Committee Page

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Mechanisms of Coexistence Between Native and Exotic Plant Species

submitted by Jens Johnson in partial fulfillment of the requirements for the degree of Master of Science in Geography

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Abstract

One of the primary goals of ecology is to understand the processes that maintain biological diversity. The development of a modern coexistence theory has helped to advance this understanding by proposing a set of specific mechanisms that enable coexistence, specifically, species can coexist when niche differences between species are large enough to overcome fitness differences between species. Recent advances have used fully parameterized demographic studies to explain how traits, phenology, and evolutionary history contribute to niche and fitness differences, but there is a lack of empirical evidence of how competition and the environment interactively influence coexistence outcomes. Moreover, there is little empirical evidence of how indirect interactions between species mediate coexistence outcomes.

Using an outdoor pot experiment and observational data from natural plant communities I explored the interactions between a pair of native (Plectritis congesta) and exotic (Valerianella locusta) co-occurring, annual plant species. With this system I answered the following four questions: (1) Can Plectritis and Valerianella coexist over the long run? (2) Does environmental variation change the intrinsic interaction between these species? (3) Does environmental variation enable coexistence by providing each species with an opportunity for positive low density growth rate in certain spaces or at certain times? (4) Do indirect interactions with pollinators destabilize or promote coexistence?

The pot experiment predicted that Plectritis will exclude Valerianella over the long run. Although the coexistence outcome did not change between environmental treatments, the parameters used to calculate niche and fitness differences experienced significant changes. I did not find any evidence that Valerianella maintains abundances through variation in the environment in natural communities. Additionally, I did not find any evidence that niche differences are decreased through indirect interactions with pollinating insects.

These species are still observed to co-occur at the site level and thus Plectritis may limit, but not totally eliminate, the abundance of Valerianella. Moreover, my experiment showed how vital rates and interaction coefficients depend on the environmental context, emphasizing that abundances are driven not only by competition and environment, but also through the interaction between competition and environment.
Lay Summary

Closely related, functionally similar plant species - native, *Plectritis congesta*, and exotic, *Valerianella locusta* - co-occur in the Garry oak ecosystems of BC. However, their abundances show an inverse relationship at the fine scale, suggesting that one species might competitively exclude the other. Using a combination of experimentation and field data, I quantified the differences between these species that might enable or preclude their coexistence. Due to competitive differences that outweigh niche differences, native *Plectritis congesta* is expected to exclude the exotic *Valerianella locusta*. Although this outcome did not depend on the environmental context of soil moisture, the parameters that are used to estimate niche and fitness differences do shift between treatments, highlighting an interaction between environment and competition that may influence coexistence. Additionally, I found no evidence that indirect interactions mediated by insect mutualists promote coexistence between these species.
Preface

This thesis is original, unpublished work by the author, Jens C. Johnson. Supervision and guidance for this research was provided by Dr. Jennifer L. Williams (UBC Geography).

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Table of Contents

Abstract ................................................................................................................................. iii
Lay Summary ........................................................................................................................ iv
Preface .................................................................................................................................... v
Table of Contents ................................................................................................................ vi
List of Tables ........................................................................................................................ vii
List of Figures ....................................................................................................................... viii
Acknowledgements ............................................................................................................... ix
Introduction .......................................................................................................................... 1
Methods and Materials ......................................................................................................... 4
  Study Species and Study Region ....................................................................................... 4
  Resource Competition Experiment ................................................................................. 5
  Growing Condition Details .............................................................................................. 8
  Field Abundance and Demography Survey ................................................................. 9
  Pollination Experiment to Test for Negative Frequency-Dependence ................... 10
  Data Analysis .................................................................................................................. 10
Results .................................................................................................................................... 13
  Resource Competition Experiment .............................................................................. 13
  Field Abundance and Demography Survey ................................................................. 14
  Pollination Experiment to Test for Negative Frequency-Dependence ................. 18
Discussion ............................................................................................................................. 20
Conclusions ........................................................................................................................ 23
Bibliography ......................................................................................................................... 24
Appendixes .......................................................................................................................... 28
  Appendix 1 ....................................................................................................................... 28
  Appendix 2 ....................................................................................................................... 29
List of Tables

Table 1: Estimates of density-dependent population growth rate parameters……………………14

Table 2: Coexistence predictions from a controlled experiment with dry and wet soil moisture conditions……………………………………………………………………………….15
List of Figures

Figure 1: Experiment Design........................................................................................................6

Figure 2: Pollination Experiment Treatment................................................................................8

Figure 3: Density-dependent seed production of *Plectritis* in *Valerianella*
in dry and wet soil moisture conditions......................................................................................14

Figure 4: *Plectritis* and *Valerianella* abundances in 0.1 m² and 1 m² plots in
Garry Oak plant communities..................................................................................................16

Figure 5: Density-Dependent Seed Production in Natural Plant Communities.............17

Figure 6: Relationships between predicted seed production and variation in
the community and environment composition........................................................................18

Figure 7: Pollen Limitation and Density-Dependence in a Natural Plant
Community....................................................................................................................................19
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Introduction

One of the primary goals of ecology is to understand the processes that maintain biological diversity. In order for diversity to persist, species in biological communities must interact such that they do not drive each other toward local extinction. Consequently, understanding patterns of diversity requires an ability to predict how the abundance of one species will affect the abundance of another. The classic ecological theory of limiting similarity predicts that the most strongly competing species will exclude other species from the community when their resource requirements overlap (MacArthur et al. 1967). This theory has proved useful in predicting the coexistence of species across a range of taxa and climates (Wilson 2007), and has been used to explain non-random patterns of community assembly from the larger regional pool of species (Diamond 1975). However, limiting similarity cannot explain the instances where two seemingly similar species occur in the same community (Godoy et al. 2014b, Thompson 2010).

The development of a modern coexistence theory (Chesson 2000) has helped to resolve the gaps in limiting similarity theory by proposing a set of specific mechanisms that enable coexistence. Modern coexistence theory focuses on identifying two types of species differences that determine the stability of species coexistence: average fitness differences and niche differences (Adler et al. 2007). Average fitness differences are those differences that allow one species to access a shared resource more efficiently than another species. Here, fitness is used in an ecological rather than evolutionary sense, and populations are the unit of comparison rather than individuals (Levine and HilleRisLambers 2009). Niche differences, on the other hand, reduce the degree of overlap in resource requirements between species. Niche differences simultaneously increase intraspecific competition and reduce interspecific competition (Levine and HilleRisLambers 2009). When stabilizing niche differences are greater than average fitness differences, population growth rates exhibit negative frequency-dependence (HilleRisLambers et al. 2012). This prevents the species with highest average fitness from excluding inferior competitors by providing an advantage to growth rate when abundance is low, thereby promoting coexistence (HilleRisLambers et al. 2012). Under this theoretical framework, studies that parameterize population dynamics models with vital rates – the stages in a plant life cycle that influence population growth rates – directly quantify average fitness differences and niche differences to predict community patterns and dynamics. In doing so, these studies identify underlying mechanisms that destabilize or promote coexistence, such as particular functional traits (Adler et al. 2010, Kraft et al. 2015) or phenology patterns (Godoy et al. 2014a).

Modern coexistence studies primarily explore mechanisms of coexistence in species pairs with a history of shared interaction, meaning that the species in those systems have had time to evolve adaptive differences that function to reduce interspecific competition. In contrast, if and how exotic species, those that have been recently introduced to a system, can coexist with similar members of the native
community has been less explored (Germain et al. 2016). In a study of a California annual plant community, only one of 16 native and exotic species pairs were expected to coexist in the long run (Godoy et al. 2014b). In this system, the winner of competition was best predicted by relative differences in growing phenology, regardless of native versus exotic origin (Godoy et al. 2014b). In another case, a native and exotic species pair were projected to coexist through co-evolutionary processes that increase niche differences relative to average fitness differences (Huang et al. 2018).

One major challenge in studying species interactions is that changes in the environment through space and time can influence their outcome. Environmental variation can influence the intrinsic values of vital rates or alter the coefficients of species interactions (Maron et al. 2014), which are used to calculate niche and fitness differences (Godoy et al. 2014b). Consequently, recognizing the environmental conditions in which species interactions occur is critical towards forming conclusions about coexistence that transfer beyond the immediate system of study (Maron et al. 2014).

While environmental heterogeneity within and between communities poses a challenge for forming more general conclusions, environmental heterogeneity within a community may allow for patchy coexistence (Chesson 2000). The storage effect occurs when species hold trait differences that provide a competitive advantage at certain times (Angert et al. 2009, Godoy et al. 2014a) or in certain microsites (Pake and Venable 1995, Adler et al. 2006, Sears et al. 2007, Adler et al. 2009, Staples et al. 2016). The unique responses of species, due to differences in functional trade-offs such as relative growth rate versus water use efficiency, cause environmental conditions and competition to co-vary (Angert et al. 2009). As a result, the abundances of each species in a community can hold positive average growth rates when considered at a broad enough scale (Chesson 1994, Chesson 2000). Thus, through a storage effect, a species pair that is not expected to coexist at the scale of a competition experiment (e.g. Adler et al. 2010 or Godoy et al. 2014b) may still coexist through storage effects (Chesson 2000). Coexistence studies that have complimented competition experiments with data on environmental variability and the abundances of species in different sites (Staples et al. 2016) or different years (Godoy et al. 2014a) find evidence for coexistence through spatial and temporal resource partitioning despite high average fitness difference and low niche difference measured in the coupled competition experiment, showing how species may coexist through partitioning at larger scales beyond those of immediate pairwise interactions.

Indirect interactions with other species also have the potential to shift the outcome of coexistence. One relatively unexplored mechanism of coexistence is through insect-mediated interactions. Modes of pollination are considered to be a major driver of plant diversity by encouraging speciation, but only recently have studies asked if modes of pollination contribute to plant diversity by allowing overlapping species to coexist (Pauw 2012). Plant abundance is tied to insect-mediated pollination through
seed production (Ashman et al. 2004). When plants are pollen limited, i.e. the production of seeds is limited by the quantity or quality of pollen delivery, population growth may cease or decline (Groom 1998). Pollination and mating system evolution have been theorized to promote coexistence in plant communities if these systems cause pollen-limitation to decrease as relative abundance in the community decreases. This pattern would place negative frequency-dependence on population growth rates, thereby limiting the dominance of species that become abundant and providing an advantage to allow populations to rebound when their abundances decline (Pauw 2012). Thus, pollinator niche differentiation could act similarly to niche differentiations that reduce direct interaction for resources (Pauw 2012).

In this study I used experimental and observational approaches to examine evidence for coexistence and the underlying mechanisms between two closely related annual forbs in the Valerianaceae family, *Plectritis congesta* (hereafter, *Plectritis*) and *Valerianella locusta* (hereafter, *Valerianella*). These species, which have similar growth forms and life histories (Jacobs 2010), form a particularly interesting combination for study because they are of different geographic origins. Although they currently overlap in range in western North America where *Plectritis* is native, *Valerianella*, has been recently introduced to the region from Eurasia via escape from cultivated sources (Jacobs 2010). *Plectritis* and *Valerianella* occur at similar rates, present in 13% and 15% of 1 m² survey plots across seven sites in the study region in the oak savanna of southwestern British Columbia, Canada (MacDougall and Turkington 2005). These data show these species co-occur in this region, however, this does not speak to whether these species can coexist.

With this native versus invasive species pair, I tested the competitive effects of conspecific and heterospecific neighbors with an outdoor pot experiment, and corroborated these results with field data on plant abundances, demography, and environmental conditions to answer the following four questions: (1) Can *Plectritis* and *Valerianella* coexist over the long run, and at what spatial scales? I expected the exotic *Valerianella* would competitively exclude *Plectritis* because disturbance and change in this ecosystem where they co-occur has provided opportunities for invasive exotics to come to dominate plant communities (MacDougall and Turkington 2005). If this outcome were supported by the experiment, I would predict that abundances of these species would be negatively correlated in natural plant communities and, furthermore, I would predict that demographic performance of *Plectritis* would be more negatively impacted by *Valerianella* than by its conspecific neighbors in natural plant communities. (2) Does environmental variation change the intrinsic interaction between these species? Because soil moisture is a key limiting factor in this ecosystem (MacDougall and Turkington 2005) - I predicted that changes in the spatial or temporal distribution of water might allow for a greater capacity for niche differentiation - potentially enabling coexistence when this resource availability is high. (3) Does environmental variation enable coexistence by providing each species with an opportunity for positive low density growth rate in certain spaces or at certain times? Because functional trade-offs
may allow species to respond uniquely to environmental heterogeneity (Staples et al. 2016; Angert et al. 2009), I predicted that natural variation in key environmental factors such as soil moisture, soil depth, and/or invasive grass abundance would enable coarse scale coexistence by providing an advantage to each species in different spatial patches (4) Do indirect interactions destabilize or promote coexistence? I predicted that Plectritis pollination would show signs of negative density-dependence because high flower densities may exceed insect-pollinator availability. Since Valerianella is self-pollinating (a density-independent reproduction mode), negative density-dependence in Plectritis pollination would increase niche-differentiation and, thereby, increase the propensity for these species to coexist.

Methods and Materials

Study Species and Study Region

The Garry Oak savanna ecosystem found in southwestern British Columbia is part of a climate and vegetation complex that extends south along Pacific lowlands toward California. Seasonal variation in Pacific Ocean currents creates a sub-Mediterranean climate with wet cool winters and warm dry summers. Climate change projections for the Garry Oak ecosystems are for warmer temperatures throughout the year, with wetter winters but drier summers. Drier, warmer summers may actually increase total suitable area for Garry Oak savannas (Lea 2006). Local-scale environmental heterogeneity including soil depth, soil moisture, and shade cover, drive strong local variability in water availability from a meter to meter or finer scale (MacDougall and Turkington 2005, Vellend 2008). The vegetation of Garry Oak savanna is dominated by grasses and a diverse community of early-spring flowering herbaceous plants (Vellend 2008). Today, native flora typically constitute less than 10% of all species cover in site remnants (Trowbridge et al. 2017), and in some cases, native species have been completely extirpated.

The annual forb Plectritis congesta (sea blush) is native and common in Garry Oak communities (Erickson and Meidinger 2007). Plectritis is a winter annual that lacks dormancy and typically germinates in the fall or, alternatively, in the early spring (Young-Mathews 2012). Plectritis flowers between March and June and then sets seed and dies by the end of the summer (Young-Mathews 2012). Plectritis has floral adaptations to attract pollinators and promote outcrossing, including conspicuous flowers that are visited by pollinating insects such as bees and bee flies, protandrous flowering phenology that separates the production of pollen and the receptivity of the stigma within a flower, and a fragrant odor combined with nectar production (Ganders et al. 1977). The plants are self-compatible, and can self-pollinate in the absence of insects, but seed set of exclusively self-pollinated plants is considerably lower than seed set in populations in the field, meaning that the breeding system of the species has the potential for mixed selfing and outcrossing (Ganders et al. 1977). These plants do not reproduce vegetatively (Ganders et al. 1977).
Valerianella locusta (corn-salad) shares a recent evolutionary history with Plectritis as part of the Valeriana subfamily of the Valerianaceae, and exhibits a similar growth form and phenology. It was introduced to the Pacific Northwest region of North America as early as the 1880’s (Consortium of Pacific Northwest Herbaria 2017) and records indicate that it has spread throughout the Garry Oak ecosystem (MacDougall and Turkington 2005). All plants in this subfamily share traits such as sympetalous, bilaterally symmetric to strongly asymmetric flowers with an inferior, compound ovary. Other shared traits include iridoid compounds contained in the vegetative tissues that may act as anti-herbivory or anti-microbial defenses (Jacobs et al. 2010). Valerianella and several other species in the genus have relatively inconspicuous flowers and are primarily self-pollinating, although flower visitors have been observed including flies, bees, beetles and butterflies (Ernet 1977). Pollinating insects rarely, if ever, visit Valerianella in a natural Garry Oak ecosystem setting (Parachnowitsch and Elle 2005).

Resource Competition Experiment

To determine whether these species can coexist under direct competition (question 1), I set up an outdoor experiment in pots to grow Plectritis and Valerianella in density gradients of conspecific or heterospecific neighbors. From this experiment, I quantified two demographic vital rates to parameterize population dynamic models: density-independent germination rates \( g \) and density-dependent seed production \( F \). Parameter estimates from the population dynamic models – specifically, intrinsic population growth rate \( \lambda \) and intra-/interspecific interaction coefficients \( \alpha \) – were then used to calculate the average fitness differences and niche differences that underlie the outcome of species interaction.

To evaluate species’ germination rates \( g \), I sowed and monitored 432 seeds of each species (72 pots per species with 3 seeds per pot). The germination rates were determined on April 12, 2017, 32-36 days after sowing, by counting the proportion of sown seeds that had successfully germinated and survived (a small number of individuals that germinated but died before producing true leaves at this date were counted as failed germinants). Pots were kept outside on the University of British Columbia campus, Vancouver, BC, and allowed to experience natural environmental and weather conditions during the germination period.

To determine density-dependent seed production \( F \), I also sowed seeds in 7.6 litre pots located outside on the University of British Columbia campus, Vancouver, BC. In the center of each pot I planted 1 focal individual of either species to quantify seed production at the end of the growing season. For each species, I assembled communities at four neighbor density levels: (1) 16 pots with no neighbors; (2) 12 pots with 4 heterospecific neighbors and 12 pots with 4 conspecific neighbors; (3) 8 pots with 10 heterospecific neighbors and 8 pots with 10 conspecific neighbors; and (4) 8 pots with 20 heterospecific neighbors and 8 pots with 20 conspecific neighbors (Figure 1). The background neighbors were initially sown at seeding densities above these levels of 4, 10, and 20, and then thinned following germination so as to ensure sufficient...
densities and consistent spatial arrangements with respect to the focal plants. Higher $n$ for low neighbor densities were selected due to higher expected variation in low-density growth. The densities across the gradient were chosen to bracket natural densities observed in the field (NCC Cowichan Garry Oak Preserve, Duncan, BC, Charlotte Trowbridge, unpublished data).
Figure 1: Experiment Design. (A) *Plectritis* grown against a background of conspecific neighbors or with *Valerianella*. (B) *Valerianella locusta* grown against a background conspecific neighbors or *Plectritis*. These setups were conducted under either wet or dry conditions. I replicated the no competition pots 16 times, the low density pots 12 times, and the medium density and high density pots 8 times.

To explore whether the average fitness differences and niche differences between these species are context-dependent (question 2), I replicated the above density-gradient set up under a different watering regime. As natural rainfall decreased over the course of the experiment, I provided ample water to one treatment group (hereafter, the wet treatment) and decreased watering regularity and duration in the other (hereafter, the dry treatment). Additionally, I erected a 30% shade cloth over the wet treatment block to reduce moisture loss and reduce the high daytime temperatures that occurred during this last time period of the experiment.

I allowed the plants to continue growing under these watering regimes and then collected the seeds of the focal individuals at the end of the growing season. Following the flowering period, plants were observed daily for seed collection. I collected seeds non-invasively from focal plants as they matured, turning from green to brown, by gently shaking the inflorescence over a paper envelope or, when the last seeds were remaining on the last senescing inflorescences, by removing the reproductive structures. All seeds were then cleaned and counted by hand in the lab.

I also collected trait data on the focal individual in each pot. I measured the number of flowers, the number of inflorescences, the height of the flowering stem from base to top of the inflorescence and the main inflorescence size for all of the focal individuals during the peak flowering period. Immediately after collecting the last seeds from a plant, I harvested aboveground biomass to provide supporting evidence for differences in individual growth and performance.

To assess the potential for pollen limitation in the outdoor site, a parallel pollen supplementation experiment was carried out in twenty pots, each with 10 *Plectritis*. In each pot, I deposited pollen to the tips of all receptive stigma of two plants in each pot every other day during the duration of the flowering period (Figure 2). I collected pollen from surplus individuals grown at the experiment site using a fine brush and transferred to the stigma of each flower on the pollination treatment individuals using a toothpick. I collected and counted the seeds as the plants senesced. Seeds of two additional untreated plants from each pot were collected and used for comparison. I also measured the number of flowers, the number of inflorescences, the plant height, and the main inflorescence size for all of these plants.
Growing Condition Details

For both the germination rates and the density gradient, I planted seeds in Sunshine Mix #1 soil medium on March 10th - 13th, 2017. I used 7.6 L planting pots with a diameter of 22.9 cm, depth of 22.9 cm and a 0.041 m² surface area. I obtained *Plectritis* seeds from Saanich Native Plants (Victoria, BC) and *Valerianella* seeds from Salt Spring Seeds (Salt Spring Island, BC). To ensure at least one individual of desired species identity at the center of the pot for data collection, I sowed three focal individual seeds around a marker at the center of the pot. When one of these seeds germinated, the remaining two seeds or germinants were immediately removed from the marker area to eliminate any interaction. The seeds of both species were sown directly on the surface of the soil, as recommended for *Plectritis* (Saanich Native Plants, personal communication; Young-Mathews 2012). Bird netting was placed over the pots to avoid seed predation.

Following the germination period, the pots were arranged on a 10 m x 8 m watering grid. Pots were placed in rows with 23 cm spacing and surrounded with a 15 cm mulch layer to moderate temperature and moisture fluctuations. Water inputs were supplied via Netafim pressure compensated spray stakes (Southern Drip Irrigation), with flow rates of 12.1 litres/hour (recommended by manufacturer for pots of 3.8 - 19 litre size) and a spray radius of ~25 cm. Pots were rotated randomly through the watering grid (within wet or dry treatment blocks) weekly to reduce any effects of small variation in spray stake water delivery. A temporary fence was constructed around the experiment area to deter herbivory from geese or other large animals.
All pots from both treatments were exposed to natural outdoor rainfall conditions from the start of the experiment until June 1, 2017, near when natural precipitation conditions shifted from near daily and constant to infrequent and ephemeral. Precipitation patterns generally become more infrequent and variable later in the growing season in the region’s Mediterranean dry summer climate (Lea 2006). At this date, plants were separated into wet and dry treatment groups. The semi-exposed aboveground pots dry more quickly than the soil, and thus artificial watering was necessary to maintain soil moisture conditions that would occur at ground level without any rainfall. Plants in the dry treatment received no water for 10 days, and then were maintained with 5 minutes of water every other day until the end of the experiment. Plants in the wet treatment received no water for 5 days, and then were maintained with 12 minutes of water every other day from until the end of the experiment. I added 0.25 liters of 100ppm, 20-8-20 fertilizer solution to all pots on June 5th, 2018, to replenish soil nutrients (See Appendix 1 for soil moisture conditions).

**Field Abundance and Demography Survey**

To investigate whether spatial heterogeneity in natural communities might contribute to coexistence through a resource partitioning effect (question 3), I surveyed the abundances and fitness proxies of *Plectritis* and *Valerianella* at three locations in the southeastern area of Vancouver Island, BC: Nature Conservancy of Canada Cowichan Garry Oak Preserve, Thetis Lake Regional Park, and Stoney Hill Regional Park. The meadow in the Cowichan Preserve was managed with a prescribed fire and the plant community is in an early phase of re-establishing (NCC, personal communication). There is no known history of recent, prescribed fire-management where I surveyed at Thetis Lake or Stoney Hill Regional Parks.

Across these three sites I quantified plant abundance and environmental conditions and collected demographic data in sixty-nine 1 m² plots. Additionally, I collected these same data in two smaller 0.1 m² plots nested inside of the 1 m² to investigate correlations at two different spatial scales. In both the smaller and larger plots, I counted the number of *Plectritis* and *Valerianella*. I then measured number of inflorescences, plant height, and main inflorescence size for 10 individuals of each species in each smaller 0.1 m² plot (or as many individuals as possible if there were fewer than 10). I used these measures as proxies for fecundity.

In each plot, I assessed environmental conditions by measuring: soil depth, soil moisture, percent grass cover, percent shrub cover, and species diversity. Using a marked measuring rod, I categorically measured soil-depth in the bottom-right and top-left corners of each plot as either <7.6 cm, between 7.6 cm and 12 cm, and >12 cm. I used a soil-moisture probe to measure percent volumetric water content (%VWC) at the bottom-right and top-left corners of each plot at depths of 7.6 cm and 12 cm. I did not test soil moisture if the soil depth was less than 7.6 cm. I estimated percent grass cover and percent shrub cover by visual approximation. I estimated species diversity by counting the number of species present in each plot.
Pollination Experiment to Test for Negative Frequency-Dependence

To determine whether indirect interactions promote coexistence between these species (question 4), I examined the relationship between conspecific and heterospecific neighbour densities and pollen limited seed set in *Plectritis*. At the NCC Cowichan Garry Oak Preserve field site, I haphazardly selected 24 pairs of *Plectritis* individuals of relatively similar overall size and inflorescence size - and located less than 10 cm apart. Pairs were spaced at distances of 2 m or more from the next nearest pair. I measured the number of flowers, number of inflorescences, plant height, and main inflorescence size of these plants. Furthermore, I collected data on the surrounding conspecific neighbor densities, *Valerianella* neighbor densities and percent grass cover at both the 0.1 m² and 1 m² scales.

I conducted a pollen supplementation treatment on the selected plant pairs to determine if *Plectritis* seed production is limited by the quantity or quality of pollen delivery. *Plectritis* bloomed synchronously at the Cowichan site, with a peak from May 20th to May 31st, 2017. During this time, I carried out 5 rounds of hand pollination on one individual within each pair and allowed the other to be pollinated naturally. Pollen was collected from nearby neighbours using a fine brush and transferred to the stigma of each flower on the pollen supplement treatment individuals using a toothpick. At the end of the flowering period, I covered the inflorescences of all plants with fine mesh bags and supported them in an upright position with a 12” wooden stake. The mesh bag was tied so as to collect any dropped seed between the end of the pollen supplementation treatment and a return visit on June 28th, 2017, to collect seeds. I quantified seed production by counting all seeds in the bag and also those still attached to the inflorescence but matured (enlarged and brown in colour).

Data Analysis

To determine whether these species should coexist in direct competition (question 1), I used the data on the vital rates in the assembled communities to parameterize models of plant abundances. These models estimate both population growth rates in the absence of competition (λ), and the influence of neighbor density and identity on population growth rates (α_conspecific_neighbors and α_heterospecific_neighbors). The population dynamics of an annual plant species with no seed bank can be described as (Chesson 1990, Godoy et al. 2014a):

**Equation 1:**

\[
\frac{N_{i,t+1}}{N_{i,t}} = (1 - g_i) s_i + g_i F_i
\]

Here, \(N_{i,t}\) represents the number of ungerminated seeds for species \(i\). The per capita growth rate for the population ((\(N_{i,t} + 1) / (N_{i,t})\)) is expressed as a function of the average of two vital rates: \(s_i\), the survival of ungerminated seed in the soil, and \(F_i\), the fecundity or the viable seeds produced per germinated individual. These terms are weighted by the average germination of the species, \(g_i\) (Godoy et al. 2014a). To
determine how species affect the performance of one another, the per-germinant fecundity, \( F_i \), can be expanded into a function that considers the effect of competing individuals in the system (Godoy et al. 2014a):

**Equation 2:**  
\[
F_i = \frac{\lambda_i}{1 + a_{ii} g_{i1} N_{i,t} + a_{ij} g_{j1} N_{j,t}}
\]

Here, \( \lambda_i \) represents the per-germinant fecundity in the absence of competition. \( \lambda_i \) decreases when neighboring individuals of either the same species or the other species negatively impact the performance of plants. These interaction coefficients are represented by \( a_{ii} \) (an intraspecific interaction coefficient for species \( i \)), and \( a_{ij} \) (an interspecific interaction coefficient for species \( i \)). I used fecundity data from the experiment to fit equation 2 and then estimated values of \( \lambda \) and \( a \) for both *Plectritis* and *Valerianella* using generalized nonlinear regression with a negative binomial distribution (“gnlr()” function) in the “gnlm” R package.

These demographic measurements were then synthesized into estimates of the stabilizing niche differences and fitness differences that determine the outcome of competition, following Godoy et al. (2014a). Niche overlap (\( \rho \)) is defined as:

**Equation 3:**  
\[
\rho = \sqrt{\frac{a_{jj} \cdot a_{ji}}{a_{ij} \cdot a_{jj}}}
\]

The demographic ratios, which describes the degree to which one species produces more seeds per seed loss due to death or germination, are defined as:

**Equation 4:**  
\[
demographic\ ratio = \frac{\lambda_i \cdot g_i}{1 - (1 - g_i)} / \frac{\lambda_j \cdot g_j}{1 - (1 - g_j)}
\]

The competitive response ratio, which describes the degree to which one species produces more seeds per seed loss due to death or germination, are defined as:

**Equation 5:**  
\[
competitive\ response\ ratio = \sqrt{\frac{a_{jj} \cdot a_{ii}}{a_{ij} \cdot a_{ji}}}
\]

Fitness differences (\( \kappa \)) are defined as the product of the demographic ratio between species and the competitive response ratio between species:

**Equation 6:**  
\[
\kappa = demographic\ ratio \times competitive\ response\ ratio
\]

Finally, coexistence conditions are considered satisfied when:

**Equation 7:**  
\[
\rho < \kappa < \frac{1}{\rho}
\]
Given Equation 7, coexistence is possible when niche overlap ($\rho$) is low, that is, when $\rho$ approaches 0, and the fitness ratio ($\kappa$) is relatively even between species, that is, when $\kappa$ approaches 1.

To determine whether the outcome of interaction is dependent on the resource environment (question 2), I fit Equation 2 using data from the second watering treatment and then re-estimated the population parameter estimates. I used Equations 3, 4, 5, and 6 to estimate new niche differences and fitness differences and then used Equation 7 to again predict whether these species could coexist in the long run. Using this estimation approach, I could calculated confidence intervals for values of $\lambda$’s and $\alpha$’s.

To further address question 1, I used the data from the field surveys on the abundances and fitness proxies for Plectritis and Valerianella. I first tested whether there was a negative relationship between Plectritis and Valerianella abundances at both the 0.1 m$^2$ scale and 1 m$^2$ using a linear model for Plectritis abundance as a function of Valerianella abundance. To meet linear model assumptions of homoskedacity and normality, abundances were log transformed (plus 1 to handle abundances of 0 in the data set).

I fit models for predicting seed production using my seed counts alongside measurements of the number of inflorescences, plant height, and main inflorescence size. For Plectritis, I used the seed counts and measurements from the untreated plants in the field pollination experiment; for Valerianella, I used the seed counts and measurements from the focal individuals in the pot experiment, pooled across all densities, because I lacked seed counts from the field site. I selected the best models for seed count for each species using generalized linear models with negative binomial distributions (“glm.nb()” function) for fitness proxies in the “MASS” R package and comparing AIC scores of all possible nested models. The best model for Plectritis included only plant height as the predictor of seed count, while the best model for Valerianella included number of inflorescences, plant height, and main inflorescence size (Appendix 2). With these two models, I predicted the number of seeds each Plectritis and Valerianella plant in the field plots would produce given the fitness proxies I measured.

I used these predicted seed counts to see how Plectritis and Valerianella seed production was driven by conspecific and heterospecific densities in the field. I used generalized linear models with negative binomial error distribution (“glm.nb()” function) to determine how the density of each species impacted the average predicted seed production of each species. Here, I treated site as a random effect, and did not include the data from Thetis Lake where Valerianella was not found. Next, I used linear models to evaluate the impact of each plant density on the variation in seed production of each species (quantified as the absolute value of the residual). Again, I treated site as a random effect, and did not include the Thetis Lake data. Further, I looked at how the soil moisture and depth conditions, as well as the grass and shrub cover influenced average seed production of each species.
I evaluated whether *Plectritis* and *Valerianella* responded uniquely to environmental heterogeneity (question 3) by determining whether environmental conditions (soil moisture, soil depth, grass cover and shrub cover) differentially influenced either the abundances or predicted seed production in *Plectritis* and *Valerianella* using generalized linear models with negative binomial error distribution ("glm.nb()" function). Here, I treated site as a random effect, and excluded the Thetis Lake data.

To examine the prevalence of pollen limitation and its potential connection to coexistence (question 4), I used data from the field site to evaluate the magnitude and density-dependence of pollen-limited seed set. I tested for the presence of pollen limitation by comparing the AIC scores of nested models for seed production as a function of flowers per plant, with and without pollen treatment included as a fixed-effect (and with spatial area of the NCC Cowichan site held in both models as a random-effect). Some plants made more seeds than flowers which may be due to flowers emerging after the initial counts near the beginning of the flowering phenology window.

The pollen limitation of *Plectritis* would only affect coexistence if its magnitude were density-dependent. To determine if the magnitude of pollen limitation was density-dependent, I first quantified the magnitude of per plot pollen limitation as the increase in seed set of a pollen supplemented plant (relative to its flower number) in comparison to the seed set of the paired untreated plant from the same plot (relative to its flower number). Then, I evaluated the effect of conspecific densities (at 0.1 m$^2$ and 1 m$^2$ scales) on these magnitudes of pollen limitation using a linear model.

All statistics and modeling were done in R, version 3.3.1 (R Development Core Team 2016).

**Results**

**Resource Competition Experiment**

(1) *Can Plectritis and Valerianella coexist over the long run?* (2) *Does environmental variation change the predicted outcome?*

In the competition experiment, I found that seed production for both species was negative density-dependent under all combinations of neighbor species identity and water treatment (Figure 3). Intrinsic population growth rate ($\lambda$) of *Plectritis* was 17% greater in the wet treatment versus the dry treatment, while intrinsic population growth rate ($\lambda$) of *Valerianella* was 110% greater in the dry treatment versus the wet treatment (Table 1). The only value of $\alpha_{xx}$ that changed significantly (non-overlapping confidence intervals) between treatments was $\alpha_{Valerianella \times Valerianella}$ (Table 1). Density-independent germination rates were 67.0% for *Plectritis* and 89.1% for *Valerianella*. 
Figure 3: Density-dependent seed production of *Plectritis* in *Valerianella* in dry (A) and wet (B) soil moisture conditions. Seed production of *Plectritis* (light green) and *Valerianella* (dark green) is plotted for all combinations of competing neighbor species and treatment. Seed production values against *Plectritis* neighbors are denoted with circles, while seed production values against *Valerianella* neighbors are denoted with triangles. Declines in seed production due to intraspecific competition are denoted with solid lines and declines in seed production due to interspecific competition are denoted with dashed lines. Dots were jittered for each neighbor density to improve legibility. Data points for 0 neighbor densities were used to model both intra- and interspecific competition and thus each data point for zero neighbor densities are plotted twice.

Table 1: Estimates of density-dependent population growth rate parameters. Standard deviations for each estimate are noted in parenthesis. See Equation 2 in methods for details on parameter estimation.
The results from the experiment predicted that these species cannot coexist, that is 
Plectritis
will exclude Valerianella in both wet and dry conditions over the long run
(Table 2), although the contribution of the underlying components differed between
 treatments. In the dry treatment, the demographic ratio favored Valerianella, while the
 competitive response ratio favored Plectritis, resulting in an overall fitness ratio that
 favored Plectritis (Table 2). The high niche overlap (low niche difference) in the dry
treatment violates the coexistence conditions (Table 2). In the wet treatment, the
demographic ratio again favored Valerianella, while the competitive response ratio
again favored Plectritis (Table 2). In the wet treatment, the niche overlap decreased;
however, the fitness ratio decreased by 0.18, meaning that Plectritis had an even
greater fitness advantage in the wet treatment (Table 2).

Table 2: Coexistence predictions from controlled experiment with dry and wet soil
moisture conditions. Coexistence is possible when niche overlap (ρ) is low, i.e. when ρ
approaches 0, and the fitness ratio (κ) is relatively even between species, i.e. when k
approaches 1. (See Equations 3, 4, 5, 6, and 7 in methods for details on parameter estimation).

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<td>Fitness ratio (κ)</td>
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<td>0.70</td>
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<td>Outcome (coexistence predicted if: ρ &lt; κ &lt; 1/ρ)</td>
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<td>coexistence not predicted</td>
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</table>

Field Abundance and Demography Survey

(1) Can Plectritis and Valerianella coexist over the long run?

In the natural plant communities I found that the abundances of Valerianella and
Plectritis showed a negative relationship at both the 0.1m² scale (F₁, 105 = 37.69, P <
0.01) (Figure 4A) and at the 1m² scale (F₁, 106 = 18.84, P < 0.01) (Figure 2B). The
highest abundances of Valerianella occurred when Plectritis was absent and likewise
the highest abundances of Plectritis occurred when Valerianella was absent (Figure 4A
and Figure 4B). I did not find Valerianella at one of the sites, Thetis Lake, and as such I
did not include Plectritis abundance data in these analyses.
Figure 4: *Plectritis* and *Valerianella* abundances in 0.1 m² and 1 m² plots in Garry Oak plant communities. Using data from two plant communities where *Plectritis* and *Valerianella* co-occurred, I tested the relationship between *Plectritis* abundance and *Valerianella* abundance at the 0.1 m² scale (A) and at the 1 m² (B). Survey plots from the NCC Garry Oak Preserve are mapped in dark blue, and survey plots from Stoney Hill Regional Park are mapped in light blue.

I examined the effect of *Plectritis* density and *Valerianella* density on predicted *Plectritis* and *Valerianella* seed production and found that *Plectritis* density has a negative impact on predicted *Valerianella* reproductive output ($F_{1, 56} = 9.74, P < 0.01$), but no impact on predicted *Plectritis* reproductive output ($F_{1, 56} = 0.71, P = 0.40$) (Figure 5A). *Valerianella* density has a positive impact on predicted *Valerianella* reproductive output ($F_{1, 55} = 4.50, P < 0.05$) but no impact on predicted *Plectritis* reproductive output ($F_{1, 55} = 0.07, P = 0.79$) (Figure 5C). Although I found no relationship between seed production in *Plectritis* and density of either neighbor species, I found that variation in the number of seeds per *Plectritis* individual is influenced by *Plectritis* density. At low densities, predicted *Plectritis* fecundities range widely. This range of variation tends to...
decrease as the density of *Plectritis* increases ($F_{1, 56} = 13.2, P < 0.01$) (Figure 5B). In contrast, variation in *Plectritis* fecundity does not change across *Valerianella* densities ($F_{1, 55} = 0.01, P = 0.94$) (Figure 5D). I found no evidence for variation in predicted seed production in *Valerianella* with respect to the density of either species (not shown).

![Graphs showing density-dependent seed production](image)

**Figure 5: Density-Dependent Seed Production in Natural Plant Communities.** Using data from two natural communities where *Plectritis* and *Valerianella* co-occurred, I examined the effect of *Plectritis* densities (A) and *Valerianella* densities (C) on predicted seed production of *Plectritis* (light green) and *Valerianella* (dark green). I also tested the impact of *Plectritis* densities (B) and *Valerianella* densities (D) on the variation in predicted seed production of *Plectritis*.

(3) Does environmental variation enable coexistence by providing each species with an opportunity for positive low density growth rate in certain spaces or at certain times?

Grass cover increased the predicted seed production in both *Plectritis* ($F_{1, 49} = 6.62, P < 0.05$) and in *Valerianella* ($F_{1, 55} = 5.02, P < 0.05$) (Figure 6A), but soil moisture at either a depth of 7.6 cm (*Plectritis*: $F_{1, 39} = 2.76, P = 0.10$; *Valerianella*: $F_{1, 43} = 0.18, P = 0.67$) (Figure 6C) or 12 cm (*Plectritis*: $F_{1, 23} = 2.60, P = 0.12$; *Valerianella*: $F_{1, 30} = 0.19, P = 0.67$) (Figure 6D). When I compared fecundity of plants growing in soils
shallower versus deeper than 12 cm, I found that these species exhibited unique responses in regard to soil depth: seed production increased in deeper soils in *Plectritis* ($F_{1, 49} = 7.28, P < 0.01$), but showed no difference in *Valerianella* ($F_{1, 51} = 0.05, P = 0.83$) (Figure 6B). I did not find any relationships between percent grass cover, soil moisture, or soil depth and the abundances of either species.

**Figure 6**: Relationships between predicted seed production and variation in the community and environment composition. I evaluated the relationship between predicted seed production and grass cover (A), soil depth (B), soil moisture at 7.6 cm depth (C), and soil moisture at 12 cm depth (D) for *Plectritis* (light green) and *Valerianella* (dark green) growing in natural plant communities.

**Pollination Experiment to Test for Negative Frequency-Dependence**

(4) Do indirect interactions destabilize or promote coexistence?

I found that including pollination treatment (pollen supplemented versus control) significantly improves a model for seed set given the number of flowers per plant ($\chi^2_{1} = 10.94, P < 0.01$) (Figure 7A). I found that pollen limitation in *Plectritis* was not dependent on conspecific neighbor densities in the surrounding 1 m$^2$ area ($F_{1, 20} = 0.003, P = 0.96$)
or in the surrounding 0.1 \( m^2 \) area \( (F_{1,20} = 1.78, P = 0.20) \) (Figure 7C). The magnitude of *Plectritis* pollen limitation was not dependent on any of the other community and environmental conditions that I considered, including *Valerianella* densities, grass cover, shrub cover and soil moisture.

Figure 7: Pollen Limitation and Density-Dependence in a Natural Plant Community. I evaluated the relationship between seed production and individual flower count for pollen supplemented plants (dark yellow) and untreated control plants (light yellow) (A). I quantified pollen limitation of *Plectritis* as the difference in seeds per flower of control versus pollen supplemented plants, and then modeled its relationship with conspecific densities in the surrounding 1 \( m^2 \) area (B) or in the surrounding 0.1 \( m^2 \) area (C). Some plants made more seeds
than flowers per plant, which may be due to flowers emerging after the initial counts near the beginning of the flowering phenology window.

**Discussion**

Native *Plectritis* is predicted to exclude exotic *Valerianella* over the long run.

The mechanisms that allow a diversity of species to coexist in ecological communities, especially for closely-related and functionally-similar species to coexist in those communities, are still being explored. Theory demonstrates that species must have sufficiently high niche differences and/or sufficiently low average fitness difference to coexist at the scale of direct interaction (Chesson 2000). My experimental and observational data support the hypothesis that these species cannot coexist in direct competition due to low niche differences and/or high average fitness differences. The results from my experiment predict that *Plectritis* will tend to exclude *Valerianella* in the long run, due to a fitness difference imbalance in favor of *Plectritis* that overcomes the margin of niche difference (Table 2). The lack of response of *Plectritis* seed production to densities of either species and the negative response of *Valerianella* seed production to *Plectritis* density (Figure 5A and 5C) suggests that *Plectritis* regulates the abundance of *Valerianella* more strongly than it regulates its own abundance. This supports the idea that *Plectritis* should competitively exclude *Valerianella* abundances where and when they co-occur.

These results are surprising given the exotic origins of *Valerianella*. Previous work shows that between allopatrically derived species, phylogenetic distance has no effect on niche differences while driving an increase in average fitness differences (Germain et al. 2016). Overall, then, the phylogenetic distance between this species pair should drive an imbalance in average fitness that would destabilize coexistence. I would have predicted that in this pair, exotic *Valerianella* would be expected to exclude native *Plectritis* via a higher average fitness, because the competitive effect of invasive species on native species is typically stronger than the effect of native species on invasive species (Vila and Weiner 2004, Maron and Marlor 2008). In this system, it appears that native *Plectritis* may not resist *Valerianella*, but does play a role in regulating its abundance through direct interaction. This result supports previous studies that found that while ecological interactions often do not resist invasions, they can constrain the abundances of invasive species once they have established (Levine et al. 2004).

I found an inverse relationship between the abundance of *Plectritis* and *Valerianella* (at the 0.1 m² and 1 m² scales) across two natural communities (Figure 4), which supports the prediction that these species cannot coexist at the scale of direct interaction. However, these data also acknowledge that *Plectritis* and *Valerianella* co-occur at the site scale (and occasionally at the 0.1 m² and 1 m² scales), which means that other processes must limit the complete competitive exclusion of exotic *Valerianella*. Analyzing other elements of demographic performance that I did not
measure might be important to gain a more complete understanding of how patterns of these species abundances arise. In many systems, populations are more limited by space for seeds to germinate rather than by the production of seeds (Ashman et al. 2004). If this were true for *Plectritis* and *Valerianella*, testing the effect of the density of the plant community on germination rates would contribute to more accurate demographic models, especially in sites where non-native grasses dominant ground cover (MacDougall and Turkington 2005). If density-dependent germination strongly structures the dynamics in this system, it could limit the ability of *Plectritis* to spread locally to exclude *Valerianella*.

Additionally, *Plectritis* showed variation in seed production at low densities and this variation decreased as density increased (Figure 5C). Thus, at low densities the population dynamics of *Plectritis* are possibly linked to demographic stochasticity which can reduce spread rates (Palamara et al. 2016, Sullivan et al. 2017). Along with higher intraspecific competition when densities increase (Pachepsky and Levine 2011) these expansion limitations might also keep *Plectritis* from spreading locally to completely exclude *Valerianella*.

**Soil moisture context changes niche and fitness differences, but not enough to alter the long-term outcome of interaction.**

I conducted my experiment under two different soil-moisture regimes to understand whether coexistence or exclusion was context-dependent. Although the outcome of competitive interaction remained the same in both treatments, I found that niche and fitness differences changed with water availability (Table 1). Environmental drivers such as patterns of precipitation and temperature are being increasingly recognized in their role in predicting species distributions and abundances (Ehrlen and Morris 2015). It has become clear that environmental drivers influence population dynamics through their controls on vital rates and transitions between life cycle stages (e.g. Doak and Morris 2010, Nicole et al. 2011, Dahlgren et al. 2016, Crone et al. 2018), that is, through the demographic potential of a species as quantified here. This experiment shows that environmental drivers can also influence population dynamics by altering the sensitivity of species to competition from neighbors. Changes in competitive interaction coefficients that are not proportional between species will alter the second half of the fitness difference between species, the competitive response ratio. Because a change in the fitness difference that overcomes the niche difference may change whether a species pair can coexist, understanding species abundances and distributions also requires knowledge of how the environmental context will shape aspects of intraspecific competition relative to interspecific competition. The results from this experiment, along with other context-dependent coexistence outcomes, highlight the potentially narrowed scope of studies of niche and fitness difference as measured under one set of controlled environmental circumstances (e.g. Staples et al. 2016), or niche and fitness difference as measured across environmental conditions in
heterogenous field-based experiments (e.g. Godoy et al. 2014a and Godoy et al. 2014b).

Although it was not enough to shift the outcome towards coexistence for these species, niche differences increased in the wet versus the dry treatment. Although the functional mechanism that increased the niche difference is unknown, increased soil moisture may have allowed these species more room to differentiate water acquisition through space or time. Phenology in invasive and native plants in another Mediterranean climate system plays a large role in coexistence, with relatively later growing species excluding earlier growing species through a fitness advantage (Godoy et al. 2014a). However, increased within-species variation in phenology or decreased overlap of between-species phenology might increase niche differences, and thus promote coexistence. Comparisons between the phenologies of the plants in my wet versus dry treatments might provide a link between the change in the environmental context and the change in the estimated niche difference.

Due to an inability to determine natural conditions in advance of the experiment, my wet treatment was in actuality wetter than any of the plots surveyed at the three field sites (Appendix 2) while the dry treatment was near the average soil moisture conditions observed. Presuming that the field measurements taken this year were representative of typical years, this means that the dry treatment represents average soil moisture conditions while the wet treatment represents a wet extreme. It would be interesting to test the outcome of competition with a third, drier extreme treatment. Given that the gap between fitness and niche differences decreased in the dry treatment here, if this trend were to continue, coexistence would be predicted under drier conditions.

**Plectritis and Valerianella respond similarly to variation in environmental conditions, with the exception of soil depth.**

Separately from the balance between niche and average fitness differences, spatial or temporal heterogeneity may allow species to coexist (Chesson 2000). I observed co-occurrences of *Valerianella* with *Plectritis* at the site scale (and occasionally at the 0.1 m² and 1 m² scales) (Figure 4); this may be explained by spatial or temporal heterogeneity that provides an advantage to *Valerianella* in particular places or at particular times. I did not however, observe any evidence for a unique response of *Valerianella* that would promote stable abundances. I did not observe any influence of soil moisture on the fecundity or abundances of either species in the field. Perhaps soil moisture is too variable at the local scale and two readings from a 0.1 m² plot are not fully indicative of the conditions that these plants are experiencing, or alternatively, the measurements from one time period may not reflect the soil moisture conditions of the entire growing season. Deeper soil depths improved the seed production of *Plectritis*, but not *Valerianella*. This unique response of *Plectritis* and inflexible response of *Valerianella* would provide an advantage to the already dominant *Plectritis*, furthering its ability to exclude *Valerianella*. Grass cover had a positive effect on seed production per plant of both species. It would be interesting to separate out the relationship between
grasses and the performance of these species by grass origin or functional type to test if invasive grasses are related to increased *Valerianella* performance but not *Plectritis*, since particular suites of interacting species may moderate coexistence through intransitivity (Stoufer et al. 2018). Alternatively, the diversity of co-occurring plants may be a more identifiable metric of experienced environmental difference versus abiotic measures (Staples et al. 2016).

**Indirect interactions do not stabilize coexistence**

I investigated whether indirect interactions via pollinators might stabilize coexistence. Although I found evidence for the presence of pollen limitation in a natural plant community (Figure 7A), its occurrence was not density-dependent (Figure 7B and 7C). Thus pollination dynamics are unlikely to affect competitive interaction coefficients in this system. However, the presence of pollen supplementation (if imposed through increased pollinator activity) or further pollination loss (through loss of pollinators in the community) would affect the intrinsic rate of population growth (\(\lambda\)) and thus might shift the outcome of coexistence via the average fitness difference.

**Conclusions**

My experiment predicts that native *Plectritis* excludes invasive *Valerianella* where they co-occur because of an average fitness advantage that outweighs the margin of niche difference between these species. These results are supported by the influence of *Plectritis* densities on *Plectritis* and *Valerianella* fecundities in natural plant communities. These species are still observed to co-occur at the site level and thus *Plectritis* may limit but not totally eliminate the abundance of *Valerianella* in natural plant communities. Some possible explanations for this pattern are that other population dynamics not considered here such as density-dependent germination rates and demographic stochasticity may limit the spread of *Plectritis* at the local level, limiting its ability to interact with *Valerianella*. I found no evidence for a storage effect that allows *Valerianella* to maintain stable abundances at the site scale, but more encapsulating or specific measures of abiotic and community patterns may be able to provide evidence for this mechanism of coexistence. Furthermore, I found no evidence for indirect interactions with pollinators to provide a density-dependent population response that would regulate *Plectritis* abundances and stabilize coexistence. Moreover, my experiment showed how vital rates and interaction coefficients depend on the environmental context, emphasizing that environmental conditions drive abundances through density-independent mechanisms (demographic potential), but also through density-dependent mechanisms (niche difference and competitive response). To make more generalizable and transferable conclusions, future coexistence studies should consider the context of interaction.
Bibliography


Appendices

Appendix 1: Soil moisture conditions for competition experiment. I watered the plants every other day for 5 and 12 minutes for the dry and wet treatments during June and July. I used data from the pots gathered on an afternoon in early July on a day where the plants received water and again on the following day when the plants did not receive water and then I compared the % VWC at 7.6 cm depth for the dry and wet treatment groups to confirm the effectiveness of my different watering regimes using a two-sample t-test.

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Appendix 2: Model selection for seed production in *Plectritis* and *Valerianella*. I chose the best models for seed production based on the lowest relative AIC score (bolded and starred).

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