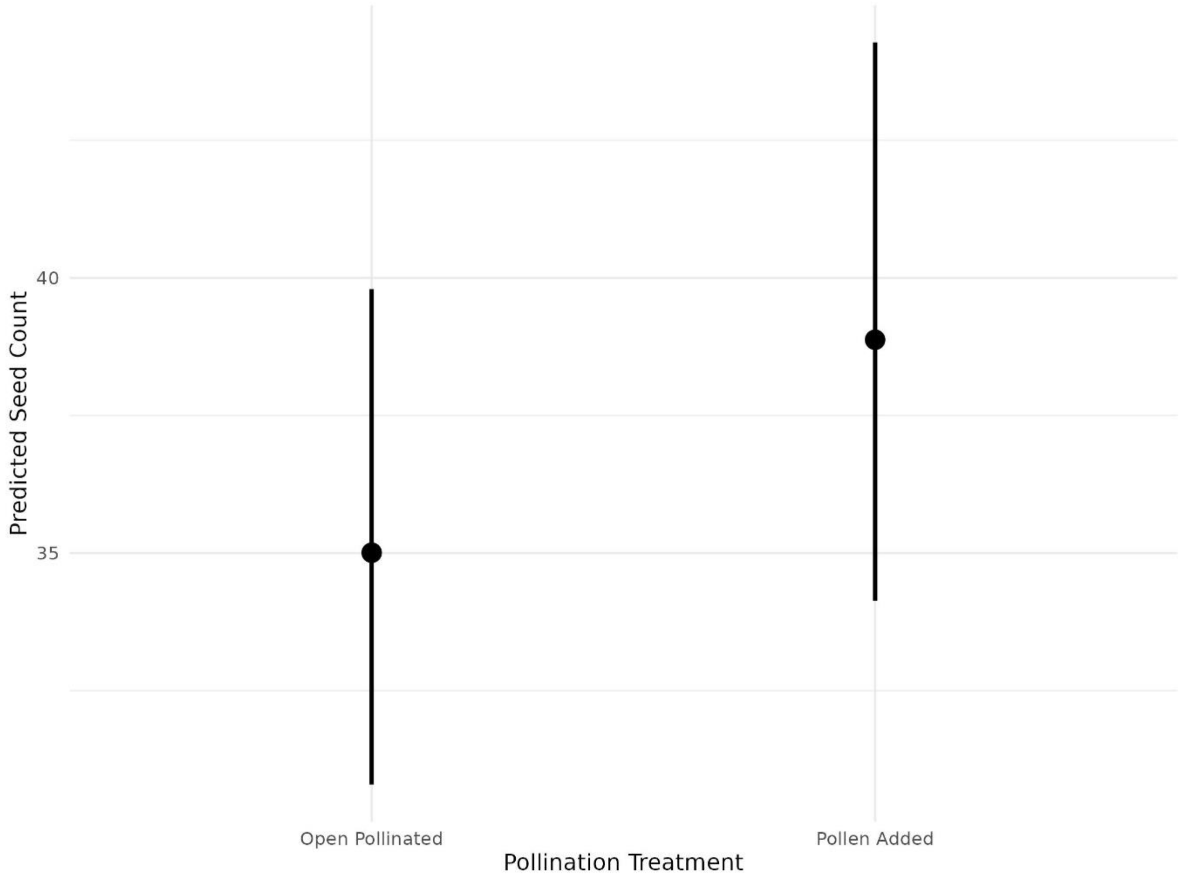

Figure 4. Predicted seed production for the open and pollen added treatments, after controlling for other variables in the model. These values are calculated at mean elevation and mean flower number.

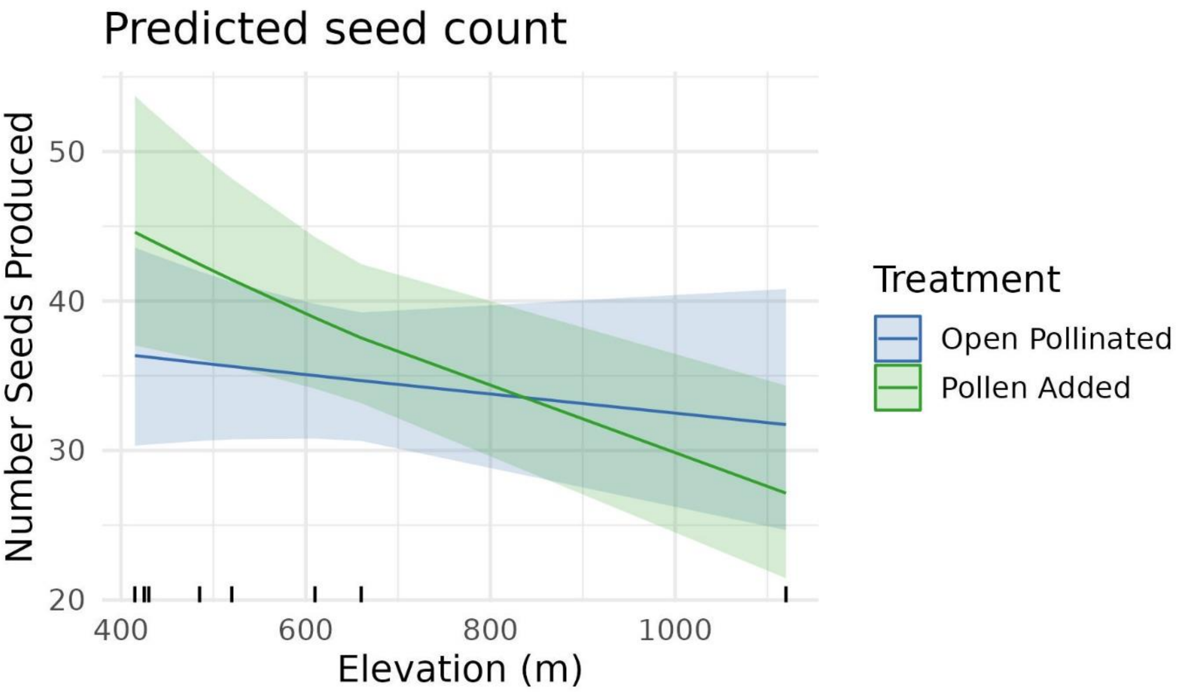

Figure 5. Predicted number of seeds produced across the elevation gradient (ticks on the x axis represent each site's elevation). There is a trend towards pollen limitation at low elevations (pollen added plants producing more seed than open pollinated plants), but this was not significant. There was an overall trend of decreased seed production as elevation increased.

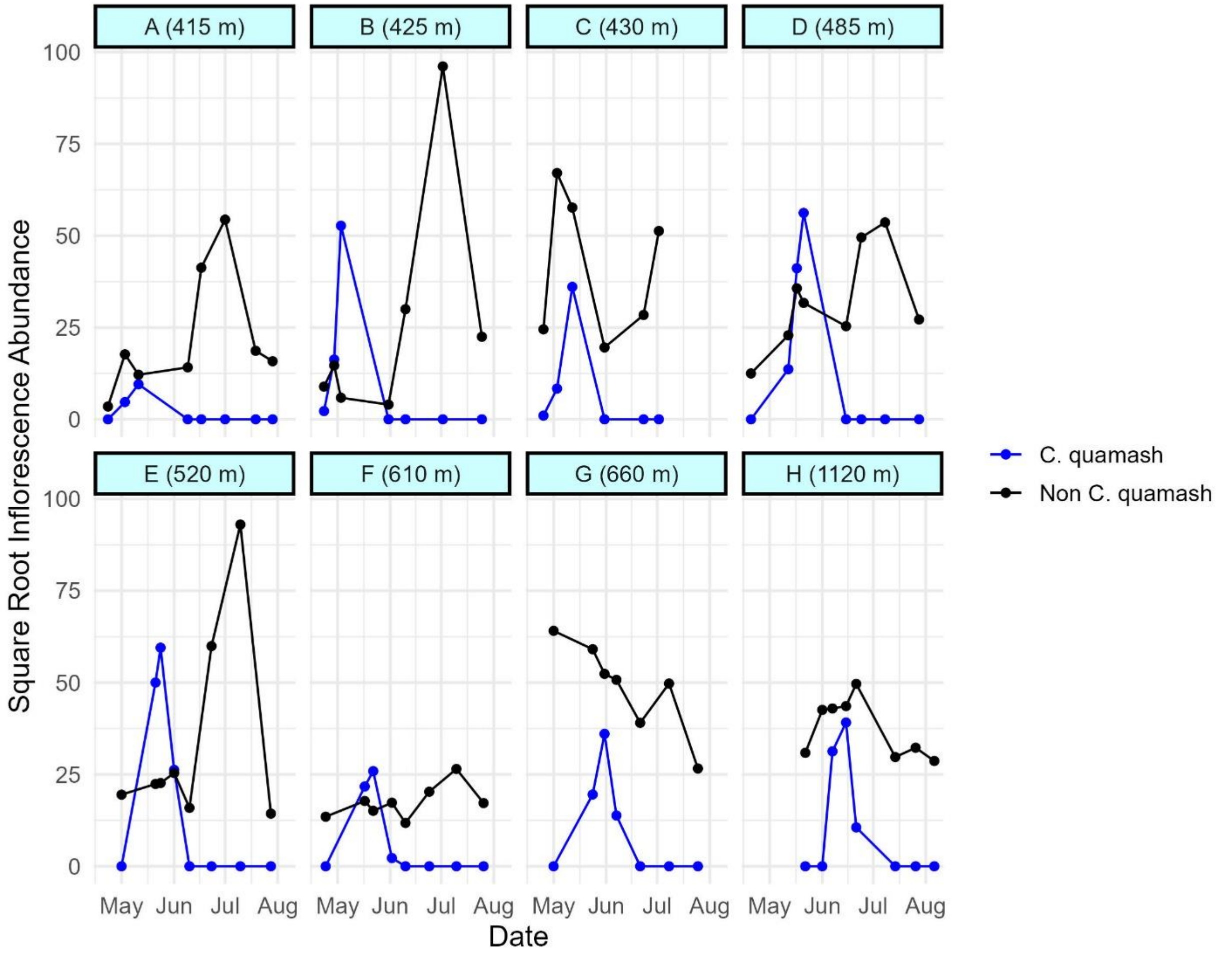

Figure 6. The square root of inflorescence abundance throughout the season, with camas in blue, and inflorescences of all other species in black.

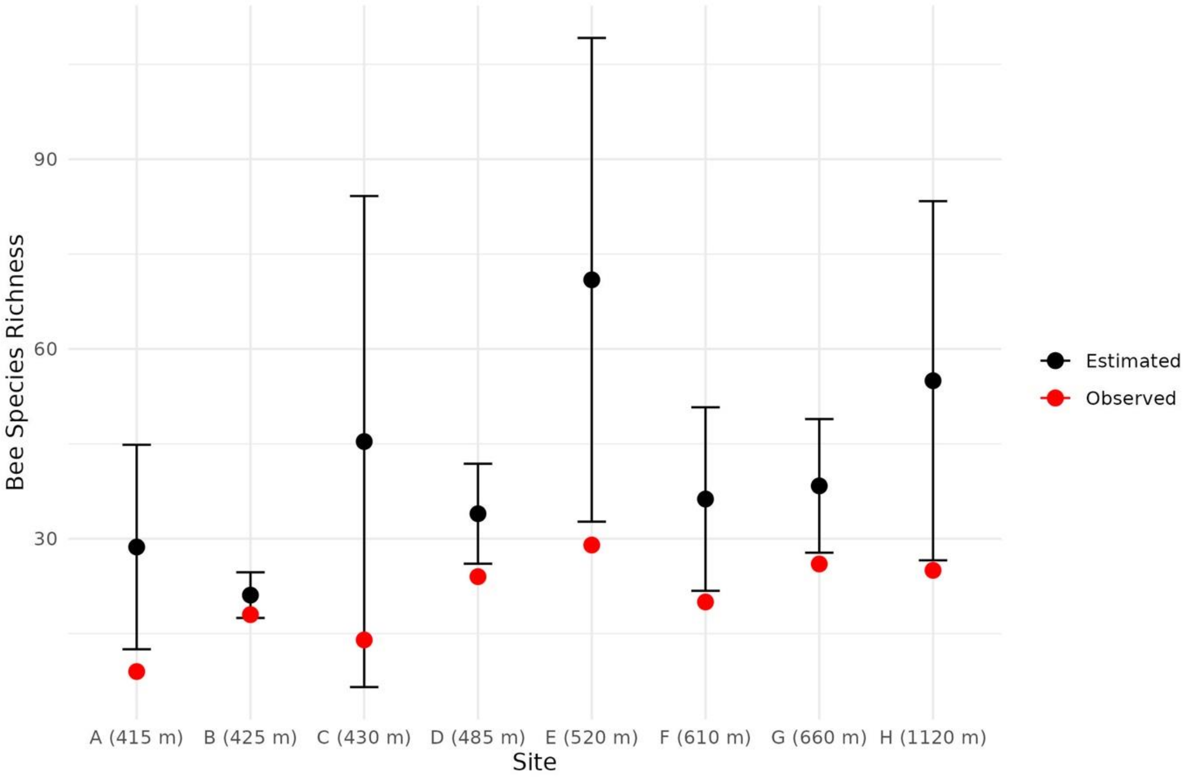

Figure 7. Estimated and observed bee species richness at each site in order of increasing elevation (categorical). Red dots represent observed bee species richness, black dots represent iNEXT estimated bee species richness, and error bars represent the estimated value +/- standard error.

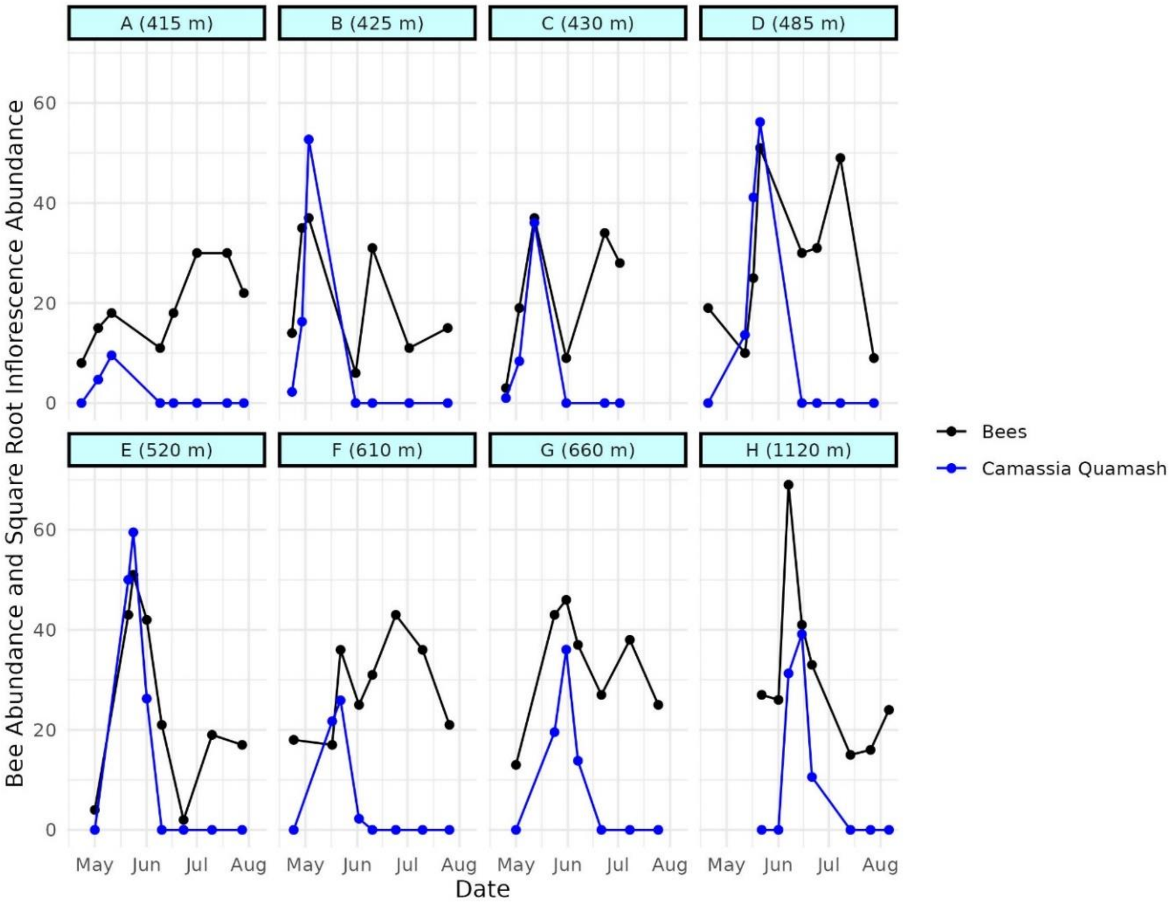

Figure 8. Bee abundance and square root of camas inflorescence abundance throughout the season, with camas abundance in blue, and bee abundance in black.

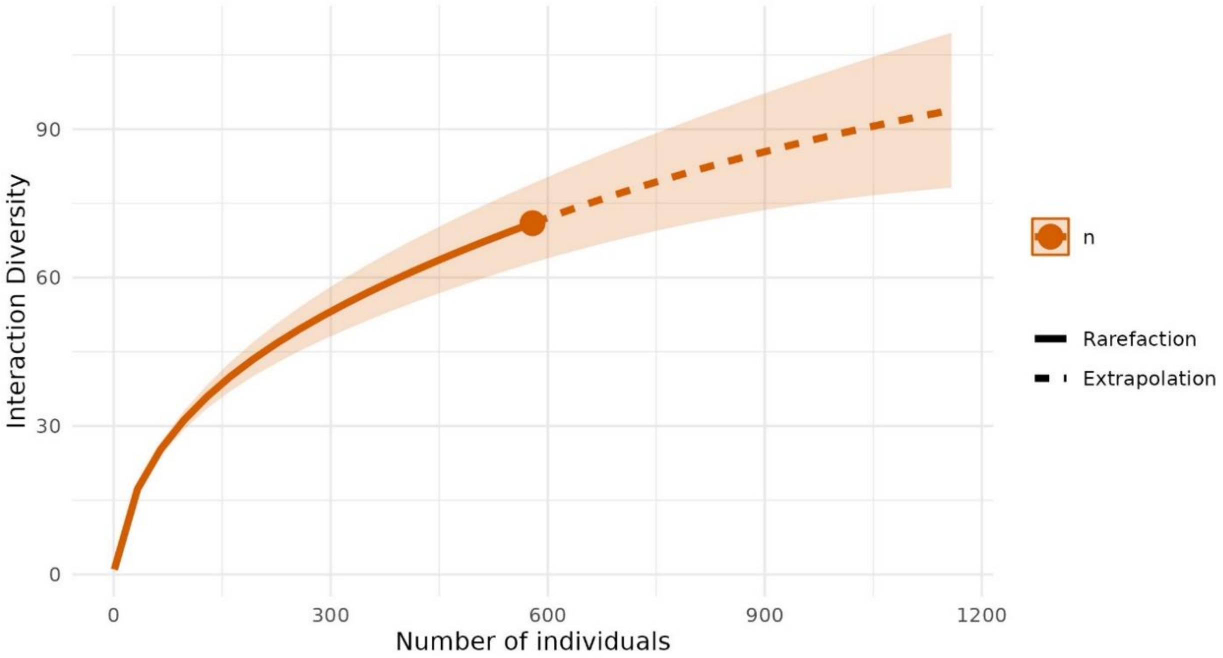

Figure 9. The accumulation curve of camas-bee interactions in relation to bees sampled across all sites. The point n represents the number of interactions detected and is not located upon a plateau in the interaction accumulation curve, suggesting that there are additional camas-bee interactions that our sampling did not detect.

Tables

Table 1. The parameters evaluated in the simple pollen limitation model.

Term Type	**Pollen Limitation Model**	**Seed Production Model**
Location	Treatment Elevation Number of flowers Number pollinated	Treatment Elevation *V. villosa* abundance Number flowers Bee abundance Bee spp. richness Floral abundance Floral spp. richness Extrapolated bee richness
Scale	Site	Site Treatment
Zero-inflation	Treatment	Treatment *V. villosa* abundance Elevation

Table 2. Numbers of plants (percentage of total in brackets) that successfully produced at least one seed vs. those that did not, for each treatment.

Treatment	**Succeeded**	**Failed**	**Missing**	**Total**
No-pollination	4 (11)	30 (86)	1 (3)	35
Open	91 (52)	42 (24)	42 (24)	175
Added	102 (59)	28 (16)	43 (25)	173

Table 3. AIC and deviance of simple pollen limitation models evaluated and in bold, the model selected as the final model. The response variable was number of seeds produced per plant.

Model	**Deviance**	**AIC**
Treatment * elevation + number flowers	**1630.8**	**1660.8**
Treatment * elevation + number flowers + number flowers pollinated	1629.8	1661.8

Table 4. The results of the pollen limitation model. The pollen added treatment was the reference level of the factor (i.e., the intercept), so the open treatment term represents the difference in mean seed production of the open pollinated treatment relative to the pollen added treatment.

Term	**Term Type**	**Link function**	**Ho Interpretation**	**Estimate**	**p**
Intercept - location	Location	log	Intercept 0	**3.69**	**<0.01**
Treatment (open)	Location	log	No difference	**-0.42**	**0.06**
Elevation	Location	log	No effect	**-0.0007**	**<0.01**
Number Flowers Per Inflorescence	Location	log	No effect	**0.05**	**0.01**
Treat X Elevation	Location	log	No interaction effect	**0.0005**	**0.09**
Intercept – zero-inflation	Zero-inflation	logit	Intercept 0	**-2.37**	**<0.01**
Elevation	Zero-inflation	logit	No effect	**0.001**	**0.03**
Dispersion intercept - Site G (ADR)	Dispersion	log	Intercept level of factor	**-1.26**	**<0.01**
Site A (BCR)	Dispersion	log	Variation not different	-0.78	0.15
Site B (KPI)	Dispersion	log	Variation not different	0.53	0.23
Site C (MIL)	Dispersion	log	Variation not different	1.78	0.14
Site D (CRV)	Dispersion	log	Variation not different	**-1.49**	**0.01**
Site E (SEC)	Dispersion	log	Variation not different	**2.58**	**<0.01**
Site F (MAR)	Dispersion	log	Variation not different	**1.31**	**<0.01**
Site H (GCR)	Dispersion	log	Variation not different	-0.1	0.8

Table 5. The variables that were of interest for their relationships with seed production. Species richness and abundance values (excluding extrapolated richness) represent the number observed during bloom and are divided by the number of visits. Many of these variables were correlated with elevation and were necessarily excluded from the final model.

Site	Elev (m)	Non-camas floral abund.	Non-camas floral spp. richness	Flowers per inflorescence	Number pollinated	Bee abund.	Bee spp. richness	Extrap. bee spp. richness	Camas abund.	Vicia villosa abund.	Total precip. (mm)	Prop. rainy days
BCR	415	230.28	2.5	7.06	1.29	16.5	19.0	51.9	86	411	27.80	0.82
KPI	425	124.7	4.0	8.43	2.87	36.0	8.5	23.6	3014	1698	26.50	0.57
MIL	430	3323.64	10.0	10.00	2.83	37.0	12.0	21.9	1343	379	25.95	0.75
CRV	485	1138.04	4.5	8.77	4.45	38.0	14.5	29.0	5035	0	15.35	0.43
SEC	520	507.82	9.5	11.64	6.95	47.0	10.0	38.5	6732	1664	13.45	0.50
MAR	610	271.88	7.5	10.09	2.50	26.5	12.0	44.7	1143	0	16.50	0.50
ADR	660	2744	16.0	7.57	2.31	46.0	10.0	28.9	1851	209	8.15	0.56
GCR	1120	1873.8	7.5	7.70	2.45	55.0	11.0	77.6	2614	0	56.15	0.82

Chapter 3 - Does removing introduced plants destabilize networks?

1 Introduction

Biotic interactions are key to maintaining functional ecosystems (Schweiger et al., 2010) but are being disrupted by several aspects of global change (Blois et al., 2013). Pollination is a key biotic interaction that provides crucial ecosystem services (Kremen, 2005) by facilitating the reproduction of most flowering plant species (Ollerton et al., 2011). Global change factors such as climate change, land-use change, pesticides, and invasive species are generally associated with negative outcomes for pollinators (Herrera, 2020; Janousek et al., 2023; Ulyshen & Horn, 2023). Plant invasions occur when species are introduced to new habitats, whether incidentally or intentionally (Radosevich et al., 2003), and possess traits that allow them to aggressively spread, to a degree that reaches a threshold considered disruptive to the existing ecosystem (Richardson et al., 2000). Plant invasions often significantly alter community structure (MacDougall & Turkington, 2005), have wide-ranging, typically negative impacts on ecosystem services (Pejchar & Mooney, 2009), and are known to directly disrupt interactions between plants and pollinators (Schweiger et al., 2010).

Plant-pollinator interaction networks collectively describe the interactions that make up the pollination occurring in a system. Introduced and invasive species are known to infiltrate networks (Memmott & Waser, 2002) and in some cases become highly visited network members important for supporting pollinators (Vilà et al., 2009). Invaded habitats have also been known to support more bee species in greater abundance than before invasion (Tepedino et al., 2008; Russo et al., 2014; but see Parker, 1997; Kaiser-Bunbury et al., 2009 for the reverse). Despite pollinators sometimes benefiting from introduced floral resources, other impacts of invasive species on ecosystems may mean that their removal is necessary to address loss of biodiversity and ecological function (Weidlich et al., 2020). Such efforts are increasingly becoming a global priority (Chazdon & Brancalion, 2019), but it is not clear how removing the abundant floral resources provided by introduced or invasive plants will impact the pollinators and interaction networks that have come to depend on them.

The patterns of plant-pollinator interactions can be described by bipartite network analysis, which uses various metrics to describe the structure and properties of networks (Dormann et al., 2009). Network level metrics can provide measures of ecological qualities, for example, the stability of an interaction network (described by the metric robustness) represents the ability of a network to absorb species loss and is associated with greater ecosystem function (Ross et al., 2021), while the metric H_2' describes the specialization of the ecological relationships present in a network (Blüthgen et al., 2006). Table 6 provides a glossary of network-related terms used in this study.

Robustness describes the ability of a network to resist disturbance. It is measured by the rate at which removing species from one level (e.g., plants) causes losses of species from the other level (e.g., pollinators) that are reliant upon those removed. If losing only a few species leads to similar losses of reliant species (e.g., pollinators each visit a single plant species, and are lost as soon as their single preferred plant is removed), the network has low robustness. If losing several species does not initially lead to many losses until a collapse point late in the removal sequence (e.g., pollinators each visit several plants and are not lost until all of their options are lost), the network is considered more robust (Burgos et al., 2007; Dormann et al., 2009).

H_2' or network specialization describes, at the network level, whether plant-pollinator interactions are occurring in a specialized or random fashion (Dormann, 2011) (Table 6). Low H_2', or network specialization, implies that pollinators are randomly visiting plants, while high H_2' implies that pollinators are only visiting their respective preferred plants (Blüthgen et al., 2006).

Networks with higher H_2' values may be more likely to contain specialist pollinators of conservation concern (Biesmeijer et al., 2006).

Evidence for the impact of invasions on network structure has been mixed, with reports of altered interactions and decreased specialization (Lopezaraiza-Mikel et al., 2007; Bartomeus et al., 2008) as well as increased nestedness (Wang et al., 2023) and robustness (Albrecht et al., 2014). Several authors contest that network structure (e.g., robustness and specialization) is relatively unimpacted by invasion, despite networks shifting to states where invasive plants have become highly visited and central to networks (Vilà et al., 2009; Russo et al., 2019; Parra-Tabla & Arceo-Gómez, 2021). While invaded networks do not always show changes in structure despite changes in interactions, these networks are likely to experience loss of introduced species through control efforts, the presence of biocontrol agents, or other unpredictable factors that decrease their abundance (e.g., Ortega & Pearson, 2011; Seastedt, 2015).

When introduced species have become highly visited and important interaction partners in networks, their removal risks altering pollination networks. Experimental studies have found that flower visitation and network specialization decline in response to the removal of highly visited plant species (Goldstein & Zych, 2016; Biella et al., 2019), with simulations also finding that network robustness declines fastest when removing the most visited species (Memmott et al., 2004). Studies specifically testing network responses to the removal of introduced vegetation are limited. Two studies have shown changes in pollinator visitation, but network impacts are unclear (Baskett et al., 2011; Ferrero et al., 2013). An additional study found that networks were more robust after removing introduced plants, but the removed plants were unimportant to pollinators, despite being dominant in abundance (Kaiser-Bunbury et al., 2017). Together, these results suggest that highly visited plant species are important in maintaining network structure, and though introduced species can become dominant, it is unclear whether this dominance results in them becoming central to network stability, and consequently, how strongly their removal will impact stability in relation to native species.

Studies that simulate the removal of taxa to explore impacts on pollination and network structure tend to remove entire taxa in a single step (e.g., Biella et al., 2019), which may not be a typical restoration outcome. Instead, it may be more realistic to consider scenarios where control of invasive plants is only partially successful, i.e., when invasive plants have decreased in abundance and thus importance in networks, but have not been entirely extirpated. Including both scenarios allows us to investigate the drivers of changes in network structure upon removal of introduced species. While the robustness metric is independent of abundance changes and dependent on changes in species, H_2' is expected to be influenced by changes in both abundance and quantity of species.

To examine the impacts of plant invasion on pollination networks, we collected plant-pollinator network data at eight sites across two years, all of which contained abundant pollinator-attracting introduced plant species. First, we examine whether quantity of introduced plants was related to network structure, using networks generated from each visit to each site as our sampling units. Second, we use aggregated yearly plant-pollinator networks to investigate the consequences of removing introduced and native plant species, losses which are likely to influence the community of pollinators supported, ultimately driving changes in network structure. To achieve this goal, we simulate random loss of either native or introduced plant associated units of networks and compare the impacts of removals on network stability (robustness) and specialization (H_2').

We hypothesize that introduced plants have not only become dominant in abundance, but dominant in terms of visitation in the networks of our study system, altering interaction patterns such that pollinators have come to depend on them as key network members. Consequently, we expect that simulating the removal of highly visited introduced plant species will more strongly impact network structure than removing variably visited native plant species. Specifically, we predict the following:

a) With greater quantities of introduced plants, there will be mixed impacts on observed network structure. Robustness will be maintained (if introduced plants become heavily visited by replacing existing highly visited plants), or increase (if introduced plants become additional highly visited plants, without replacing existing species). Specialization is expected to decrease as introduced plants form interactions with many pollinator species, i.e., integrate as generalists, and increase the proportion of generalists in the network relative to the existing mixture of generalists and specialists (Figure 10).
b) Because introduced species are expected to become dominant in networks, and the removal of dominant species is thought to destabilize networks (Memmott et al., 2004), we expect that removal of introduced species will lead to declines in network robustness relative to removing native species, which will show only a moderate impact of removal due to consisting of a mixture of abundant, highly visited species, and less common, less frequently visited species (Figure 11, Panel B).
c) Removing introduced plants that have formed interactions with many pollinators (i.e., generalized interactions) will increase network specialization relative to removing only native species, which are more likely to be involved in specialized plant-pollinator relationships (Figure 11, Panel A).

2 Methods

2.1 Study system

Our study took place in eight meadows in the West Kootenay region of British Columbia, Canada (Figure 1). The region is mountainous, containing a variety of habitats between the low elevation floodplains and the alpine peaks. The study meadows are defined by the presence of *C. quamash* and are often referred to as camas meadows. In the West Kootenay, these meadows occur in floodplains and on the lower slopes of mountains, representing unique snowmelt fed wet meadows among dry, shrubby to forested habitats. Meadows occurring on slopes can be categorized as bedrock meadows, which are known to support significant plant diversity (Pätsch et al., 2022), though their pollinator diversity is poorly known. The bee diversity in this region is high, with our past work finding upwards of one third of the bee taxa known from the entirety of British Columbia (BC) in our study sites (Rampton et al., 2023).

Each site was visited multiple times throughout two growing seasons. In 2021, five visits took place between May 10th and July 10th, while in 2022, seven to eight visits took place between April 20th and August 6th.

2.2 Collecting plant-pollinator network samples and associated floral data

Plant-pollinator interactions were sampled for one person-hour at each site visit. Collections focused on bees, which were the dominant pollinators in our study system and likely contributed most of the pollination services provided to flowering plants (Bischoff et al., 2013). All bees observed touching the reproductive parts of flowers were caught with hand nets, with the identity of the visited flower recorded. Collecting took place between 10:00 and 17:00, only when weather conditions were adequate for bee activity, defined as wind less than 3 m/s, temperature above 13 C, no precipitation, and enough light that shadows were visible. The sampling hour involved only time spent searching and excludes time processing specimens. Searching for interactions involved systematically walking through each focal site (see description in Chapter 2 methods). Approximately 30 seconds were spent at each patch of floral resources before moving to the next. Floral resources were treated equally, such that a given patch of floral resources was subject to a similar amount of sampling to all other patches. Each pollinator visitation sample was complemented by quantifying available floral resources at each visit (at most 3 days later). To quantify floral resource availability, open inflorescences of all plant species flowering within three 25 x 2 metre transects were counted.

2.3 Pollinator identification

Bee identifications to species were confirmed from pinned specimens by experienced bee taxonomist Lincoln Best, using a variety of taxonomic resources, including Ascher and Pickering (2013), Bouseman and LaBerge (1978), de Silva (2012), Gibbs (2010), Hurd and Michener (1955), LaBerge (1969; 1973; 1980; 1985; 1986; 1989), LaBerge and Ribble (1975), McGinley (1986), Roberts (1973a), Roberts (1973b), Sheffield et al., (2011), Stephen (1954). In cases where all resources failed to delineate species, taxa were assigned genera/subgenera-morphospecies codes.

2.4 Building networks

Site visit plant-bee networks were constructed for each visit to each site (n = 35 in 2021; n = 60 in 2022), representing snapshots of network structure for use in observed network structure analyses. Yearly plant-bee networks were also constructed by aggregating each year’s site visits (n = 2, aggregated from n = 35 samples for 2021, and n = 60 for 2022) and were used for simulation analyses. We treated the two years as separate networks because sampling effort and timing varied between the two. Spring arrived early in 2021, and by the time it was possible to begin sampling, camas bloom was nearly complete at some sites. Spring arrived late in 2022, allowing sampling to start prior to camas bloom. Each year was therefore sampled under different conditions. However, even if conditions had been identical, network structure is known to change significantly from year to year (Alarcón et al., 2008). The *bipartite* package in R (Dormann et al., 2009) was used to calculate network metrics, using the functions *robustness* and *second.extinct* to calculate robustness, a measure of network stability (Table 6) and the function *H2fun* to calculate network specialization (H_2') values. The functions r*obustness* and *second.extinct* randomly remove bees from a network, then calculate resulting losses of plants (i.e., which plants lack pollination after a pollinator species is removed). This allowed us to assess whether simulated plant removal corresponds to a change in the ability of the bee community to maintain pollination.

Within networks, plants were assigned as native or introduced using the descriptions found in the Illustrated Flora of British Columbia (Douglas et al., 1998). R 4.1.3 (R Core Team, 2022), and ggplot2 (Wickham, 2016) were used to analyze and visualize data, respectively.

2.5 Observed network analysis

To assess whether introduced species altered network structure, we calculated the network metrics robustness and specialization (H_2') for each network sample (i.e., site and visit combination, n = 60 in 2022, n = 35 in 2021). We separated each year's site visit samples for the reasons described above, then compared the network metrics of each sample with associated measurements of introduced and native plant diversity and abundance. Networks were not equal in size (number of interacting plant and pollinator species), meaning that direct comparisons of metrics across samples would be misleading due to correlations between network size and network metric values (Dormann et al., 2009). To control for such relationships, we used a standard bipartite null modeling approach, where an observed interaction network is repeatedly randomized, creating a null-network distribution, which is then used to calculate z-scores (see Table 6). These scores describe to what degree an observed network deviates from the distribution of randomized networks (Pellissier et al., 2018). Z-scores are calculated by subtracting the mean of the randomized network metric distribution from the observed metric value, then dividing by the standard deviation of the randomized network metric distribution (as in Lara-Romero et al., 2019; Classen et al., 2020). To calculate z-scores, we used the *shuffle.web* null model from the *bipartite* package (Dormann et al., 2009) to generate 100 randomized networks for each observed network. We then calculated z-scores for both robustness and H_2', acknowledging that null models may not perfectly control for size differences between networks (Dormann et al., 2009; Pellissier et al., 2018). Comparisons between networks were made using the resulting z-scores, e.g., robustness in relation to a randomized network. For robustness, higher z-scores indicate relatively more stable networks. For specialization, higher z-scores indicate relatively more specialized networks.

We used the R package *glmmTMB* (Brooks et al., 2017) to fit generalized linear models which evaluate the impact of plant community (and pollinator visitation to the plant community) on network metrics (robustness and H_2'), where each of our site visit networks was an observation in these models (Figure 15). We included a site-by-visit interaction as a random effect to control for variation between sites and visits. Before running models, we examined correlations between the measures describing introduced and native plant diversity and abundance. If correlations between variables were 0.6 or greater, we did not include variables in a single model. Each of the sampling years (2021 and 2022) were modelled separately, with sets of models examining robustness and specialization within each year (Table 7).

2.6 Removal from networks

To assess the impacts of removing introduced plants from networks, we simulated iteratively removing portions of each year's aggregated plant-pollinator network (Appendices 3 and 4) and evaluated changes in network robustness and specialization (H_2') across the removal sequence.

We simulated two scenarios of iterative observation removal to assess whether either species removal or quantity of individuals removed were driving outcomes. Each scenario removed a different portion of the network one step at a time, with the two scenarios described below and illustrated in Figure 12. The respective portion of the network iteratively removed in each scenario is referred to as a removal unit (RU).

Scenario 1: removing one plant species at a time; associated removal unit: RU 1 - all observations associated with one plant.

Scenario 2: removing one individual plant-bee observation at a time; associated removal unit: RU 2 - one observation of a plant-pollinator interaction (essentially an individual bee).

For each year's aggregated network, we carried out iterative removals for each scenario (i.e., removing one plant and one observation), within which one replicate removed only native plant associated RUs, and a paired replicate removed only introduced plant associated RUs (Figure 13). The same quantity of RUs were removed for each of the paired plant type replicates, even though there were often more native associated RUs than introduced RUs (e.g., more native plant species than introduced plant species, in which case the number of introduced plant species was the number of species removed for both replicates). Each replicate followed the removal process illustrated in Figure 14, where a plant type was selected, then one RU was removed, metrics describing the resulting network were calculated (including null modelling comparison to 100 randomized networks), then another RU removed, iterating until the process reached the maximum quantity of RUs removed, as described above. This process was then repeated to produce 100 removal simulations for each plant type (i.e., native or introduced) within each network year-removal scenario (Figure 13). Network metrics were calculated after every plant (Scenario 1) removal but were calculated every five observation removals (Scenario 2) to decrease computational intensity.

We then used generalized linear models to evaluate the impacts of removals on network robustness and specialization. These models allowed inclusion of a random effect term necessary to account for variation between simulations which differed in removal sequence, as well as an AR1 term that accounted for within-simulation sequential autocorrelation throughout the removal sequence (i.e., a pair of metrics early in the removal process are more similar than a pair consisting of one metric early in the process and one late in the process).

The two removal scenarios were modeled separately, but the model formula was identical for both. We modeled the relationship between the z-scores of each of the network metrics (robustness and specialization) in relation to a main effect including the following variables: network year, number of RUs removed, and the type of associated plant loss – native or introduced. In addition to the main effect, we included a random intercept term for simulation number (i.e. which of the 100 repeated simulations a point belonged to), a random slopes term for the number of units removed (reflecting that each species removed will influence the network in a different way), as well as an AR1 (autocorrelation) term where the time component was number of units removed, and the process was modeled for each of the replicates as described above. Pairwise post-hoc comparisons of network metric rates of change (metric by iteration rate of change) for each year and plant type were completed using the R package *emmeans* (Lenth, 2023).

3 Results

3.0 Plant and pollinator community

In the 2021 network year, there were 139 bee taxa and 62 plant species, while in 2022, the network contained 156 bee taxa and 71 plant species. The top three most visited introduced species in each year made up 63% and 64% of the total interactions with introduced plants (2021 and 2022, respectively), and represent species that are considered invasive weeds (e.g., *Berteroa incana, Centaurea stoebe, Potentilla recta* & *V. villosa)*. For native plants, camas was by far the most visited in both years, representing 30% of interactions with native plants in 2021, and 51% in 2022. In both years, the most abundant bees were almost always generalists, including species such as *Bombus vancouverensis*, *Ceratina acantha,* and *Andrena nigrocaerulea.* Specialist bees were also present in the networks, including *Andrena astragali* which only visited *Toxicoscordion venenosum*, as well as *Andrena crataegi* which we only observed visiting *Physocarpus malvaceus.* The remaining bees that were found to visit only one flower were uncommon species observed one to three times, limiting our ability to describe their degree of specialization with confidence. Further descriptions of the plant and pollinator communities can be found in Rampton et al. (2022 & 2023).

3.1 Network structure related to degree of invasion

Our sampling of bee-plant interactions produced 35 site visit network samples in 2021, and 60 site visit network samples in 2022. Networks generated from site visit samples contained 2 to 53 plant-bee observations in 2021, and 2 to 69 plant-bee observations in 2022. Three network samples in 2021 and eight samples in 2022 contained too few individual bees to calculate network metrics and were excluded from sample-level analysis (though their observations were included later in aggregated networks). Across site visit networks, visitation to introduced plants ranged from no visitation (i.e., when only native plants were visited) to visitation of only introduced plants, with a range of ratios between the two extremes. Introduced and native plant abundance, species richness, and quantity of bee visitation associated with each site visit network are presented in Appendix A, Tables A1 and A2. One site's network samples for each visit are illustrated in Figure 15.

3.1.1 Prediction: invasion does not alter robustness, but increases specialization

To evaluate prediction (a), we tested whether sample network robustness and specialization z-scores were related to introduced or native plant richness, abundance, and quantity of bee interactions with pollinators.

Correlations were present between the three native plant measures, as well as between the three introduced measures ($0.5 < r < 0.8$). To avoid unstable parameter estimates, we created models MR1-MR6 and MH1-MH6 as seen in Table 7. Due to model instability, we were unable to evaluate models MR3, MR6, & MH6, with stable variants of each presented in Table 7 below. Additionally, the site by sample visit random effect was reduced to a random effect containing only sample visit, as site had a negligible impact on variation controlled for.

For robustness, we found no relationship with native or introduced plant abundance, richness, or quantity of bee interactions with pollinators (Table 7).

Specialization related to all measures except introduced plant richness but was best explained by quantity of bee interactions with native plants in 2022, and bee interactions with both native and introduced plants in 2021 (Table 7).

For the 2021 network samples, specialization was significantly related to native species richness, native and introduced inflorescence abundance, plus both native and introduced interactions. Model MH3 was selected as the final model (Table 8), where specialization is significantly positively related to quantity of bee interactions with both native and introduced plants after controlling for differences in network size and a random effect of sampling visit.

For the 2022 network samples, network specialization was positively related to quantity of bee interactions with native plants. It was also marginally positively related to native inflorescence abundance but was not related to other variables. Model MH6b (Table 8) was selected as the final model, in which specialization is positively related to the amount of bee interactions with native plants, after controlling for network size and a random effect of sample visit.

3.2 Removal from networks

We aggregated sample networks from each year and used them to test predictions (b) and (c) by simulating removal of both native and introduced plants and evaluating resulting changes in network robustness and specialization. We found that removing introduced and native associated network units had different impacts on rates of robustness change, which differed between years and removal scenarios (Figure 16, panels A to D). There was little evidence that removing introduced associated network units altered network specialization relative to removing native associated network units (Figure 16, panels E to H).

The aggregated networks are described in Table 9 and visualized in Appendices 3 and 4. The proportion of introduced plants was similar in both year's networks, with approximately 35% of interactions involving introduced plants in 2021, and approximately 37% of interactions involving introduced plants in 2022. Despite the similar proportions, the distribution of dominant interactions between native and introduced species differed between years (Table 9). The majority of dominant plants in the 2022 network were native plants, both in abundance and number of species, while in 2021, there was a relatively even distribution.

In models of removal, we initially included a random slopes term for the number of RUs removed, but the estimate for this term ended up being negligibly small (~1 x 10^-15), so it was excluded from all removal models. We also scaled the number of RUs removed to allow for comparisons between the two years of differing network size and accordingly, different absolute numbers of RUs removed.

3.2.1 Prediction: Removing introduced plants will decrease robustness faster than removing native plants.

We found support for prediction (b) in 2021 (Figure 16, panels A and C), but not in 2022 (Figure 16, panels B and D). Removing introduced plants decreased robustness faster than removing native plants in 2021 ($p < 0.01$, Figure 16, panel A), while the opposite was true in 2022 ($p < 0.01$, Figure 16, panel B). The impacts of removing individual observations were less clear but directionally similar, with introduced associated removal decreasing robustness in 2021 faster than native associated removal (though with a small effect size and $p = 0.02$, Figure 16, panel C), while in 2022, removing introduced plants increased robustness relative to removing native plants ($p < 0.01$, Figure 16, panel D).

3.2.2 Prediction: Removing introduced plants will increase specialization faster than removing native plants

We did not find clear support for prediction (c). In all cases, specialization increased when RUs were removed, but there were conflicting differences between years and removal scenarios, and the effect sizes of differences were small.

Removing introduced plants increased specialization faster than removing native plants did in 2021 (with a moderate effect size, $p < 0.01$, Figure 16, panel E), but not in 2022, where the rates were not significantly different ($p = 0.99$, Figure 16, panel F). There was no difference in the rate of specialization increase between removing observations associated with introduced and native plants in 2021 ($p = 0.71$, Figure 16, Panel G), while in 2022, removing observations associated with introduced plants increased specialization faster than removing observations associated with native plants ($p < 0.01$), but the effect size of the difference was small (Figure 16, panel H).

4 Discussion

We found no evidence that networks involving more invasive plants were more sensitive to species loss (i.e., had lower robustness). The tendency of species within networks to interact with particular partner species (i.e., network specialization) was best explained by bee visitation patterns and not degree of invasion. Networks with introduced species removed were more susceptible to further species loss (i.e., less robust) than networks with native species removed, though only in one of our two network years, which happened to contain higher proportions of dominant introduced interactions. Simulated removal of introduced plants from networks mostly increased specialization at the same rate as removing native species, though removing introduced plants increased specialization faster than removing native plants in the network year containing higher proportions of dominant introduced plants. In other words, as plants or observations are lost, the remaining interactions tend to be between species that are one another’s preferred interaction partners. In this system, introduced plants have few initial impacts on network structure, but subtly alter interaction patterns such that their future removal risks decreasing the ability of pollination networks to resist species loss, though potentially only when introduced plants have become highly visited members of networks.

4.1 Network structure related to degree of invasion

4.1.1 Prediction: invasion does not alter robustness, but increases specialization

We predicted that network sensitivity to species loss would not differ or decrease (i.e., network robustness would remain stable or increase) in relation to the quantity of introduced plants networks contained. Our prediction of stable robustness was supported, with no relationship between quantity of introduced plants and network robustness (Table 7). These results agree with past studies showing invasions do not alter robustness (Parra-Tabla et al., 2019; Corcos et al., 2020), but contrast with other studies which found higher robustness in invaded sites (Albrecht et al., 2014), or lower robustness in invaded sites (Kaiser-Bunbury et al., 2017). Greater robustness is associated with networks where some plant species interact with many pollinator species, and some plant species only interact with the pollinators that visit the most plants (i.e., nested networks as in Bartomeus et al., 2008). This study's networks are consistent with such patterns, where highly (and diversely) visited plant species were present, while less common plants were usually visited by a subset of common generalist pollinators. Highly visited species of both native and introduced origin were distributed throughout our network samples, which may explain the lack of a relationship between robustness and native or introduced composition; robustness was likely maintained by native species in some networks, and by introduced species in others. This distribution (of highly visited species being spread through samples and not clustered in few samples of high richness) may also explain why we did not see a relationship as in Corcos et al., (2020) where plant species richness related to increased robustness.

We predicted that species would tend to interact more with preferred interaction partners (greater network specialization) in less invaded networks relative to more invaded networks. We did not find evidence that specialization related to invasion, and instead, network specialization was best explained by bee visitation to plants. Specifically, network specialization was explained by quantity of bee interactions with native plants in 2021 and 2022, and also by quantity of bee interactions with introduced plants in 2021, but not 2022 (Table 8). In contrast to our prediction, more bee interactions with introduced plants in 2021 increased network specialization instead of decreasing it. Past studies mostly agree with our results, finding no relationship observed between invasion and specialization (Emer et al., 2015; Parra-Tabla et al., 2019), though Corcos et al., (2020) found species level specialization declined with invasion. It is possible that our network samples are not sampled thoroughly enough to adequately describe specialization, such that when introduced species were abundant, our sampling was not adequate to detect rare interactions with non-dominant plants. This leads to networks where sampling has only detected pollinators visiting the dominant introduced plant(s), making pollinators appear to prefer only such species, ultimately producing more specialized networks. Further investigation of the specialists (or apparent specialists) present in the network and their visitation patterns would be necessary to fully understand the drivers of differences between the two years.

Of our descriptors of introduced plants, quantity of interactions with bees best predicted specialization, which suggests that floral resource availability of native and introduced species, while correlated with pollinator visitation, do not necessarily drive changes in network specialization, which instead appears to be regulated by the floral resources that pollinators choose to visit. Our results agree with studies that show specialization increases with floral richness and are consistent with the idea that bees narrow (or at least maintain) diet breadth to decrease interspecific competition, even when additional floral resources are available (Brosi, 2016; Gómez-Martínez et al., 2022). They are also consistent with another study which found that abundance of introduced floral resources does not necessarily relate to high pollinator visitation (Kaiser-Bunbury et al., 2009).

4.2 Removal from networks

4.2.1 Prediction: removing introduced species will decrease robustness

We predicted that simulated removal of introduced species from networks would decrease robustness more quickly than removing native species. This was true in 2021, where robustness decreased when removing introduced portions of the network relative to native associated portions, though this relationship was stronger when removing entire plant species. An opposing result was observed in 2022, where removing introduced associated RUs increased robustness, and removing native associated RUs decreased or did not change robustness (depending on removal scenario, Figure 16, panels A to D). The other study we are aware of that simulated removal of native and introduced plants from networks did not find any differences between removal of the two types of plants (Parra-Tabla et al., 2019). The authors suggest that the presence of highly generalist honeybees may have contributed to maintaining robustness despite loss of plant species, and the low honeybee frequency, and indeed lack of a single highly dominant generalist bee species in camas meadows may provide an explanation for why our results were qualitatively different.

The contrasting results we observed between 2021 and 2022 can likely be explained by initial network composition, in particular, the plants that are visited by the most pollinator species. These species are thought to provide stability to the rest of the network (Burgos et al., 2007), and the identity (i.e., native or introduced) of species within this key group will have important implications for the impacts of introduced species removal. In our 2021 network, sampling began near the end of peak early season bloom, underrepresenting native species, and effectively overrepresenting introduced plants among the most visited species (Table 9). The higher proportion of introduced plants among the most visited plants in 2021 relative to 2022 may explain the results observed, where robustness in 2021 was sensitive to removal of introduced species (removal of introduced associated RUs led to decline in robustness in all cases), while the opposite was observed in 2022, when native plants dominated the top interactions. They highlight the importance of temporally resolved sampling in describing and making conclusions about plant-pollinator networks (e.g., in Prendergast & Ollerton, 2022b), but also suggest that future studies should target networks with not only high abundance of introduced flowers, but also high visitation to such flowers. Given that the existing experimental study focuses on the opposite case (Kaiser-Bunbury et al., 2017), completing experimental removal studies in networks where introduced plants have become key to pollinators, will allow a more complete understanding of how loss of introduced species impacts network structure.

Our approach also does not account for the ability of pollinators to shift their visitation patterns upon loss of a plant they previously visited, a phenomenon known as rewiring, which increases network robustness (Kaiser-Bunbury et al., 2010), and has been documented in experimental (Goldstein & Zych, 2016) and observational studies (CaraDonna et al., 2017), plus natural history records, where specialized bees have been observed switching to alternative plants when their preferred floral resources are unavailable (Thorp, 1969). Our robustness analysis therefore represents a worst-case scenario of removal, with bees likely to shift interactions to different flowers if forced to, effectively maintaining network robustness.

4.2.2 Prediction: removing introduced species will increase specialization.

We predicted that removing introduced species would increase specialization relative to removing native species. In contrast to our prediction, the impacts of removal were generally similar, with specialization increasing in both scenarios and for both plant types (Table 10). The only notable difference was plant removal in 2021, where removing introduced plants increased specialization slightly faster than removing native plants (Figure 16, panel E). This difference may be related to initial network composition as described above for robustness, where the 2021 network consisted of a higher quantity of generalist introduced species relative to more often specialized native species, leading to a modest increase in rate of specialization increase when removing introduced species relative to native species. This contrasts with 2022, which contained a large contribution of generalist interactions from a highly abundant native plant, and moderate contributions from several generalist introduced species, likely resulting in little difference between native and introduced removal.

It is also possible that our null model analysis does not adequately control for changes in network size. We used the shuffle.web algorithm in the bipartite R package, which has been shown to increase specialization, and produce “over-randomized” specialization values at low specialization relative to high specialization (Dormann et al., 2009). Consequently, we expect that our z-scores will be underestimating low values of specialization relative to high values of specialization, and the strength of the relationship will be overestimated. However, the positive relationship between specialization and removing network units is clear (Figure 16, panels E to H), and agrees with the results of another study examining specialization in relation to plant community (Gómez-Martínez et al., 2022). Caution in interpretation is appropriate as both studies’ results could be explained by known relationships between specialization and network size that have not been adequately controlled by null modelling, where network specialization increases as networks get smaller (Dorado et al., 2011; Dormann, 2011).

To our knowledge, this is the first study that simulates removal of introduced species and evaluates the impact on network level specialization (H_2') and further research is necessary to examine whether our results hold in other systems. A productive exploration may involve investigating impacts of removal in networks with favorable characteristics for specialization changes, e.g., a highly generalized plant invading a network composed of relatively specialized native species.

4.2.3 Differences observed between removal scenarios

Both specialization and robustness appeared more sensitive to species level (Scenario 1) than observation level (Scenario 2) losses, with differences in impacts of removal between introduced and native associated observations less pronounced than for plant equivalents. For robustness, this is not particularly surprising, as metric calculations are at the species level, independent of abundance and thus any removals in Scenario 2 that do not remove a species

(Dormann et al., 2009). Using available network metrics, Scenario 2 does not provide a perfect comparison of native and introduced associated observation removal. This is because a single observation removal can sometimes remove an entire species, but usually removes only one individual of a species. Combined with our criteria to end iterative removal (i.e., when no species in one group were left), observation removal removes all species in one plant type (introduced associated observations), but only portions of species in the other (native associated observations). Scenario 1 should thus be considered the more reliable one, with Scenario 2 a necessary, yet currently imperfect investigation into realistic scenarios of only partial removal success.

4.3 Implications for management

While examining network metrics provides an understanding of the ecological interactions in pollination systems post invasion, a measure more relevant to management may be reproductive success of the plants and pollinators in the network. Studies have examined the impacts of removing invasive floral resources on the pollination success of remaining native plants, but impacts appear to be system dependent, with one study finding positive impacts on native seed set and visitation despite lower pollinator abundance (Baskett et al., 2011), and another finding seed set of some native species declined after removal despite network metrics remaining constant (Ferrero et al., 2013). Linking changes in network metrics to outcomes in plant reproduction remains a challenge, with little association between network level metrics and seed production (Theodorou et al., 2017), though relationships have been found between species level metrics and plant reproduction (Gómez & Perfectti, 2011; Tur et al., 2013).

Studies suggest that the association between robustness and nestedness depends upon the species with the most interactions having low probabilities of being lost (Memmott et al., 2004; Burgos et al., 2007; Albrecht et al., 2014). In camas meadows, several of the most abundant introduced species are noxious weeds, and are often subject to targeted control, in which case, the above statement no longer applies. In systems where networks have become dominated by interactions with introduced species, management decisions that remove introduced species risk decreasing the ability of pollination networks to resist further disturbance. Our results suggest that when dominant pollinator-attractive native floral resources are also available (in this case camas), networks are able to maintain robustness even when dominant introduced species are lost. Further experiments should examine systems lacking extant native floral resources, and test whether pairing removal of introduced plants with native floral resource replacement is a viable method for managers to mitigate the risk of network destabilization.

Management decisions to remove introduced species at a site should weigh the potential for both negative impacts and positive impacts. Negatives include destabilized networks as we have shown, and fewer resources for pollinators (Baskett et al., 2011). Positives include decreased competition with native plants for pollinators (Baskett et al., 2011) and increased pollinator visitation or pollination quality (Brown et al., 2002; Wang et al., 2023). Vanbergen et al., (2018) outline factors which increase the risk that introduced plants will negatively impact the pollination of native plants; in summary, if introduced plants are functionally similar and bloom at similar times of year, pollination of native plants is more likely to suffer, shifting the cost-benefit analysis towards removing introduced species. These points provide initial guidelines for weighing the impact of introduced species removal on pollination systems, but further studies are needed to verify that decisions made using these criteria will result in the desired outcomes.

5 Conclusion

This study examined the consequences of plant invasions on pollination network structure. We used a series of real-world network samples collected across two growing seasons to examine network structure in relation to the presence of introduced plants and simulated the impacts of their removal in relation to native species. We found the degree to which networks were invaded was not related to their robustness (i.e., the ability of a network to resist species loss was not related to the quantity of introduced plants it contained), while network specialization (i.e., to what degree interactions are with preferred interaction partners) was most clearly related to bee visitation. The impacts of removing introduced plants from networks relative to removing native plants differed by year, potentially in relation to whether the most dominant interactions involved mostly native or mostly introduced plants. These results need experimental verification but suggest that the impacts plant invasions have on network structure will be limited if invading plants are attractive to pollinators, but removal of such plants may have impacts on the ability of networks to resist further species loss. Invasive plant removal programs should consider the reliance of pollinators on introduced species when retaining pollination service is a concern.

6 Figures and Tables

Figures

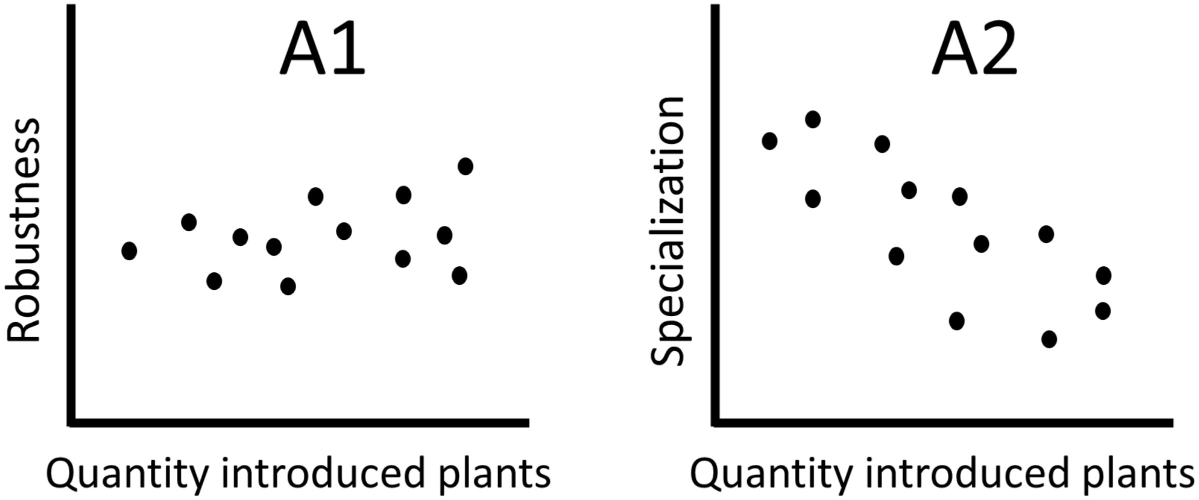

Figure 10. Expected relationships between network metrics and the quantity of introduced plants. We expect that introduced plants will integrate into networks, forming interactions with many pollinator species, maintaining, or even increasing robustness if they form interactions in excess of those previously present (A1). When introduced species integrate into networks and form interactions with many pollinators (i.e., form generalized interactions), network specialization will decrease (A2).

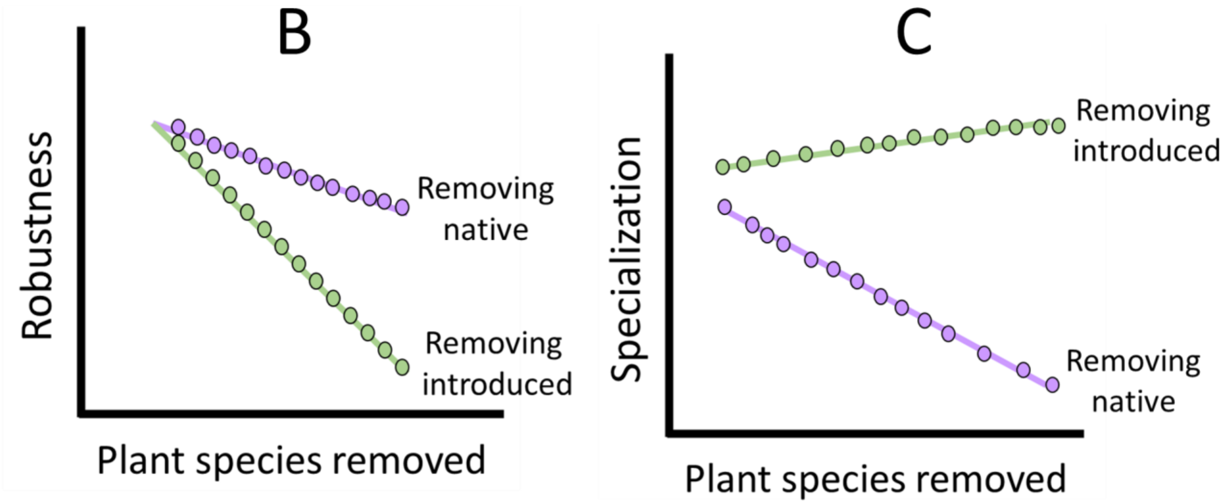

Figure 11. Expected relationships between removal and network metrics for predictions (B) and (C). We expect that introduced species have become dominant and are acting as generalists in our networks. Upon removal of introduced plants, robustness will decrease (B) due to loss of their dominant interactions, and specialization will increase (C) due to the removal of their generalist interactions. Native species are expected to contain a wider mixture of dominant/non-dominant and generalist/specialist species, with their removal decreasing robustness less rapidly (B) and decreasing specialization (C).

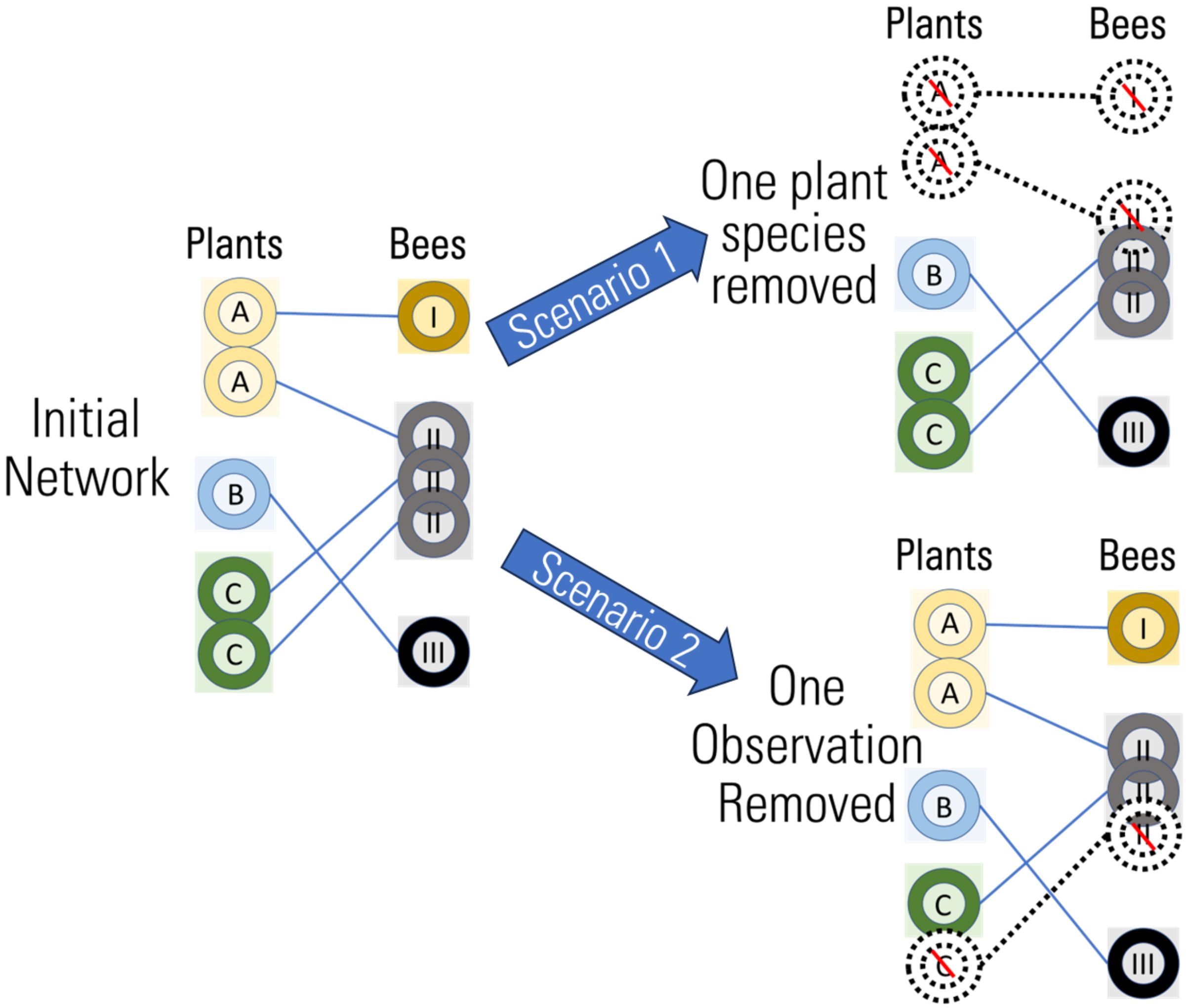

Figure 12. Left: a simplified network pre-removal. Right: the two scenarios of removal, with removed individuals shown with dashed lines and red slashes. Scenario 1 involves iterative removal of a plant species and its associated observations. Here removal of plant A removes bee species I, as well as one individual observation of bee species II. Scenario 2 removes one observation at a time, in this case one individual of plant C which removes an individual of bee species II.

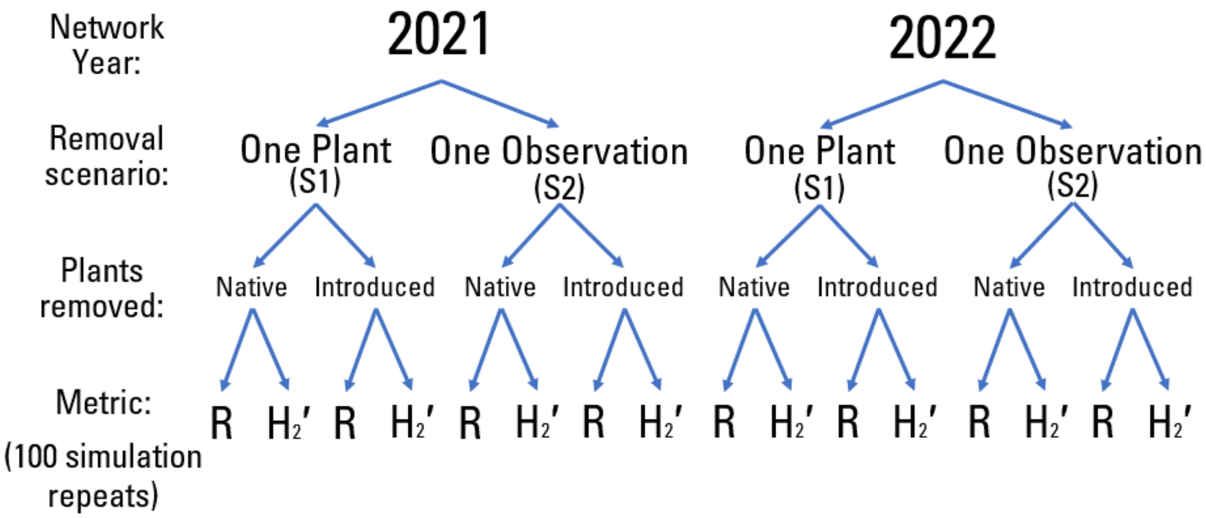

Figure 13. The two removal scenarios and associated runs of simulations that were completed. R represents robustness, and H_2' represents network specialization. S1 and S2 are Scenario 1 and Scenario 2, respectively.

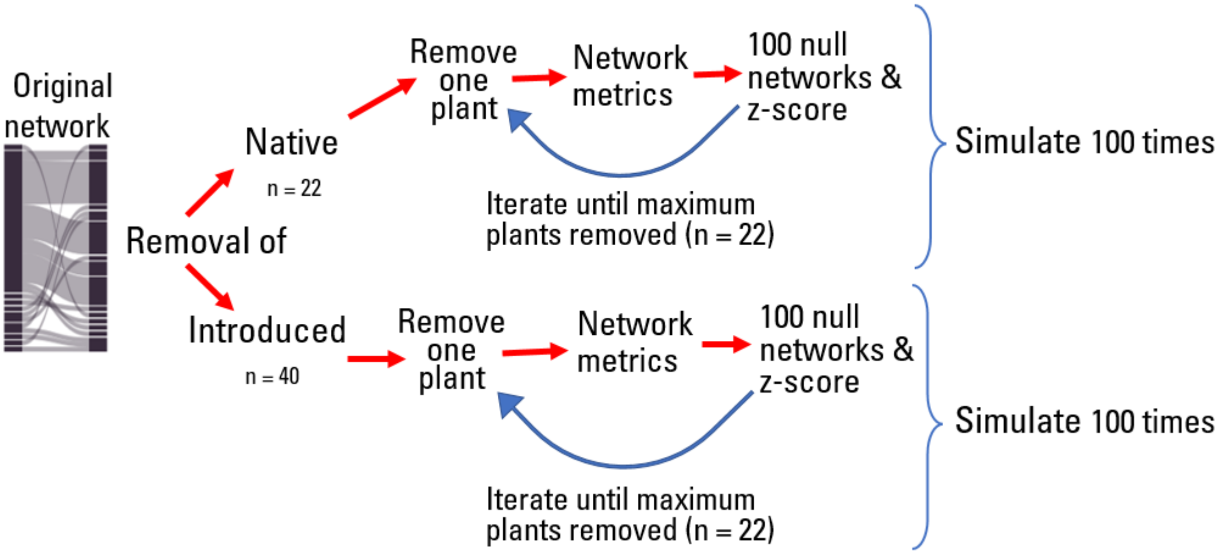

Figure 14. The process of iterative removal of units from the network, using plant removal (Scenario 1) as an example. Note that the maximum number of plant species removed (i.e., iterations) was determined by the lesser of introduced plant richness and native plant richness. Two network metrics (robustness and H_2') and their z-scores were calculated after each plant species was removed, until the maximum number of species (iterations) had been reached.

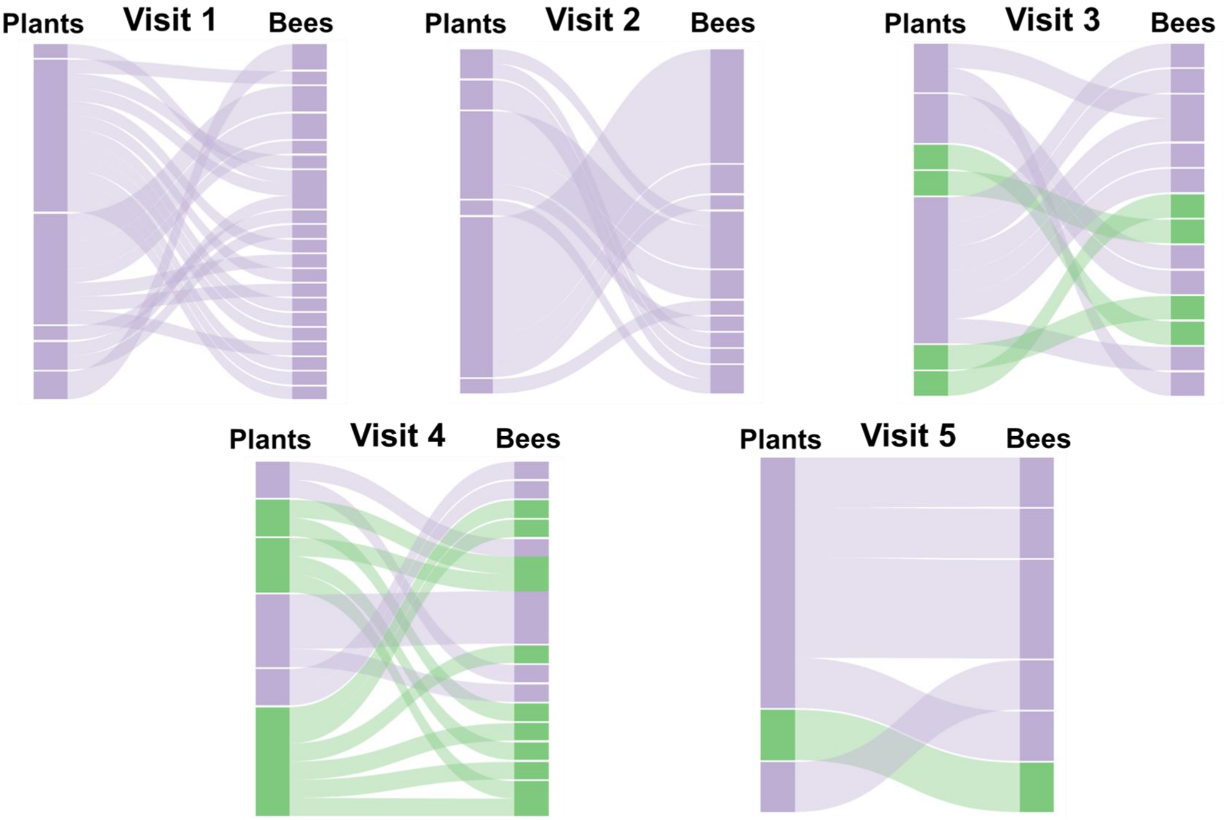

Figure 15. One site's visit level networks in 2021. Plants (left) are connected to bee taxa (right) when a bee was recorded visiting the plant (connection thickness proportional to frequency of interaction). The height of each bar represents the number of times a plant-bee interaction was observed. Purple indicates native plants and their interactions, and green indicates introduced plants and their interactions.

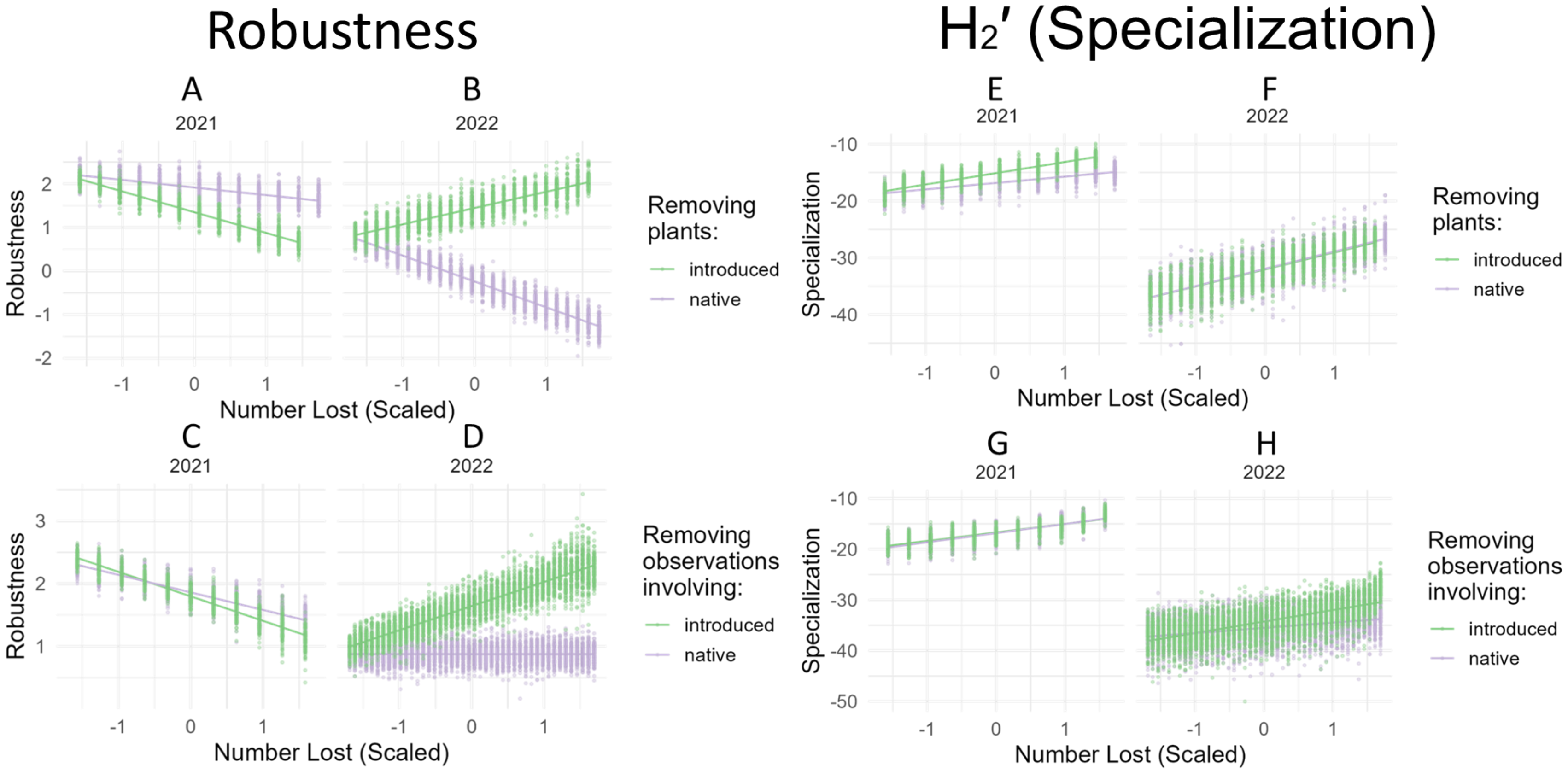

Figure 16. The change in robustness and specialization Z-scores as native plant species (A, E), native plant associated observations (C and G), introduced plant species (B, F), or introduced plant associated observations (D, H), are removed from each network year. The x axis is scaled to allow comparisons in number lost between network years of different sizes. In 2021, removing introduced plants decreased robustness faster than removing native plants (A), but not for observations (C). In 2022, removing introduced plants increased robustness relative to removing native plants (B) and observations (D). Removal consistently increased specialization, and in 2021, removing introduced plants increased specialization faster than removing native plants (E), but there was no difference when removing observations (G). In 2022, there was no difference between removing either type of plant species (F), but removing introduced observations increased specialization slightly faster than removing native associated observations (H).

Tables

Table 6. Glossary of network terms, and computational functions. Definitions are summarized from Dormann et al., 2009.

Term	**Definition**	**Relevance**
Level	One of the two groups of species that make up bipartite networks (i.e., links in the network are between levels).	This study's networks are bipartite, with one level being pollinators, and the other being plants.
Robustness	Network metric describing ability to randomly lose species, without secondary losses; calculated using the *second.extinct()* function (see below)	Provides a measure of network capability to absorb random loss of species without collapse (i.e., a measure of stability)
second.extinct() (function)	Function from *bipartite* package; calculates the number of species in one level of the network that are lost as species are randomly removed from the other level one-at-a-time.	Used with *robustness()* to calculate all robustness values in this study
robustness() (function)	Function from *bipartite* package; calculates network robustness, converts the rate from *second.extinct()* into a value (i.e., area under the curve)	Used with *second.extinct()* to calculate all robustness values in this study
H_2' - Network specialization	Measures whether species are interacting randomly (e.g., by abundance) or instead by other criteria (preferred species, morphological specialization etc.)	Provides a measure of the ecological complexity of networks; species in random networks are interchangeable, while specialized networks require relationships between taxa, potentially involving taxa of conservation concern
H2fun()	Function from *bipartite* package to calculate H_2' (network specialization)	Used to generate all H_2' values in this study
Null model	Randomizes networks according to null hypotheses	Provides a way to compare observed networks that differ in size by standardizing them against randomized networks
shuffle.web()	Function from *bipartite* package to randomize observed network,	Generated the randomized networks used to calculate z-scores in this

	while keeping the amount of interactions constant	study
Z-score	Describes how many standard deviations an observation falls from the mean of a distribution	Z-scores are used to compare an observed network to a distribution of randomized networks created using null models
Nestedness	A metric describing to what degree uncommon species in networks visit (or are visited by) a subset of highly visited (or highly visiting) species	Nestedness is thought to be related to robustness, and high nestedness is a common property of networks
Generalization	Inverse of specialization	Implies network interactions are due to simple probabilities of interaction based on abundance, or describes a species' tendency to interact with many other species

Table 7. Results of models evaluating the impacts of introduced and native species on robustness and specialization in site visit networks of 2021 and 2022. To avoid model instability, models MR6 and MH6 were split into a and b variants. A simplified version of model MH4 (MH4s) was created to ensure that AIC comparisons with model MH6a/b were reasonable (i.e., ensuring MH4 did not contain non-significant predictors driving up the AIC). Selected models are bolded.

Model	Predictor variables	AIC
MODEL SET 1 - Robustness (2021)		
MR0.1	**Intercept only**	**82**
MR1	Quantity of bees interacting with native plants	84
MR2	Introduced inflorescence abundance & native inflorescence abundance	86
MR3	Introduced plant species richness & native plant species richness	86
MODEL SET 2 – Robustness (2022)		
MR0.2	**Intercept only**	**161**
MR5	Introduced plant species richness & native plant species richness	164
MR4	Introduced inflorescence abundance & native inflorescence abundance	164
MR6a	Quantity of bees interacting with introduced plants	162
MR6b	Quantity of bees interacting with native plants	163
MODEL SET 3 – H_2': Network Specialization (2021)		
MH3	**Quantity of bees interacting with introduced plants & quantity of bees interacting with native plants**	**135**
MH2[1]	Native plant species richness	142
MH1	Introduced inflorescence abundance & native inflorescence abundance	143
MODEL SET 4 – H_2': Network Specialization (2022)		
MH6b	**Quantity of bees interacting with native plants**	**205**
MH4s	Native inflorescence abundance	207
MH4	Native inflorescence abundance & introduced inflorescence abundance	209
MH6a	Quantity of bees interacting with introduced plants	210
MH5	Native species richness + introduced species richness	212

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[1] Model MH2 failed to fit when including introduced plant richness and was fit without the offending term.

Table 8. The selected models for specialization site visit samples in 2021 (model MH3) and 2022 (model MH6a). In model MH3, specialization related positively to quantity of bee interactions with both native and introduced plants. In model MH6a, specialization increased as the quantity of bees interacting with native plants increased. Both models also include a random effect of sample visit.

Term	**Estimate**	**P**
Selected Specialization Model (2021): <u>MH3</u>		
Intercept	-1.25	0.09
Quantity of bees interacting with native plants	0.17	**<0.01**
Quantity of bees interacting with introduced plants	0.13	**<0.01**
Selected Specialization Model (2022): <u>MH6b</u>		
Intercept	-1.14	0.099
Quantity of bees interacting with native plants	0.04	**0.01**

Table 9. The number of bees, bee species and plant taxa that made up constructed yearly networks. Also included is the percentage of the top 10 most visited plant species that were introduced, and the proportion of the top 10 interactions by abundance that involved introduced plants (counts are displayed in brackets). In 2021, introduced and native plants made up a similar proportion of the most common interactions, while in 2022, introduced plants made up a smaller proportion than native plants.

Year	**Number Bees**	**Bee Taxa**	**Plant Taxa**	**Percentage Introduced Species in Top 10**	**Percentage Introduced Plant-Bee Observations in Top 10**
2021	791	139	62	50% (5)	43% (198)
2022	1646	157	71	30% (3)	24% (273)

Table 10. (next page). Removal model results. Removal had differing impacts on robustness and specialization, related to interactions between plant type, scenario, and treatment year. In 2021, removing both introduced plant associated observations and plant species decreased robustness relative to removing native equivalents. In 2022, removing both native plant associated observations and species decreased robustness relative to removing introduced equivalents. Removal positively impacted network specialization in all cases, but only small effect sizes differentiated the impact of removing each of the two plant types for each scenario.

		(a) Robustness		(b) Specialization	
Removal unit	**Term**	**Estimate**	**p**	**Estimate**	**p**
Plant species	Intercept	1.348	**<0.001**	-15.13	**<0.001**
	Number lost (scaled)	-0.48	**<0.001**	1.97	**<0.001**
	Network year[2]	0.10	0.15	-16.90	**<0.001**
	Removing native plants[3]	0.57	**<0.001**	-1.72	**<0.001**
	Number lost * network year	0.85	**<0.001**	1.02	**<0.001**
	Number lost * removing native plants	0.30	**<0.001**	-0.85	**<0.001**
	Network year * removing native plants	-2.25	**<0.001**	1.82	**<0.001**
	Number lost * network year * removing native plants	-1.27	**<0.001**	0.90	**<0.001**
Observation (single bee)	Intercept	1.80	**<0.001**	-16.70	**<0.001**
	Number lost (scaled)	-0.39	**<0.001**	1.68	**<0.001**
	Network year[2]	-0.15	**0.005**	-17.58	**<0.001**
	Removing native plant associated observations[3]	0.06	0.30	-0.13	0.31
	Number lost * network year	0.78	**<0.001**	0.58	**<0.001**
	Number lost * removing native plant associated observations	0.11	**0.003**	0.13	0.28
	Network year * removing native plant associated observations	-0.83	**<0.001**	-1.11	**<0.001**
	Number lost * network year * removing native plant associated observations	-0.50	**<0.001**	-1.36	**<0.001**

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[2] The reference network year was 2021

[3] The reference condition was removing introduced plants

Chapter 4 – Summary

In this thesis, I set out to investigate whether predicted negative impacts of global change can be detected in the pollination systems of previously unstudied camas meadows in the West Kootenay region of BC. I focused on potential impacts of climate change via phenological shifts (Forrest, 2015), and of invasive species via disruption of pollination networks (Vanbergen et al., 2018; Parra-Tabla & Arceo-Gómez, 2021). To assess whether phenological shifts were altering synchrony between camas and its pollinators, I used a pollen limitation experiment to assess pollination related reproductive output of camas over an elevation gradient varying in phenology. To examine whether invasive species altered pollination network structure, I collected plant-pollinator interaction data in camas meadows which varied in quantity of introduced plants, built plant-pollinator networks, and related the resulting network metrics to plant community. I also simulated the removal of introduced species to examine potential impacts of invasive species control.

In Chapter Two, I found a slight, non-significant trend towards pollen limitation of camas at lower elevations, but camas generally received enough pollen to maximize its seed production given the resources available. I did not find evidence that synchrony is at risk of disruption across the elevation gradient, as bees were available before, after, and during camas bloom at all sites. One interesting finding is that seed production declined overall as elevation increased, suggesting camas reproduction is limited by growing conditions as it approaches its high elevation range limit. The marginally significant pollen limitation observed at low elevation supports this idea, with pollination approaching being the limiting factor as conditions become less harsh.

In Chapter Three, I did not find evidence that introduced species alter either the ability of networks to resist disturbance, or patterns in the specialization of species at the network level. In one of the network years, where introduced species were key members of the network, their subsequent removal led to a decline in the ability of the network to resist species loss. However, in the year where sampling more completely described the pollination network, and camas was a dominant network member, this relationship was not observed, with native species removal decreasing the ability of the network to resist species loss faster than removal of introduced species. This result suggests that conservation of camas populations is crucial to maintaining network robustness, though if dominant invasive species are to be removed from camas meadows as part of restorations, consideration should be given to replacing invasive floral resources with native floral resources possessing shared phenology and the ability to support many pollinators.

Together, these results suggest that while the aspects of global change we studied do have the potential to impact this system, they are not currently enacting strong negative forces upon pollination. It is possible that pollination has already declined in this system, but historical data to study such a question does not exist. Our data should be useful as a baseline for future studies to compare to, given that global change effects are likely to persist. In fact, climate change is predicted to cause spring to continue to advance earlier, with weather (i.e., spring conditions conducive to pollination) becoming less predictable (Gehne et al., 2016). It remains to be seen whether a tipping point will be reached when either plants or pollinators can no longer track the rate of climate change and phenological asynchrony occurs (Forrest, 2015).

Invasions are also occurring at a higher rate than in the past (Ricciardi, 2007) and do not appear to be slowing down (Seebens et al., 2017). This raises the possibility that novel introduced species could invade camas meadows, including invasive plants possessing characteristics associated with declines in native plant pollination (Vanbergen et al., 2018). In addition to the impacts we studied, camas meadows face a third driver of global change: land-use change. There have already been major shifts in this region, with the installation of dams altering the hydrology of the rivers (Bottom et al., 2005, Irvine et al., 2015) and permanently flooding much of the low elevation floodplain habitat. The vegetation of the southern part of the region also experienced major alteration due to air pollution during the early 1900s (Archibold, 1978). The most immediate threat facing camas meadows is development, yet these meadows lack any formal protection, and if studies of this region are completed in the future, the loss of habitat may be the most alarming impact of global change. My work provides justification for conservation, highlighting the diversity of plants and pollinators present, plus their involvement in complex pollination networks, and describing the intact provision of pollination services.

My research has explored the resilience of camas meadows to two potential global change impacts. The ability of camas to reproduce successfully while supporting many bees provides optimism for the ability of these meadows to self-sustain well into the future. Pollination networks in camas meadows are currently structurally sound, though when introduced species have become highly visited network members, their removal has the potential to disrupt network structure. However, camas itself is the most visited floral resource, and appears to be the key to retaining both network structure, and the pollination function of these meadows.

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Appendices

Appendix A: Data associated with Chapter 3 network modeling.

Table A1. Data used to model network metrics for the 2022 network samples, including their site and visit, network z-scores, measures of native and introduced plant abundance and richness, and quantity of bees interacting with plants. Sampling visits with NA (missing) values for robustness or specialization were excluded from analysis.

Sampling visit	Site	Robustness (Z score)	Specialization (Z score)	Introduced plant species	Native plant species	Introduced inflorescence abundance	Native inflorescence abundance	Quantity of bees interacting with native plants	Quantity of bees interacting with introduced plants
1	G	0.02	1.50	1	4	1	4107	13	0
2	G	0.14	2.07	3	13	2	3872	43	0
3	G	1.01	2.59	5	12	2	4041	46	0
4	G	-1.73	3.43	4	12	2	2766	37	0
5	G	-0.33	1.26	9	13	40	1484	26	1
6	G	-0.13	5.31	10	8	2043	432	10	28
7	G	1.35	2.84	7	6	247	462	17	8
1	A	NA	NA	1	1	0	12	8	0
2	A	0.98	1.06	2	3	0	335	14	1
3	A	-1.65	-0.11	2	3	0	238	18	0
4	A	NA	NA	2	0	200	0	0	11
5	A	NA	NA	2	1	1703	1	0	18
6	A	-0.20	2.07	3	0	2956	0	0	30
7	A	-0.31	2.18	4	2	154	194	22	8
8	A	-1.88	1.43	1	2	8	242	17	5
1	D	-0.83	0.05	1	4	0	156	19	0
2	D	2.48	-1.30	5	7	35	675	10	0
3	D	-0.08	2.45	4	6	59	2904	25	0
4	D	0.48	2.34	3	6	18	4144	51	0
5	D	-1.21	2.55	6	8	12	630	28	2
6	D	-1.24	6.58	3	6	10	2441	28	3
7	D	2.88	3.76	10	6	713	2161	28	21
8	D	NA	NA	5	5	587	151	0	9
1	H	-0.33	0.11	0	5	0	954	27	0
2	H	-0.37	4.12	0	8	0	1813	26	0
3	H	-2.01	4.13	0	12	0	2825	69	0
4	H	-1.32	3.33	0	15	0	3433	41	0
5	H	-1.10	2.76	0	14	0	2577	33	0
6	H	0.89	1.21	3	12	53	831	9	6
7	H	0.47	3.52	2	9	85	956	5	11

8	H	0.66	1.60	2	2	109	713	8	16
1	B	0.25	-0.61	7	2	14	70	2	12
2	B	-1.04	3.04	6	3	45	435	30	5
3	B	NA	NA	5	2	30	2782	37	0
4	B	-1.15	1.19	6	1	16	0	5	1
5	B	-0.66	5.60	3	1	899	0	10	21
6	B	-0.85	0.81	4	0	9231	0	0	11
7	B	0.80	2.55	5	0	505	0	0	15
1	F	-1.21	1.25	4	6	2	180	7	11
2	F	-1.37	0.81	7	7	6	782	17	0
3	F	1.22	0.29	5	8	6	893	35	1
4	F	-0.17	2.66	7	8	7	297	25	0
5	F	-0.36	2.47	8	7	4	135	31	0
6	F	-0.69	1.70	8	9	273	139	9	34
7	F	-1.22	4.01	7	5	509	193	20	16
8	F	-0.74	0.89	6	3	258	38	0	21
1	C	NA	NA	5	3	6	595	0	3
2	C	0.00	-0.94	8	3	20	4545	18	1
3	C	-2.31	4.95	8	3	50	4574	34	3
4	C	-1.18	0.35	9	4	7	375	2	7
5	C	0.07	2.43	7	2	806	1	1	33
6	C	-1.66	3.84	7	2	2626	3	1	27
1	E	0.71	NA	5	6	3	377	3	1
2	E	1.18	1.08	5	13	4	3000	43	0
3	E	-0.82	-0.48	4	12	3	4051	51	0
4	E	0.70	2.82	4	13	3	1331	42	0
5	E	-1.26	1.50	7	16	22	231	21	0
6	E	NA	NA	7	11	3436	157	1	1
7	E	-1.54	1.94	10	8	8245	409	12	7
8	E	-0.29	-0.35	5	5	137	68	0	17

Table A2. Data used to model network metrics for the 2021 network samples, including their site and visit, network z-scores, measures of native and introduced plant abundance and richness, and quantity of bees interacting with plants. Sampling visits with NA (missing) values for robustness or specialization were excluded from analysis.

Sampling visit	Site	Robustness (Z score)	Specialization (Z score)	Introduced plant species	Native plant species	Introduced inflorescence abundance	Native inflorescence abundance	Quantity of bees interacting with native plants	Quantity of bees interacting with introduced plants
1	G	0.37	1.24	3	11	2	2233	0	25
2	G	-1.06	4.99	7	12	3	2011	0	23
3	G	-1.38	-0.54	8	8	28	166	4	10
4	G	-0.63	0.05	7	9	119	229	11	8
5	G	-1.07	1.15	4	4	5	10	1	6
1	D	1.99	0.26	3	9	12	912	1	24
2	D	-0.54	2.25	4	9	0	211	0	15
3	D	0.65	0.25	6	8	3	227	1	18
4	D	0.20	3.20	8	4	33	260	0	23
5	D	NA	NA	2	5	2	94	1	1
1	H	-0.35	-0.43	0	10	0	580	0	12
2	H	0.23	3.16	0	16	0	1646	0	25
3	H	0.46	4.75	2	10	3	1374	1	28
4	H	-0.36	0.59	1	8	50	1546	3	14
5	H	0.17	-1.08	1	3	34	24	9	2
1	B	-0.98	-0.90	4	2	17	46	1	5
2	B	-0.62	2.26	4	3	202	15	9	19
3	B	0.02	1.53	4	2	233	4	10	0
4	B	0.23	0.69	4	2	192	2	10	1
5	B	-0.32	2.39	4	2	53	135	18	6
1	F	0.76	1.98	6	12	5	790	0	36
2	F	-0.39	5.53	6	11	2	261	0	20
3	F	0.37	1.61	5	7	5	34	8	15
4	F	0.14	-1.19	5	4	179	69	19	6
5	F	-0.65	-0.65	2	2	3	22	0	3
1	C	-0.56	2.99	9	4	22	1398	16	17
2	C	1.04	0.83	10	4	25	46	6	2
3	C	-1.50	0.90	7	2	96	13	30	2
4	C	0.65	2.34	11	0	165	0	19	1
5	C	0.50	0.67	3	0	51	0	6	0
1	E	NA	NA	2	16	2	5727	0	32
2	E	-1.56	6.24	7	20	5	435	2	35
3	E	-0.90	5.43	5	10	632	253	19	8
4	E	-1.20	7.41	4	10	1371	326	45	8
5	E	NA	NA	3	2	20	78	0	9

Appendix B: Plant-pollinator network visualizations

Figure B1. A visualization of the 2021 network used for simulation analyses, intended to show relative proportions of interactions involving native (purple lines) and introduced (green lines) plants plus display the diversity and complexity present. Each bar represents a species, with plants on the left, and bees on the right. Lines connect species observed interacting.

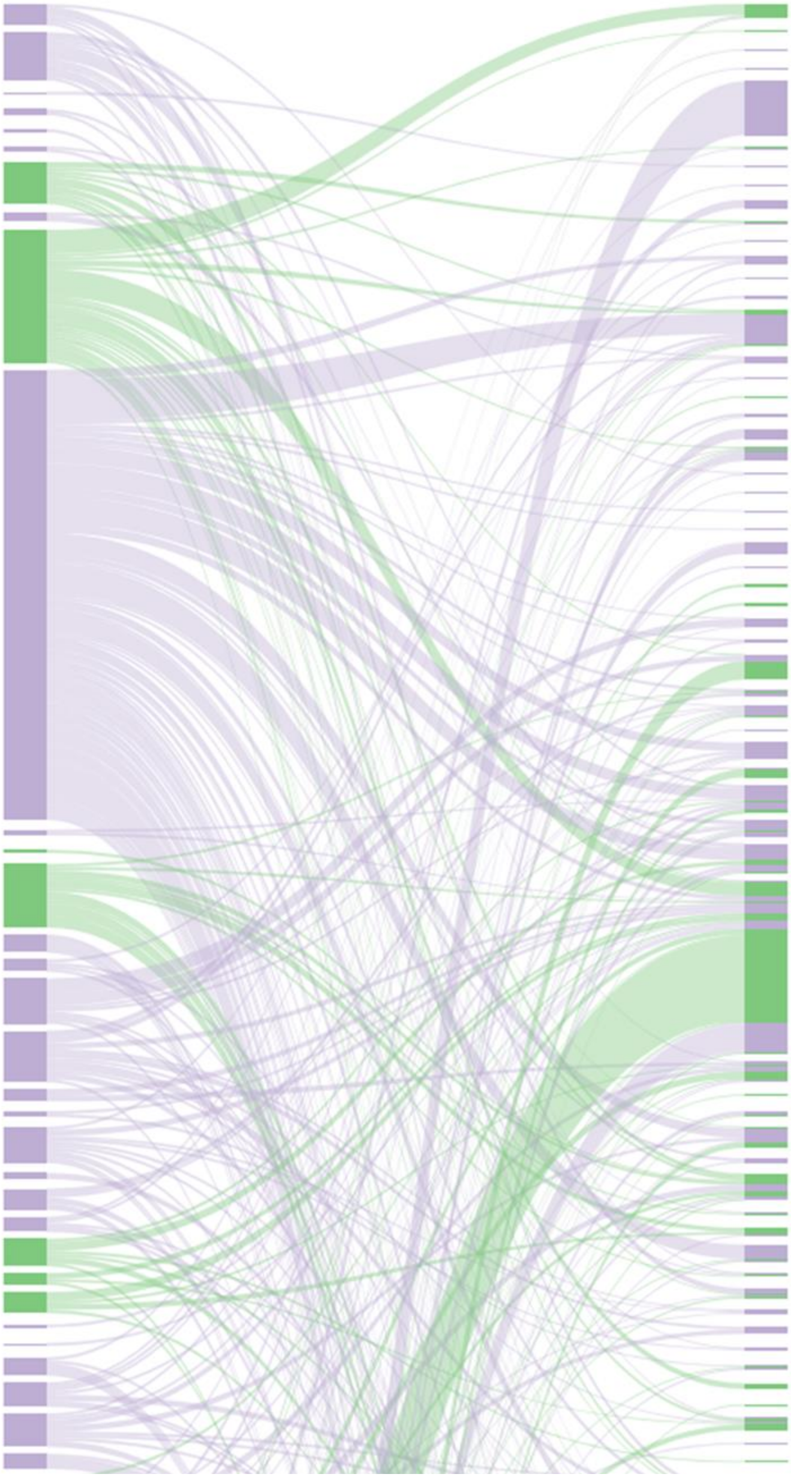
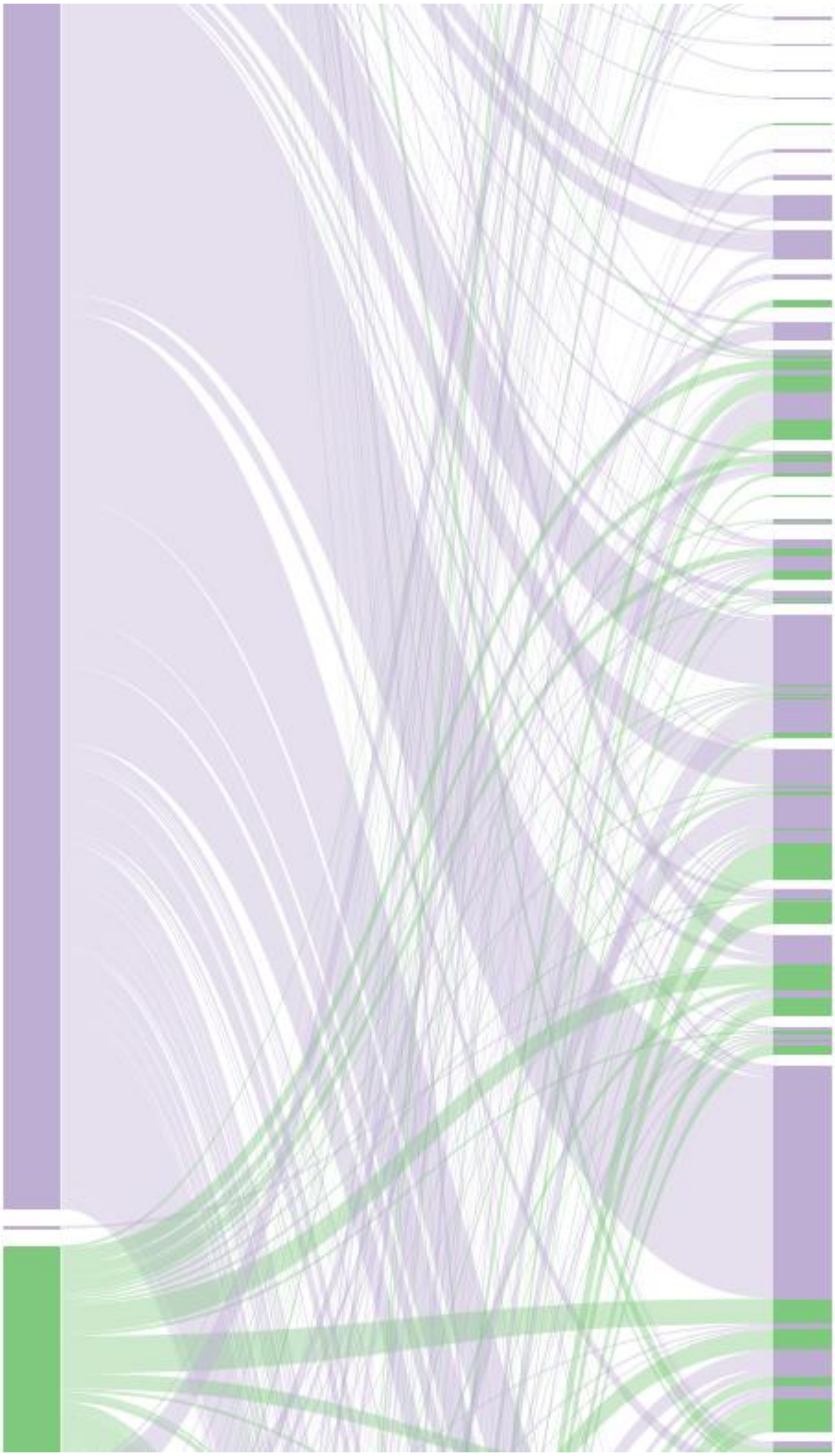
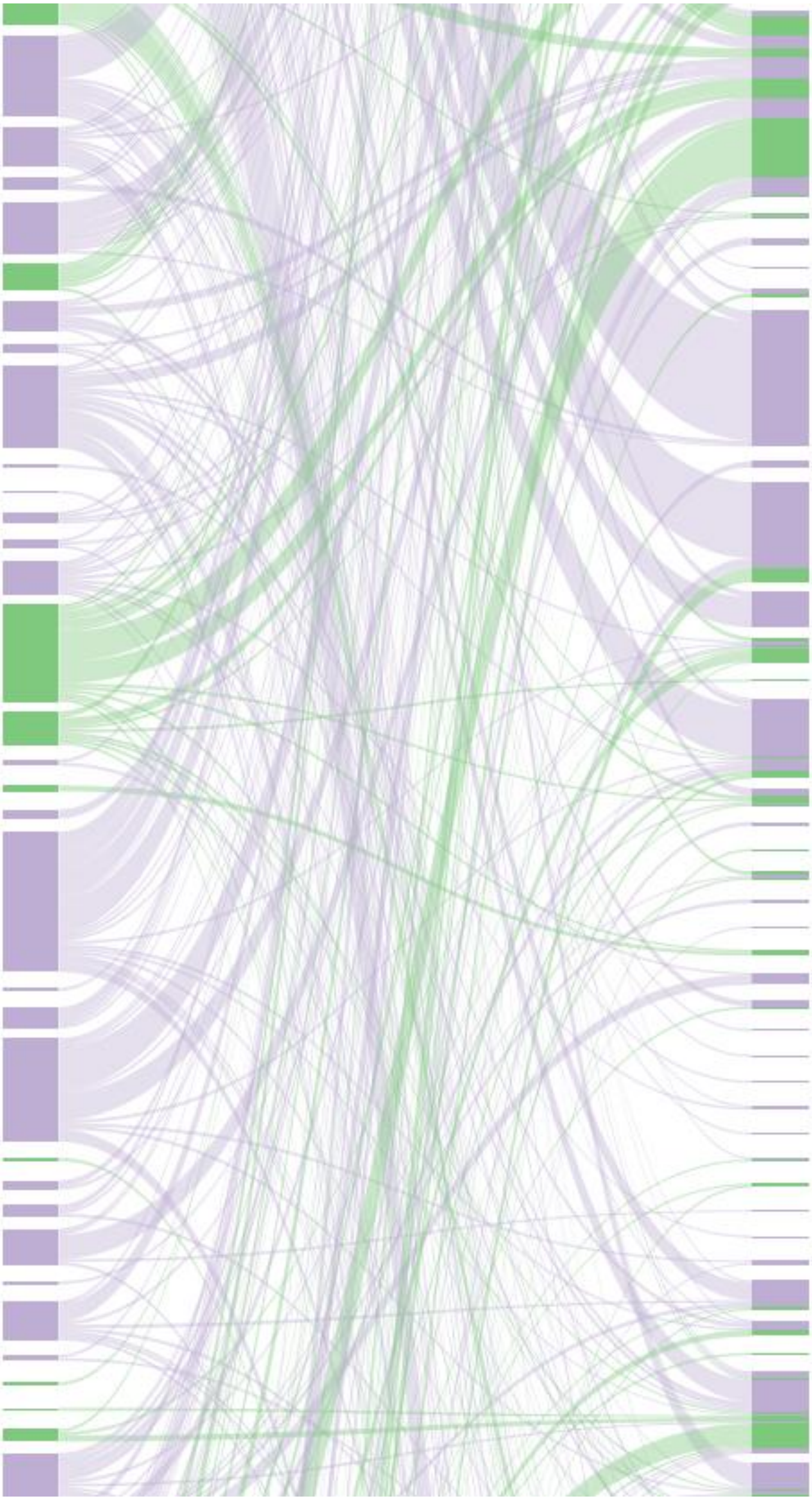
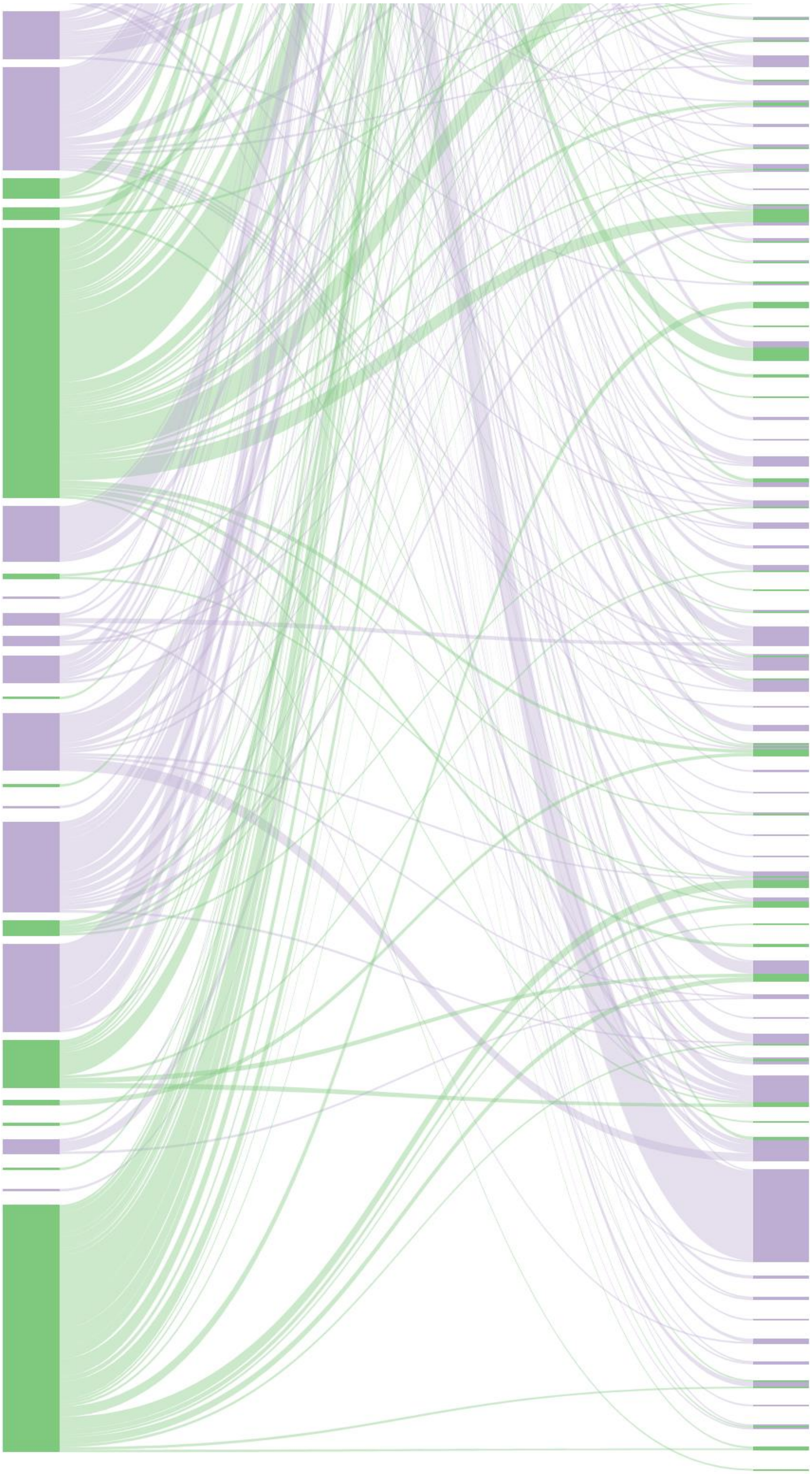


Figure B2. A visualization of the 2022 network used in simulation analyses, intended to show relative proportions of interactions involving native (purple lines) and introduced (green lines) plants plus display the diversity and complexity present. Each bar represents a species, with plants on the left, and bees on the right, lines connect species observed interacting.







Appendix C: Camas meadow photographs

Figure C1. Images of camas meadows: A) high elevation meadow on slopes of mountain, B) Camassia quamash portrait, C) low elevation meadow near river, D) Andrena males on camas waiting for weather to improve, E) Bombus occidentalis visiting camas, F) hand pollination with inset camas stigma. Photos by R. Rampton except where noted.