

**SPATIAL HETEROGENEITY IN NATURAL SELECTION AND LOCAL  
ADAPTATION TO UNGULATE HERBIVORY IN *PLECTRITIS CONGESTA***

by

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## Abstract

Understanding how organisms respond to environmental change via genetic and plastic responses can help predict species occurrence and persistence in changing landscapes. I quantified phenotypic and genotypic variation in the annual plant *Plectritis congesta* to test for the effects of spatial variation in ungulate herbivory on plant traits. I first surveyed 285 island and mainland populations in British Columbia, Canada, to estimate how ungulates, climate, and population isolation affect fruit phenotype and plant height. I then tested for local adaption in common gardens open to and protected from deer, and for adaptive plasticity in common gardens protected from herbivores, using populations exposed and naïve to ungulate herbivory. I then estimated genetic variance, heritability, evolvability and plasticity for plant height, shape and branch number, and assessed how these traits changed in response to intraspecific competition. Ungulate occurrence explained substantial population-level variation in phenotype, but climate and isolation had minor effects. In island populations, plants naïve to ungulate browsers were 2.6 times taller and 3.4 times more likely to produce winged fruits than plants from historically exposed populations. I observed local adaptation in common gardens open to and protected from herbivores, wherein plants from naïve populations were three times more abundant than plants from exposed populations after five years of protection from browsing. In contrast, plants from exposed populations survived three times better and were twice as fecund as plants from naïve populations when browsed, due to later bolting and flowering. Trade-offs in plant height and fecundity occurred in response to intraspecific competition: height increased 1.5 to three times as density increased but led to a ~20-30% decrease in fecundity. Moderate additive genetic variance and evolvability in traits under selection suggest a capacity for rapid evolution in 2-18 generations, similar to that shown in island populations of other taxonomic groups. My results suggest that spatial heterogeneity in browsing

by ungulates can drive local adaptation in *P. congesta* populations, resulting in context-dependent trade-offs that influence fitness and elicit adaptive plasticity. Existing variation between island populations of *P. congesta* has the potential to provide long-term stability when faced with rapid environmental change.

## Lay Summary

Garry oak and maritime meadows of the Georgia Basin are one of the most threatened ecosystems in British Columbia and are distributed throughout an island archipelago. My work demonstrates that the presence or absence of ungulates on these islands is likely the main factor causing observed population-level differences in the plant *Plectritis congesta*. Specifically, plants from islands with ungulates are short with mostly wingless fruits and survived best in environments with ungulates, whereas plants from islands without ungulates are taller with mostly winged fruits and survived best in habitats without ungulates. The timing of when plants increased height was a key contributor to the differences in survival but resulted in trade-offs between herbivore avoidance and competitive ability for light and pollinators. With rapid environmental changes, the existing variation between populations has the potential to provide long-term stability for the species and help maintain diversity within Garry Oak and maritime meadows.

## Preface

The observed patterns of trait variation in the Gulf Islands was first observed by Dr. Peter Arcese over a decade ago. He documented observations of fruit phenotype from 2005 onwards and conducted the first common garden experiment at Totem Field in 2006. I joined in 2013 to conduct the exclosure experiment on Sidney Island, which was an idea initially conceived by Dr. Peter Arcese. Subsequently, Dr. Arcese and I have worked together to develop research questions and experimental design to complete a geographic survey of *Plectritis congesta* populations throughout the Georgia Basin, establish the methodology for the Sidney Island exclosure experiment, establish a second common garden in Totem Field (2015), and conduct numerous growth chamber trials. Since 2013, I have collected much of the data, with Dr. Arcese often accompanying to assist in data collection and help further develop the research questions. I conducted all the statistical analyses, often accompanied by conversations with Dr. Arcese and my doctoral committee to enhance the analyses relative to the research question being addressed.

A version of chapter 2 has been published. Skaen, C. L. and Arcese, P. (2018) Spatial variation in herbivory, climate and isolation predict plant height and fruit phenotype in *Plectritis congesta* island populations. *Journal of Ecology*, 106: 2344-2352. Dr. Arcese and I conceived the ideas, designed methodology and collected the data. I analyzed the data. I wrote the initial manuscript, with substantial editing contributions from both Dr. Arcese and myself.

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## Dedication

I dedicate this thesis to the dozens of animals (both domestic and wild) that I have had the pleasure of sharing my life and unconditional love with over the past 3 decades. I secondly dedicate my thesis to the mountains and forests of British Columbia, and elsewhere around the world, that I have had the luxury of exploring for leisure and work. Without these animals and these ecosystems, my passion for biology would not exist.

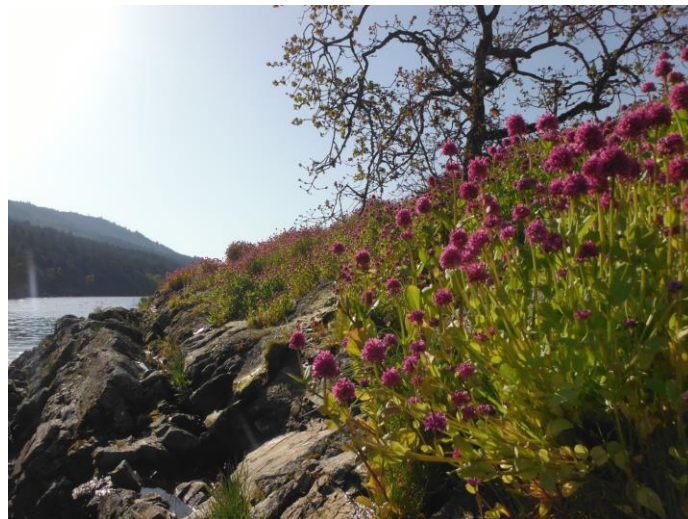


Photo credit: Cora Skaien

# Chapter 1: Introduction

## 1.1 Rationale

Understanding mechanistic drivers of evolutionary change and factors that influence differences in traits observed within and between populations is critical to predicting how species or populations will respond to changing environmental conditions (Endler 1980, Lande and Shannon 1996, Aitken and Whitlock 2013, Germain et al. 2018). For specific species or ecosystems, more studies are needed that describe: (1) environmental factors driving local adaptation in nature (e.g., Hughes et al. 2008; Whitlock 2015); (2) the degree to which canalized responses versus adaptive plasticity is expressed within locally adapted populations (Valladares et al. 2014, Palacio-López et al. 2015); and (3) the influence of these factors on population persistence and species distribution (Aitken et al. 2008, Franks et al. 2014, Bonamour et al. 2019). In this thesis, I investigate potential drivers of rapid evolutionary change and local adaptation in morphology and phenology of the annual plant *Plectritis congesta* in island and mainland populations in threatened Garry oak and maritime meadow ecosystems of western Canada. My main hypothesis is that the presence or absence of ungulate herbivores in island populations has driven differences in phenology and morphology in *P. congesta* via local adaptation and adaptive plasticity. To investigate this hypothesis, I estimate (1) influences of multiple environmental factors on morphology, (2) the genetic contributions to phenology and morphology, (3) the potential for rapid adaptation, and (4) the potential for adaptive plasticity in morphological and phenological traits in response to intraspecific competition with plants from contrasting selective environments (i.e., populations with and without ungulate herbivores). Additionally, by investigating local adaptation, adaptive phenotypic plasticity, and the likely role of gene flow between populations in different



environments, I am able to suggest ways to augment genetic diversity of populations requiring conservation and restoration (Rice and Emery 2003, Weeks et al. 2011, Aitken and Whitlock 2013).

In the following sections, I provide an overview of relevant background information pertaining to my main hypothesis. I first review background theory and empirical work related to genetic variation and natural selection, local adaptation, phenotypic plasticity, temporal and spatial heterogeneity in natural selection, and influences of herbivory and competition on plant traits. I then describe my study system and study species. Finally, I outline my thesis chapters and key hypotheses.

## **1.2 Background**

### **1.2.1 Genetic Variation and Natural Selection**

The strength and direction of natural selection depends on both the selective agent and the amount of genetic variation present within a population or species (Wright 1968, 1982). Natural selection can be particularly effective in large populations where genetic variation is often high, and differential fitness of alleles allows for adaptive evolution (Wright 1982). Genetic variation can increase in populations slowly via mutation (de Vries 1901) or more quickly through gene flow, both of which can increase genetic variation (Grant and Price 1981, Wright 1982) and can facilitate adaptation in response to environmental change (Barrett and Schluter 2008). The pace of adaptive evolution can sometimes be rapid (e.g., beak size in *Geospiza fortis* in 22 years, Grant and Grant 2006; scape length in *Primula farinosa* in 8 years, Ågren et al. 2013; toe pads of *Anolis* lizards in 20 generations, Stuart et al. 2014; floral attractiveness to pollinators and conspicuousness to

herbivores in *Brassica rapa* in 8 generations, Ramos and Schiestl 2019), with changes occurring in only a few to hundreds of generations (Hendry and Kinnison 1999, Reznick and Ghalambor 2001, Hendry et al. 2008). Rapid adaptation is more likely to act on standing genetic variation than on mutations, given low mutation rates for most species (Barrett and Schluter 2008).

Conversely, genetic variation can be depleted if natural selection was strong historically and eliminated alleles with low fitness (Barton and Turelli 1989). This may prevent populations from responding to future environmental change or lead to local extirpation (Gomulkiewicz and Holt 1995, Kellermann et al. 2009). Genetic variation can alternatively be reduced through rapid environmental change, reducing population size and creating genetic bottlenecks (i.e., periods of time when allelic diversity is low, Willi et al. 2006; e.g., song sparrows, Keller et al. 1994, 2001; Marr et al. 2006). Neutral processes such as random genetic drift can also reduce genetic variation, leading to the fixation of alleles by chance, particularly in isolated populations experiencing little to no gene flow (Kimura 1962, Willi et al. 2007). Ultimately, sufficient genetic variation is necessary for adaptive evolution to occur, but strong natural selection or neutral processes can deplete genetic variation.

### **1.2.2 Local Adaptation and Phenotypic Plasticity**

Natural selection can lead to local adaptation, in which the mean fitness of resident ('local') genotypes in their local environment is higher than that of nonresident ('foreign') genotypes originating from other habitats (i.e., local vs foreign comparison, Kawecki and Ebert 2004). Local adaptation has been commonly observed (Hereford 2009), particularly in plant species (Leimu and Fischer, 2008; e.g., *Chamaecrista fasciculata*, Galloway and Fenster 2000; *Carlina vulgaris*,

Becker et al. 2006; *Clarkia xantiana*, Gould et al. 2014). Locally adapted traits can substantially enhance local fitness, but also reduce fitness when expressed in novel environments (fitness trade-offs and cost of phenotype; e.g., Bennett and Lenski 2007, Callahan et al. 2008, Rodríguez-verdugo et al. 2014, Murren et al. 2015, Bontrager and Angert 2018). Understanding how local adaptation arises and is maintained in metapopulations (e.g., loci influencing coat colour and predation risk in mice, Barrett et al. 2019) is necessary to predict population responses to environmental change, and to identify potential limits on species distribution (Endler 1980, Lande and Shannon 1996, Siepielski et al. 2013, Olivieri et al. 2016).

Most traits are influenced by both genetics and environment, and the degree to which trait expression is influenced by environmental conditions is referred to as phenotypic plasticity (Bradshaw 1965, Schlichting 1986). Locally adapted traits may express phenotypic plasticity given that (1) plastic changes in a trait can have a genetic basis that is often adaptive (Hendry 2015) and (2) habitat quality and annual variation in conditions impact plant performance dramatically (Maschinski et al. 1997, Siepielski et al. 2009, 2011). Three main types of phenotypic plasticity have been described: (1) perfect adaptive plasticity, where a similar phenotype is expressed in the same environment regardless of population of origin (i.e., no local adaptation observed); (2) adaptive plasticity, where resident and nonresident populations respond similarly but maintain baseline differences between populations (can be paired with local adaptation), and (3) nonadaptive plasticity, where populations demonstrate plastic responses that reduce their fitness compared to ancestral phenotype or is in a maladaptive direction (Levins 1968, Ghalambor et al. 2007). Phenotypic plasticity provides insight to the range of environmental conditions a particular population can persist in without requiring natural selection to optimize traits through canalized

responses (Lande 2015, Bonamour et al. 2019, Fox et al. 2019), but many studies suggest that phenotypic plasticity may not be sufficient or adaptive to future changes (e.g., Duputié et al. 2015). Investigating both local adaptation and phenotypic plasticity of traits is therefore particularly informative to our understanding of the mechanisms causing population differentiation in temporally or spatially heterogeneous environments, yet investigating both aspects in the same populations has garnered little attention until more recently (e.g., Becker et al. 2006, Franks et al. 2014, Gould et al. 2014, Merilä and Hendry 2014, Valladares et al. 2014).

### **1.2.3 Temporal and Spatial Heterogeneity in Natural Selection**

Trait expression and phenotypic divergence can be influenced by temporally varying selection and by gene flow between populations in spatially heterogeneous environments (Siepielski et al. 2009, 2013). Gene flow introduces genetic variation into populations, which enhances the evolutionary potential of a population to respond to temporal variation in selection (e.g., Lenormand 2002). However, high levels of gene flow between populations in patchy environments subject to opposing selective pressures can lead to gene swamping, which can impede adaptive divergence and local adaptation (Slatkin 1987, Lenormand 2002, Débarre et al. 2013, Siepielski et al. 2013). This impediment can be particularly strong in marginal or edge populations (Garcia-Ramos and Kirkpatrick 1997, Alleaume-Benharira et al. 2006). Divergence in phenotypes and genotypes can persist in adjacent patches experiencing gene flow if natural selection is sufficiently strong to select against less fit immigrants or hybrids and thus reduce the potential for gene swamping (Slatkin 1985, Star et al. 2007). With consistent or strong natural selection, population-level differences in trait expression are commonly observed in island populations where barriers to gene flow exist that facilitate adaptation through restricted gene flow (Wright's Shifting Balance Theory, Wright

1982; Warren et al. 2015). As a result, island populations may be particularly susceptible to changing conditions if gene flow is insufficient to re-introduce the genetic variation required for natural selection to act on. However, these populations may persist if traits exhibit adaptive plasticity. Sultan and Spencer (2002) suggest that plasticity is in fact favored over canalized local adaptation if migration is common between populations in spatially heterogeneous environments. Scheiner (2013) suggests that plasticity can be particularly strong with spatial variation in abiotic and biotic conditions and migration between islands. Consequently, recent studies have highlighted the importance of incorporating phenotypic plasticity in models predicting population persistence (Chevin et al. 2010). This is also relevant in considering the rate of gene flow between populations in spatially heterogeneous environments when predicting locally adapted responses (Ronce and Kirkpatrick 2001, Débarre et al. 2013).

#### **1.2.4 Herbivory and Competition**

Herbivory affects plant fitness and is widely suggested to drive local adaptation in traits linked to a plant's ability to resist or tolerate herbivores (e.g., Stinchcombe and Rausher 2001, Vourc'h et al. 2001, Prendeville et al. 2015). Resistance traits enhance survival by reducing the probability of herbivory, whereas tolerance traits enhance relative fitness by improving the capacity for regrowth and reproduction given herbivory (van der Meijden et al. 1988). Resistance and tolerance traits have been demonstrated in response to herbivory from insects (e.g., in *Oenothera biennis*, Johnson et al. 2009; *Asclepias incarnata*, Agrawal et al. 2008; *Asclepias syriaca*, Bingham and Agrawal 2010), rabbits (e.g., *Arabidopsis thaliana*, Weinig et al. 2003) and ungulates (e.g., *Odocoileus virginianus*, Martin et al. 2015). Such traits include delays in bolting and maintaining a short stature (e.g., *O. biennis*, Parker et al. 2010), delays in flowering (e.g., *O. biennis*, Agrawal et al.

2012; *Brassica rapa*, Schiestl et al. 2014), reducing the flowering period (e.g., *Impatiens capensis*, Martin et al. 2015), increasing the production of branches following herbivory (e.g., *Impomopsis aggregata*, Paige and Whitham 1987, Juenger and Bergelson 2000; *Thuja plicata*, Stroh et al. 2008) and chemical defenses to deter herbivores (e.g., *T. plicata*, Vourc'h et al. 2001). Many species use resistance and tolerance traits in a mixed defense strategy to co-exist with herbivores (Núñez-Farfán et al. 2007), but the expression of these traits can lead to fitness trade-offs when grown in herbivore-free environments.

Plants that exhibit traits to resist herbivory often exhibit decreased competitive ability. For example, *Tithonia tubaeformis* populations appear to trade-off resistance to herbivory (shorter stem) for increased competition for light (longer stem, Boege 2010). Intraspecific competition is hypothesized to result in stem elongation at high planting densities as a response to increased shading via adaptive phenotypic plasticity (e.g., Casal and Smith 1989), but this adaptive response comes at a fitness cost (Dudley and Schmitt 1996). Similarly, *Primula farinosa* produced shorter scapes that were less likely to be browsed where ungulates were present, but produced taller scapes that were more attractive to pollinators where ungulates were absent (Ågren et al. 2013). The presence of both bee pollinators and herbivores selected for self-compatibility and increased selfing rates in *Brassica rapa*, but in the absence of herbivores, bee pollinators selected for increased floral attractiveness (Ramos and Schiestl 2019). Trade-offs in the fitness value of traits that increase plant tolerance or resistance to herbivory or increase competitive ability for light or pollinators are therefore likely to occur in plant populations distributed throughout archipelagos, where variation in island size, isolation and history enforce marked spatial variation in the

occurrence of ungulate browsers (e.g., Gonzales and Arcese 2008, Martin et al. 2011, Arcese et al. 2014).

### **1.3 Study System and Species**

#### **1.3.1 Study System: Garry Oak and Maritime Meadow Ecosystems**

The Garry oak maritime meadows comprise a patchy ecosystem once distributed throughout the Georgia Basin and Willamette Valley of western North America (BC MELP 1993, GOERT 2012), with only 1-5% of its original extent remaining (Fuchs 2001, Lea 2006). This severe degradation is due to human land conversion and the cessation of First Nation's land management (BC MELP 1993, Lea 2006, GOERT 2012). The most intact sites are currently found along the Georgia Basin of British Columbia, many of which are on islands and islets of various size throughout the San Juan or Gulf Island Archipelagos (Bennett et al. 2012, 2013, Bennett and Arcese 2013, Bennett 2014).

In many parts of the Georgia Basin, deer densities have increased well-above historic levels. Ungulates historically occurred at low densities prior to the arrival of European settlers (Arcese et al. 2014). Ungulate densities increased because of the introduction of novel diseases reducing the populations of Indigenous peoples and the subsequent cessation of Indigenous land stewardship (Koch et al. 2019), and dramatic increases in the abundance of domestic, exotic, and native herbivores in association with the extirpation of large predators (Hatter and Janz 1994, MacDougall 2008, Martin et al. 2011, Arcese et al. 2014). Subsequently, deer densities are now as high as ~100-150 deer/km<sup>2</sup> (McTaggart Cowan 1945, Hatter and Janz 1994, MacDougall 2008,

Martin et al. 2011, Arcese et al. 2014). Such densities reduce native plant species occurrence and diversity (Gonzales and Arcese 2008). The persistence and recovery of native herbaceous and woody species in this ecosystem will likely require deer densities  $\leq 7\text{-}10$  deer/km<sup>2</sup> (Martin et al. 2011, Arcese et al. 2014). However, islands in the Georgia Basin have either high ungulate densities ( $>10$  deer/km<sup>2</sup>, typically on larger islands without deer predators or hunting), no ungulate herbivores (typically smaller, semi-isolated islands that lack sufficient resources to sustain resident deer populations) or temporally varying ungulate densities with ungulates briefly visiting or residing in an area before relocating.

### **1.3.2 Study Species: *Plectritis congesta***

*Plectritis congesta* (Lindl.) DC (seablush, Valerian family) is an iconic winter annual of Garry oak maritime meadow and savanna habitats of Northwestern North America. Within this ecosystem, it frequently co-occurs with camas spp. (*Camassia quamash*, *C. leichtlinii*), death camas (*Zigadenus venenosus*), monkey flower spp. (*Mimulus guttatus*, *M. alsinoides*), shooting star (*Dodecatheon* spp.), white fawn lily (*Erythronium oregonum*), nodding onion (*Allium cernuum*), brodiaea spp. (*Brodiaea coronaria*, *B. hyacinthina*), and many other species. *Plectritis congesta* also often co-occurs with deer and other ungulate species (e.g., sheep), but can be rapidly extirpated under high grazing pressure (Gonzales and Arcese 2008). This species is highly variable throughout the range, expressing two fruit phenotypes and substantial variation in plant height and flowering phenology.

Inflorescences of varying size are found at the end of the terminal branch and any additional side branches in *P. congesta*. These inflorescences can contain as few as one and as many as over one hundred flowers that will produce fruits when fertilized. *Plectritis congesta* is pollinated by an



abundance of insects, but can also self-pollinate, with an estimated outcrossing rate of 48-75% in island populations near Nanaimo, BC where pollinators are abundant (Ganders et al. 1977a). Each *P. congesta* plant produces one of two fruit phenotypes, with or without wing-like appendages (Ganders et al. 1977a, Jacobs et al. 2010), based on Mendelian dominance at a single locus with two alleles (Ww, WW = winged, ww = wingless, Ganders et al. 1977a, Carey and Ganders 1980). The two fruit phenotypes tend to vary in size, with winged fruits being larger than wingless fruits due to the wing-like appendages. As a result, inflorescence size and fruit phenotype are likely to impact herbivore attraction and pollination success, given previous findings that larger inflorescences in other plant species attract more pollinators and increase outcrossing rates, but conversely decrease survival in the presence of herbivores (Ågren et al. 2013, Ramos and Schiestl 2019). At present, the main dispersal mechanisms for *P. congesta* fruits is unknown, but wind, water and animal dispersal likely contribute.

Variation in plant height and flowering phenology have been observed in *P. congesta* throughout the Pacific Northwest of North America. Carey (1983) reported high heritabilities for plant height ( $h^2 = 0.44-0.58$ ) in *P. congesta* from Vancouver Island populations (mean height  $22.4 \pm 4.5$  cm) and created selected lines 150% taller and 50% as tall as controls in just five generations. This suggests the potential for rapid evolution. Carey and Ganders (1980) also demonstrated modest plasticity in plant height (ranging from 18.66 to 26.9 cm tall) relative to variable growing conditions (warm dry vs. cool wet) in *P. congesta* from Saturnina Island (an island with resident ungulates) when grown in controlled environments. Plasticity was also observed in flowering phenology in response to latitudinal variation in local temperature throughout Oregon and Washington, USA (Reed et al. 2019). Together, these findings suggest that *P. congesta* has a

potential for rapid evolution for plant height and other traits linked to herbivore resistance, but also demonstrates phenotypic plasticity in morphology and phenology. Therefore, this species is particularly well-suited to address my research questions to be highlighted in the next section.



**Figure 1.1** Garry oak and maritime meadow dominated by *P. congesta* (seablush). Photo credit: Cora Skaien.

## **1.4 Thesis Chapters**

Each of the data chapters of my thesis investigates factors contributing to population differentiation of *Plectritis congesta* in a spatially heterogeneous island archipelago, including: (1) determining the relative contribution of multiple factors influencing trait distributions (e.g., Hughes et al. 2008); (2) investigating mechanisms leading to local adaptation (e.g., Whitlock 2015); and (3) investigating the contributions of both local adaptation and phenotypic plasticity (e.g., Valladares

et al. 2014, Palacio-López et al. 2015) in spatially and temporally heterogeneous environments. In Chapter 2:, I use data collected from 285 populations over 77 island and 44 mainland sites throughout the Georgia Basin to infer the relative contributions of multiple drivers of selection (i.e., variation in ungulate presence and climate) and population isolation on population-level variation. Specifically, I tested the hypothesis that spatial variation in ungulate herbivory is the dominant factor associated with phenotypic and morphological differences in *P. congesta* throughout the Georgia Basin, with additional contributions from climate and population isolation. In Chapter 3:, I used split-plot common garden enclosures on Sidney Island, British Columbia to identify mechanisms driving local adaptation of morphological and phenological traits in 12 island populations experiencing spatial heterogeneity in selective pressures (6 populations historically exposed to ungulate herbivory, 6 historically naïve to ungulate herbivory). Specifically, I tested the hypothesis that morphological and phenological differences among *P. congesta* island populations represent adaptations arising as a consequence of spatial variation in the occurrence of browsing ungulates (i.e., selection due to herbivory) and may reflect trade-offs between traits likely to affect competitive ability and tolerance to browsing. In Chapter 4:, I use two common gardens protected from ungulate herbivores (2006-2007, 2015-2016) at Totem Field (UBC) with 44 populations (16 historically exposed to ungulate herbivory, 28 historically naïve to ungulate herbivory) to assess the roles of genetic differentiation and phenotypic plasticity in explaining population-level variation in an environment experiencing temporal and spatial heterogeneity in selective pressures. I hypothesize that population-level differences in traits suggested to be local adaptations to either resist ungulate herbivory or increase competition for light (i.e., height, phenology) arise due to genetic differences among populations. Additionally, I hypothesize that all populations exhibit adaptive phenotypic plasticity in their ability to elongate stems as a response

to increased intraspecific competition. Together, these chapters suggest that variation in natural selection in an island archipelago has led to population-level variation of *P. congesta* through both local adaptation and adaptive plasticity that will likely influence population persistence and response to future changes.

## Chapter 2: Spatial Variation in Herbivory, Climate and Isolation Predict

### Plant Height and Fruit Phenotype in *Plectritis congesta* Populations on Islands

#### 2.1 Summary

Climate and herbivory can each drive natural selection on plant traits but may also interact to give rise to different patterns in trait distributions across island populations. These different patterns may arise because the occurrence of ungulate herbivores often varies across archipelagos, potentially leading to strong and abrupt spatial heterogeneity in the direction or intensity of natural selection. In contrast, climate tends to vary gradually and thus is more likely to lead to gradual clines in trait values. Population isolation may also affect trait values, given that random genetic drift may fix alleles or traits in the absence of gene flow, or because gene flow between populations with similar or opposing selection pressures may augment or swamp the effects of selection. Here, I estimate the independent effects and interactions of ungulate browsing, climate and isolation on fruit phenotype and plant height in 285 *Plectritis congesta* populations at 77 island and 44 mainland sites in western North America. Fruit phenotype and plant height were well-predicted by ungulate occurrence; plants in populations with resident ungulates were short ( $15.0 \pm 1.1$  cm) and mainly expressed wingless fruits ( $73.0 \pm 4.0$  %), whereas plants in populations without ungulates were 2.6 times taller ( $38.9 \pm 5.3$  cm) and only  $9.0 \pm 1.6$  % expressed wingless fruits. Wingless fruits were more common in drier conditions with less seasonal variability in temperatures, whereas winged fruits were more common in wetter, more seasonally variable climates. In contrast, population isolation was unrelated to fruit phenotype, except in populations rarely exposed to ungulates, where plants expressed phenotypes more like those in populations without

ungulates as isolation increased. My results are consistent with the hypothesis that spatial variation in browsing by ungulates, or other factors correlated with it, contributes to population-level variation in fruit phenotype and plant height in *P. congesta*, and that climate causes a modest spatial gradient in plant height.

## 2.2 Introduction

Theory suggests that spatial variation in the intensity or direction of natural selection can promote population-level differences in plant traits, particularly if selection acts consistently on heritable traits and is not overwhelmed by random genetic drift or gene flow from populations subject to opposing selection pressures (e.g., Wright 1968, Wade and Kalisz 1990, Yeaman and Jarvis 2006). Selection intensity or direction can vary spatially either (1) continuously, leading to gradual clines in trait values surveyed across populations, or (2) abruptly, leading to threshold relationships between traits and the drivers of selection at fine spatial scales (Siepielski et al. 2013). For example, Etterson (2004) studied the annual plant *Chamaecrista fasciculata* across a climate gradient to show that individuals achieved peak fitness when planted into common gardens nearer their source, revealing a clinal relationships between environmental factors and fitness traits. In contrast, Schamske and Bierzychudek (2007) reported abrupt differences in flower colour in *Linanthus parryae* on opposite sides of a ravine despite substantial gene flow, indicating a threshold relationship between environment and phenotype. These and other studies suggest that the influence of natural selection on plant traits can be inferred by examining how trait values vary in populations distributed across regions. Here, I describe trait distributions in 285 island and mainland populations of *Plectritis congesta* to test whether spatial patterns in morphology are

consistent with the hypothesis that spatial variation in browsing by ungulates contributes to population-level variation in traits.

Natural selection may act in synergy or opposition to gene flow to affect population-level variation in trait distributions (e.g., Yeaman and Jarvis 2006) and, in small or isolated populations, random genetic drift may drive trait values and the fixation of alleles at functional loci (Wright 1968). Population-level differences in polygenic traits can also arise via phenotypic plasticity and can be difficult to tease apart from natural selection without experimentation (Wade and Kalisz 1990). Consequently, quantifying the roles of natural selection, gene flow, genetic drift, and phenotypic plasticity as mechanisms underlying population-level differences in trait distributions can be tricky, but documenting such patterns in nature may provide a basis on which to test general expectations prior to engaging in more detailed study. Studies of natural populations that successfully attribute variation in trait distributions to the effects of multiple drivers of selection are particularly powerful and informative for estimating population dynamics, especially while also controlling for the potential effects of population isolation (Hughes et al. 2008). Surveys of island populations offer excellent opportunities to do so, given gradual variation in abiotic factors potentially affecting phenotype, variation in the frequency and occurrence of species likely to affect individual fitness (e.g., herbivores, predators, competitors or symbionts, Darimont et al. 2004), and variable levels of gene flow between island populations as a consequence of isolation by water barriers reducing dispersal (reviewed in Warren et al. 2015). For example, Stuart et al. (2014) showed that native *Anolis* lizards on islands invaded by a non-native congeneric competitor expressed heritable differences in micro-habitat selection and toe shape due to rapid evolution when compared to islands without the congener.

Herbivory is also a potent selective force affecting plant traits (e.g., *Ipomoea hederacea*, Stinchcombe and Rausher 2002; *Asclepias syriaca*, Agrawal 2005; *Primula farinosa*, Ågren et al. 2013; *Campanulastrum americanum*, Prendeville et al. 2015; *Brassica rapa*, Ramos and Schiestl, 2019), and many studies of ungulate herbivores have shown that herbivore occurrence often varies with island size and isolation in island archipelagos (Darimont et al. 2004, Mudrak et al. 2009, Arcese et al. 2014). For example, *Primula farinosa*, a short-lived perennial herb, rapidly evolved shorter stipes when exposed to mammalian herbivores, but longer stipes when protected from herbivores as a response to selection on survival and pollination success (Ågren et al. 2013). Additionally, western red cedars (*Thuja plicata*) responded plastically to deer browsing by increasing branching and stem number compared to plants protected from browsing (Stroh et al. 2008), but also displayed inherited differences in constitutive, chemical defenses (Vourc'h et al. 2001). Studying morphological and other differences in traits between island populations of plants can be particularly informative when predicting drivers of evolutionary change and consequences of future environmental changes.

I recorded fruit phenotype and plant height in 285 populations of *P. congesta* from 77 island and 49 mainland sites throughout the Georgia Basin to identify factors contributing to phenotypic variation in this highly variable species (Ganders et al. 1977a, Carey and Ganders 1980, 1987). Each *P. congesta* plant produces one of two fruit phenotypes, with or without wing-like appendages (Ganders et al. 1977a, Jacobs et al. 2010), based on Mendelian dominance at a single locus with two alleles (Ww, WW = winged, ww = wingless, Ganders et al. 1977a, Carey and Ganders 1980). Carey (1983) reported high heritability in plant height ( $h^2 = 0.44-0.58$ ) in *P. congesta* and lines selected for increased or decreased plant height were 150% taller and 50% as tall as controls in



just five generations. Carey and Ganders (1980) also demonstrated modest plasticity in plant height in *P. congesta* grown in controlled environments relative to environmental conditions. Lastly, *P. congesta* are highly palatable to ungulate herbivores which can drive their rapid extirpation (Gonzales and Arcese 2008), suggesting the potential for ungulate herbivores to influence trait distributions.

Given qualitative observations linking fruit phenotype, plant height and ungulate herbivores in *P. congesta*, I hypothesise that spatial variation in ungulate herbivory is the dominant factor associated with phenotypic and morphological differences in *P. congesta* throughout the Georgia Basin, with additional contributions from climate and population isolation. Specifically, I expect to observe threshold responses in plant height and fruit phenotype to the presence or absence of ungulate herbivores in an island archipelago, but gradual clinal effects of climate on these traits at regional scales. Moreover, given the Mendelian basis of fruit phenotype, high heritability in plant height, and the potential for gene flow among populations, I also predict that as populations become more isolated from each other by water, I will observe plant height and the fraction of plants bearing either fruit phenotype to be at the extremes of each trait distribution within populations. Specifically, I expected that *P. congesta* on islands with resident ungulates would be shorter and more often bear wingless fruits compared to *P. congesta* on islands without ungulates, on average, but that these differences would be more pronounced in more isolated populations. However, because Carey and Ganders (1980) also demonstrated modest plasticity in plant height in *P. congesta* grown in controlled environments, I further expect that variation in the height of *P. congesta* observed among populations might reflect variation in soil depth, climate or other factors linked to growing conditions.

## **2.3 Methods**

### **2.3.1 Sampling Locations**

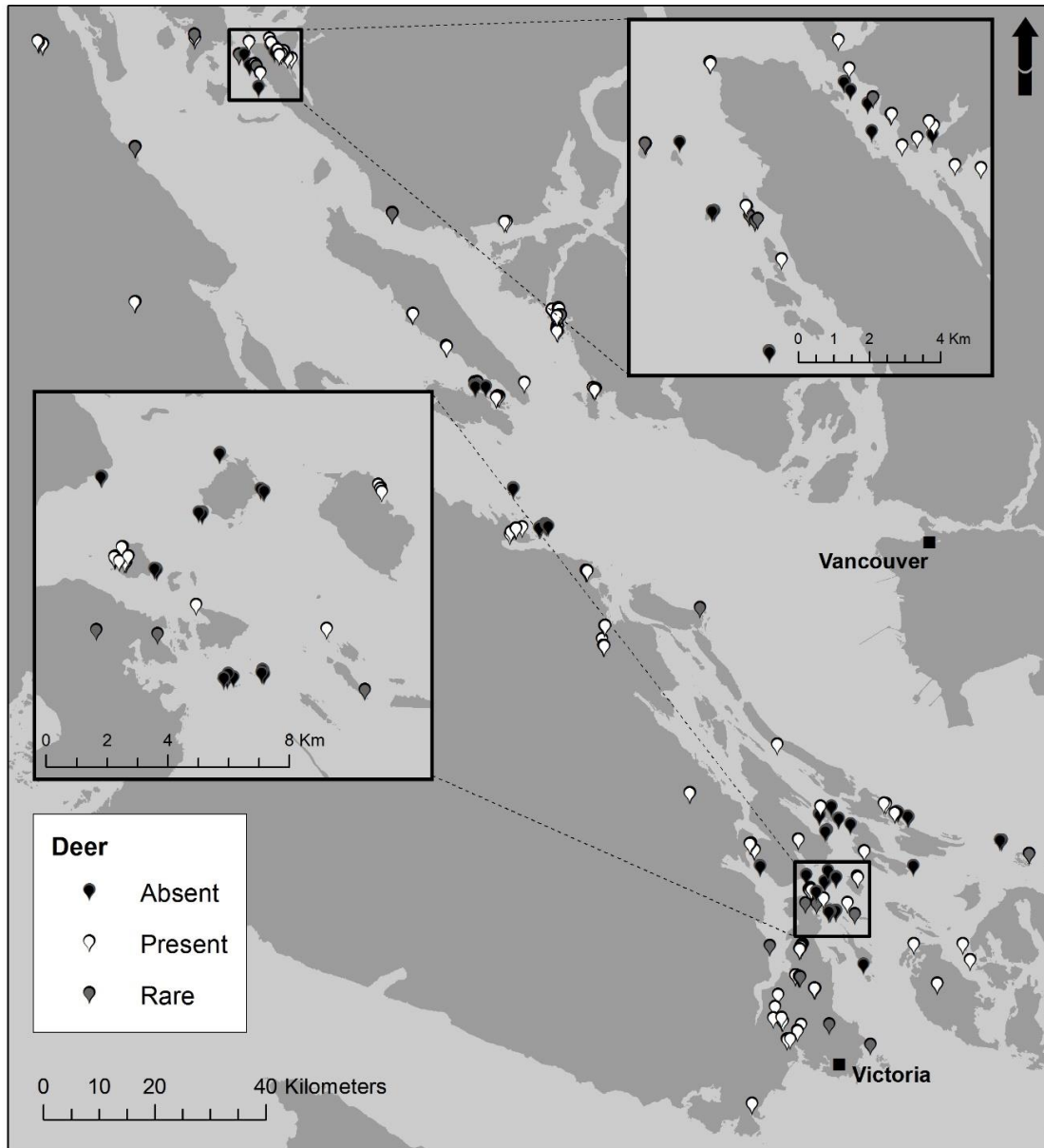
I sampled *P. congesta* populations in Garry oak (*Quercus garryana*) and maritime meadow habitats of the Georgia Basin and Puget Sound Lowlands (Gonzales and Arcese 2008, Bennett et al. 2012, Arcese et al. 2014) selected opportunistically via public data sources (e.g., eFlora 2013), personal communications and surveying ideal habitat throughout the Georgia Basin. Densities of Sitka black-tailed deer (*Odocoileus hemionus sitchensis*), exotic fallow deer (*Cervus dama*), and occasionally feral sheep (*Ovis aries*), can exceed densities of 100 individuals per square kilometer, due to the extirpation of predators and prohibitions on hunting (Martin et al. 2011, Arcese et al. 2014), and are well-above historic levels (McTaggart Cowan 1945, Hatter and Janz 1994, MacDougall 2008, Martin et al. 2011, Arcese et al. 2014). In addition to ungulates, all islands also hosted gastropod and insect herbivores, although none were surveyed systematically. A few sites also supported exotic lagomorphs (domestic rabbits), but casual observations suggest that lagomorphs are not likely herbivores of *P. congesta*.

### **2.3.2 Data Collection**

From 2005 to 2014, 285 *P. congesta* populations were surveyed in 77 island and 49 mainland sites where ungulate herbivores were known to be resident, absent or rarely present (Figure 2.1; Arcese et al. 2014). A site was defined as a geographically distinct entity, such as an island or demarcated reserve. A population was defined as a continuous patch of ~100 to > 10,000 individual plants, separated from other patches by  $\geq 50$  meters of forested or urban habitat without *P. congesta*. I was rarely able to estimate population size precisely because most populations were large and widely-distributed and appeared to contain >1000 individuals, with populations of >10,000

individuals common. To the best of my ability and where possible, I surveyed populations with and without resident ungulates in each geographic region of my overall study area to disentangle the effects of herbivory, climate and population isolation statistically. Populations with ungulates present were those known to host resident deer or sheep (*Ovis aries*, one island). Populations where ungulates were absent were those from islands on which no ungulate sightings or sign (e.g., pellets, browsed plants) were observed in the past 20 years, or which had physical barriers such as shoreline cliffs preventing access by ungulates (similar to "historically protected" populations in Martin et al. 2015). We had an additional category in which ungulate presence was classified as rare, and these were sites where ungulate populations were known to not be resident, but for which signs of ungulates (e.g., pellet piles, browsed vegetation, direct sightings followed by a lack thereafter on sufficiently small islands) had been observed occasionally in the past fifteen years.

In each site, I estimated the fraction of wingless fruits in populations by conducting 5 *in situ* surveys of 20 plants separated by  $\geq 1$  m. Each survey of 20 plants was located haphazardly within the known extent of the population being surveyed. In 15 populations where I detected fewer than 100 plants, fruit phenotype was determined to be the fraction of all plants bearing wingless fruits. For populations surveyed in multiple years, I used the most recent survey in analyses presented here because exploratory analyses offered no evidence of variation in fruit phenotype among years. In 37 populations surveyed in June 2014, I measured the height of 13 to 40 plants (mean = 32 plants) on a haphazardly located 1 x 0.2 m belt transect to test for correlations between plant height, fruit phenotype and soil depth. Soil depth was averaged from five measurements along the 1 m belt transect taken at 20 cm intervals.



**Figure 2.1** Sampled locations where ungulates were absent, present or rare throughout the Georgia Basin.

### 2.3.3 Statistical Analyses

To estimate the relative contributions of ungulate herbivory and climate on trait distributions, I obtained local climate data for all populations (Climate BC, Wang et al. 2012), including mean annual precipitation and temperature, number of frost free days, evaporation metrics, and mean

seasonal and monthly precipitation and temperature measurements. A Principal Components Analysis (PCA) of Climate BC data performed in SYSTAT (Wilkinson 1992) indicated that PC1 explained 92% of variation, leading us to adopt PC1 as a representation of climate to predict phenotype, wherein increasing values indicate drier conditions and less variation in temperature among months, and lower values indicate wetter conditions, warmer summers, and colder winters (Appendix 1).

I estimated the isolation of populations as the percent of area within a 1 km radius of the population centroid identified as salt water using ArcGIS (ESRI 2011) and a 1:20,000 terrain map (GeoBC 2017). A 1 km buffer maximized variation in my data, avoided zero-inflation, and aimed to represent potential water barriers to gene flow, following Bennett et al. (2013) and Schuster and Arcese (2013) who used buffers to infer dispersal limitation in plant and bird communities in this area. I did not estimate distance to all adjacent *P. congesta* populations due to the patchy nature of populations and limits on search effort and access due to terrain and land ownership.

To quantify spatial trends in the fraction of plants bearing wingless fruits and ungulates, I first compared the fraction of plants bearing wingless fruits on islands and mainland populations relative to ungulate presence or absence, with Vancouver Island grouped with mainland populations. I next used weighted logistic regression in a generalized linear model (R 3.1.0 Statistic Package, R Core Team 2014), with the weight being the total number of individuals counted in a population, and a binomial distribution, with 0 representing no wing-like appendages on fruits (i.e., wingless fruits) and 1 representing wing-like appendages on fruits (i.e., winged fruits) for each individual of the total counted. Fixed effects were: a) categorical variable of ungulate presence,

absence or rare occurrence; b) climatic variation expressed as the value of PC1; c) area of salt water in a 1 km radius of each surveyed population to represent population isolation; and d) interactions between ungulate presence and climate or isolation. Continuous variables were standardized (mean = 0, standard deviation = 1) using the `scale()` function in the “standardize” package (Eager 2017) to facilitate the comparison of model coefficients (Appendix 2). All reported means and coefficients in results are standardized and expressed as mean  $\pm$  standard error.

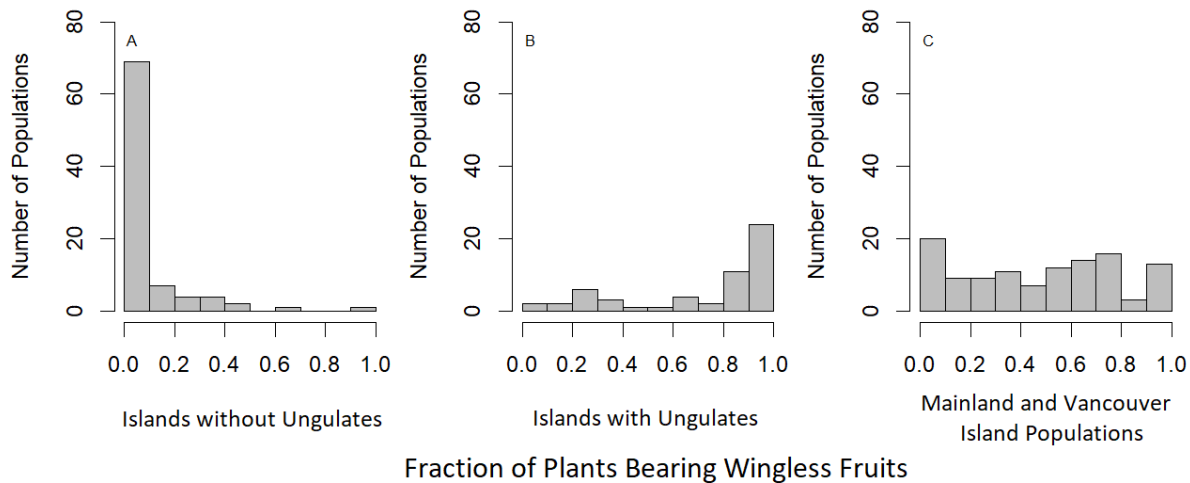
I characterized variation in the natural logarithm of mean plant height spatially using a linear model (R 3.1.0 Statistic Package, R Core Team 2014). Fixed effects included were: a) Ungulate presence, absence or rare occurrence; b) climatic variation as represented by PC1; c) population isolation as estimated by the area of salt water in a 1 km radius of each surveyed; d) average soil depth; and e) interactions between ungulate presence and variables (b) and (c) above (Appendix 3). Continuous variables were standardized as noted above.

## **2.4 Results**

Of 285 *P. congesta* populations surveyed, 158 (55.4%) were in sites with resident ungulates ( $n = 158$ ), 38 (13.3%) were on islands rarely visited by ungulates, and 89 (31.2%) were on islands with no current or historical evidence of ungulates. Throughout the Georgia Basin, the mean fraction of plants bearing wingless fruits was  $37.7 \pm 2.1\%$  and mean plant height was  $26.7 \pm 1.1$  cm over all populations, but these values varied dramatically with ungulate presence, climate and soil depth.

### 2.4.1 Spatial Variation in the Fraction of Plants Bearing Wingless Fruits

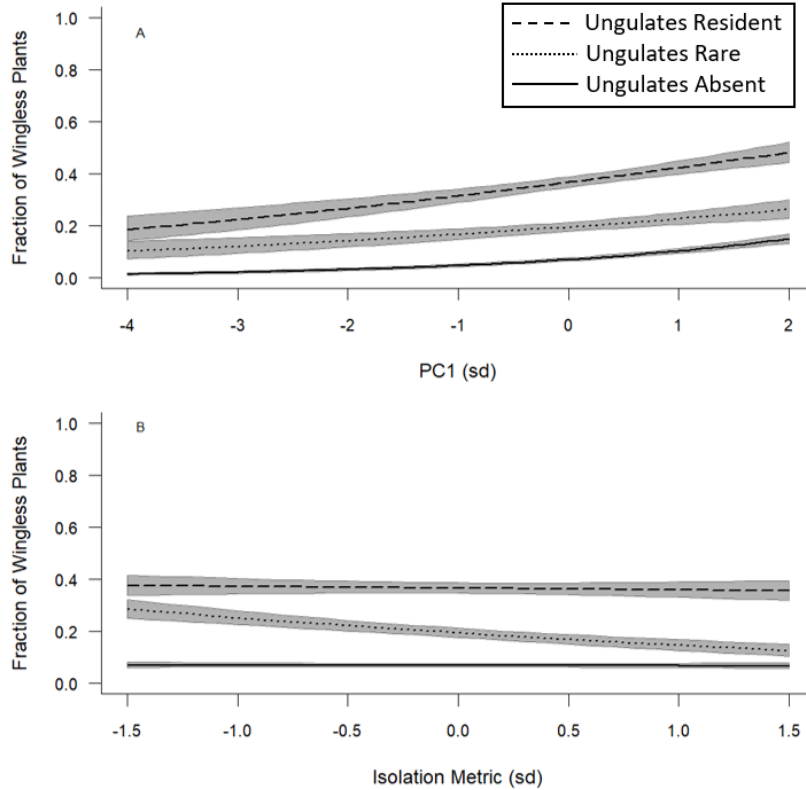
The average number of individuals producing wingless fruits in *P. congesta* populations was less than 10% on islands without ungulates ( $9.0 \pm 1.6 \%$ ,  $n = 88$ ), compared to 73% ( $\pm 4.0 \%$ ,  $n = 56$ ) on islands with resident ungulates across the Georgia Basin, resulting in a bi-modal distribution in plant phenotype across all islands (Figure 2.2a, b). In contrast, populations on the mainland and Vancouver Island displayed a roughly uniform distribution of fruit wing phenotypes (Figure 2.2c). Over all sites (island and mainland), the fraction of plants bearing wingless fruits was more than six times higher where ungulates were present ( $57.1 \pm 2.6 \%$ ,  $n = 158$ ) than absent ( $9.2 \pm 1.6 \%$ ,  $n = 89$ ), whereas populations that rarely hosted ungulates had intermediate values ( $23.8 \pm 4.6 \%$ ,  $n = 38$ ).



**Figure 2.2** Distribution of the fraction of plants bearing wingless fruits within *P. congesta* populations on islands without ungulates (A), islands with ungulates (B) and in mainland and Vancouver Island populations, both with and without ungulates (C). Island populations demonstrate a bi-modal distribution relative to ungulate presence, whereas mainland and Vancouver Island populations demonstrate a uniform distribution.

The effect of ungulates presence on fruit phenotype was modified by climate and isolation, as revealed by statistical interactions between ungulate presence and climate PC1 (Figure 2.3a) and ungulate presence and population isolation (Figure 2.3b; Appendix 2). Wingless fruits were more common where local climate was seasonally less variable and drier, but the correlation was strongest where ungulates were absent ( $\beta_{\text{PC1, ungulates resident}} = 0.23 \pm 0.07$ ,  $\beta_{\text{PC1, ungulates rare}} = 0.19 \pm 0.08$ ,  $\beta_{\text{PC1, ungulates absent}} = 0.42 \pm 0.06$ ; Appendix 2; Figure 2.3a). I found no association between the fraction of plants with wingless fruits and isolation in populations with either resident or no ungulates ( $\beta_{\text{isolation, ungulates resident}} = -0.03 \pm 0.09$ ,  $\beta_{\text{isolation, ungulates absent}} = -0.02 \pm 0.09$ ; Appendix 2; Figure 2.3b). However, the fraction of plants with wingless fruits on islands that rarely hosted ungulates was similar to values observed in populations hosting resident ungulates when less isolated, and similar to values observed in populations without ungulates when more isolated ( $\beta_{\text{isolation, ungulates rare}} = -0.34 \pm 0.10$ ; Appendix 2; Figure 2.3b).



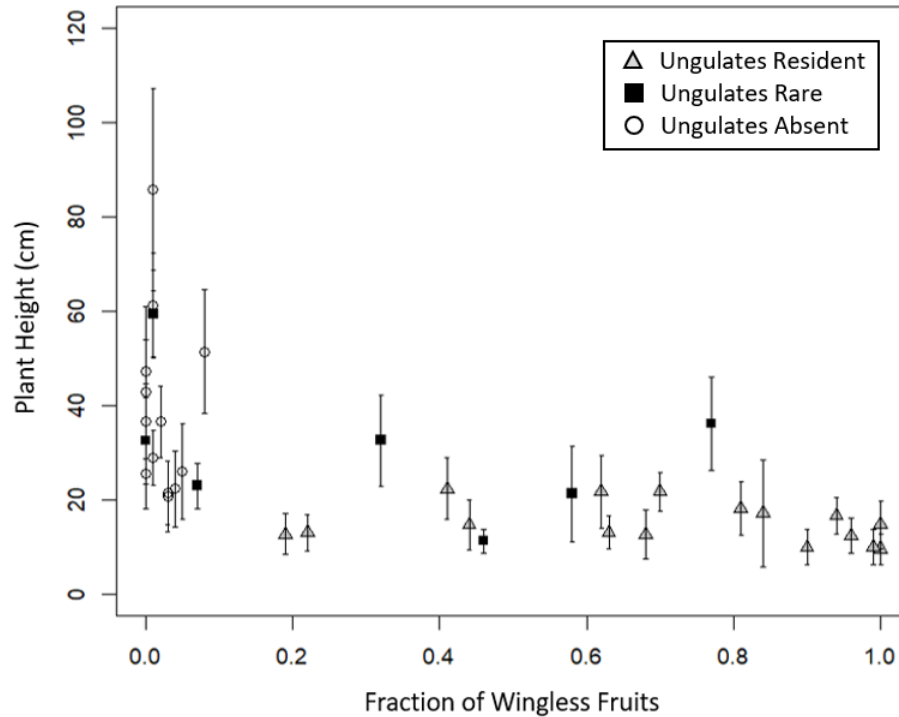


**Figure 2.3 Relationship between the fraction of plants bearing wingless fruits and (a) climate (standardized PC1 values) and (b) population isolation (standardized values), given mean value of other continuous variables (Appendix 2). Grey bars represent model generated standard errors. The fraction of wingless fruits increased with drier and less seasonally variable climates (increasing PC1 values), but was unaffected by isolation except in populations where deer were rare.**

## 2.4.2 Spatial Variation in Plant Height

Plant height also varied with ungulate presence (Figure 2.4). Plants in populations with resident ungulates were less than half as tall on average ( $15.0 \pm 1.1$  cm; range, 9.5 - 22.3 cm.  $n = 13$ ) as populations that were never exposed to ungulates ( $38.9 \pm 5.3$  cm; range = 20.7 - 85.2 cm,  $n = 16$ ; Figure 2.4). Plants were intermediate in height on islands that rarely hosted ungulates (11.2 - 59.4

cm, average  $30.8 \pm 5.7$  cm,  $n = 7$ ; Figure 2.4). The fraction of plants with wingless fruits was negatively related to average plant height ( $r = -0.59$ ,  $t_{34} = -4.3$   $p = 0.0001$ ,  $N = 37$ ; Figure 2.4).



**Figure 2.4 Mean plant height ( $\pm$  SE) in relation to the fraction of plants bearing wingless fruits and ungulate occurrence. Plants from populations where ungulates were absent tended to be taller and fewer produced wingless fruits than plants from populations where ungulates were present.**

Plant height increased with soil depth and plants were taller where soils were deeper regardless of ungulates presence (Appendix 3). Average soil depths did not differ between sites where ungulates were present, absent or rare ( $7.89 \pm 0.95$  cm,  $8.20 \pm 0.90$  and  $7.87 \pm 1.40$ , respectively). There was also an interaction between climate PC1 and ungulate presence on plant height (Appendix 3), such that I observed a positive association between PC1 and height in populations without ungulates ( $\beta_{PC1, \text{ungulates absent}} = 0.20 \pm 0.11$ ), but a negative association in populations where ungulates were

rare ( $\beta_{PC1, \text{ungulates rare}} = -0.29 \pm 0.19$ ), and no effect in populations with resident ungulates ( $\beta_{PC1, \text{ungulates resident}} = 0.06 \pm 0.14$ ). Thus, in populations without ungulates, plants were taller where climate was drier and less variable, but in populations where ungulates were rare, plants were taller where climate was wetter, with warmer summers and colder winters. Lastly, I found no correlation between population isolation and plant height (Appendix 3).



**Figure 2.5** Populations of *P. congesta* where ungulates are present (left) and absent (right). Photo credit: Cora Skaien.

## 2.5 Discussion

I found that fruit phenotype and plant height were well-predicted by ungulate presence in 285 *P. congesta* populations distributed across island and mainland sites in the Georgia Basin (Figure 2.2; Figure 2.4), confirming my prediction of threshold relationships between ungulate herbivory, fruit phenotype and plant height across populations. *Plectritis congesta* in sites with resident ungulates

were shorter and produced mainly wingless fruits, in contrast to populations rarely or not exposed to ungulates (Figure 2.2; Figure 2.4). Because these patterns were stronger in island than mainland populations (Figure 2.2), my results also suggest that spatial heterogeneity in the occurrence of ungulate herbivory is lower in mainland than island populations, that there are fewer barriers to gene flow than between mainland than island populations, or that both conditions apply. I also observed that climate, or factors linked to it, predicted a gradual cline in the frequency of wingless fruits across the Georgia Basin, wherein the fraction of wingless fruits increased as conditions became warmer and more seasonally variable (Figure 2.3a). In contrast, I found no effect of isolation by water on fruit phenotype or plant height in *P. congesta*, except on islands where ungulates were rarely present (Figure 2.3b). On such islands, the fraction of wingless fruits declined and became more similar to values observed in populations without ungulates as their isolation by water increased (Figure 2.3b). This result is consistent with the idea that isolation reduced the occurrence of ungulates on islands where they were rare, reduced gene flow from adjacent populations with resident ungulates and a preponderance of recessive alleles, or had both effects. Although it is possible that genetic drift and founder effects also contribute to variation at the fruit wing locus in the *P. congesta* populations I surveyed, the strong associations that I report between fruit phenotype and ungulate occurrence suggest that herbivory by ungulates, or another factor highly correlated with ungulates, drives much of the variation observed by selecting against plants with winged fruits directly, or against traits linked to fruit phenotype via pleiotropy or linkage disequilibrium.

Our observation that *P. congesta* in populations with resident ungulates were only 20% as tall as plants in populations without ungulates resembles the results of Ågren et al. (2013), who reported

rapid evolution in stipe length in *P. farinosa* populations subject to or protected from ungulate herbivores in island populations located in Sweden. Variation in plant height might represent a constitutive or induced response to herbivory (e.g., Agrawal 2007, 2011), and I suggest that the differences in mean height that I observed among *P. congesta* populations are an expected outcome of spatial variation in natural selection via ungulate herbivory, given high heritability in plant height and the demonstrated ability of *P. congesta* to respond rapidly to artificial selection on plant height (Carey 1983). However, I also found that plant height increased with soil depth and was positively correlated with drier conditions and reduced climatic seasonality where ungulates were absent, and with colder winters, warmer summers and wetter climate where ungulates were rare. Similarly, Carey and Ganders (1980) also found that *P. congesta* collected from one island population and grown in herbivore-free growth chambers grew taller in cooler, wetter conditions than in warmer and drier conditions, further confirming phenotypic plasticity in height due to environmental conditions. In contrast, I found no difference in the nature of the response of *P. congesta* to increasing soil depth in populations with or without ungulates present, and mean soil depths did not differ between these sites. Although the variation in mean plant height observed between populations is largely consistent with patterns expected via an evolutionary response to ungulate herbivory, I cannot rule out that other factors highly correlated with ungulate herbivory drove these patterns via direct environmental or gene by environment interactions. Selective factors favoring greater height in *P. congesta* populations in the absence of ungulates might include a positive correlation between plant height and fecundity (Carey 1983), intraspecific competition for resources, light, or pollinator services, or other factors. To help resolve these issues, I estimate genetic and environmental components of variation in the phenology and morphology of *P. congesta* using common gardens in my next chapters.

In contrast to plant height, fruit phenotype is under strict Mendelian control in *P. congesta* (Ganders et al. 1977a). Thus, given that populations with a high fraction of wingless phenotypes also tended to be shorter than populations wherein wingless phenotypes were rare (Figure 2.4), it is possible that population-level differences in fruit phenotype and plant height represent a co-adapted response to herbivory in *P. congesta* or these traits may be pleiotropic (see Smith 2016). Johnson et al. (2009) reported correlational selection on multiple traits in the evening primrose (*Oenothera biennis*); this and other studies suggest substantial potential for co-adaptation in quantitative traits linked to individual fitness and phenotype which could be readily explored in *P. congesta* using common gardens (e.g., Simms and Bucher 1996, Fineblum and Rausher 1997, Conner 2002, Stinchcombe and Rausher 2002, Agrawal 2005, Campitelli and Stinchcombe 2013)

Spatial heterogeneity in natural selection can increase genetic variance in fitness traits within populations in the absence of barriers to gene flow (e.g., lodgepole pines, Yeaman and Jarvis 2006). However, *P. congesta* populations on islands with and without ungulates differ strongly in the frequency of fruit phenotypes, consistent with the hypothesis that isolation by water reduced gene flow among island populations often subject to different conditions with respect to herbivory. In contrast, a nearly uniform distribution in fruit phenotypes across mainland populations (Figure 2.2) suggests that spatial heterogeneity in herbivory by ungulates is reduced in mainland as compared to island populations, that gene flow is higher among mainland than island populations, or that both of these conditions prevail in mainland as opposed to island populations. Although the role of genetic drift on population-level variation in fruit phenotype and plant height in *P. congesta* remains uncertain, it might be estimated in future by comparing neutral genetic markers in

populations subject to different selective environments (e.g., Campitelli and Stinchcombe 2013, Stock et al. 2014).

The potential role of fruit wings and their relationship to herbivory by ungulates or climate in *P. congesta* is unclear. Wingless fruits might survive mastication better and pass more rapidly than winged fruits; however, no fruits were observed to successfully germinate in 8 trials wherein 800 winged or wingless *P. congesta* fruits were fed to sheep (Arcese unpubl. res.). Although *P. congesta* with winged fruits were more common where annual temperature was more variable seasonally and precipitation higher (Figure 2.3a), I do not know the mechanism driving this pattern. Morey (1962) suggested that fruit wings in *P. congesta* facilitate dispersal in wind or rainwater. Winged fruits were dispersed further (1.5 meters) than wingless fruits (0.5 meters) at wind speeds of ~15 km/h (Arcese unpubl. res.), suggesting a three-fold effect, but short distance dispersal overall. Pollinators might also select for winged fruits if their services are limited on islands and fruit wings increase the detectability of inflorescences because the volume of inflorescences with winged fruits tends to be higher than that of inflorescences with wingless fruits (Appendix 14.2). Given Ågren et al.'s (2013) demonstration of fitness trade-offs involving pollination success and the avoidance of herbivory, my results imply that similar trade-offs may occur across the *P. congesta* populations that I studied.

In summary, my results are consistent with the hypothesis that ungulate herbivory is a key factor driving phenotypic differences in plant height and fruit phenotype among *P. congesta* populations in the Georgia Basin. However, I also found that climate, soil depth and population isolation influenced these traits, indicating plasticity in plant height and for a potential influence of physical

barriers to gene flow influencing plant traits in more and less isolated populations. Circumstances suggests that the intensity of herbivory in *P. congesta* populations has increased in the last century, particularly on islands where the extirpation of large predators and regulation of human hunting has led to over-abundant ungulate populations and local extirpation of palatable plants (Martin et al. 2011, Arcese et al. 2014). Common garden and transplant experiments are analyzed in subsequent chapters of this dissertation to estimate additive genetic and environmental components of variation affecting morphological traits in *P. congesta*, and the influences of fruit phenotype, plant origin, herbivory by ungulates and intraspecific competition on local adaptation and adaptive plasticity of *P. congesta* populations. These subsequent chapters lead to informed predictions as to how these populations will respond to human-induced change in climate and herbivory.



## **Chapter 3: Local Adaptation to Herbivory in Island Populations of *Plectritis congesta* that Differ in Historic Exposure to Ungulates**

### **3.1 Summary**

Spatial variation in the occurrence of browsing by ungulates can drive local adaptation in traits affecting fitness but may also lead to trade-offs among traits that affect competitive ability versus tolerance to browsing in heterogeneous selective environments. *Plectritis congesta* populations that co-occur on islands with or without ungulate browsers in the Pacific Northwest of North America offer a particularly striking example of population-level variation in traits likely to affect fitness, such as plant height and fruit morphology. I monitored split-plot common gardens exposed to and protected from browsing ungulates for five years to test for evidence of local adaptation (local vs. foreign comparison) in *P. congesta* by comparing the survival and fecundity of 4392 sown fruits from six island populations where browsing ungulates were present (“historically exposed”) and six where they were absent (“historically naïve”). My results indicate that local adaptation to browsing in *P. congesta* favoured rosette formation, delayed bolting and flowering, and the production of wingless fruits, all of which likely contributed to the higher survival, fecundity, and estimated population growth rate in plants from populations historically exposed to ungulate browsers as compared to plants from historically naïve populations. In contrast, plants from historically naïve populations displayed higher relative fitness in the absence of ungulates, bolted and flowered earlier, and produced fewer but larger, winged fruits, often in large terminal inflorescences. My results suggest that ungulate browsers can drive rapid adaptation in plant populations on islands and that context-dependent trade-offs exist in the fitness value of traits

conferring resistance or tolerance to herbivory versus traits conferring success in competition for light, pollinators or other resources. Broadly, my results imply that gene flow between populations that experience different selective environments, or are subject to temporally fluctuating selective environments, should enhance population growth and persistence under environmental change but reduce population growth and persistence in populations only experiencing directional selection due to isolation, topography, or human history.

### **3.2 Introduction**

Spatial variation in biotic and abiotic factors affecting individual fitness is ubiquitous in nature and can drive heterogeneity in natural selection (Wade and Kalisz 1990), lead to population-level differences in phenotype and genotype (Schluter 2000, Thompson 2005), maintain or deplete genetic variation within and among populations (Wright 1968, 1982), and affect the adaptive potential of populations (e.g, Rice and Emery 2003, Yeaman and Jarvis 2006, Aitken et al. 2008, Aitken and Whitlock 2013, Bontrager and Angert 2018). However, precise demonstrations of the mechanisms underlying local adaptation in nature remain scarce despite much practical and theoretical interest (e.g., Schluter 2010, Savolainen, Lascoux and Merilä 2013, Whitlock 2015, Bontrager and Angert 2018; see recent work on coat colour in mice, Barrett et al. 2019). I identified mechanisms driving local adaptation in morphology, phenology, and fitness in the winter annual *Plectritis congesta*, which occurs throughout the San Juan and Gulf Island Archipelagos of western North America. To do so, I monitored common gardens in plots open to and protected from ungulates for five years to test for local adaptation and estimate population-specific survival, fecundity, and growth rate, using six populations historically exposed and six historically naïve to ungulate browsers.

Given sufficient genetic variation in inherited traits under selection, populations are expected to express locally adapted traits to the extent that random genetic drift, inbreeding depression, or gene flow do not over-ride the effects of selection (e.g., Anderson and Geber 2009), and that fitness trade-offs between traits do not constrain evolution (e.g., Lowry et al. 2009). Local adaptation, often defined as the fitness advantage of local vs. foreign genotypes (Kawecki and Ebert 2004, Blanquart et al. 2013), is widely reported (Leimu and Fischer 2008, Hereford 2009, Savolainen et al. 2013), and recent examples indicate that the pace of local adaptation can sometimes be rapid (e.g., beak size in *Geospiza fortis* in 22 years, Grant and Grant 2006; scape length in *Primula farinosa* in 8 years, Ågren et al. 2013; toe pads of *Anolis* lizards in 20 generations, Stuart et al. 2014; floral attractiveness to pollinators and conspicuousness to herbivores in *Brassica rapa* in 8 generations, Ramos and Schiestl, 2019). Within-environment, local vs. foreign comparisons can facilitate tests for local adaptation (e.g., Galloway and Fenster 2000, Anderson et al. 2015) while accounting experimentally for the potential effects of habitat and environmental quality on performance (Maschinski et al. 1997, Siepielski et al. 2009, 2011, Savolainen et al. 2013). Given prior work on the species (Chapter 2), I adopted a within-environment, local vs. foreign common garden design to test my hypothesis that spatial variation in ungulate occurrence drives population-level variation in the distribution of several traits affecting plant morphology, phenology, and fitness in island populations of *P. congesta*. Such results provide insight in predicting how gene flow can facilitate or impede population persistence and adaptive change given habitat heterogeneity and future changes to climate and community membership.

Herbivory affects plant fitness and is widely suggested to drive local adaptation in traits linked to a plant's ability to 'resist' or 'tolerate' herbivores (e.g., Stinchcombe and Rausher 2001, Vourc'h

et al. 2001, Prendeville et al. 2015). Resistance traits enhance survival by reducing herbivory, whereas tolerance traits enhance relative fitness by improving the capacity for regrowth and reproduction given partial predation (van der Meijden et al. 1988). Traits conferring resistance or tolerance to insect and ungulate herbivores include those linked to plant phenology and morphology (Agrawal and Fishbein 2006). For example, populations of *Oenothera biennis* vary in bolting phenology (i.e., days as a ‘rosette’), wherein late-bolting genotypes survive better in the presence of deer than individuals who bolt earlier (Parker et al. 2010). Other species are thought to form rosettes to reduce their ‘apparency’ to ungulate herbivores by favouring outward over upright growth early in the growing season (Mortenson 2013). Later flowering in *Brassica rapa* (Schiestl et al. 2014) and *O. biennis* (Agrawal et al. 2012) have also been suggested to be adaptations to avoid herbivory and maintain fecundity. *Impatiens capensis* populations historically exposed to deer exhibited tolerance to browsing by flowering for longer periods relative to populations naïve to deer (Martin et al. 2015). Although many species use resistance and tolerance traits in a mixed defense strategy to co-exist with herbivores (Núñez-Farfán et al. 2007), high rates of herbivory can still lead to population extirpation when such defenses are insufficient or not represented locally (e.g., *Trillium grandiflorum*, Augustine and Frelich 1998; Knight 2004; *Plectritis congesta*, Gonzales and Arcese 2008). Overall, plant resistance and tolerance traits may vary between populations in ways predicted by their respective browsing histories.

Tolerance and resistance traits may give rise to trade-offs related to herbivore defense versus competitive ability. For example, *Tithonia tubaeformis* populations appeared to trade-off resistance to herbivory (shorter stem) for an increased ability to compete for light (longer stem, Boege 2010). Similarly, *Primula farinosa* produced shorter scapes that were less likely to be

browsed where ungulates were present, but produced taller scapes that were more attractive to pollinators where ungulates were absent (Ågren et al. 2013). Pollination success often increases with inflorescence size (e.g., *Corydalis ambigua*, Ohara and Higashi 1994) and the production of larger inflorescences with fewer, larger seeds (e.g., *Lupinus texensis*, Schaal 1980). These larger inflorescences may lead to trade-offs between pollinator attraction and apparency to herbivores, leading to changes in inflorescence characteristics and mating systems (Johnson et al. 2015). For example, the presence of bee pollinators and herbivores selected for self-compatibility and increased selfing rates in *Brassica rapa*, but in the absence of herbivores, bee pollinators selected for increased floral attractiveness (Ramos and Schiestl 2019). Additionally, large seeds may be selected against in the presence of ungulate browsers given that small particles tend to pass more rapidly through the guts of ruminants (Martz and Belyea 1986), and because producing a larger number of small seeds may increase the probability that at least some offspring survive when in environments in which mortality is high (Janzen 1984). Trade-offs in the fitness value of traits that increase plant tolerance or resistance to herbivory but reduce competitive ability therefore appear to be common in nature, and are especially likely to occur in plant populations distributed throughout archipelagos, where variation in island size, isolation, and history enforce marked spatial variation in the occurrence of ungulate browsers (e.g., Gonzales and Arcese 2008, Martin et al. 2011, Arcese et al. 2014).

*Plectritis congesta* is an iconic winter annual of maritime meadow and savanna habitats of Northwestern North America, that often co-occurs with deer, but is often extirpated at high deer densities (Gonzales and Arcese 2008). All *P. congesta* plants produce one of two, single-seeded fruit phenotypes, with or without wing-like appendages (Jacobs et al. 2010). Fruit phenotypes

follow Mendelian dominance (one locus; Ww, WW = winged, ww = wingless, Ganders et al. 1977a, Carey and Ganders 1980), with winged fruits being larger than wingless fruits. My surveys of 285 sites throughout the Georgia Basin of British Columbia (BC) and Washington State (WA) show marked variation in population phenotype and genotype, which was particularly accentuated on islands with or without ungulates as compared to populations not isolated by water (Chapter 2). Specifically, on islands without ungulates, *P. congesta* averaged 2.6 times taller than plants from populations with ungulates present, and ~91% of plants expressed winged fruits, compared to just ~27% in populations on islands with ungulates present (Chapter 2). Additionally, the studied islands in the Georgia Basin are young geologically (<14,000 years old, Fedje et al. 2018) and ungulate populations are expected to vary over time due to colonization and extirpation by activities of large predators, humans or other factors (Martin et al. 2011, Arcese et al. 2014). Such variation provides an excellent opportunity to investigate local adaptation and trade-offs in the fitness value of traits in a geologically young, spatially heterogenous landscape.

I hypothesize that many morphological and phenological differences among *P. congesta* populations represent local adaptations arising as a consequence of spatial variation in the occurrence of browsing ungulates (i.e., selection due to herbivory) and may reflect trade-offs between traits likely to affect competitive ability and tolerance to browsing. Specifically, based on the literature and my experience with the species, I predict that (1) survival and fecundity will be lower outside versus inside exclosures for all populations, but that I will find evidence of local adaptation with plants originating from populations historically exposed to ungulates demonstrating higher relative survival and fecundity in the presence of ungulates than plants from populations historically naïve to ungulates. I further predict that (2) these differences in survival

and fecundity will arise via one or more of the resistance or tolerance mechanisms revealed in similar studies or theory. Specifically, I predict that plants from historically exposed populations will demonstrate resistance mechanisms via allocation of growth to width rather than height early in the growing season, and bolting and flowering later in the season, when compared to plants from historically naïve populations. Conversely, I predict that plants from historically naïve populations will bolt sooner but experience high mortality relative to populations historically exposed to ungulates when subject to browsing. I also predict that (3) in the absence of ungulates, plants from historically naïve populations will bolt earlier and contain larger inflorescences, resulting in higher fitness and survival as expected given a hypothesis that competition for light and pollinators confers high relative fitness in the absence of ungulate browsers. Because plant height, ungulate herbivore occurrence and fruit phenotype were correlated in natural populations, I also predict that (4) plants with smaller, wingless fruits will be more fecund in the presence of ungulates, and that plants with larger winged fruits will have higher fecundity in the absence of ungulates, given a hypothesized trade-off in apparency to herbivores and pollinators. Finally, I also predict that (5) inflorescence volume will be larger for plants bearing winged versus wingless fruits, due to differences in fruit size.

### **3.3 Methodology**

#### **3.3.1 Study Site**

Sidney Island (9 km<sup>2</sup>; BC, Canada) supports native black-tailed (*Odocoileus hemionus columbianus*) and non-native fallow deer (*Dama dama*), at estimated combined densities of 97 and 62 deer / km<sup>2</sup> in 2012 and 2014, respectively (unpublished results, Sallas Forest Partners). These densities are 6-10 times higher than densities compatible with the persistence of native plant

communities typical of the region prior to European settlement ( $<10$  deer /  $\text{km}^2$ ; Allombert et al. 2005, MacDougall 2008, Martin et al. 2011, Arcese et al. 2014). Current densities are above historic levels following the declines of indigenous people from diseases introduced by Europeans (Koch et al. 2019) and reduced stewardship of their lands. The extirpation of large predators (*Felis concolor*, *Canis lupus*, *Ursus americanus*) also increased exotic, domestic and native herbivore populations (Martin et al. 2011, Arcese et al. 2014). These densities are not uncommon given that the densities of black-tailed deer on islands regionally are often 13-38 deer/ $\text{km}^2$  and can be as high as 105-280 deer/ $\text{km}^2$  (Martin et al. 2011, Arcese et al. 2014). Prior to this study, Sidney Island did not host any *P. congesta* populations, although neighbouring small islets such as Eagle Islet and Sallas Rock do. Sidney Island was selected due to the suitable Garry oak and maritime meadow ecosystems, the lack of *P. congesta* populations to complicate results, and a partnership with local land owners.

### **3.3.2 Experimental Design**

Two exclosures (23 x 27 m, 20 x 20 m) were established on Sidney Island to exclude deer from replicated patches of south-exposed, shallow soil, maritime meadow habitat in May 2012 (~2.5m tall, reinforced plastic deer fencing; 10 U 479419 E 5382235 N, 10 U 479716 E 5382220 N). Exclosures were ~300 m apart, representative of the larger habitat complex, and qualitatively indistinguishable in terms of plant community, slope and habitat composition to adjacent control sites at the time of construction (see comparison of site characteristics in Appendix 4). Although deer were excluded, insects, rodents and birds had unobstructed access in and outside exclosures.



Twelve *P. congesta* populations, six from locations where ungulates were historically present (“historically exposed”) and six where ungulates were historically absent (“historically naïve”; Appendix 5), were represented in and outside exclosures by 12-20 families (open pollinated fruits collected from a single parent plant) per population, representing both fruit phenotypes (i.e., winged and wingless; 6-12 families of each when possible). “Historically exposed” populations were those known to host resident deer or sheep (*Ovis aries*, one island) and “historically naïve” populations were those from islands on which no ungulate sightings or sign (e.g., pellets, browsed plants) were observed in the past 20 years, or which had physical barriers such as shoreline cliffs preventing access by ungulates (similar to “historically protected” populations in Martin et al. 2015). Four of the six populations with resident ungulates hosted only black-tailed deer, one population hosted both the native black-tailed and non-native fallow deer species, and one population hosted resident sheep instead of deer, but ungulate densities were within natural observed ranges for the region in all historically exposed populations (Martin et al. 2011, Arcese et al. 2014). Because populations tend to predominantly have either more winged or wingless fruits based on browsing history (Chapter 2), I was not able to equally represent both fruit phenotypes in all populations (Appendix 5). Resultant pooled populations from historically exposed and naïve populations had 53% (391 of 729) and 41.8% (308 of 737) of planting locations having wingless fruits, respectively (47.8% of all planting locations). With two browsing histories (i.e., historically exposed and naïve) and two fruit phenotypes represented in this study, there are four ‘fruit phenotype by origin’ groups of interest (i.e., historically exposed winged, historically exposed wingless, historically naïve winged, historically naïve wingless).

Planting locations were spaced at  $\geq 0.75$  m intervals on 42 parallel transects across each pair of enclosed and open plots (21 transects per exclosure, ~50 m length; excluding sites  $<1$  m of fence), totaling 4392 fruits and 1464 planting locations. Each family was replicated three times within and three times outside exclosures, with each location sown with three single-seeded fruits to increase the chances of germination success at each planting location. At each planting location I recorded soil depth (a minimum of 4 cm required) using a probe, and classified plant communities in three categories ('moss' as  $\geq 80\%$  cover of moss and  $<10\%$  grass; 'grass' as  $\geq 20\%$  cover of grass and  $<30\%$  cover of moss; or 'moss and grass' as an intermediate mixture of moss and grass with  $< 20\%$  grass cover), because increased soil depth and moisture positively influence plant height in *P. congesta* (Carey and Ganders 1980, Chapter 2).

Each planting location was surveyed to record germination, survival, plant height, plant width and flowering phenology of each plant in December 2013, and March and May 2014. Flowering phenology of surviving plants was assessed at each planting location on an 11-point scale, with higher numbers representing more developed buds, flowers or fruits (Appendix 6). Because more than one germinated plant was detected in 6.8% of 1464 planting locations in March 2014, I used scissors to randomly prune all but one plant at each location to eliminate intraspecific competition as a confounding factor. In May 2014, I recorded the height at which signs of ungulates browsing were evident on browsed plants, the height and width of each plant's terminal inflorescence and counted the number of florets each plant produced to estimate fecundity. Each floret produces a single-seeded fruit; therefore, the number of florets is strongly correlated to the number of possible viable seeds, assuming high fertilization rates from a mixture of selfing and outcrossing (Carey and Ganders 1980). I re-visited all locations to record the number of plants that germinated in

subsequent generations at each planting location in December 2014 and 2015. Subsequent generations were surveyed annually in May 2015, 2016 and 2018 to count all surviving plants and measure the height of up to 20 randomly selected plants at each planting location. Because dispersal distances were short on average (2014 dispersal:  $19.4 \pm 14.0$  cm, mean  $\pm$  SD,  $n = 2212$ , my unpubl. results), and relatively few planting locations had surviving plants (resulting in patches often being separated by several meters), I was confident in my ability to associate plants in subsequent generations with the planting locations they originated from. Additionally, although plants can outcross, I assume that plants in subsequent years were more likely either (1) self-fertilize (outcrossing rates 48-75%, Ganders et al. 1977b), or (2) breed with direct neighbours (that were 1-20 cm away) that share the same genetic history as opposed to breeding with those from other patches (typically greater than five meters away, although some patches were only 1 meter away). However, some outcrossing between planting locations likely occurred.

### **3.3.3 Statistical Analyses**

All analyses (except for flowering phenology) were conducted with the glmmADMB package (Skaug et al. 2018) in the R Statistical Program (R 3.1.0 Statistic Package, R Core Team 2014). I estimated the effects of: (1) browsing history (i.e., fruits originating from historically exposed or naïve populations; fixed effect); (2) current exposure to browsing (i.e. inside or outside of enclosures preventing deer access; fixed effect); and (3) fruit phenotype (i.e. winged or wingless; fixed effect) on: (A) germination success and subsequent survival; (B) the number of florets produced per plant (fecundity); (C) the volume of the terminal inflorescence; (D) bolting phenology (as estimated by exponential growth curves); (E) plant height; (F) growth form (height to width ratio, H:W ratio; representing rosette or tall growth forms, with rosettes being plants that

have a H:W ratio  $< 1$ ); and (G) flowering phenology (following Appendix 6). I estimated survival, plant height, growth form and bolting phenology relative to the fruit phenotype of the sown fruit and not that of the plant itself because I was unable to determine the phenotype of plants that did not survive or produce fruits in May. I was, however, able to use the fruit phenotype of surviving plants to estimate fecundity and inflorescence volume because these plants survived to produce mature fruits. All models included full-factorial interactions of the variables of interest, and results were interpreted at the highest order interaction that was statistically significant ( $\alpha = 0.05$ ). Soil depth was often included as a covariate, including an interaction with current exposure to browsing, because I expected that soil depth would impact plant height and subsequent survival outside exclosures (e.g., Chapter 2). Visually depicted means and standard errors were calculated from model outputs. All analysis of variance (ANOVA) results and model predicted values can be found in the relevant cited appendices.

To estimate germination and survival over time in 2013-14, I included measurement date as a fixed effect in a four-way interaction with browsing history, current exposure to browsing and fruit phenotype of sown fruit (Appendix 7). All planting locations were included in the analysis, assuming a maximum of one plant at each planting location due to pruning ( $n = 1464$  locations where a fruit was sown at each measurement date;  $n = 4392$  for full analysis). I used a binomial distribution in the model, with 0 representing the absence of a plant and 1 representing the occurrence of a plant at each measurement date. I also included an interaction between soil depth and current exposure to browsing because soil depth impacted plant height (Chapter 2) and I predicted that increased plant height will reduce survival. To control for confounding environmental influences, I included substrate as a random effect (germination/survival  $44.4 \pm 2.2$

% in moss,  $19.3 \pm 2.2\%$  in grass and  $33.2 \pm 1.9\%$  in a mixture of moss and grass). Additional random effects included current exposure to browsing nested within enclosure ID (i.e., east or west; nesting accounting for split-plot design), family ID nested within population of origin (accounting for relatedness between individuals), and individual plant ID nested within measurement date (to account for repeated measures of each individual).

To estimate fecundity in May 2014 (as estimated by the number of florets or fruits), I used only plants that survived until May 2014 ( $n = 237$ ). I tested a three-way interaction among browsing history, current exposure to browsing and fruit phenotype of surviving plants, including all two-way interactions between these variables (Appendix 8). The model used a Poisson distribution and a log link. The fruit phenotype of 6 plants (2.5% of total) was not observed, but instead I predicted what the fruit phenotype most likely was based on the population of origin, fruit phenotype of sown fruit and dominant fruit phenotype at that planting location in subsequent years (assuming Mendelian inheritance). I believe this estimate approximated the truth because 70% of plants followed the phenotype of the sown fruit, particularly if that was the dominant phenotype of the source population (77-90% of plants matched parental phenotype if that was the dominant phenotype of that population), and I assumed random mating within each patch to utilize Mendelian inheritance patterns given the observed fruit phenotypes in the subsequent generation. Random effects included substrate, current exposure to herbivory nested within enclosure ID (for split-plot design) and population of origin.

I estimated the volume of the terminal inflorescence for all plants in May 2014 that produced an inflorescence ( $n=200$ ), testing a three-way interaction between browsing history, current exposure

to browsing, and fruit phenotype of surviving plant (Appendix 9). The model used a Gaussian distribution, using log transformed values of estimated inflorescence volume assuming an ellipsoid ( $V = (4/3) \cdot abc$ , where  $a$  is the distance from the midpoint to the top of the inflorescence, and  $b$  and  $c$  are the distance from the midpoint to the side of the inflorescence). Random effects included substrate and population of origin.

I quantified bolting phenology in 2013-14 by estimating the exponential growth rate of each individual plant that survived from December 2013 to May 2014 ( $n = 228$ ) by converting the measurement date to the number of days since sowing (i.e., December = 105, March = 200, May = 270) and log transforming both the number of days since sowing and plant height. I obtained estimates for the growth rate (i.e. exponential power function) for each individual plant using a fixed-intercept model. I then tested for differences in the exponential power function with a three-way interaction between browsing history, current exposure to browsing and fruit phenotype of surviving plant (Appendix 10). I included soil depth as a covariate with an interaction with current exposure to browsing. Substrate, current exposure to herbivory nested in enclosure ID (accounting for split plot design), and family nested in population of origin were included as random effects.

To test how height and growth form (expressed as H:W ratio) were affected by browsing history, current exposure to browsing and fruit phenotype of sown fruit, I conducted separate analyses at each time period using a three-way interaction (December, March and May; Appendix 11, Appendix 12). Models used a Gaussian distributions and log transformations of height and the H:W ratio (representing growth form;  $n_{\text{December}} = 441$ ;  $n_{\text{March}} = 327$ ;  $n_{\text{May}} = 242$ ;  $n_{\text{total}} = 1010$ ). I included an interaction between soil depth and current exposure to browsing. Random effects

variables included in both series of models were substrate and current exposure to herbivory nested in enclosure ID (for split-plot design). Population was included as an additional random effect in the model assessing height in May 2014, but models for December and March failed to converge with this factor included and thus it was removed. Family nested in population of origin was included as additional random effects in all three models assessing growth form.

Flowering phenology was assessed using the ‘multinom’ function in the nnet package (Venables and Ripley 2002), using flowering phenology classes as multinomial responses (Appendix 6). I tested for influences of browsing history, current exposure to browsing and fruit phenotype of sown fruit, with full-factorial interactions (Appendix 13). I used only plants that survived to each measurement date and did not have the terminal inflorescence browsed by herbivores and I tested for differences independently for March ( $n = 328$ ) and May ( $n = 222$ ); all plants were in the leaf stage in December. I included substrate as random effect.

### **3.3.4 Population Growth, Selection and Persistence**

I estimated population growth ( $\lambda$ ) as:  $\lambda = P[\text{germination}] \times P[\text{survival to fruiting}] \times \text{fecundity}$  by creating stochastic distributions of  $\lambda$  ( $n_{\text{trials}} = 10,000$ ) using rates drawn from the observed mean and standard deviation of these variables from three growing seasons between December 2013 to May 2016. Using estimates over multiple years allows for a more representative estimate of population growth that accounts for annual variation in climate. Expected population growth ( $\lambda$ ) was independently estimated for all combinations of browsing history, current exposure to browsing and fruit phenotype (i.e., eight groupings) by taking population means for each metric (i.e., using six historically exposed and six historically naïve populations, for all other

combinations of current exposure to browsing and fruit phenotype). Probability of germination was estimated for each group using germination rates in the first two years (i.e., 2013 to 2014 and 2014 to 2015) when I was able to track the success of independent fruit phenotypes, comparing known number of fruits at each planting location at the end of each growing season to the number of plants observed in the following December. The probability of survival was estimated using the mean number of germinated plants from each population in 2013, 2014 and 2015 that survived and produced at least one fruit the subsequent May, taking only those not pruned in the first year as candidates for 2013-14 estimates. The standard deviation of the mean probabilities for germination and survival were estimated using the formula for a binomial distribution and pooling all plants together within each of the four fruit phenotype by origin groups, inside and outside of exclosures independently (eight total groups), as  $SD = \text{square-root}([Probability\ of\ Germination\ or\ Survival] * [1 - Probability\ of\ Germination\ or\ Survival] * N)$ , where N is the number of plants being observed in each of the eight groups. Fecundity was estimated from the mean number of florets or fruits produced in each of the eight different groups. In 2014, I counted the number of florets on all plants that survived to bloom. In 2015, I estimated fecundity for each plant of known height and fruit phenotype using a regression estimating florets from plant height established using 2013-14 data because I did not count them directly (Appendix 14). We also created a regression to estimate fruit number relative to inflorescence volume (Appendix 14).

I estimated the strength of selection on each fruit phenotype by origin group independently in and out of exclosures, utilizing the equation  $S = 1 - w$ , where  $S$  is selection and  $w$  is the relative fitness of each group compared to the group with the highest fitness (separate estimates in and out of exclosures). To do so, I estimated overall fitness by creating stochastic distributions of fitness



utilizing the probability of survival and the estimated fecundity for each group (as previous;  $n_{\text{trials}} = 10,000$ ). Within each iteration, I compared all 4 groups inside exclosures, and then all 4 groups outside exclosures, to obtain estimates of relative fitness for each group in relation to the current exposure to browsing. Using these relative fitness estimates, I was able to estimate  $S$  from stochastic simulations. Higher values of  $S$  indicate stronger selection against that phenotype.

### **3.4 Results**

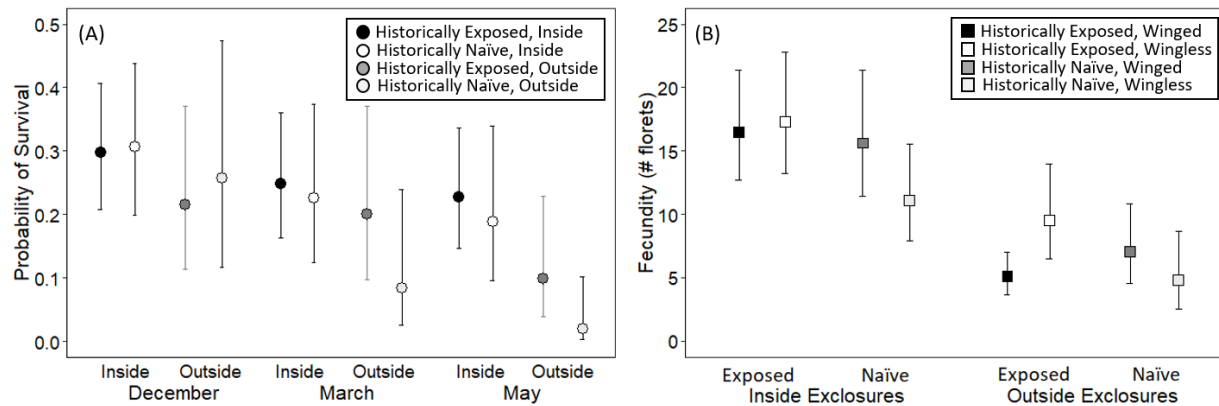
#### **3.4.1 Germination, Survival and Fecundity**

Germination was low in 2013 for all populations, with 16.2% of 4392 fruits sown detected as small plants, and 34.1% of 1464 planting locations producing one or more plants by December. Germination averaged  $13.8 \pm 1.5\%$  and  $17.9 \pm 1.6\%$  for historically exposed populations (winged and wingless fruits, respectively), similar to rates for historically naïve populations ( $16.1 \pm 1.5\%$  and  $16.2 \pm 1.7\%$ , respectively). However, plants from historically exposed populations either germinated later or went undetected in December more often than plants from historically naïve populations, because over twice as many plants from historically exposed populations were not detected until March (8.3% of 169 and 13.7% of 182 of plants in and out of exclosures, respectively), as compared to plants from historically naïve populations (3.4% of 169 and 4.8% of 182 plants in and outside exclosures, respectively).

Model predicted plant survival outside exclosures was two to five times higher among plants from historically exposed populations compared to historically naïve populations, despite being low for all populations (Figure 3.1a; Appendix 7). In contrast, browsing history had no influence on

survival inside the exclosures, which declined only modestly from December to May (Figure 3.1a), and survival was unrelated to fruit phenotype in or outside of exclosures (Appendix 7).

Model predicted plant fecundity was up to 70% lower outside of exclosures as compared to plants inside, but the magnitude of this effect was largest in plants from historically naïve populations (Figure 3.1b). Plants from historically exposed populations produced 1.4 to two times more fruits than plants from historically naïve populations when both were exposed to herbivores (Figure 3.1b; Appendix 8), and this pattern was strongest for plants bearing wingless fruits. In the absence of herbivores, fecundity was similar for plants bearing both winged and wingless fruits, except it was 35% lower for plants from historically naïve populations bearing wingless fruits (Figure 3.1b; Appendix 8).

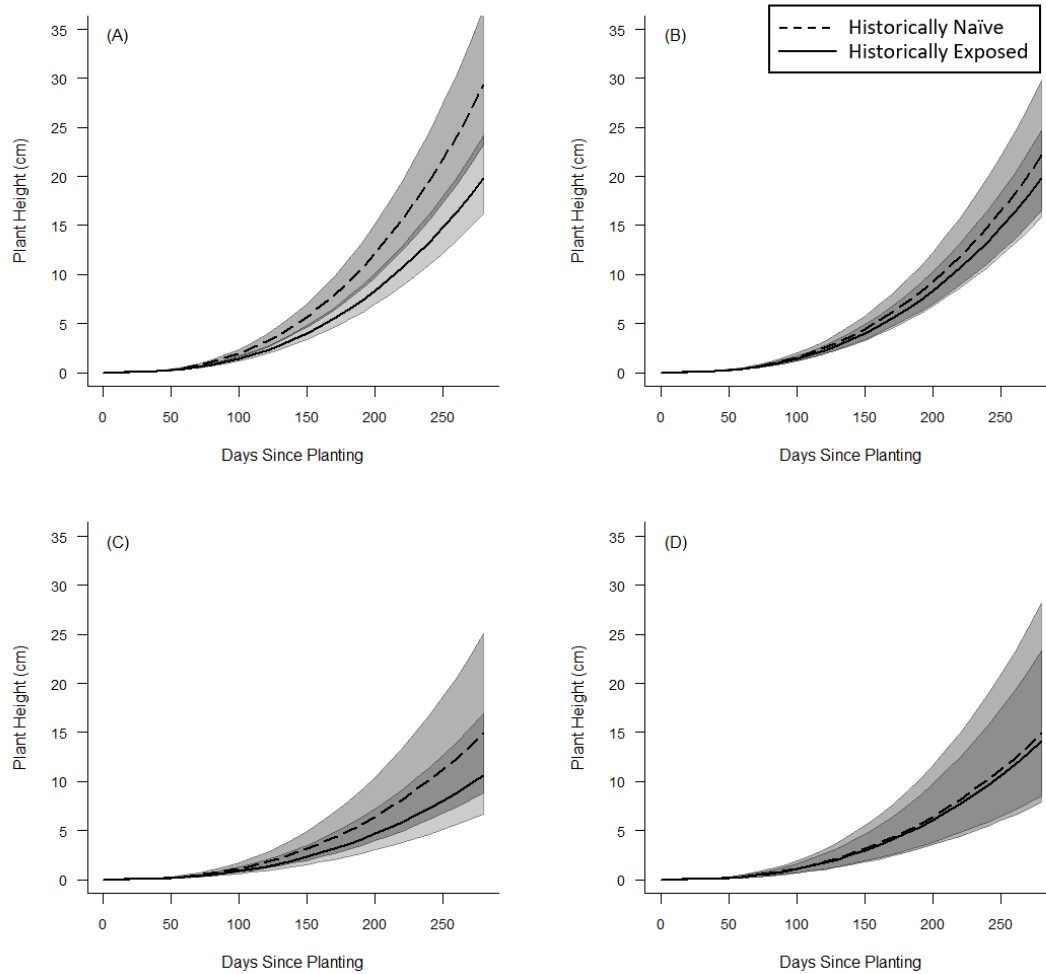


**Figure 3.1** Model predicted plant survival over time (A; Appendix 7) and fecundity relative to phenotype of the sown fruit (B; Appendix 8), inside and outside exclosures. Survival decreased over time outside of exclosures for all populations, but particularly for historically naïve populations. Overall, fecundity was highest for winged fruits inside exclosures and for wingless fruits outside of exclosures.

### **3.4.2 Plant Morphology and Phenology**

Inflorescence volume averaged 3.1 times larger in plants from historically naïve than historically exposed populations (Appendix 9). Inflorescences bearing winged fruits were up to 5.5 times larger than inflorescences bearing wingless fruits in historically naïve populations, with little difference in inflorescence volume for plants bearing winged or wingless fruits in historically exposed populations (Appendix 9).

Model predicted phenology of bolting differed dramatically among populations, with plants from historically naïve populations bolting earlier than plants from historically exposed populations (Figure 3.2; Appendix 10). Plants with winged fruits also bolted earlier than plants with wingless fruits (Figure 3.2). Surviving plants inside of exclosures also bolted earlier than plants outside of exclosures (Figure 3.2; Appendix 10), probably because plants that bolted later survived longer in the presence of ungulates or non-lethal browsing delayed bolting.

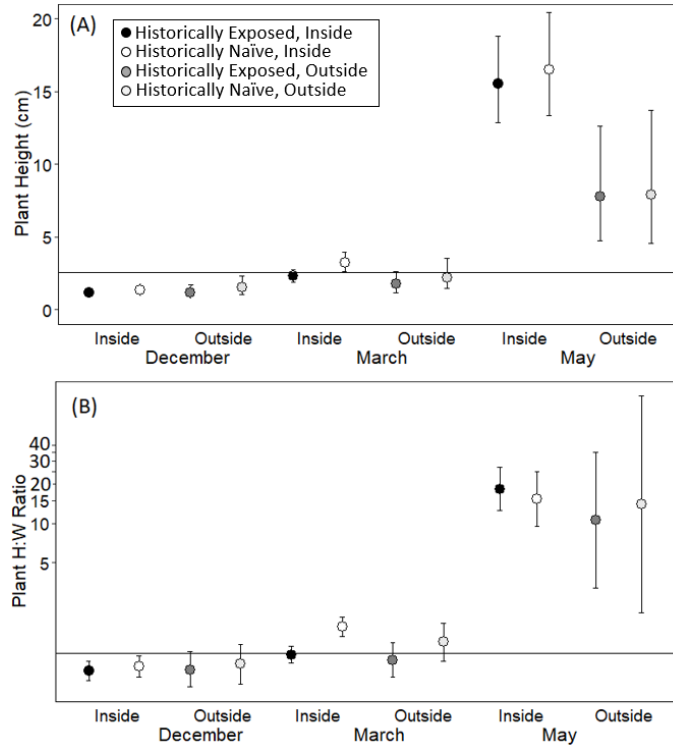


**Figure 3.2 Model predicted growth rates (bolting phenology) of plants (Appendix 10) with winged fruits (A, C) or wingless fruits (B, D), both in (A, B) and out (C, D) of exclosures. Plants from historically naïve populations and those bearing winged fruits bolted earlier than their counterparts.**

Browsing by ungulates outside exclosures caused a 1.8 to 2.6 fold reduction in model predicted mean plant height outside versus inside exclosures in May 2014, but with substantial overlap in model predicted standard errors (Figure 3.3a; Appendix 11). Additionally, the height of intact plants in May did not differ by browsing history (Figure 3.3a; Appendix 11). Plant heights were similar in December 2013, when all plants remained below the mean height at which I observed

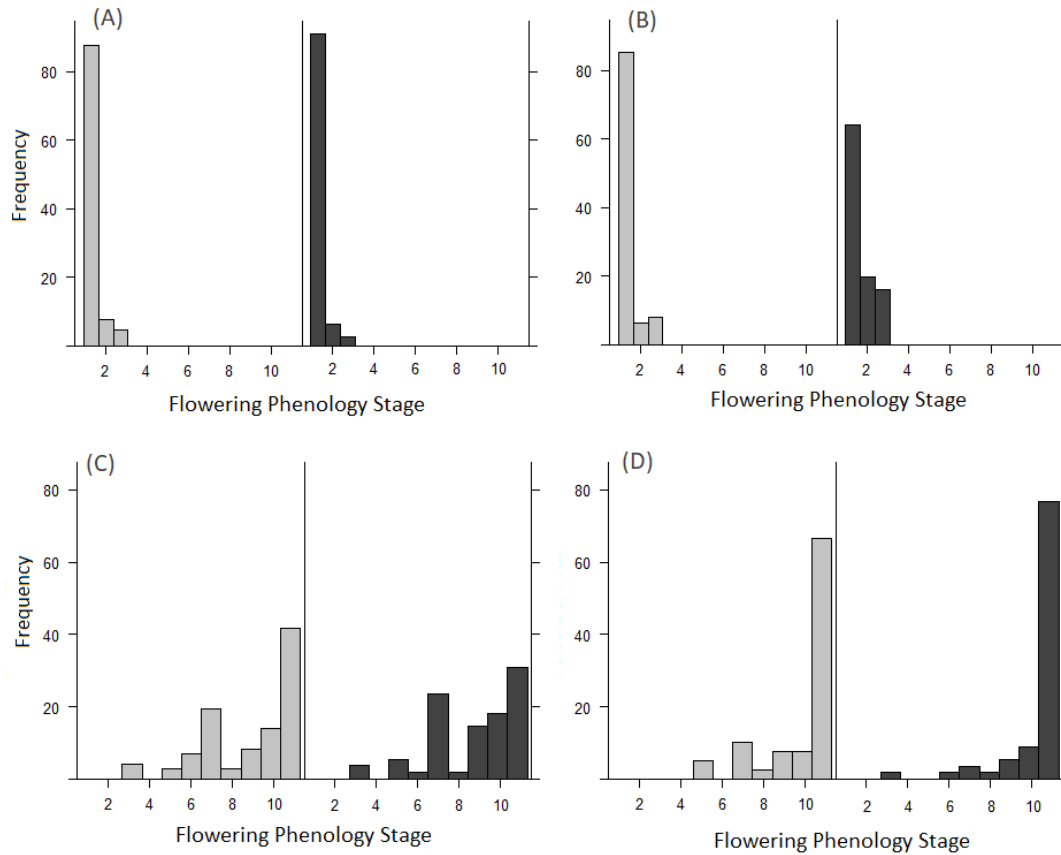
signs of browsing by deer (i.e.,  $2.62 \pm 0.38$  cm;  $n = 18$ ; Figure 3.3a). By March, plants from historically naïve populations were consistently taller than plants from historically exposed populations, with plants from historically naïve populations inside of exclosures averaging  $3.27 \pm 0.67$  cm, exceeding the mean height of browsed plants (2.62 cm; Figure 3.3a). In comparison, plants from historically exposed populations averaged  $2.29 \pm 0.39$  cm inside exclosures, and all plants surviving outside exclosures were relatively short ( $1.77 \pm 0.60$  and  $2.34 \pm 0.92$  cm, historically exposed and naïve, respectively; Figure 3.3a). Plant height was unaffected by the phenotype of sown fruit and soil depth did not impact plant height in December, March or May (Appendix 11).

Plants from historically exposed populations often expressed rosette-like growth forms emphasizing outward over upward growth (H:W ratio  $< 1$ ) in March 2014, whereas plants from historically naïve populations tended to be taller than wide (H:W ratio  $> 1$ ; Figure 3.3b; Appendix 12). Additionally, plants outside of exclosures also more often expressed rosette-like growth forms compared to plants inside of exclosures in March (Appendix 12). In contrast, H:W ratios were similar among populations in December, prior to bolting by most plants, and similar in May when all plants had reached their final height (Figure 3.3b; Appendix 12). These patterns did not vary in or outside exclosures in December and May or by fruit phenotype at any measurement time (Appendix 12).



**Figure 3.3 Model predicted height (A; Appendix 11) and growth form (H:W ratio) (B; Appendix 12) in and out of exclosures over time. The mean height at which ungulate damage was detected outside exclosures (2.62 cm) is represented by the solid black line in Panel A. Plants below a H:W ratio of 1 (line in panel B) are wider than they are tall. Plant height was lower in surviving plants currently exposed to ungulate herbivores. Plants from historically exposed populations allocated more growth to width than height early in the growing season.**

Plants from historically naïve populations and winged fruits were slightly more advanced in bud or flower development in March 2014 than plants from historically exposed populations or those with wingless fruits on average, indicating that they flower earlier (Figure 3.4; Appendix 13). Although similar trends appeared in May with respect to browsing history and fruit phenotype, those differences were not statistically significant (Figure 3.4c, d; Appendix 13). I detected no effects of exclosures on flowering phenology (Appendix 13).



**Figure 3.4** Frequency of plants at 11 stages of flowering (Appendix 6) in March (A, B) and May 2014 (C, D) for historically exposed (A, C) and historically naïve (B, D) populations (Appendix 13). All plants in and outside exclosures pooled together. Grey and black bars represent wingless and winged fruits, respectively. Plants from historically naïve populations and those bearing winged fruits demonstrated earlier flowering phenology and more advanced flower development at each survey time than plants from historically exposed populations or bearing wingless fruits.

### 3.4.3 Population Growth, Selection and Persistence

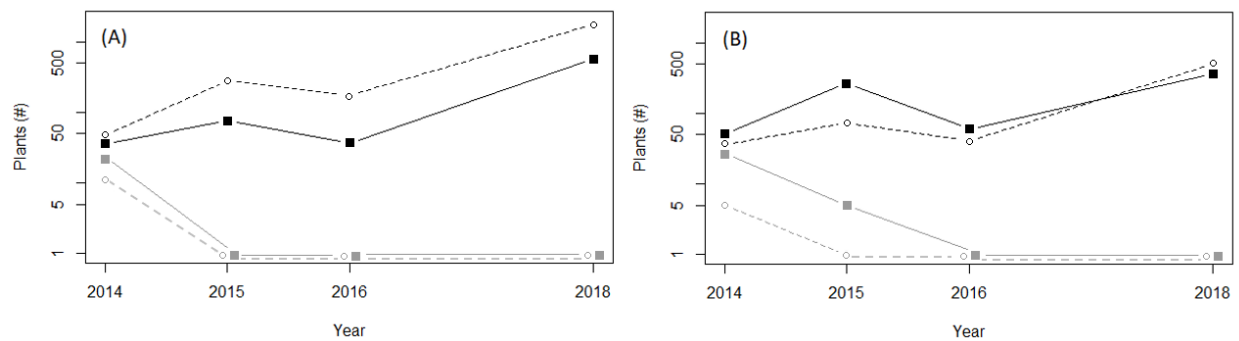
Monitoring the progeny of plants that germinated in subsequent years allowed us to quantify change in fruit wing phenotype frequencies to May 2018, and to subsequently estimate lambda and selection (Table 3.1; Figure 3.5). Inside exclosures by 2018, *P. congesta* plants with winged

fruits and derived from historically naïve populations ( $n = 1744$ ) were 3 times more abundant than plants with winged fruits from historically exposed populations ( $n = 571$ ), 3.5 times more abundant than plants with wingless fruits from historically naïve populations ( $n = 499$ ), and 4.8 times more abundant than plants with wingless fruits from exposed populations by 2018 ( $n = 365$ ; Figure 3.5). *P. congesta* were extirpated outside of exclosures by 2016, although only plants bearing wingless fruits survived in 2015, with five of the six plants being from populations historically exposed to ungulates (Figure 3.5).

Our findings above suggest that the highest rates of population growth ( $\lambda$ ) in the absence of ungulate browsers is expected in populations comprised of plants with winged fruits and originating from historically naïve populations. The highest population growth rate by ranked order of predicted means was indeed highest for this group, largely due to higher mean germination and fecundity (Table 3.1). Outside exclosures, plants with wingless fruits and originating from historically exposed populations had the highest estimated population growth rate, due to higher survival and fecundity as compared to other groups (Table 3.1; Appendix 15). High variance in estimated population growth rate reflect both micro-site and annual variation (Appendix 15), and are consistent with substantial variation between years in observed population growth rates. For example, all four groups inside exclosures exhibited population growth between 0.22 and 0.62 in 2014-15 and between 2.02 and 5.15 in 2015-16. This variation resulted in overlapping confidence intervals for population growth rate for all groups inside exclosures. Therefore, the rank order of which group performs best is as expected in and out of exclosures, but population growth rates are not substantially different between groups inside exclosures.



The rank order of predicted selection ( $S$ ) is as predicted, with populations from historically naïve populations bearing winged fruits most favoured inside exclosures, and historically exposed populations bearing wingless fruits most favoured outside of exclosures (Table 3.1). However, selection estimates also displayed substantial overlap in standard deviations because of annual variation in survival and fecundity (Table 3.1), resulting in these estimates not being significantly different from each other.



**Figure 3.5** Total number of winged (A) and wingless (B) plants detected in four surveys over five years inside (black lines) and outside (gray lines) exclosures. Plants from populations historically exposed (black squares, solid line) or naïve (open circles, hatched line) to ungulate browsers. Plants bearing winged fruits and originating from historically naïve populations dominated inside exclosures after five years. Plants bearing wingless fruits and from historically exposed populations survived best outside of exclosures for the first three years, but then all populations were extirpated.

**Table 3.1** Estimated germination, survival, fecundity, population growth rate ( $\lambda$ ), absolute fitness and selection ( $S$ ) of historically exposed ( $n_{\text{populations}} = 6$ ) or naïve ( $n_{\text{populations}} = 6$ ) populations of *P. congesta* relative to fruit phenotype. Rank order suggests that plants from historically naïve populations and bearing winged fruits perform best inside exclosures, whereas those from historically exposed populations bearing wingless fruits perform best outside of exclosures. However, there is substantial overlap in estimated standard deviations.

	<i>Germination</i>	<i>Survival</i>	<i>Fecundity</i>	$\lambda$	<i>Absolute Fitness</i>	<i>S</i>
<b><i>Inside Exclosures</i></b>						
<i>Historically Exposed, Wingless</i>	$0.23 \pm 0.02$	$0.42 \pm 0.05$	$43 \pm 46$	$4.52 \pm 3.79$	$19.76 \pm 16.71$	$0.51 \pm 0.42$
<i>Historically Exposed, Winged</i>	$0.16 \pm 0.02$	$0.51 \pm 0.06$	$30 \pm 29$	$2.74 \pm 2.20$	$16.55 \pm 13.46$	$0.58 \pm 0.39$
<i>Historically Naïve, Wingless</i>	$0.16 \pm 0.02$	$0.49 \pm 0.06$	$23 \pm 16$	$1.82 \pm 1.24$	$11.42 \pm 7.59$	$0.61 \pm 0.31$
<i>Historically Naïve, Winged</i>	$0.19 \pm 0.01$	$0.50 \pm 0.06$	$54 \pm 44$	$5.32 \pm 3.81$	$28.21 \pm 20.01$	$0.31 \pm 0.39$
<b><i>Outside Exclosures</i></b>						
<i>Historically Exposed, Wingless</i>	$0.16 \pm 0.03$	$0.33 \pm 0.06$	$10 \pm 4$	$0.54 \pm 0.28$	$3.53 \pm 1.57$	$0.14 \pm 0.34$
<i>Historically Exposed, Winged</i>	$0.19 \pm 0.02$	$0.18 \pm 0.06$	$8 \pm 7$	$0.30 \pm 0.25$	$1.80 \pm 1.33$	$0.38 \pm 0.47$
<i>Historically Naïve, Wingless</i>	$0.15 \pm 0.01$	$0.12 \pm 0.04$	$3 \pm 3$	$0.05 \pm 0.05$	$0.55 \pm 0.32$	$0.55 \pm 0.47$
<i>Historically Naïve, Winged</i>	$0.15 \pm 0.01$	$0.10 \pm 0.05$	$6 \pm 5$	$0.10 \pm 0.09$	$0.74 \pm 0.63$	$0.42 \pm 0.46$

### 3.5 Discussion

My results support the hypothesis that spatial heterogeneity in the occurrence or intensity of browsing by ungulates has led to local adaptation in plant populations with context-dependent trade-offs in the fitness value of traits. Specifically, I estimated survival, fecundity, and population growth for *P. congesta* populations with different browsing histories in common gardens exposed to or protected from ungulate browsers (Figure 3.1, Figure 3.5; Table 3.1). Outside exclosures, the ‘home environment’ for historically exposed populations, plants from historically exposed populations survived five times better (Figure 3.5) and were 1.4 to two times more fecund than plants from historically naïve populations (Figure 3.1). Inside exclosures, representing the ‘home environment’ for populations historically naïve to ungulate herbivory, plants from historically naïve populations were 2.5 times more abundant than plants from historically exposed populations after five growing seasons (Figure 3.5). These differences led to selection estimates favoring plants currently residing in their ‘home environment’, particularly if the plant produced the fruit phenotype most common from its native population; however, these estimates had substantial overlap in their standard deviations between groups (Table 3.1). The home site advantages observed in survival, fecundity and long-term persistence suggest that the populations used in this study are locally adapted to the presence or absence of herbivores (following guidelines in Kawecki and Ebert 2004, Blanquart et al. 2013), with annual variation in environmental conditions further influencing fitness for all groups. The differences among populations in survival and fecundity leading to local adaptation depended on environmental context and were linked to morphological and phenological traits known or assumed to be heritable (e.g., Carey and Ganders 1980, Carey 1983).

I observed several morphological and phenological traits consistent with local adaptation to resist ungulate herbivory. Specifically, *P. congesta* plants from populations historically exposed to ungulates germinated later, bolted later and allocated more energy to outward than upward growth early in the growing season (Figure 3.2, Figure 3.3), similar to resistance mechanisms in *O. biennis* (Parker et al. 2010, Agrawal et al. 2012) and *B. rapa* (Schiestl et al. 2014). Additionally, individual *Lathyrus vernus* plants that flowered earlier were more likely to be grazed compared to later flowering individuals (Ehrlén and Münzbergová 2009), a pattern that we also observed outside of exclosures here. Similarly, I speculate that fruits from historically exposed populations evolved to germinate later as a mechanism to reduce the total amount of time the plant is exposed to herbivory over its short lifetime. Low stature and growth form (H:W ratio) of *P. congesta* from historically exposed populations are also similar to observed differences for reduced scape-length in *P. farinosa* as a response to herbivory by deer (Ågren et al. 2013) and noted for other species (Mortenson 2013). Overall, my current and prior results (Chapter 2) support my hypothesis that population-level differences in plant architecture (Figure 3.5) and phenology (Figure 3.2, Figure 3.4) in *P. congesta* represent locally adapted traits that have evolved in response to browsing by ungulates in the San Juan and Gulf Island Archipelagos of western North America.

Locally adapted traits that confer a fitness advantage in one environment often result in a fitness disadvantage in contrasting environments (e.g., Murren et al. 2015, Bontrager and Angert 2018). Such differences are particularly noteworthy in island ecosystems, which often experience temporal variation in selective environments or gene flow between populations from contrasting selective environments (Warren et al. 2015). Spatial variation in ungulate densities is striking in the San Juan and Gulf Island Archipelagos (Martin et al. 2011, Arcese et al. 2014), which suggests

that trade-offs should be apparent in trait expression between populations with and without ungulate herbivores. Blossey and Notzold (1995) hypothesized that browsing pressure could lead to trade-offs in which traits that increase plant resistance or tolerance to browsing would reduce competitive ability in an environment without herbivores (the foreign environment for these plants). My results provide support for this idea, where plants from historically naïve populations germinated and bolted earlier than those from historically exposed populations (Figure 3.2), likely increasing their risk of being browsed in the presence of ungulates (Figure 3.1a). In the absence of ungulates, *P. congesta* from historically naïve populations were 2.4 times more abundant than those from historically exposed populations after five years (Figure 3.5). This increase in abundance was likely due to earlier bolting (Figure 3.2), earlier flowering (Figure 3.4) and larger inflorescences, which are traits associated with local adaptation to intraspecific competition for light and pollinators in other species (e.g., Ohara and Higashi 1994, Boege 2010, Ågren et al. 2013, Johnson et al. 2015, Ramos and Schiestl 2019). In the next chapter of my dissertation, I will investigate the direct influences of intraspecific competition on these traits and plant fecundity.

My results suggest that populations locally adapted to a specific selective pressure can be extirpated when selective pressure is too strong despite the evolution of locally adapted traits. Specifically, I estimated population growth rates of  $\lambda < 1$  for all populations outside of exclosures on Sidney Island (Table 3.1; Appendix 15), and found that no *P. congesta* survived in plots open to browsing after 3 years (Figure 3.5). Reductions in survival and fecundity outside exclosures appeared to be due to the loss of inflorescences and plant tissue, and the selective removal of larger plants by browsers. The fact that all individuals from all 12 source populations were eventually extirpated in the absence of protection from browsing suggests that ungulate densities on Sidney

Island ( $\sim 60$  deer/km<sup>2</sup>; unpublished results, Sallas Forest Partners) were sufficient to drive local extinction in *P. congesta*, despite the relative fitness advantage observed for populations historically exposed to browsing. However, I also acknowledge that the locations of the exclosures on Sidney Island may represent habitat that is drier than other sites throughout the Georgia Basin (Appendix 4), and that the studied plants may have therefore been physiologically stressed in ways that may additionally impact their survival, fecundity and morphological traits. For example, mean plant height for both historically exposed and naïve populations protected from herbivores inside exclosures was only  $\sim 17$  cm (Figure 3.3), whereas plant height in native populations without herbivores averaged 39 cm, and reached over 1 m in some populations (Chapter 2). Overall, given earlier suggestions that deer densities greater than 10/km<sup>2</sup> lead to dramatic reductions in plant species richness, diversity, and structural complexity in the Gulf, San Juan, and Haida Gwaii Archipelagos of western North America (Allombert et al. 2005, Martin et al. 2011, Arcese et al. 2014), my current results suggest that densities below at least 60 deer/km<sup>2</sup> are indeed necessary to prevent extinction in this and other highly palatable species in habitat patches without refuges from herbivores (e.g., Augustine and Frelich 1998, Knight 2004, Gonzales and Arcese 2008).

My results suggest that fruit phenotype affected fitness directly or indirectly in *P. congesta* given that phenotype predicted long-term persistence and fecundity in the presence or absence of deer (Figure 3.1, Figure 3.5; Table 3.1). Specifically, plants that germinated from wingless fruits achieved up to two times higher fitness outside exclosures (Figure 3.1b; Table 3.1) and were the only fruit phenotype persisting outside of exclosures in 2014 (Figure 3.5). Conversely, plants bearing winged fruits had up to 1.5 times higher fitness (Figure 3.1b) and were 2.7 times more abundant inside exclosures after five years (Figure 3.5; Table 3.1). These differences may reflect

trade-offs in fruit size, where larger fruits are more likely to result in larger flowers that attract pollinators (e.g., Ohara and Higashi 1994) and smaller fruits are more likely to escape herbivory (e.g., Janzen 1984) or pass through the gut of herbivores unharmed (Martz and Belyea 1986). These differences in survival by fruit phenotype may lead to long-term evolutionary change in rates of selfing versus outcrossing (e.g., Johnson et al. 2015). For example, herbivores selected for self-compatibility and increased selfing rates in *Brassica rapa*, but bee pollinators selected for increased floral attractiveness and outcrossing in the absence of herbivores (Ramos and Schiestl 2019). A closely related species, *Plectritis brachystemon*, possesses mostly wingless fruits, short stature, reduced floral structures and high selfing rates of 2-4% (Ganders et al. 1977b, Layton and Ganders 1984), suggesting that long-term selection from herbivory or other factors can lead to the evolution of a syndrome composed of traits linked to reduced floral apparency. However, I suggest that it is also possible that these differences in survival according to fruit phenotype are due at least partially to pleiotropic effects or genetic linkage between the fruit wing locus and genes affecting plant height, bolting or flowering phenology.

Adaptation in morphological traits can evolve within a few to hundreds of generations (Hendry and Kinnison 1999, Hendry et al. 2008), particularly on islands where barriers to gene flow can facilitate local adaptation given sufficient standing genetic variation in traits under selection (Wright 1982, Warren et al. 2015). In island populations of *P. congesta*, plant height has the potential to adapt rapidly to variation in browsing intensity given that Carey (1983) reported a 150% increase and 50% decline in the mean height of plants after five generations of artificial selection. Many of the locally adapted morphological and phenological traits described here also likely evolved locally within the last ~300 years. This is because ungulates occurred at relatively

low densities prior to the arrival of Europeans (Arcese et al. 2014), but subsequent declines in Indigenous peoples after the introduction of novel diseases resulted in the cessation of Indigenous land stewardship (Koch et al. 2019) and was followed by dramatic increases in the abundance of domestic, exotic, and native herbivores in association with the extirpation of large predators (Hatter and Janz 1994, MacDougall 2008, Martin et al. 2011, Arcese et al. 2014). Natural and human-assisted changes affecting ungulate density on islands are therefore likely to play a strong role in the distribution, abundance, and persistence of *P. congesta* populations in future, in combination with other variables such as independent impacts of climate and population dynamics.

Taken together, my results suggest that several morphological and phenological traits that can be easily observed in *P. congesta* populations within the Georgia Basin of western North America (Chapter 2) have evolved in response to spatial variation in natural selection by browsing ungulates. The fitness advantages estimated in the respective home environments of historically exposed and naïve populations were sometimes large, but also involved context-dependence trade-offs in the fitness value of traits affecting resistance to herbivory versus success in competition for light or pollinators. I also observed links between fruit phenotype and fecundity by showing that plants produced from small, wingless fruits displayed high relative fecundity in the presence of browsers, whereas plants producing larger winged fruits were 2.7 times more abundant in the absence of ungulate herbivores after five years. Overall, the results of this chapter add to the growing literature identifying evolutionary mechanisms responsible for the rapid evolution of population-level variation in life history, linked to spatial heterogeneity in the selective environment (see also, Ågren et al. 2013, Savolainen et al. 2013, Campbell et al. 2014, Bontrager and Angert 2018). The strong associations demonstrated here (Chapters 2, 3) between the



occurrence of *P. congesta* populations and traits expressed therein suggest that this species could serve as an excellent indicator of the current and historic environments experienced by the species and its more and less palatable community members. Such understandings can contribute to the conservation of critically-endangered threatened Garry oak and maritime meadow ecosystems of western North America and San Juan and Gulf Island archipelagos.

My findings offer broad support for the idea that in heterogeneous environments, trade-offs in the fitness value of locally adapted traits have the potential to dramatically influence population growth under changed conditions. Because such changes are common in terrestrial and marine systems following the eradication or introduction of keystone predators (Estes et al. 2011, Martin et al. 2011, Arcese et al. 2014), conservation planners will likely need to incorporate evolutionary history and local adaptation into decisions regarding the conservation and restoration of populations experiencing changes in land use, climate, and communities (e.g., Rice and Emery 2003, Weeks et al. 2011, Aitken and Whitlock 2013, Johnson et al. 2018). Further, my results suggest that gene flow between populations experiencing different selective environments will likely add further complexity to predicting and managing the consequences of change, given that gene flow might be expected to either reduce relative fitness in populations experiencing a stable selective environment with consistent directional selection due to isolation, topography, or human history, or to enhance capacity for adaptive response, population growth, and persistence in populations subject to rapidly fluctuating selection.

## **Chapter 4: Local Adaptation to Herbivory and Phenotypic Plasticity Drive Population-Level Variation in Genotype, Phenotype and Fitness in Island Populations of the Annual Plant *Plectritis congesta***

### **4.1 Summary**

Species respond to temporal and spatial variation in the environment via a combination of genetic differentiation and phenotypic plasticity. Understanding the relative roles of inheritance and phenotypic plasticity in local adaptation across multiple populations distributed over spatially heterogeneous selective environments can improve predictions about population responses to environmental change and help identify limits on species distributions. In this chapter, I monitor 3544 *P. congesta* plants from 435 families originating from populations historically exposed to ungulate browsing ( $n = 16$ ) and naïve to browsing ( $n = 28$ ) grown in two common gardens (2006-07, 2015-16) to explore the genetic and plastic contributions to phenotype. Both local adaptation and adaptive plasticity appear to maintain population-level differences in phenotype observed among island populations of *P. congesta* subject to variation in the occurrence of browsing ungulates. Specifically, historically exposed populations were ~40% shorter, tended to form rosettes, delayed flowering, and produced twice as many branches close to the ground compared to historically naïve populations. Predicted evolvabilities were relatively high for all traits (~3-30% change per generation), suggesting that rapid changes in the mean value of some traits could be selected for in 2-18 generations, matching estimates for rapid adaptation in island populations of birds, lizards and other plant species. However, these traits also displayed high coefficients of phenotypic variation ( $CV_p = 36$  to 149%) that were much greater than their coefficients of additive

genetic variance ( $CV_a = 23$  to  $36\%$ ), indicating that environmental factors had a strong influence on trait expression. I also detected adaptive plasticity in response to plant density in which plants from all populations were able to increase final plant height with increased density, but at a 20-30% fitness cost. My results support our hypothesis that *P. congesta* can adapt rapidly and exhibits both local adaptation and adaptive plasticity in response to environmental conditions, but that there are costs to expressing specific phenotypes and adaptive plasticity. Differences in fitness associated with phenotypes and plasticity in contrasting environments can dramatically influence population persistence when conditions change, such as with fluctuations in herbivore density in island ecosystems. I suggest that reducing ungulate densities or eliminating ungulates entirely in at least some patches of the Garry oak and maritime meadow ecosystems will be required to maintain genetic diversity across the range and successfully restore this species to sites where herbivores are unnaturally abundant.

## **4.2 Introduction**

Identifying the genetic and environmental factors affecting population differentiation in heterogenous environments can improve predictions about population responses to environmental change and help identify limits on species distributions (Endler 1980, Lande and Shannon 1996, Germain et al. 2018). Species respond to temporal and spatial variation in the environment via a combination of genetic differentiation and phenotypic plasticity (Franks et al. 2014, Grenier et al. 2016). However, the efficiency of natural selection can vary dramatically with the amount of genetic variation in populations, gene flow among them, and spatial and temporal variation in the fitness-value of particular traits (Wright 1982, Kawecki and Ebert 2004, Gould et al. 2014). One metric used to predict population response to selection is narrow-sense heritability ( $h^2$ ), which

estimates the proportion of the observed variance in phenotype that is explained by inheritance (Visscher et al. 2008). Conversely, phenotypic plasticity is observed when trait expression is environmentally dependent and does not require genetic differentiation (Bradshaw 1965, Schlichting 1986), although the underlying cause of differences in plastic responses can be due to genetic differences between populations (Hendry 2015). Quantifying phenotypic plasticity can provide insight regarding the range of environmental conditions in which a populations can be expected to persist in the absence of additional genetic differentiation (Chevin et al. 2010, Lande 2015, Bonamour et al. 2019, Fox et al. 2019), but many studies suggest that plasticity will be insufficient to accommodate ongoing environmental change experienced by many species (Duputié et al. 2015). As a consequence, there is a need to understand the relative roles of inheritance and phenotypic plasticity in local adaptation, and value in comparing multiple populations distributed over spatially heterogeneous selective environments (van Kleunen and Fischer 2005, Valladares et al. 2014). Here, I use common gardens containing 3544 *Plectritis congesta* plants from 44 island populations historically exposed ( $n = 16$ ) or naïve ( $n = 28$ ) to ungulate browsers to estimate genetic and plastic contributions to trait expression among populations.

The rate of gene flow between populations is one of many factors that influences whether local adaptation or phenotypic plasticity is more often observed in spatially heterogeneous environments, with both local adaptation and phenotypic plasticity being commonly detected (Leimu and Fischer 2008, Palacio-López et al. 2015). When gene flow between populations is limited, natural selection theoretically can lead to ‘perfect local adaptation’ in which responses are canalized (i.e., entirely inherited, not influenced by environment; Palacio-Lopez et al. 2015), although most quantitative

traits are additionally impacted by environmental conditions and can still be locally adapted. Such locally adapted traits can substantially enhance local fitness, but reduce fitness when expressed in novel environments, revealing fitness trade-offs and costs of phenotypes (e.g., Bennett and Lenski 2007, Callahan et al. 2008, Rodríguez-verdugo et al. 2014, Murren et al. 2015, Bontrager and Angert 2018). Conversely, phenotypic plasticity is predicted to be observed when gene flow is extensive between populations experiencing different selective pressures (Sultan and Spencer 2002, Emery 2009, Scheiner 2013), with three defined types: (1) perfect adaptive plasticity, where a similar phenotype is expressed in the same environment regardless of population of origin (i.e., no local adaptation); (2) adaptive plasticity, where resident and nonresident populations respond in a similar manner but maintain baseline differences and allow a genotype to survive and reproduce in a variety of environmental conditions (i.e., can still be locally adapted), and (3) nonadaptive plasticity, where populations demonstrate plastic responses that reduce their fitness on average compared to ancestral phenotype or is in a maladaptive direction (Levins 1968, Ghalambor et al. 2007). Island archipelagos are particularly useful for studying local adaptation and adaptive plasticity because of barriers that restrict gene flow (Warren et al. 2015), wherein gene flow may introduce sufficient variation to either (1) maintain plastic responses to a variety of environmental stimuli, or (2) allow natural selection to act and promote local adaptation (Barton and Turelli 1989, Lenormand 2002).

Plants that express canalized locally adapted traits to resist or tolerate herbivory may experience a competitive disadvantage in the absence of herbivores. Traits related to resistance (i.e., those that enhance survival by reducing the probability of herbivory) and tolerance (i.e., those that enhance relative fitness by improving the capacity for regrowth and reproduction given partial herbivory)

can help reduce the negative impacts of herbivory (van der Meijden et al. 1988). Traits associated with resistance or tolerance to ungulate herbivory include delays in bolting and maintaining a short stature (e.g., *Oenothera biennis*, Parker, Salminen and Agrawal 2010), increasing the production of branches following herbivory (e.g., *Impomopsis aggregate*, Paige and Whitham 1987, Juenger and Bergelson 2000; *Thuja plicata*, Stroh et al. 2008), and chemical defenses to deter herbivores (e.g., *Thuja plicata*, Vourc'h et al. 2001). Many of these traits are constitutive (i.e., always present), while others are environmentally induced (i.e., plastic, Agrawal 1999). Plants that delay bolting or maintain a short stature often experience reduced fitness as a result of competition for light (e.g., Givnish 1982; *Tithonia tubaeformis*, Boege 2010) or pollinators (e.g., *Primula farinosa*, Ågren et al. 2013). Such competition is hypothesized to result in greater stem elongation at high planting densities as a response to increased shading via adaptive plasticity (e.g., Casal and Smith 1989). However, initial differences in plant height in mixed stands can also impact plant fitness. Dudley and Schmitt (1996) showed that *Impatiens capensis* plants grown to produce elongated stems had a fitness advantage over plants with non-elongated stems at high planting densities, but prior induction of stem elongation had a fitness cost when transplanted into low planting densities. Ultimately, phenotype and trait distributions are influenced by both genetics and the environment, mediated by the fitness value of specific traits or phenotypes (Callahan et al. 2008, Murren et al. 2015) and plasticity within them (DeWitt et al. 1998, Murren et al. 2015). However, examples providing evidence of adaptive plasticity are scarce despite their theorized value in spatially heterogeneous environments (van Kleunen and Fischer 2005, Palacio-López et al. 2015).

By comparing differences within and between families in common gardens, the relative contributions of genetic and environmental factors influencing traits, as well as the potential for

future selection, can be elucidated by estimating: (1) the additive genetic variance ( $V_a$ ; additive genetic contribution to phenotype, not accounting for dominance or epistatic effects); (2) narrow-sense heritability (i.e.,  $h^2 = V_a/V_p$ ; where  $V_p$  represents the total phenotypic variance, a combination of genetic, environmental and residual variance); (3) the coefficient of additive genetic variation ( $CV_A$ ; a measure of the relative additive genetic variation relative to the trait mean); (4) evolvability (i.e., ability of a population to respond to natural selection, expressed as the percent change predicted per generation given selection; Houle 1992, Hansen et al. 2003, Visscher et al. 2008); and (5) the coefficient of phenotypic variation ( $CV_p$ ; a measure of the relative phenotypic variation relative to the trait mean, including all genetic, environmental and residual variation). Genetic contributions are most strongly elucidated via  $V_a$ ,  $h^2$ , and  $CV_a$ , with evolvability predicting the rate of change in a trait per generation. Evolvability estimates allow predictions as to how many generations is required to lead to specific changes in trait means. Conversely, plasticity can be assessed by evaluating the  $CV_p$  and, additionally, by evaluating induced responses to a variety of local conditions (e.g., altering climatic variables or planting densities).

*Plectritis congesta* is a winter annual that exhibits substantial phenotypic variation relative to the presence or absence of ungulate herbivores (Chapter 2). It occurs in Garry oak and maritime meadow ecosystems throughout the San Juan and Gulf Island Archipelagos of the Georgia Basin, where variation in island size, isolation, and history enforce marked spatial and temporal variation in the occurrence of ungulate browsers (e.g., Gonzales and Arcese 2008, Martin et al. 2011, Arcese et al. 2014). All *P. congesta* plants produce one of two fruit phenotypes, with or without wing-like appendages (Jacobs et al. 2010), following Mendelian dominance at a single locus ( $Ww$ ,  $WW =$

winged, ww = wingless, Ganders et al. 1977a). Plants from historically naïve populations (i.e., those that historically do not host resident ungulates) are 2.6 times taller and bear predominantly winged fruits (~91%) compared to historically exposed populations (i.e., those that historically do host resident ungulates) which contain plants that are shorter and bear predominantly wingless fruits (~73%; Chapter 2). Carey (1983) has previously shown that plant height in *P. congesta* has the potential to adapt rapidly to variation in browsing intensity given a 150% increase and 50% decline in the mean height of plants after 5 generations of artificial selection. Differences in plant height, phenology and fruit phenotype may therefore represent adaptations to herbivory, given that plants from populations historically exposed to ungulates displayed higher relative fitness in the presence of ungulates by bolting and flowering later than plants from populations that were naïve to ungulates (Chapter 3). However, modest plasticity has also been observed in height in *P. congesta* in growth chambers (Carey and Ganders 1980), and in flowering phenology in response to latitudinal variation in local temperature (Reed et al. 2019). Prior results also suggest that herbivory is more limiting of population growth in *P. congesta* than above-ground competition with exotic grasses (Gonzales and Arcese 2008), but plastic responses to variation in intraspecific competition, which may also vary with the intensity of herbivory, has not been studied. Investigating such effects is a novel and particularly informative avenue to better understand multiple contributors to phenotype and local adaptation.

My prior results and theory suggest that population-level variation in the traits of *P. congesta* on islands likely represents the outcome of local adaptation and adaptive plasticity, mediated by the fitness value of traits in the presence or absence of ungulate herbivores. I therefore hypothesize that (1) population-level differences in traits facilitating adaptation to resist ungulate herbivory or



increase competition for light (i.e., height, phenology; Chapter 3) have arisen in populations in part via spatial variation in ungulate presence leading to genetic differentiation. If true, I expect plants from populations historically exposed to ungulates to delay bolting and flowering, achieve shorter peak heights, favour outward over upward growth (growth form), produce more branches, and have branches closer to the ground than plants naïve to ungulates. I additionally hypothesize that (2) within historically exposed and naïve populations, plants bearing winged fruits will demonstrate greater heights, higher branches and earlier phenology compared to plants bearing wingless fruits because of the dominant fruit phenotypes observed in wild populations (i.e., winged in historically naïve and wingless in historically exposed populations). Because of these expected differences, I hypothesize that (3) plant height, growth form and branch allocation will be heritable, with relatively high evolvabilities, but that these traits will also express relatively high coefficients of phenotypic variation. Such high evolvabilities will predict the capacity for rapid adaptation in few (~5-20) generations. Finally, I hypothesize that (4) populations that differ in browsing history will exhibit adaptive phenotypic plasticity via stem elongation as a response to intraspecific competition. Specifically, I predict that in addition to observing mean differences in plant height, growth form, and lowest branch height between historically exposed and naïve populations, I would observe plasticity in stem elongation, growth form, and branch height in response to plant density. I further predict that greater stem elongation will come at a fitness cost, with the cost being greater as the mean height of neighbours increases.

### **4.3 Methodology**

#### **4.3.1 Fruit Collection**

Fruits of *P. congesta* were collected from 44 populations ( $n = 16$  historically exposed;  $n = 28$  historically naïve) from Vancouver Island and the Gulf Islands of British Columbia, Canada (Appendix 16), of which 20 were collected from in 2005, 17 in 2006 and 21 in 2015. “Historically exposed” populations were those known to host resident deer or sheep (*Ovis aries*, one island) and “historically naïve” populations were those from islands on which no ungulate sightings or sign (e.g., pellets, browsed plants) were observed in the past 20 years, or which had physical barriers such as shoreline cliffs preventing access by ungulates (similar to “historically protected” populations in Martin et al. 2015). In 35 of the 44 populations, fruits were collected from 10-13 ‘families’ representing both fruit phenotypes (i.e., winged and wingless) in 2006 or 2015. Families were defined as including all fruits collected from a single parent plant. The remaining nine populations were all collected only in 2005, along with 11 populations also collected in 2006 or 2015 (20 total populations collected from in 2005), and seeds within each population were pooled together across individuals and were not used for estimates of  $V_a$ ,  $h^2$ ,  $CV_a$ ,  $CV_p$  and evolvability. All fruits were collected from plants  $> 1$  m apart in natural populations, and then sun-dried and stored at 5°C until planted.

#### **4.3.2 Experimental Design**

Two common gardens were planted, one in 2006-07 using fruits collected in 2005 and 2006, and one in 2015-16, using fruits collected in 2015. Fruits were sown 10 cm apart in 12 (2006) or 15 (2015) 1.2 x 2.4 m raised beds (previously fertilized sandy loam; Totem Field, University of British Columbia). Up to 44 fruits from each pooled population in 2005 (30 to 44, median 44 fruits per

population) were selected to represent variation in size and fruit phenotype, for a total of 714 fruits sown ( $n = 396$  winged,  $n = 318$  wingless). Families from 2006 were planted in randomized blocks, with one sibling from  $\leq 12$  families per bed, per population (range 7-12 families, median 12 families per population;  $n = 1442$  winged fruits,  $n = 625$  wingless fruits). Families from 2015 were planted similarly, with each bed sown with fruits from 12 families per population ( $n = 1713$  winged fruits,  $n = 1311$  wingless fruits).

Planting began September 25, 2006 and occurred over 11 days for the 2006-07 garden and began on September 20, 2015 over 9 days for the 2015-16 garden. In both years, beds were watered to secure fruits in soil and protected by a clear plastic canopy to prevent displacement. In 2015-16, I watered every three days to day 92 when the canopy was removed and watering ceased, allowing natural rainfall to provide water for plants. This was the same protocol followed for the 2006-07 garden. These beds were regularly weeded to eliminate interspecific competition with other plants.

Assessments for germination, morphology and phenology were made at approximately the same number of days post-planting in both the 2006-07 and 2015-16 gardens at days 55 (November), 119 (January) and 192 (late March), and in April and May. Measurements were taken two weeks earlier in April and May for the 2015-16 garden due to a warmer than normal spring. Germination was assessed for all fruits 55 days post-planting. Plant height and diameter at the widest point were recorded on day 55, 119 and 192 for all plants surviving to this stage; height was also recorded in April and May. Flowering phenology was estimated by scoring plants for the absence of buds, presence of buds, or presence of open flowers on day 192 (represented by a scale of 1, 2 or 3, respectively). In May, I counted the total number of branches and branches below 10 cm, measured

height of the lowest branch above the ground and recorded fruit phenotype of the surviving plant. Because *P. congesta* can have hundreds of flowers per inflorescence and typically mature over weeks, counting flowers or fruits was impractical and thus not recorded. I did, however, record the height and width of the terminal inflorescence in May 2015 (but not 2006) and estimated the number of fruits present relative to inflorescence volume using relationships previously determined for this species (Appendix 14). Planting density surrounding each location was not altered, but instead was determined by the natural germination success of each adjacent planting location.

### **4.3.3 Genetic Variance, Heritability, Coefficient of Variation and Evolvability**

I used a linear mixed effects model (lmer) in the lme4 package (Bates et al. 2015) in the R Statistical Program (R 3.1.0 Statistic Package, R Core Team 2014) to estimate the variance explained by the additive genetic component of genotype ( $V_a$ ) and total phenotypic variance ( $V_p$ ) for plant height (Day 192, natural log transformed), growth form (H:W ratio; Day 192, natural log transformed) and the number of branches below 10 cm (May). Random effects included in all models to partition variance were (1) family nested within population of origin and (2) bed nested within garden year. Additive genetic variance ( $V_a$ ) was estimated from family variance ( $V_f$ ) under a mixed mating system ( $V_a = 3 V_f$ ; following methods similar to Angert et al. 2014, Rubin et al. 2019).). This assumes that fruits from the same family are on average approximately 50% half siblings, where  $V_a = 4*V_f$ , and 50% full siblings, where  $V_a = 2*V_f$ . I estimated narrow-sense heritability as  $h^2 = V_a/V_P$ , where  $V_a$  is the additive genetic variance and  $V_P$  is the total phenotypic variance explained by family (including variance explained by additive genetic factors and residual variation). The coefficient of additive genetic variation was calculated as  $V_a^{0.5}/\mu_i$  and the

coefficient of phenotypic variation was calculated as  $V_p^{0.5}/\mu_i$ , where  $\mu_i$  is the mean of trait  $i$  (Houle 1992). I estimated evolvability as  $100 * (V_a / (\mu_i)^2)$  (Houle 1992). I then estimated the number of generations required for trait means in historically exposed populations to reach the trait mean in historically naïve populations in the Totem Field common garden, and vice versa, using the formula  $N_{gen} = [((\mu_1 - \mu_2) / \mu_2) * 100] / \text{evolvability}$ , where  $N_{gen}$  is the number of generations,  $\mu_1$  is the mean value observed for plants from historically exposed or naïve populations, and  $\mu_2$  is the mean value observed in the opposite selective environment.

#### **4.3.4 Statistical Analyses: Trait Variation Relative to Ungulate Herbivory**

Most analyses were conducted with the glmmADMB package (Skaug et al. 2018) in the R Statistical Program (R 3.1.0 Statistic Package, R Core Team 2014). To assess trait variation, I estimated the effects of (1) browsing history (i.e., fruits originating from historically exposed or naïve populations; fixed effect); and (2) fruit phenotype of resultant plant (i.e. winged or wingless, fixed effect) on: (A) plant height over time; (B) growth form over time (height to width ratio, H:W ratio; with greater values denoting more allocation to upward than outward growth); (C) the number of total branches in May; (D) the number of branches below 10 cm in May; (E) height of the lowest branch in May; and (F) budding phenology at Day 192 (either no buds forming, buds forming, or flowers blooming). All model results are shown in the relevant cited appendix.

To estimate plant height and growth form at each measurement date (day 55, 119, 192 for both; also April and May for plant height), I tested two-way interactions between browsing history and fruit phenotype of the resulting plant (0, Appendix 18). I used only plants that germinated and survived to each measurement date and were not damaged during sampling ( $n = 3515$  in most

models,  $n = 3408$  at day 55 due to delayed germination of some plants). Models were run with Gaussian distributions and log transformations of height and the H:W ratio (representing growth form). Growth form was only estimated for the first three measurement dates because all plants bolted by April. I included population of origin and bed ID nested within garden year as random effects.

To estimate the number of total branches and the number of branches below 10 cm height, I tested a two-way interaction between browsing history and fruit phenotype of resultant plant, using only plants that survived until May (Appendix 19, Appendix 20). The model predicting the total number of branches was assessed using log transformed data and a Gaussian distribution. The model predicting the total number of branches below 10 cm was assessed using a Poisson distribution and a log link. Population of origin and bed ID nested within garden year were included as random effects in both series of models. To estimate the height of the lowest branch, I conducted a nonparametric Kruskal-Wallis test to compare branch height between four groups: plants from historically exposed or naïve populations and those with winged or wingless fruits.

Flowering phenology at Day 192 was assessed using the ‘multinom’ function in the nnet package (Venables and Ripley 2002), using flowering phenology classes as multinomial responses where ‘1’ represented no bud formation, ‘2’ represented bud formation and ‘3’ represented the presence of blooming flowers. I tested a two-way interaction between browsing history and fruit phenotype of resultant plant (Appendix 21). I used only plants that survived to Day 192 and I included bed ID nested within garden year as random effects.

#### **4.3.5 Statistical Analyses: Intraspecific Competition and Phenotypic Plasticity**

To test for fitness differences (i.e., number of fruits) relative to browsing history, fruit phenotype and intraspecific competition, I tested two-way interactions between (1) browsing history and fruit phenotype of the focal plant, (2) the total number of neighbours and the proportion of neighbours from historically exposed populations, and (3) the total number of neighbours and the mean height of neighbouring plants (Appendix 22). Overall, there are four ‘fruit phenotype by origin’ groups of interest (i.e., historically exposed winged, historically exposed wingless, historically naïve winged, historically naïve wingless). The model used a Poisson distribution and a log link. The random effects variables were bed ID and family nested within population of origin. I only assessed fecundity for the 2015-16 garden because the 2006 garden did not include measurements for inflorescence height and width. The plants closest to the edge of each bed were removed from the analysis, as were any planting locations that failed to germinate, and any plants damaged during sampling.

Similarly, to test for phenotype plasticity relative to browsing history, fruit phenotype and intraspecific competition, I tested two-way interactions between (1) browsing history and fruit phenotype of the focal plant, (2) the total number of neighbours and the proportion of neighbours from historically exposed populations, and (3) the total number of neighbours and the mean height of neighbouring plants on: (A) plant height in May (untransformed; Gaussian distribution; Appendix 23); (B) growth form at day 192 (H:W ratio; log transformed; Gaussian distribution; Appendix 24); (C) total number of branches in May (Poisson distribution; log link; Appendix 25) and; and (D) the number of branches below 10 cm in May (Poisson distribution; log link; Appendix 26). The plants closest to the edge of each bed and plants damaged during sampling were removed

from all analyses. Random effects variables were genetic family nested in population of origin and bed ID nested within garden year.

## **4.4 Results**

I scored 3544 plants for quantitative traits in common gardens grown in two different years ( $n_{2007, \text{pooled}} = 480$ ,  $n_{2007, \text{families}} = 1589$ ,  $n_{2015, \text{families}} = 1507$ ). Germination rates were high and similar among populations in 2006-07 (~76%), but lower in 2015-16 (~51%). In contrast, survival from germination to flowering was high in both gardens (95-98%).

### **4.4.1 Additive Genetic Variance, Heritability, Coefficient of Variation and Evolvability**

Additive genetic variance and estimates of heritability were generally low, being lowest for growth form, then plant height, and finally the number of branches below 10 cm (Table 4.1). The coefficients of additive genetic variance were similar for all traits ( $CV_a = 22$  to 36%), with the coefficient of phenotypic variance being much larger for all traits ( $CV_p = 36$  to 149%; Table 4.1). Evolvability estimates were high, leading to predictions that rapid change could occur in 2-18 generations, depending on the trait (Table 4.1; Appendix 27).



**Table 4.1 Additive genetic variance ( $V_a$ ), narrow-sense heritability ( $h^2$ ), coefficient of variation for additive genetic variance ( $CV_a$ ) and phenotypic variance ( $CV_p$ ), evolvability, and the estimated number of generations needed to reach the mean value observed in populations from contrasting selective environments.  $V_a$  and  $h^2$  are at intermediate values, but evolvability estimates suggest the potential for measurable change in trait means each generation.  $CV_p$  estimates are substantially larger than  $CV_a$  estimates, suggesting large influences from environmental factors.**

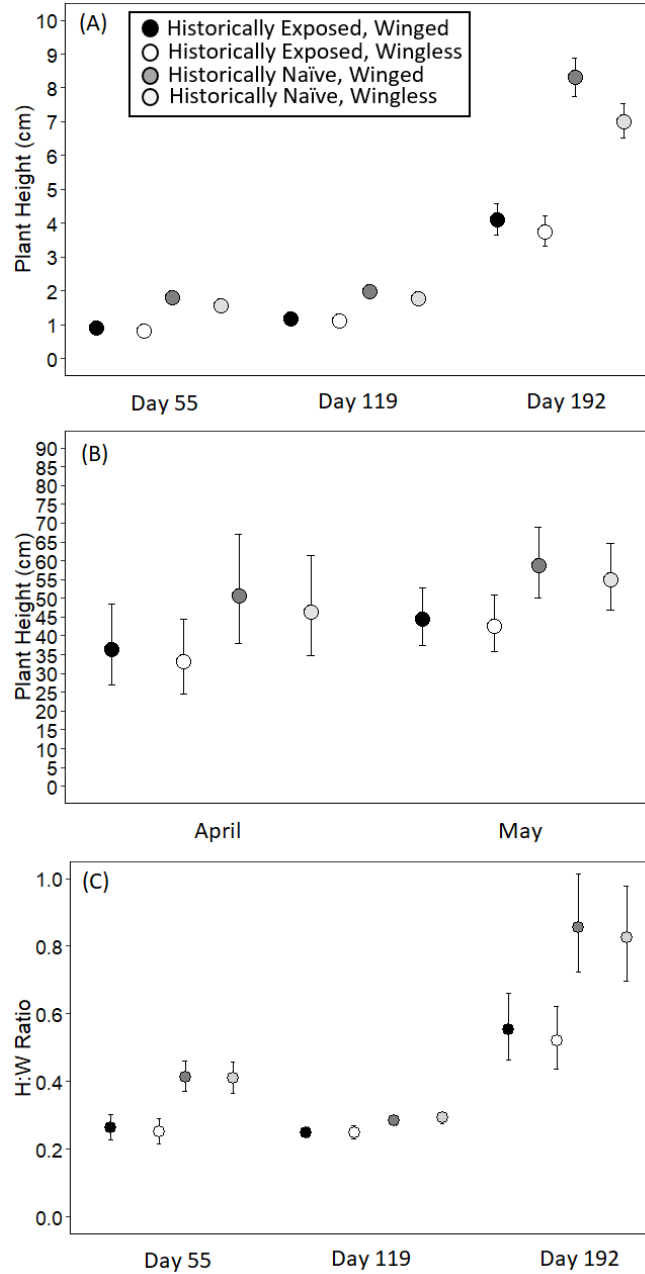
Trait	$V_a$	$h^2$	$CV_a$	$CV_p$	Evolvability	# Generations
Height D192 (logged)	0.09	0.22	22.65	36.01	2.83	12-18
H:W Ratio D192 (logged)	0.03	0.14	32.02	149.14	30.11	2-5
# Branches < 10 cm	0.21	0.26	35.57	54.26	7.79	6-10

#### 4.4.2 Trait Variation and Herbivory

Model generated estimates suggest that plants from historically naïve populations were about 28 to 40% taller than plants from historically exposed populations at all five censuses (Figure 4.1a, b; 0). Plants bearing winged fruits were also 10 to 20% taller than plants bearing wingless fruits to Day 192, and five to 10% taller thereafter (Figure 4.1a, b; 0). Models also predicted that plants from historically exposed populations allocated more energy to outward than upward growth than plants from historically naïve populations at all three survey times for which width was measured (days 55, 119 and 192; Figure 4.1c; Appendix 18). The largest differences occurred at Day 192 (60% larger H:W ratio in historically naïve vs exposed populations; Figure 4.1c). Growth form (H:W ratio) was only affected by fruit phenotype at day 192 (March), wherein plants bearing wingless fruits also allocated more growth outwards than upwards and displayed H:W ratios at ~95% the values observed for plants bearing winged fruits (Appendix 18). Additionally, early in the growing season, plants from historically exposed populations were visibly smaller and were easily distinguished from larger plants from historically naïve populations (Figure 4.2).

In addition to forming rosettes, models predicted that plants from historically exposed populations produced nearly twice as many branches below 10 cm height ( $8.0 \pm 0.4$ ) as plants from historically naïve populations ( $4.3 \pm 0.2$ ; Appendix 20), despite plants from historically naïve populations producing one to two more branches on average ( $14.0 \pm 0.7$ ) than plants from historically exposed populations ( $12.7 \pm 0.7$ ; Appendix 19). Similarly, the average height of the lowest branch was three times higher in historically naïve populations ( $3.8 \pm 0.3$  cm) than in historically exposed populations ( $1.20 \pm 0.21$  cm; Kuskal-Wallis,  $\chi^2 = 218.75$ ,  $df = 3$ ,  $P < 0.001$ ).

Model predicted estimates indicate that plants from historically naïve populations and those bearing winged fruits developed buds and flowered earlier than plants from historically exposed populations or those bearing wingless fruits (Table 4.2; Appendix 21). For example, in historically naïve populations, 62.4% of plants bearing winged fruits developed buds by Day 192 (March) and 19.6% had flowered, as compared to 30.1% and 13.0% of plants from historically exposed populations, respectively (Table 4.2).



**Figure 4.1** Plant height (0) at days 55, 119 and 192 (A) and in April and May (B), and growth form from day 55 to day 192 (C; Appendix 18) relative to browsing history and fruit phenotype. Plants from historically naïve populations were consistently taller than plants from historically exposed populations.



**Figure 4.2** Common observed differences in plant size at day 55 (December) between plants from historically naïve (left, larger) and exposed populations (right, smaller), prior to bolting. Photo credit: Cora Skaien.

**Table 4.2** Model predicted percentages of plants at each developmental stage (no bud formation, buds forming or flowers present) at day 192 for historically exposed and naïve populations of both fruit phenotypes (Appendix 21). Plants from historically naïve populations and bearing winged fruits were at more advanced flower development than those from historically exposed populations or bearing wingless fruits.

	No Buds	Pink Buds	Blooming
Historically Exposed			
Winged	57.0%	30.1%	13.0%
Wingless	66.1%	27.1%	6.8%
Historically Naïve			
Winged	20.1%	62.4%	19.6%
Wingless	51.5%	39.5%	9.0%

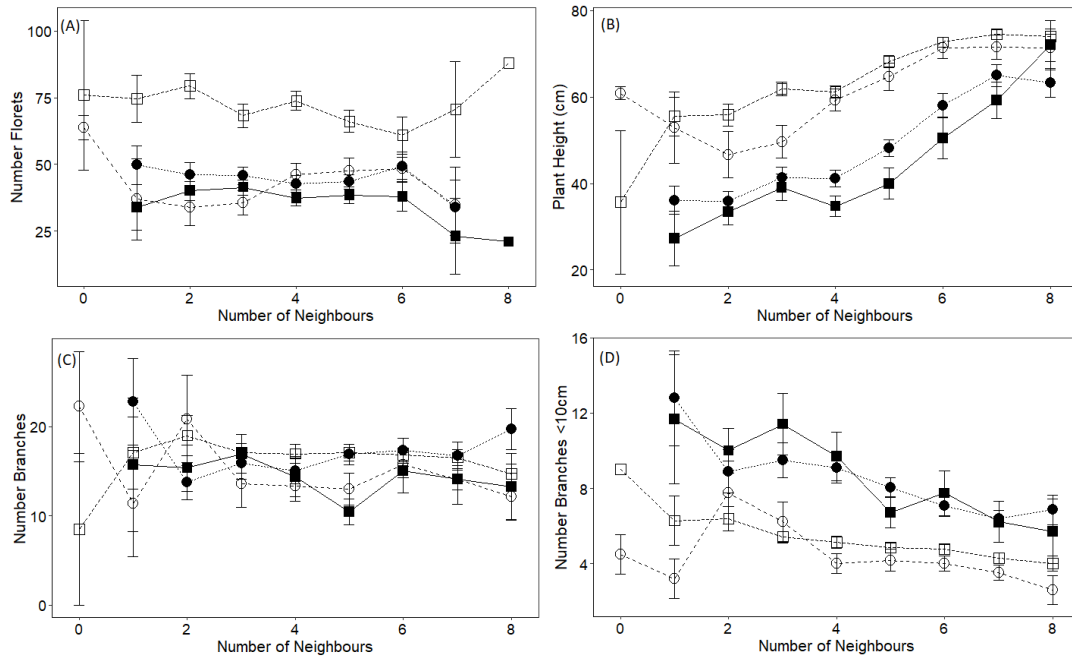
#### **4.4.3 Intraspecific Competition and Phenotypic Plasticity**

Model predictions suggest that fecundity was two to three times higher in plants bearing winged fruits and collected from historically naïve populations than all other fruit phenotype by origin groups, but it declined as neighbour density increased for all groups (Figure 4.3a; Appendix 22). Additionally, declines in fecundity were larger as the proportion of neighbours from historically naïve populations increased (Appendix 22).

Adaptive plasticity was observed wherein models predicted that all plants increased their height by a factor of 1.5 to three as the number of neighbours increased from zero to eight (Figure 4.3b; Appendix 23). This increase was most evident in historically exposed populations, which remained short when they only had one neighbour (e.g., ~25 to 35 cm), but nearly tripled their height and matched that of plants from historically naïve populations when there were eight neighbours (e.g., ~75 cm, Figure 4.3b; Appendix 23). At low planting densities, plants from historically naïve populations were two to three times taller than those from historically exposed populations (Figure 4.3b). The height of focal plants also increased as the mean height of its neighbours increased, further suggestive of an adaptive response to shading (Appendix 23). In comparison to plant height, I did not detect phenotypic plasticity in growth form, which appeared to be unaffected by intraspecific competition in this common garden (Appendix 24).

Model predicted estimates indicate that plants from historically naïve populations had approximately half as many branches below 10 cm as plants from historically exposed populations, but this number decreased by approximately half in all groups as the number of neighbours increased from zero to eight (Figure 4.3d; Appendix 26). These differences were independent from

the total number of branches produced, which was similar for all groups regardless of neighbour density (Figure 4.3c; Appendix 25).



**Figure 4.3** Fecundity (estimated number of florets; A), plant height (B), total number of branches (C) and number of branches below 10 cm (D) in May, showing mean  $\pm$  standard error of raw data. Open and closed symbols represent historically exposed and naïve populations respectively. Squares and circles represent winged and wingless fruits respectively. Plants responded plastically to increased neighbour density by increasing plant height and height of branches, but this came at a cost of reduced fecundity.

## 4.5 Discussion

My results indicate that local adaptation and phenotypic plasticity each play substantial roles in maintaining population-level variation in phenotype in island populations of *P. congesta* with and without ungulate herbivores. Moreover, the estimated evolvabilities were high for all traits examined, suggesting that rapid changes in trait distributions could be selected for within 2-18 generations (Table 4.1; e.g., Carey 1983). Such rapid changes are similar to those predicted or

observed in species of lizards (Stuart et al. 2014), birds (Grant and Grant 2006) and other plants (Ågren et al. 2013). Differences in trait expression that I previously demonstrated to be the result of local adaptation to resist herbivory (Chapter 3:) were maintained here in common gardens and were predictable based on history of exposure to ungulates. Specifically, plants from historically exposed populations were 28 to 40% shorter (Figure 4.1a, b), tended to form rosettes (Figure 4.1c), delayed flowering (Table 4.2), and produced twice as many branches close to the ground (Figure 4.3d) compared to plants from historically naïve populations. These mechanisms to resist ungulate herbivores are similar to those observed in *O. biennis* (Parker et al. 2010). However, historically exposed populations also displayed two to three times lower fecundity than plants from historically naïve populations in this herbivore-free environment (Figure 4.3a), revealing a cost to the expression of locally adapted phenotypes in environments that differed from the environment in which the phenotype evolved (e.g., Bennett and Lenski 2007, Callahan et al. 2008, Rodríguez-verdugo et al. 2014, Murren et al. 2015, Bontrager and Angert 2018). I also reported high coefficients of phenotypic variation in locally adapted traits ( $CV_p = 46$  to  $200\%$ ; Table 4.1), and observed adaptive plasticity in response to planting density (Figure 4.3), indicating that environmental factors had strong effects on trait expression and that differences were not solely based on genetic differentiation. Such differences in local adaptation and adaptive plasticity as a result of trade-offs in the fitness value of traits have led to ecological character displacement in other species (e.g., benthic and limnetic forms of stickleback, Schluter 2000), and this chapter contributes to the growing body of literature suggesting the important role of such differentiation when considering the response of populations to environmental change.

As predicted, adaptive plasticity in response to increasing plant density incurred a fitness cost (Figure 4.3; Givnish 1982). Specifically, plant height increased 1.5 to three-fold as plant density increased from zero to eight neighbours (Figure 4.3b), but at a ~20-30% reduction in fecundity (Figure 4.3a). The reduced fecundity as a result of stem elongation in response to shading mirrors that observed in *I. capensis* (Dudley and Schmitt 1996) and is similar to the costs of adaptive plasticity observed in other species (DeWitt et al. 1998, Murren et al. 2015). My findings are also similar to previous studies investigating trade-offs in fitness for the expression of traits associated with herbivore resistance and competitive ability observed in scape-length in *P. farinosa* (Ågren et al. 2013) and plant height in *T. tubaeformis* (Boege 2010). Costs of plasticity were additionally evident in that: (1) the height of focal plants increased as the mean height of neighbours increased; and (2) fecundity declined more rapidly as the fraction of neighbours from historically naïve populations increased, given that they were also taller on average. The results presented in this chapter therefore indicate that *P. congesta* exhibits both local adaptation and adaptive plasticity in response to environmental conditions, similar to findings in *Clarkia xantiana* (Gould et al. 2014), but that there are costs associated both with expressing specific phenotypes (Callahan et al. 2008) and for adaptive plasticity (DeWitt et al. 1998).

Plants bearing winged fruits were more likely to demonstrate earlier phenology for bolting and flowering than those with wingless fruits (Figure 4.1a, b; Table 4.2), both features attributed to historically naïve populations. Specifically, within exposed and naïve populations, plants bearing winged fruits were 10-15% taller to day 192 (Figure 4.1a, b) and more than twice as many plants were flowering at day 192 (Table 4.2) when compared to plants bearing wingless fruits. Plants bearing winged fruits and from historically naïve populations were also two to three times more



fecund than plants from all other groups (Figure 4.3a). These results suggest that the locus responsible for fruit phenotype (Ganders et al. 1977a) may contribute to morphological and phenological differences via pleiotropy or linkage disequilibrium. Pleiotropy has been suggested to be responsible for dictating correlated floral traits in many species. For example, six floral traits in *B. rapa* (width of petal, length of petal, corolla tube, pistil and short and long filaments) remained perfectly correlated after 9 generations of random mating, suggesting that pleiotropy explains these correlations and not linkage disequilibrium (Conner 2002). Such pleiotropic associations with floral traits can subsequently influence herbivore performance. For example, it is hypothesized that mutations that block the production of floral pigments may also block the production of defensive compounds (Fineblum and Rausher 1997), and such pleiotropic effects can negatively impact herbivore performance (Simms and Bucher 1996). To test for pleiotropic effects or linkage disequilibrium between the locus controlling fruit phenotype and genes responsible for plant height or bolting and flowering phenology in *P. congesta*, future studies may combine genetic techniques (e.g., Quantitative Trait Locus mapping, QTL) with several generations of random mating to assess the strength of correlated responses to selection.

Although I did not measure or estimate gene flow directly, gene flow is expected between island populations (Warren et al. 2015) which may maintain adaptive plasticity or promote local adaptation (Barton and Turelli 1989, Lenormand 2002). Additionally, it has been suggested that in environments where mammalian herbivore membership varies spatially or temporally, that selection may act to maintain resistance and tolerance traits at intermediate levels (Weinig et al. 2003), a consequence that is also likely to occur with intermediate rates of gene flow. The lack of a canalized response for locally adapted traits in response to herbivory in *P. congesta* suggests that

gene flow between populations of contrasting selective pressure, or temporal variation in visitation rate from ungulates, likely contributes to the maintenance of adaptive plasticity observed here. Islands that experienced temporal variation in ungulate presence expressed traits more similar to those in islands with or without ungulates depending on the degree of isolation (Chapter 2:), with increased isolation likely resulting in less gene flow. As a result, I predict that as island populations become more isolated, they will express a lower capacity for adaptive plasticity, but also lower additive genetic variance as predicted with consistently strong selection under Fisher's Fundamental Theorem (Fisher 1930). These more isolated populations will likely possess lower evolvability and require more generations for mean values to change, or otherwise may become extirpated, if herbivore community membership changes. Analyses assessing additive genetic variation and heritability by isolation are currently under way to elucidate the impacts of isolation (and correlated gene flow) on local adaptation and the potential for adaptive plasticity.

My results thus suggest that population-level variation in *P. congesta* populations on islands of the Georgia Basin is maintained by local adaptation and adaptive plasticity, and is mediated by the fitness costs of trait expression given the current environment. Specifically, differences in plant height, shape, bolting, and flowering phenology expressed in wild populations (Chapter 2:, Chapter 3:) were also expressed in common gardens protected from ungulate herbivores (Figure 4.1). Estimated  $V_a$  and evolvabilities for these traits indicate the potential for future natural selection to elicit changes in trait distribution (Table 4.1; Visscher et al. 2008). However, all plants also responded plastically to variation in shading by elongating their stems to enhance competitive ability, but did so at a cost to fecundity (Figure 4.3). This result highlights the importance of considering phenotypic plasticity when assessing the probability of population persistence (Chevin

et al. 2010). Specifically, plants from historically exposed populations may therefore be able to survive and reproduce in environments both with and without ungulate herbivores by expressing locally adapted traits that resist or tolerate herbivory, but also maintaining the adaptive plasticity to increase height in response to intraspecific competition in years with favourable conditions or following the local extirpation of ungulate herbivores. Conversely, plants from historically naïve populations appear to be much less capable of persisting in the presence of ungulate herbivores, given their poor survival and rapid extinction in two experimental studies (Gonzales and Arcese 2008, Chapter 3). As a consequence, protecting isolated populations of *P. congesta* from invasion by over-abundant or exotic herbivores may be critical to conserving the full range of genetic variation expressed in the species, particularly given historical and current understanding about how to conserve critically-endangered Garry oak and maritime meadow ecosystems of the Georgia Basin (Gonzales and Arcese 2008, Bennett and Arcese 2013, Arcese et al. 2014, Schuster et al. 2018). My work lays the ground-work for predicting how local adaptation and adaptive plasticity may contribute to the persistence of *P. congesta* populations in the face of environmental change, and highlights the need to consider herbivory pressures in formulating reliable conservation plans for island populations (Valladares et al. 2014, Bonamour et al. 2019) and helping to prioritize populations for conservation and restoration (Rice and Emery 2003, Weeks et al. 2011, Aitken and Whitlock 2013).

## Chapter 5: Conclusion

### 5.1 Overview

In this dissertation, I set out to test the hypothesis that spatial and temporal heterogeneity in ungulate herbivory is a dominant factor affecting patterns of local adaptation and adaptive plasticity in an annual plant (*P. congesta*) that occurs in an extensive system of island and mainland populations in western North America. To do so, I presented three data chapters where I tested the potential influences of ungulate herbivory, climatic variation and population isolation on plant morphology, and then investigated local adaptation and adaptive plasticity in response to ungulate herbivory using common garden experiments. Understanding the factors that influence local adaptation and adaptive plasticity is important for predicting whether populations are likely to persist, migrate or become extinct under changed biotic or abiotic conditions (Endler 1980, Germain et al. 2018), both of which are changing rapidly within my study region and globally (e.g., Arcese et al. 2014, Venter et al. 2016, Vistry et al. 2018). In the following sections, I first integrate the major findings of my three data chapters with previous work relating to spatial and temporal variability, local adaptation and adaptive plasticity. I then discuss broad implications of my findings. I finish with a discussion of the strengths and limitations of my dissertational research and suggestions for future research in this study system.

#### 5.1.1 Spatial and Temporal Variation in Natural Selection Influence Traits of *P. congesta*

*P. congesta* occur throughout an island archipelago that experiences both spatial and temporal variation in ungulate densities. Because the observed morphological and phenological differences persist between populations in a predictable manner, it is suggested that spatial variation in the

selective environment is stronger and more consistent than temporal variation (e.g., Siepielski 2013), or that selective pressure from ungulate herbivory is strong enough to overcome short-term temporal variations (Slatkin 1985). I observed that in populations of *P. congesta* on islands without resident ungulates that may have occasionally experienced a short visit from an ungulate herbivore, fruit phenotype distributions and plant height were more similar to populations with or without ungulates depending on if they were less or more isolated, respectively (Chapter 2:). This implies that: (1) temporal variation in ungulate presence maintains intermediate phenotypes; and/or (2) gene flow between populations introduces genetic variation and alters observed phenotypes. This additionally implies that islands that experience intermediate levels of gene flow or are occasionally subjected to herbivory are more likely to express intermediate phenotypes capable of resisting herbivory or enhancing competitive ability as the environment varies (e.g., Weinig et al. 2003). Population-level differences persisted among populations without temporal variation in ungulate herbivory (i.e., islands either with or without ungulates), however, suggesting that selection is sufficiently strong to select against immigrants or hybrids and prevent gene swamping (Slatkin 1985, Star et al. 2007). In archipelagos, temporal variation in ungulate abundance and colonization and extinction dynamics linked to variation in human and natural depredation rates (Darimont et al. 2004, Arcese et al. 2014) should both contribute to maintaining genetic variation in phenotype, with the effect enhancing local and meta-population persistence.

### **5.1.2 *P. congesta* Exhibits Local Adaptation and Adaptive Plasticity to Herbivory and Competition**

*P. congesta* populations demonstrated local adaptation and adaptive plasticity to resist herbivory or grow taller when experiencing competition for light (Chapter 3:, Chapter 4:). I observed home

vs. away advantages in plants from both populations historically exposed and naïve to ungulates when grown in environments mimicking that of their evolutionary history (Chapter 3:, Chapter 4:; Kawecki and Ebert 2004). Local adaptations specific to herbivore resistance included delayed bolting and flowering, shorter peak heights and maintaining branches closer to the ground, similar to herbivore resistance traits observed in other plant species (Paige and Whitham 1987, Juenger and Bergelson 2000, Parker et al. 2010, Agrawal et al. 2012, Schiestl et al. 2014, Martin et al. 2015). Local adaptations specific to competitive advantage for light and pollinators included earlier bolting and flowering, larger inflorescences and greater peak heights, similar to traits observed in other species (Blossey and Notzold 1995, Boege 2010, Ågren et al. 2013, Ramos and Schiestl 2019). However, intraspecific competition resulted in stem elongation at high planting densities in all populations as a response to increased shading (Chapter 4:; Casal and Smith 1989). Such elongation came at a 20-30% reduction in fitness, similar to findings in other plant species (Dudley and Schmitt 1996). Together, the above results highlight that *P. congesta* populations throughout the Georgia Basin are locally adapted to the presence or absence of herbivores, but that those from historically exposed populations maintain the capacity to increase height and compete with taller plants. However, plants from historically naïve populations had a greater mean height even at low planting densities, suggesting that these populations have genetic differences leading to greater baseline differences that make them more susceptible to the presence of ungulates, and that these populations would likely be extirpated with the introduction of ungulates.

## **5.2 Applications of Research**

Many species are experiencing rapid environmental changes, many of which are human-driven, that can threaten population or species persistence. For example, human-driven forest

fragmentation and vertebrate defaunaution has been suggested as the driving factors leading to decreased seed size in keystone Palm Species of Brazil in under 100 years, with negative consequences for palm regeneration (Galetti et al. 2013). Although such rapid change can have negative consequences, it also suggests the potential for evolutionary rescue (i.e., when a population or species faced with changing conditions is saved from extinction through genetic changes, Martin et al. 2013). Translocations or assisted gene flow are two options that have the potential to mitigate the negative consequences of climate change or other human-driven environmental change (Weeks et al. 2011, Aitken and Whitlock 2013), largely through introducing alleles that are adapted to the new conditions present at the site. Acquiring an understanding of the evolutionary history of a population can therefore inform management plans that can better protect extant biodiversity (Olivieri et al. 2016). Ultimately, A holistic understanding of how genetic variation, phenotypic plasticity and gene flow influence a population's capability to respond to environmental change is essential when making restoration decisions (Rice and Emery 2003).

In my dissertation, I further highlight the importance of understanding how local adaptation, phenotypic plasticity and gene flow between populations in a spatially heterogenous island ecosystem influence traits that impact fitness in ways that may threaten population persistence with changing conditions. With this knowledge, we can predict population-wide responses to changes in herbivore membership, which can help to better inform prioritization of populations for conservation and restoration (Rice and Emery 2003, Weeks et al. 2011, Aitken and Whitlock 2013). Additionally, protecting isolated populations of *P. congesta* from invasion by over-abundant or exotic herbivores may be critical to conserving the full range of genetic variation expressed in the species, particularly given historical and current understanding about how to

conserve critically-endangered Garry oak and maritime meadow ecosystems of the Georgia Basin (Gonzales and Arcese 2008, Bennett and Arcese 2013, Arcese et al. 2014, Schuster et al. 2018). My dissertation also offers practical suggestions for restoration and conservation of *P. congesta*. Specifically, I recommend using a mixture of fruits from populations both with and without herbivores when restoring sites to maximize genetic variation, or selecting fruits from multiple populations that are already best adapted to the herbivore environment of the restoration site (e.g., Weeks et al. 2011).

### **5.3 Strengths and Limitations of Thesis**

The first major strength of my dissertation is the use of an island archipelago because archipelagos offer an opportunity to test contrasting selective pressures in distinct populations with varying levels of gene flow (Warren et al. 2015). Archipelagos provide contrasts between environments of similar climatic conditions, but differences in community membership of herbivores or predators. Additionally, greater trait plasticity is expected in more variable environments (Hendry 2015), which is likely to be observed in islands that experience temporal variation in the presence or absence of herbivores or predators. The Georgia Basin offered an ideal arena because it experiences abrupt differences in the presence or absence of ungulates among dozens of islands at varying degrees of isolation. This region is also geologically young (<14,000 years old, Fedje et al. 2018), with dramatic changes in predator and herbivore abundance over the last few hundred years (Martin et al. 2011, Arcese et al. 2014), suggesting that most differences observed could be a result of rapid evolution.



The second major strength of this dissertation is the study organism. *P. congesta* is a winter annual known to be susceptible to herbivory (Gonzales and Arcese 2008) that is iconic to the Garry oak and maritime meadows of the San Juan and Gulf Island Archipelagos. Having a short generation time (1 year) and distinct cohorts makes it easier to study evolutionary change in response to specific mechanisms and in a short period of time. Additionally, I had three ideal traits to work with: (1) fruit phenotype, which follows Mendelian dominance (Ganders et al. 1977a); (2) plant height, which can be rapidly selected for in as few as 5 generations (Carey 1983); and (3) phenology in bolting and flowering, which responds plastically to environmental conditions (Carey and Ganders 1980, Reed et al. 2019).

The third major strength of my dissertation is the breadth of approaches utilized to answer my main hypothesis. I was able to utilize observational studies across a large geographic region (Chapter 2:) to determine the potential drivers of population-level differences. I was then able to isolate the main factor hypothesized to be dictating this pattern (ungulate herbivory) and test for local adaptation (Chapter 3:) and adaptive plasticity (Chapter 4:) of key traits linked to resistance to deal with ungulate herbivory and competition for light in common gardens in which many environmental conditions can be held constant.

There are also limitations to my dissertation. In Chapter 2:, it is possible that there are other environmental factors influencing traits in *P. congesta* that were untested and may be correlated with my hypothesized variables; however, I suggest that ungulate herbivory is likely the dominant factor driving the observed differences in fruit phenotype distributions and plant height given observed local adaptation in subsequent chapters (Chapter 3:, Chapter 4:). In Chapter 3:, I only

had two exclosures, both located on the same island, which leaves the possibility that outcomes may have differed with lower ungulate densities or the presence of only one species of deer (native Black-tailed deer). Because *P. congesta* was extirpated outside of exclosures on Sidney Island after three growing seasons, I was also unable to comment on what ungulate densities may allow population persistence in locally adapted populations. Local conditions on Sidney Island demonstrated that habitat quality and annual variation in conditions impact plant performance dramatically (Maschinski et al. 1997, Siepielski et al. 2009, 2011), with low germination success and plants rarely exceeding 30 cm in height despite plants reaching 45 to 100 cm in wild populations (Chapter 2:) or previously fertilized raised beds (Chapter 4:). Finally, I was not able to fully test how fluctuations in ungulate densities may impact species distributions of *P. congesta* and other meadow species, although my findings provide an excellent baseline for further investigation.

## **5.4 Next Steps**

My thesis establishes a baseline from which to continue investigating evolutionary questions related to spatial variation in natural selection and rapid adaptation using *P. congesta*, and pertaining to how to best proceed with restoration and conservation in the threatened Garry oak and maritime meadow ecosystems. To address evolutionary questions, further research could investigate: (1) the function of fruits wings (e.g., dispersal, nutrient stores, etc.); (2) presence and function of secondary metabolites; and (3) the evolutionary relationship between floral display, herbivory and pollinators and subsequent consequences. For example, recent studies suggest that the presence of both bee pollinators and herbivores can select for reduced floral display and increased selfing rates (Johnson et al. 2015, Ramos and Schiestl 2019). Our observations thus raise

intriguing questions about the potential roles of herbivory in the evolution of other palatable species within the Valerianaceae, such as *P. brachystemon*, a species once described as a subspecies of *P. congesta* that almost exclusively expresses wingless fruits, short stature, reduced floral structures, and high selfing rates (2-4%, Ganders et al. 1977b, Layton and Ganders 1984). Additional studies could also investigate (4) the influences of climatic factors and other abiotic conditions on traits suggested to be local adaptations to herbivory. For example, many studies have demonstrated that earlier flowering has occurred in response to climate change in 385 British plant species (Fitter and Fitter 2002) and *B. rapa* (Franks et al. 2007), suggesting potential compounding influences between climate change and herbivory on flowering phenology. An additional avenue for investigation would be to (5) determine the genes responsible for stem elongation and phenological shifts. Similarly, studies could investigate (6) the roles of maternal effects and epigenetic changes causing transgenerational plant resistance. For example, Herrera and Bazaga (2011) observed correlations between epigenetic variation and herbivore damage in the plant *Viola cazorlensis*. Similarly, maternal effects were observed in radish plants, *Raphanus raphanistrum*, wherein progeny produced by plants damaged by herbivores displayed greater herbivore resistance than those from undamaged controls (Agrawal 2002). Future studies may also wish to (7) artificially select for observed locally adapted traits (e.g., plant height, branch height, phenology) in controlled environments to assess how rapidly these traits can evolve to herbivory, intraspecific competition or other factors of interest. Additionally, although I suggest that the observed adaptive plasticity (Chapter 4) can contribute to the ability of *P. congesta* to respond to modest environmental change, additional simulations or experiments are necessary to (8) estimate the resilience of populations and impacts of changing ungulate densities. Additionally, populations experiencing opposing browsing histories often exist adjacent to each other in nature, indicating

that (9) many opportunities exist to quantify factors affecting gene flow, isolation, selection, and evolution precisely with modest additional work, similar to methods followed by Stock et al. (2014) and others. Current work is indeed underway using microsatellite markers to estimate gene flow between populations of varying degrees of isolation and its influences on trait means of locally adapted traits. Specifically, we predict that more isolated populations will have lower genetic variation and experience less gene flow with neighbouring populations. Additionally, we predict that neighbouring island populations of contrasting browsing histories will experience higher gene flow, and therefore, express traits at intermediate values between those expected for more isolated populations exposed or naïve to herbivory. Lastly, from a conservation perspective, future work could (10) attempt to create fruit mixes with differing compositions and restore them into sites with differing deer densities to determine which mixes might be best for specific abiotic and biotic conditions. This work could also aim to determine what the lowest deer densities are that allow persistence of *P. congesta*.

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## Appendices

### Appendix 1: Principal Components Analysis for Climatic Variables throughout Georgia Basin (Chapter 2)

**Table A1.1** Principal components analysis results for climatic variables in the Georgia Basin (Chapter 2). PC1 explains 92% of the variation. PC2 explains 25% of the variation in the data (with overlap with PC1). Variable acronyms presented, and associated names can be found in Climate BC (Wang et al. 2012).

	<b>TMAX02</b>	<b>TMAX03</b>	<b>TMAX04</b>	<b>TMAX05</b>	<b>TMAX06</b>	<b>TMAX07</b>	<b>TMAX08</b>	<b>TMAX09</b>	<b>TMAX10</b>	<b>TMAX11</b>
<b>PC 1</b>	0.941	0.872	0.533	0.079	-0.24	-0.447	-0.414	0.575	0.912	0.955
<b>PC 2</b>	0.024	0.098	0.366	0.571	0.461	0.39	0.266	-0.142	-0.051	0.075
	<b>TMAX12</b>	<b>TMIN01</b>	<b>TMIN02</b>	<b>TMIN03</b>	<b>TMIN04</b>	<b>TMIN05</b>	<b>TMIN06</b>	<b>TMIN07</b>	<b>TMIN08</b>	<b>TMIN09</b>
<b>PC 1</b>	0.958	0.953	0.976	0.973	0.902	0.572	0.041	-0.232	-0.152	0.48
<b>PC 2</b>	0.095	0.08	-0.064	0.104	0.342	0.785	0.95	0.882	0.888	0.625
	<b>TMIN10</b>	<b>TMIN11</b>	<b>TMIN12</b>	<b>TAVE01</b>	<b>TAVE02</b>	<b>TAVE03</b>	<b>TAVE04</b>	<b>TAVE05</b>	<b>TAVE06</b>	<b>TAVE07</b>
<b>PC 1</b>	0.91	0.973	0.987	0.979	0.982	0.956	0.822	0.4	-0.096	-0.389
<b>PC 2</b>	0.26	0.029	0.003	0.088	-0.023	0.104	0.372	0.82	0.922	0.846
	<b>TAVE08</b>	<b>TAVE09</b>	<b>TAVE10</b>	<b>TAVE11</b>	<b>TAVE12</b>	<b>PPT01</b>	<b>PPT02</b>	<b>PPT03</b>	<b>PPT04</b>	<b>PPT05</b>
<b>PC 1</b>	-0.352	0.764	0.964	0.984	0.985	-0.711	-0.884	-0.914	-0.858	-0.85
<b>PC 2</b>	0.845	0.439	0.103	0.06	0.055	-0.361	-0.074	0.033	0.126	0.441
	<b>PPT06</b>	<b>PPT07</b>	<b>PPT08</b>	<b>PPT09</b>	<b>PPT10</b>	<b>PPT11</b>	<b>PPT12</b>	<b>DD_0_01</b>	<b>DD_0_02</b>	<b>DD_0_03</b>
<b>PC 1</b>	-0.858	-0.848	-0.808	-0.814	-0.905	-0.845	-0.789	-0.961	-0.966	-0.94
<b>PC 2</b>	0.4	0.391	0.327	0.266	0.141	-0.109	-0.259	-0.139	-0.033	-0.135
	<b>DD_0_04</b>	<b>DD_0_10</b>	<b>DD_0_11</b>	<b>DD_0_12</b>	<b>DD18_04</b>	<b>DD18_05</b>	<b>DD18_06</b>	<b>DD18_07</b>	<b>DD18_08</b>	<b>DD18_09</b>
<b>PC 1</b>	-0.582	-0.623	-0.967	-0.975	0.375	0.153	-0.161	-0.404	-0.345	0.625
<b>PC 2</b>	-0.52	-0.38	-0.14	-0.106	0.483	0.677	0.921	0.862	0.865	0.481

	<b>DD18_10</b>	<b>NFFD01</b>	<b>NFFD02</b>	<b>NFFD03</b>	<b>NFFD04</b>	<b>NFFD05</b>	<b>NFFD09</b>	<b>NFFD10</b>	<b>NFFD11</b>	<b>NFFD12</b>
<b>PC 1</b>	0.698	0.93	0.967	0.957	0.832	0.65	-0.086	0.831	0.955	0.969
<b>PC2</b>	-0.109	0.129	-0.017	0.107	0.417	0.544	0.541	0.284	0.058	-0.004
	<b>PAS01</b>	<b>PAS02</b>	<b>PAS03</b>	<b>PAS04</b>	<b>PAS05</b>	<b>PAS10</b>	<b>PAS11</b>	<b>PAS12</b>	<b>EREF01</b>	<b>EREF02</b>
<b>PC 1</b>	-0.901	-0.946	-0.919	-0.668	-0.731	-0.852	-0.939	-0.928	0.832	0.882
<b>PC2</b>	-0.3	-0.166	-0.232	-0.413	-0.105	0.155	-0.196	-0.261	-0.166	-0.227
	<b>EREF03</b>	<b>EREF04</b>	<b>EREF05</b>	<b>EREF06</b>	<b>EREF07</b>	<b>EREF08</b>	<b>EREF09</b>	<b>EREF10</b>	<b>EREF11</b>	<b>EREF12</b>
<b>PC 1</b>	0.821	0.39	-0.021	-0.101	-0.021	0.044	0.5	0.776	0.859	0.884
<b>PC2</b>	-0.191	-0.06	-0.054	-0.299	-0.458	-0.546	-0.586	-0.484	-0.216	-0.046
	<b>CMD04</b>	<b>CMD05</b>	<b>CMD06</b>	<b>CMD07</b>	<b>CMD08</b>	<b>CMD09</b>	<b>TMAX_WT</b>	<b>TMAX_SP</b>	<b>TMAX_SM</b>	<b>TMAX_AT</b>
<b>PC 1</b>	0.782	0.851	0.829	0.801	0.79	0.769	0.96	0.625	-0.378	0.918
<b>PC2</b>	-0.287	-0.449	-0.471	-0.494	-0.472	-0.536	0.068	0.328	0.394	-0.016
	<b>TMIN_WT</b>	<b>TMIN_SP</b>	<b>TMIN_SM</b>	<b>TMIN_AT</b>	<b>TAVE_WT</b>	<b>TAVE_SP</b>	<b>TAVE_SM</b>	<b>TAVE_AT</b>	<b>PPT_WT</b>	<b>PPT_SP</b>
<b>PC 1</b>	0.979	0.901	-0.125	0.905	0.986	0.837	-0.275	0.977	-0.807	-0.919
<b>PC2</b>	-0.001	0.386	0.921	0.287	0.039	0.408	0.903	0.147	-0.24	0.169
	<b>PPT_SM</b>	<b>PPT_AT</b>	<b>DD_0_WT</b>	<b>DD_0_SP</b>	<b>DD_0_AT</b>	<b>DD18_SP</b>	<b>DD18_SM</b>	<b>DD18_AT</b>	<b>NFFD_WT</b>	<b>NFFD_SP</b>
<b>PC 1</b>	-0.85	-0.896	-0.973	-0.922	-0.975	0.119	-0.34	0.686	0.978	0.938
<b>PC2</b>	0.381	0.052	-0.101	-0.243	-0.14	0.537	0.893	0.356	0	0.284
	<b>NFFD_SM</b>	<b>NFFD_AT</b>	<b>PAS_WT</b>	<b>PAS_SP</b>	<b>PAS_AT</b>	<b>EREF_WT</b>	<b>EREF_SP</b>	<b>EREF_SM</b>	<b>EREF_AT</b>	<b>CMD_SP</b>
<b>PC 1</b>	0.547	0.956	-0.926	-0.932	-0.943	0.916	0.419	-0.026	0.71	0.847
<b>PC2</b>	0.407	0.143	-0.252	-0.254	-0.19	-0.223	-0.114	-0.447	-0.506	-0.393

	<b>CMD_SM</b>	<b>CMD_AT</b>	<b>MAT</b>	<b>MWMT</b>	<b>MCMT</b>	<b>TD</b>	<b>MAP</b>	<b>MSP</b>	<b>AHM</b>	<b>SHM</b>
<b>PC 1</b>	0.818	0.769	0.899	-0.367	0.979	-0.923	-0.914	-0.853	0.92	0.854
<b>PC2</b>	-0.486	-0.536	0.373	0.856	0.088	0.294	0.028	0.376	-0.083	-0.421
	<b>DD_0</b>	<b>DD18</b>	<b>NFFD</b>	<b>BFFP</b>	<b>EFFP</b>	<b>FFP</b>	<b>PAS</b>	<b>EMT</b>	<b>EXT</b>	<b>EREF</b>
<b>PC 1</b>	-0.973	-0.2	0.974	-0.941	0.955	0.951	-0.934	0.946	-0.144	0.445
<b>PC2</b>	-0.122	0.919	0.118	-0.19	0.085	0.152	-0.236	0.095	0.028	-0.418
	<b>CMD</b>									
<b>PC 1</b>	0.836									
<b>PC2</b>	-0.467									

## Appendix 2: ANOVA Results for Estimating Fruit Phenotype throughout the Georgia Basin (Chapter 2)

Table A2.1 ANOVA table for fixed effects variables in estimating the fraction of plants bearing wingless fruits throughout the Georgia Basin, using Type III tests. Bold p-values denote significant differences (Chapter 2).

Fixed Effects Variable	Df	Chi-Square	P-value
Intercept	1	770.59	<b>&lt;0.0001</b>
Deer P/A/R	2	492.21	<b>&lt;0.0001</b>
PC1 (standardized)	1	42.90	<b>&lt;0.0001</b>
% Water 1 km radius (standardized)	1	0.05	0.83
Deer * PC1 (standardized)	2	12.24	<b>0.002</b>
Deer * % water 1 km radius (standardized)	2	12.98	<b>0.002</b>

Table A2.2 Beta coefficients ( $\beta$ ) for fixed effects variables in estimating the fraction of plants bearing wingless fruits throughout the Georgia Basin (Chapter 2), using standardized variables.

Variable	$\beta$	Standard Error	Z-value	P-value
Intercept	-2.59	0.093	-27.76	<b>&lt;0.0001</b>
Deer: present	2.04	0.095	21.60	<b>&lt;0.0001</b>
Deer: rare	1.17	0.10	11.61	<b>&lt;0.0001</b>
PC1 (standardized)	0.42	0.065	6.55	<b>&lt;0.0001</b>
% Water 1 km radius (standardized)	-0.02	0.089	-0.21	0.83
Deer: present * PC1 (standardized)	-0.19	0.066	-2.85	<b>0.004</b>
Deer: rare * PC1 (standardized)	-0.23	0.077	-3.04	<b>0.002</b>
Deer: present * % water 1 km radius (standardized)	-0.0095	0.091	-0.11	0.92
Deer: rare * % water 1 km radius (standardized)	-0.32	0.097	-3.26	<b>0.001</b>

### Appendix 3: ANOVA Results for Estimating Plant Height Throughout the Georgia Basin (Chapter 2)

**Table A3.1 ANOVA table for fixed effects variables in estimating plant height throughout the Georgia Basin, using Type III tests. Bold p-values denote significant differences (Chapter 2).**

Fixed Effects Variable	Sum of Squares	Df	F-value	P-value
Intercept	81.99	1	772.65	<b>&lt;0.0001</b>
Deer P/A	4.22	2	19.86	<b>&lt;0.0001</b>
PC1 (standardized)	0.38	1	3.58	0.07
% Water 1 km radius (standardized)	0.08	1	0.72	0.40
Average soil depth (standardized)	0.70	1	6.62	<b>0.02</b>
Deer * PC1 (standardized)	0.78	2	3.66	<b>0.04</b>
Deer * % water 1 km radius (standardized)	0.28	2	1.29	0.29
Residuals	2.76	26		

**Table A3.2 Beta coefficients ( $\beta$ ) for fixed effects variables in estimating plant height throughout the Georgia Basin (Chapter 2), using standardized variables.**

Variable	$\beta$	Standard Error	Z-value	P-value
Intercept	3.51	0.13	27.80	<b>&lt;0.0001</b>
Deer: present	-0.82	0.15	-5.35	<b>&lt;0.0001</b>
Deer: rare	-0.05	0.19	-0.27	0.79
PC1 (standardized)	0.20	0.11	1.89	0.07
% Water 1 km radius (standardized)	0.15	0.17	0.85	0.40
Average soil depth (standardized)	0.16	0.06	2.57	<b>0.02</b>
Deer: present * PC1 (standardized)	-0.26	0.14	-1.92	0.07
Deer: rare * PC1 (standardized)	-0.49	0.19	-2.56	<b>0.02</b>
Deer: present * % water 1 km radius (standardized)	-0.10	0.20	-0.52	0.61
Deer: rare * % water 1 km radius (standardized)	0.13	0.20	0.62	0.54

## Appendix 4: Site Characteristics of Exclosures on Sidney Island (Chapter 3)

**Table A4.1** Site characteristics for the two exclosures on Sidney Island (Chapter 3). Values are mean  $\pm$  standard deviation. Values are acquired from 2m<sup>2</sup> units from 2006 Lidar data. Heatload is a value bounded by 0-1 representing how topographic change effects direct sunlight, with higher values having more sunlight.

Exclosure	Location	Total Area (m <sup>2</sup> )	Elevation (m)	Slope (°)	Aspect (°)	Heatload
West	Inside	462	29.14 $\pm$ 2.93	22.37 $\pm$ 4.23	194.75 $\pm$ 8.70	0.91 $\pm$ 0.04
	Outside	489	28.49 $\pm$ 2.66	20.29 $\pm$ 4.89	204.08 $\pm$ 13.58	0.88 $\pm$ 0.05
East	Inside	629	37.44 $\pm$ 1.96	16.66 $\pm$ 3.95	201.62 $\pm$ 12.24	0.85 $\pm$ 0.04
	Outside	629	37.26 $\pm$ 1.58	13.74 $\pm$ 4.52	195.29 $\pm$ 38.35	0.80 $\pm$ 0.06



**Figure A4.1** Photographs of inside (left) and outside (right) the west exclosure in 2019 to demonstrate similarity in habitat. Note that natural recruitment of *Arbutus* has occurred in the past few years, after construction of the exclosures. Photo credit: Cora Skaien.



## Appendix 5: Sampling Locations and Fraction of Plants Bearing Either Fruit Phenotype in Populations Sown on Sidney Island (Chapter 3)

Table A5.1 Locations of 12 source populations planted into common gardens open to and excluding deer on Sidney Island, BC (Chapter 3), percentage of plants in those populations bearing wingless fruits, and the number of families collected from each by fruit phenotype (see Methods).

Population	UTM (N, E)	% Plants with Wingless Fruits	Families (wingless, winged)
<b>Historically Exposed (With Deer)</b>			
Crow's Nest (Salt Spring Island)	5403824, 466848	94%	6, 8
Dean Park (Vancouver Island)	5384977, 467621	93%	6, 7
Moresby Island	5397061, 477525	98%	7, 6
Pender Island	5401676, 478716	94%	11, 7
Piers Island	5394805, 469211	90%	7, 8
Prevost Island	5409749, 470845	99%	6, 8
<b>Historically Naïve (Without Deer)</b>			
Chades Island	5398192, 472230	3%	6, 7
Clive Island	5394341, 470151	4%	6, 6
Musgrave Island	5399003, 460040	1%	2, 14
Owl Island	5408240, 470681	9%	6, 7
Shell Island	5390933, 472504	3%	6, 6
Port Washington Island	5406547, 476287	1%	6, 8

## Appendix 6: Flower Phenology Classes (Chapter 3)

Table A6.1 Flowering phenology classes of *P. congesta* used for Sidney Island (Chapter 3).

Phenology Class	Description
1	Only leaves present; no buds.
2	Inflorescence forming, but no definable pink buds
3	Pink buds present
4	Inflorescence: 75-90% budding and 10-25% blooming
5	Inflorescence: 50% budding and 50% has bloomed
6	Inflorescence: 10-25% budding and 75-90% blooming
7	Inflorescence: 100% blooming
8	Inflorescence: 75-90% blooming and 10-25% fruiting
9	Inflorescence: 50% blooming and 50% fruiting
10	Inflorescence: 10-25% blooming and 75-90% fruiting
11	Inflorescence: 100% fruiting

## Appendix 7: ANOVA Results and Predicted Values for Germination and Survival on

### Sidney Island (Chapter 3)

**Table A7.1 ANOVA results for the model predicting germination and survival on Sidney Island (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	2.39	0.12
Measurement Date	2	4.43	0.11
Browsing History	1	0.01	0.90
Current Exposure to Browsing	1	0.29	0.59
Fruit Phenotype of Sown Fruit	1	2.86	0.09
Soil depth	1	0.92	0.34
<b>Two-way Interactions</b>			
Measurement Date*Browsing History	2	1.00	0.60
Measurement Date*Current Exposure to Browsing	2	2.34	0.31
Browsing History*Current Exposure to Browsing	1	0.30	0.59
Measurement Date*Fruit Phenotype of Sown Fruit	2	0.16	0.95
Browsing History*Fruit Phenotype of Sown Fruit	1	1.36	0.24
Current Exposure to Browsing*Fruit Phenotype of Sown Fruit	1	3.34	0.07
Current Exposure to Browsing*Soil Depth	1	3.92	<b>0.048</b>
<b>Three-way Interactions</b>			
Measurement Date*Browsing History*Current Exposure to Browsing	2	13.03	<b>0.001</b>
Measurement Date*Browsing History*Fruit Phenotype Sown Fruit	2	0.18	0.92
Measurement Date*Current Exposure to Browsing* Fruit Phenotype of Sown Fruit	2	0.64	0.72
Browsing History*Current Exposure to Browsing*Fruit Phenotype of Sown Fruit	1	3.34	0.07
<b>Four-way Interaction</b>			
Measurement Date*Browsing History*Current Exposure to Browsing*Fruit Phenotype of Sown Fruit	2	3.19	0.20

**Table A7.2 Variance accounted for by random effects variables in the model predicting survival on Sidney Island (Chapter 3).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Substrate	0.33	0.57
Exclosure ID	$1.1 \times 10^{-7}$	$3.3 \times 10^{-4}$
Exclosure ID/Current Exposure to Browsing	$1.3 \times 10^{-6}$	$1.1 \times 10^{-3}$
Population	$2.3 \times 10^{-2}$	0.15
Population/Family	0.42	0.65
Measurement Date: Plant ID	$7.29 \times 10^{-7}$	$8.5 \times 10^{-4}$

**Table A7.3 Back-transformed model predicted values and standard errors (SE) for germination and survival (%) on Sidney Island (Chapter 3).**

<b>Browsing History</b>	<b>Current Exposure to Browsing</b>	<b>Measurement Date</b>	<b>Fruit Phenotype</b>	<b>Model Predicted Mean (%)</b>	<b>SE Lower</b>	<b>SE Upper</b>
Historically Exposed	Inside	December	Wingless	29.8	20.8	40.6
			Winged	20.6	13.0	31.2
		March	Wingless	24.9	16.3	36.0
			Winged	17.8	9.8	30.2
		May	Wingless	22.8	14.6	33.7
			Winged	16.7	8.8	29.3
	Outside	December	Wingless	21.6	11.4	37.0
			Winged	24.2	11.6	43.8
		March	Wingless	20.1	9.7	37.1
			Winged	19.3	7.1	42.7
		May	Wingless	9.9	3.4	22.9
			Winged	10.0	2.8	30.2
Historically Naïve	Inside	December	Wingless	30.6	20.0	43.8
			Winged	30.3	16.8	48.3
		March	Wingless	22.6	12.5	37.4
			Winged	20.4	8.1	42.7
		May	Wingless	18.9	9.5	33.9
			Winged	19.4	6.8	44.3
	Outside	December	Wingless	25.7	11.7	47.5
			Winged	20.9	6.7	49.1
		March	Wingless	8.4	2.6	23.9
			Winged	9.3	1.5	40.4
		May	Wingless	2.0	0.4	10.2
			Winged	3.4	0.3	31.3

## Appendix 8: ANOVA Results and Predicted Values for Fecundity on Sidney Island

### (Chapter 3)

**Table A8.1 ANOVA results for the model predicting fecundity on Sidney Island (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	115.01	<b>&lt;0.001</b>
Browsing History	1	0.085	0.77
Current Exposure to Browsing	1	29.37	<b>&lt;0.001</b>
Fruit Phenotype of Surviving Plant	1	0.51	0.48
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	1	2.66	0.10
Browsing History*Fruit Phenotype of Surviving Plant	1	14.57	<b>&lt;0.001</b>
Current Exposure to Browsing*Fruit Phenotype of Surviving Plant	1	9.31	<b>0.002</b>
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	1	4.31	<b>0.04</b>

**Table A8.2 Variance accounted for by random effects variables in the model predicting fecundity on Sidney Island (Chapter 3).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Substrate	0.11	0.09
Exclosure ID	$7.7 \times 10^{-3}$	$8.8 \times 10^{-2}$
Exclosure ID/Current Exposure to Browsing	$1.5 \times 10^{-2}$	0.12
Population	$8.3 \times 10^{-2}$	0.29

**Table A8.3 Back-transformed model predicted values for fecundity (number of florets/fruits) on Sidney Island (Chapter 3).**

<b>Browsing History</b>	<b>Current Exposure to Browsing</b>	<b>Fruit Phenotype</b>	<b>Model Predicted Mean</b>	<b>SE lower</b>	<b>SE upper</b>
Historically Exposed	Inside	Wingless	17	13	23
		Winged	16	13	21
	Outside	Wingless	10	7	14
		Winged	5	4	7
Historically Naïve	Inside	Wingless	11	9	15
		Winged	15	11	21
	Outside	Wingless	5	3	9
		Winged	7	5	11

## Appendix 9: ANOVA Results and Predicted Values for Inflorescence Volume on Sidney

### Island (Chapter 3)

Table A9.1 ANOVA results for the model predicting inflorescence volume on Sidney Island (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Intercept	1	4.52	<b>0.03</b>
Browsing History	1	3.89	<b>0.049</b>
Current Exposure to Browsing	1	0.02	0.88
Fruit Phenotype of Surviving Plant	1	0.13	0.72
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	1	0.21	0.65
Browsing History*Fruit Phenotype of Surviving Plant	1	2.93	0.09
Current Exposure to Browsing*Fruit Phenotype of Surviving Plant	1	0.38	0.54
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	1	0.05	0.82

Table A9.2 Variance accounted for by random effects variables in the model predicting inflorescence volume on Sidney Island (Chapter 3).

Random Effects Variable	Variance	SD
Substrate	0.19	0.44
Population	0.03	0.16
Residual	1.77	0.09

**Table A9.3 Mean values and standard errors for inflorescence volume (cm<sup>3</sup>) on Sidney Island (Chapter 3) using raw data.**

<b>Browsing History</b>	<b>Current Exposure to Browsing</b>	<b>Fruit Phenotype</b>	<b>Mean (cm<sup>3</sup>) ± SE</b>
Historically Exposed	Inside	Wingless	2.67 ± 0.10
		Winged	1.45 ± 0.16
	Outside	Wingless	0.44 ± 0.01
		Winged	0.91 ± 0.26
Historically Naïve	Inside	Wingless	3.16 ± 0.26
		Winged	7.78 ± 0.38
	Outside	Wingless	0.31 ± 0.08
		Winged	0.75 ± 0.19

**Table A9.4 Back-transformed model predicted values and standard errors for inflorescence volume (cm<sup>3</sup>) on Sidney Island (Chapter 3).**

<b>Browsing History</b>	<b>Current Exposure to Browsing</b>	<b>Fruit Phenotype</b>	<b>Model Predicted Mean</b>	<b>SE lower</b>	<b>SE Upper</b>
Historically Exposed	Inside	Wingless	0.40	0.20	0.82
		Winged	0.34	0.20	0.56
	Outside	Wingless	0.25	0.05	1.13
		Winged	0.38	0.14	1.09
Historically Naïve	Inside	Wingless	0.34	0.11	1.10
		Winged	0.94	0.45	1.93
	Outside	Wingless	0.17	0.01	2.55
		Winged	0.58	0.10	3.44



## Appendix 10: ANOVA Results for Bolting Phenology on Sidney Island (Chapter 3)

**Table A10.1** ANOVA results for the model predicting bolting phenology on Sidney Island (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Browsing History	1	8.49	<b>0.004</b>
Current Exposure to Browsing	1	4.89	<b>0.03</b>
Fruit Phenotype of Surviving Plant	1	0.12	0.73
Soil Depth	1	3.39	0.07
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	1	0.11	0.75
Browsing History*Fruit Phenotype of Surviving Plant	1	2.51	0.11
Current Exposure to Browsing*Fruit Phenotype of Surviving Plant	1	3.96	<b>0.047</b>
Soil Depth * Current Exposure to Browsing	1	0.02	0.89
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	1	0.02	0.88

**Table A10.2** Variance accounted for by random effects variables in the model predicting bolting phenology on Sidney Island (Chapter 3).

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Substrate	$2.0 \times 10^{-4}$	$1.4 \times 10^{-2}$
Exclosure	$1.1 \times 10^{-7}$	$3.4 \times 10^{-4}$
Exclosure/Current Exposure to Browsing	$1.1 \times 10^{-7}$	$3.3 \times 10^{-4}$
Population	$5.6 \times 10^{-4}$	$2.4 \times 10^{-2}$
Population/Family	$3.2 \times 10^{-7}$	$5.6 \times 10^{-4}$
Residual	$6.9 \times 10^{-2}$	$3.3 \times 10^{-3}$

## Appendix 11: ANOVA Results and Predicted Values for Plant Height on Sidney Island

### (Chapter 3)

**Table A11.1 ANOVA results for the model predicting plant height (natural log transformed) on Sidney Island in December (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	0.28	0.60
Browsing History	1	1.95	0.16
Current Exposure to Browsing	1	0.02	0.88
Fruit Phenotype of Sown Fruit	1	0.003	0.95
Soil depth	1	0.55	0.46
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	1	0.88	0.35
Browsing History*Fruit Phenotype of Sown Fruit	1	2.14	0.14
Current Exposure to Browsing*Fruit Phenotype of Sown Fruit	1	1.89	0.17
Current Exposure to Browsing*Soil Depth	1	0.04	0.83
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	1	0.09	0.77

**Table A11.2 Variance accounted for by random effects variables in the model predicting plant height on Sidney Island in December (Chapter 3).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Substrate	$2.4 \times 10^{-7}$	$4.9 \times 10^{-4}$
Exclosure ID	$4.1 \times 10^{-3}$	$6.4 \times 10^{-2}$
Exclosure ID/Current Exposure to Browsing	$1.1 \times 10^{-7}$	$3.3 \times 10^{-4}$
Residual	0.52	$1.7 \times 10^{-2}$

**Table A11.3 ANOVA results for the model predicting plant height (natural log transformed) on Sidney Island in March (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	30.85	<b>&lt;0.0001</b>
Browsing History	1	13.01	<b>0.0003</b>
Current Exposure to Browsing	1	1.94	0.16
Fruit Phenotype of Sown Fruit	1	0.00	0.99
Soil depth	1	0.29	0.59
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	1	0.29	0.59
Browsing History*Fruit Phenotype of Sown Fruit	1	0.87	0.35
Current Exposure to Browsing*Fruit Phenotype of Sown Fruit	1	0.15	0.69
Current Exposure to Browsing*Soil Depth	1	0.12	0.73
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	1	1.67	0.20

**Table A11.4 Variance accounted for by random effects variables in the model predicting plant height on Sidney Island in March (Chapter 3).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Substrate	$6.1 \times 10^{-3}$	$7.8 \times 10^{-2}$
Exclosure ID	$1.6 \times 10^{-7}$	$3.9 \times 10^{-4}$
Exclosure ID/Current Exposure to Browsing	$1.1 \times 10^{-7}$	$3.3 \times 10^{-4}$
Residual	0.46	$1.8 \times 10^{-2}$

**Table A11.5 ANOVA results for the model predicting plant height (natural log transformed) on Sidney Island in May (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	328.16	<b>&lt;0.0001</b>
Browsing History	1	0.38	0.54
Current Exposure to Browsing	1	1.55	0.21
Fruit Phenotype of Sown Fruit	1	0.47	0.49
Soil depth	1	0.63	0.43
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	1	0.03	0.86
Browsing History*Fruit Phenotype of Sown Fruit	1	0.15	0.70
Current Exposure to Browsing*Fruit Phenotype of Sown Fruit	1	0.08	0.78
Current Exposure to Browsing*Soil Depth	1	0.89	0.35
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	1	0.47	0.49

**Table A11.6 Variance accounted for by random effects variables in the model predicting plant height on Sidney Island in May (Chapter 3).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Substrate	$8.9 \times 10^{-3}$	$9.4 \times 10^{-2}$
Exclosure ID	$1.1 \times 10^{-7}$	$3.3 \times 10^{-4}$
Exclosure ID/Current Exposure to Browsing	$7.2 \times 10^{-6}$	$2.7 \times 10^{-3}$
Population	$1.1 \times 10^{-7}$	$3.3 \times 10^{-4}$
Residual	0.46	$2.1 \times 10^{-2}$

**Table A11.7 Back-transformed model predicted values for height (cm) on Sidney Island for December, March and May (Chapter 3).**

<b>Browsing History</b>	<b>Current Exposure to Browsing</b>	<b>Measurement Date</b>	<b>Fruit Phenotype</b>	<b>Model Predicted Mean</b>	<b>SE Lower limit</b>	<b>SE Upper Limit</b>
Historically Exposed	Inside	December	Wingless	1.18	0.98	1.43
			Winged	1.17	0.95	1.46
		March	Wingless	2.32	1.93	2.78
			Winged	2.31	1.88	2.85
		May	Wingless	15.53	12.85	18.80
			Winged	14.50	11.66	18.03
	Outside	December	Wingless	1.19	0.83	1.72
			Winged	0.97	0.65	1.46
		March	Wingless	1.77	1.20	2.63
			Winged	1.87	1.22	2.87
		May	Wingless	7.75	4.77	12.62
			Winged	7.58	4.49	12.80
Historically Naïve	Inside	December	Wingless	1.35	1.09	1.67
			Winged	1.65	1.26	2.18
		March	Wingless	3.25	3.98	2.65
			Winged	3.69	2.83	4.80
		May	Wingless	16.51	13.34	20.43
			Winged	16.28	12.33	21.49
	Outside	December	Wingless	1.56	1.05	2.34
			Winged	1.47	0.89	2.44
		March	Wingless	2.29	1.49	3.52
			Winged	2.07	1.22	3.52
		May	Wingless	7.90	4.55	13.71
			Winged	6.59	3.35	12.98

## Appendix 12: ANOVA Results and Predicted Values for Growth Form (H:W Ratio) on Sidney Island (Chapter 3)

**Table A12.1** ANOVA results for the model predicting growth form (measured as the height to width ratio, H:W Ratio; natural log transformed) on Sidney Island in December (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	6.45	0.01
Browsing History	1	0.74	0.39
Current Exposure to Browsing	1	0.01	0.92
Fruit Phenotype of Sown Fruit	1	0.00	0.99
Soil depth	1	0.11	0.74
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	1	0.02	0.88
Browsing History*Fruit Phenotype of Sown Fruit	1	1.24	0.27
Current Exposure to Browsing*Fruit Phenotype of Sown Fruit	1	1.38	0.24
Current Exposure to Browsing*Soil Depth	1	0.00	0.96
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	1	0.08	0.77

**Table A12.2** Variance accounted for by random effects variables in the model predicting growth form (measured as the height to width ratio, H:W Ratio; natural log transformed) on Sidney Island in December (Chapter 3).

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Substrate	$1.1 \times 10^{-7}$	$3.4 \times 10^{-4}$
Exclosure ID	$5.3 \times 10^{-3}$	$7.3 \times 10^{-2}$
Exclosure ID/Current Exposure to Browsing	$2.2 \times 10^{-7}$	$4.7 \times 10^{-4}$
Population	$5.1 \times 10^{-6}$	$2.3 \times 10^{-3}$
Population/Family	$3.6 \times 10^{-6}$	$1.9 \times 10^{-3}$
Residual	0.45	$1.5 \times 10^{-2}$

**Table A12.3 ANOVA results for the model predicting growth form (measured as the height to width ratio, H:W Ratio; natural log transformed) on Sidney Island in March (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	1.91	0.17
Browsing History	1	27.49	<b>&lt;0.0001</b>
Current Exposure to Browsing	1	4.88	<b>0.03</b>
Fruit Phenotype of Sown Fruit	1	0.84	0.36
Soil depth	1	3.76	0.05
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	1	2.39	0.12
Browsing History*Fruit Phenotype of Sown Fruit	1	0.27	0.60
Current Exposure to Browsing*Fruit Phenotype of Sown Fruit	1	0.10	0.75
Current Exposure to Browsing*Soil Depth	1	3.25	0.07
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	1	0.53	0.47

**Table A12.4 Variance accounted for by random effects variables in the model predicting growth form (measured as the height to width ratio, H:W Ratio; natural log transformed) on Sidney Island in March (Chapter 3).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Substrate	$1.9 \times 10^{-3}$	$4.3 \times 10^{-2}$
Exclosure ID	$1.1 \times 10^{-7}$	$3.4 \times 10^{-4}$
Exclosure ID/Current Exposure to Browsing	$1.8 \times 10^{-7}$	$4.2 \times 10^{-4}$
Population	$7.1 \times 10^{-3}$	$8.4 \times 10^{-2}$
Population/Family	$1.8 \times 10^{-2}$	0.13
Residual	0.33	$1.6 \times 10^{-2}$

**Table A12.5 ANOVA results for model predicting growth form (measured as the height to width ratio, H:W Ratio; natural log transformed) on Sidney Island in May (Chapter 3) including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	134.91	<b>&lt;0.0001</b>
Browsing History	1	0.82	0.36
Current Exposure to Browsing	1	0.00	0.99
Fruit Phenotype of Sown Fruit	1	0.04	0.84
Soil depth	1	4.96	<b>0.03</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	1	0.25	0.61
Browsing History*Fruit Phenotype of Sown Fruit	1	0.45	0.50
Current Exposure to Browsing*Fruit Phenotype of Sown Fruit	1	0.05	0.82
Current Exposure to Browsing*Soil Depth	1	0.35	0.56
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	1	1.64	0.20

**Table A12.6 Variance accounted for by random effects variables in the model predicting growth form (measured as the height to width ratio, H:W Ratio; natural log transformed) on Sidney Island in May (Chapter 3).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Substrate	$4.5 \times 10^{-2}$	0.21
Exclosure ID	$8.1 \times 10^{-4}$	$2.8 \times 10^{-2}$
Exclosure ID/Current Exposure to Browsing	$2.2 \times 10^{-4}$	$1.5 \times 10^{-2}$
Population	$2.6 \times 10^{-2}$	0.16
Population/Family	$1.1 \times 10^{-6}$	$1.0 \times 10^{-3}$
Residual	0.83	$4.2 \times 10^{-2}$



**Table A12.7 Back-transformed model predicted values for growth form (measured as the height to width ratio, H:W ratio) on Sidney Island (Chapter 3).**

<b>Browsing History</b>	<b>Current Exposure to Browsing</b>	<b>Measurement Date</b>	<b>Fruit Phenotype</b>	<b>Model Predicted Mean</b>	<b>SE Lower limit</b>	<b>SE Upper Limit</b>
Historically Exposed	Inside	December	Wingless	0.74	0.62	0.87
			Winged	0.74	0.61	0.89
		March	Wingless	0.98	0.85	1.13
			Winged	1.06	0.90	1.25
		May	Wingless	18.41	12.50	27.10
			Winged	19.16	13.09	28.03
	Outside	December	Wingless	0.76	0.55	1.05
			Winged	0.65	0.46	0.93
		March	Wingless	0.90	0.66	1.21
			Winged	0.94	0.67	1.30
		May	Wingless	10.52	3.18	34.88
			Winged	12.66	4.23	37.94
Historically Naïve	Inside	December	Wingless	0.79	0.66	0.96
			Winged	0.91	0.71	1.16
		March	Wingless	1.61	1.36	1.90
			Winged	1.63	1.32	2.02
		May	Wingless	15.26	9.42	24.72
			Winged	19.03	11.20	32.33
	Outside	December	Wingless	0.83	0.59	1.19
			Winged	0.87	0.56	1.34
		March	Wingless	1.23	0.88	1.71
			Winged	1.36	0.90	2.05
		May	Wingless	13.95	2.06	94.61
			Winged	9.30	2.12	40.86

### Appendix 13: ANOVA Results for Flowering Phenology on Sidney Island (Chapter 3)

**Table A13.1** ANOVA results for the model predicting flowering phenology in March on Sidney Island (Chapter 3), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Browsing History	7	1.76	0.42
Current Exposure to Browsing	7	0.83	0.66
Fruit Phenotype of Surviving Plant	7	3.95	0.14
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	7	1.29	0.53
Browsing History*Fruit Phenotype of Surviving Plant	7	1.12	0.57
Current Exposure to Browsing*Fruit Phenotype of Surviving Plant	7	6.72	<b>0.03*</b>
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	7	1.54	0.46

**Table A13.2** ANOVA results for the model predicting flowering phenology in May on Sidney Island (Chapter 3), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables. Bold p-values denote statistical significance.

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Browsing History	7	11.23	0.13
Current Exposure to Browsing	7	11.59	0.11
Fruit Phenotype of Surviving Plant	7	11.45	0.12
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing	7	7.09	0.42
Browsing History*Fruit Phenotype of Surviving Plant	7	7.37	0.39
Current Exposure to Browsing*Fruit Phenotype of Surviving Plant	7	11.49	0.12
<b>Three-way Interactions of Fixed Effects</b>			
Browsing History*Current Exposure to Browsing*Fruit Phenotype	7	6.19	0.52

## **Appendix 14: Estimating Number of Florets from Plant Height and Inflorescence Volume (Chapter 3)**

### **14.1 Estimating Number of Florets from Plant Height**

Regression equation for estimating the number of florets produced per plant by height,  $n = 242$ ,  $R^2 = 0.73$ , using the 2013-2014 exclosure data on all surviving plants in May 2014 on Sidney Island. Fruit phenotype was not included in the final predictive model ( $P > 0.05$ ).

$$\text{Predicted \# Florets} = \exp(-2.6708 + (2.0783 * \ln(\text{height}))) - 0.5$$

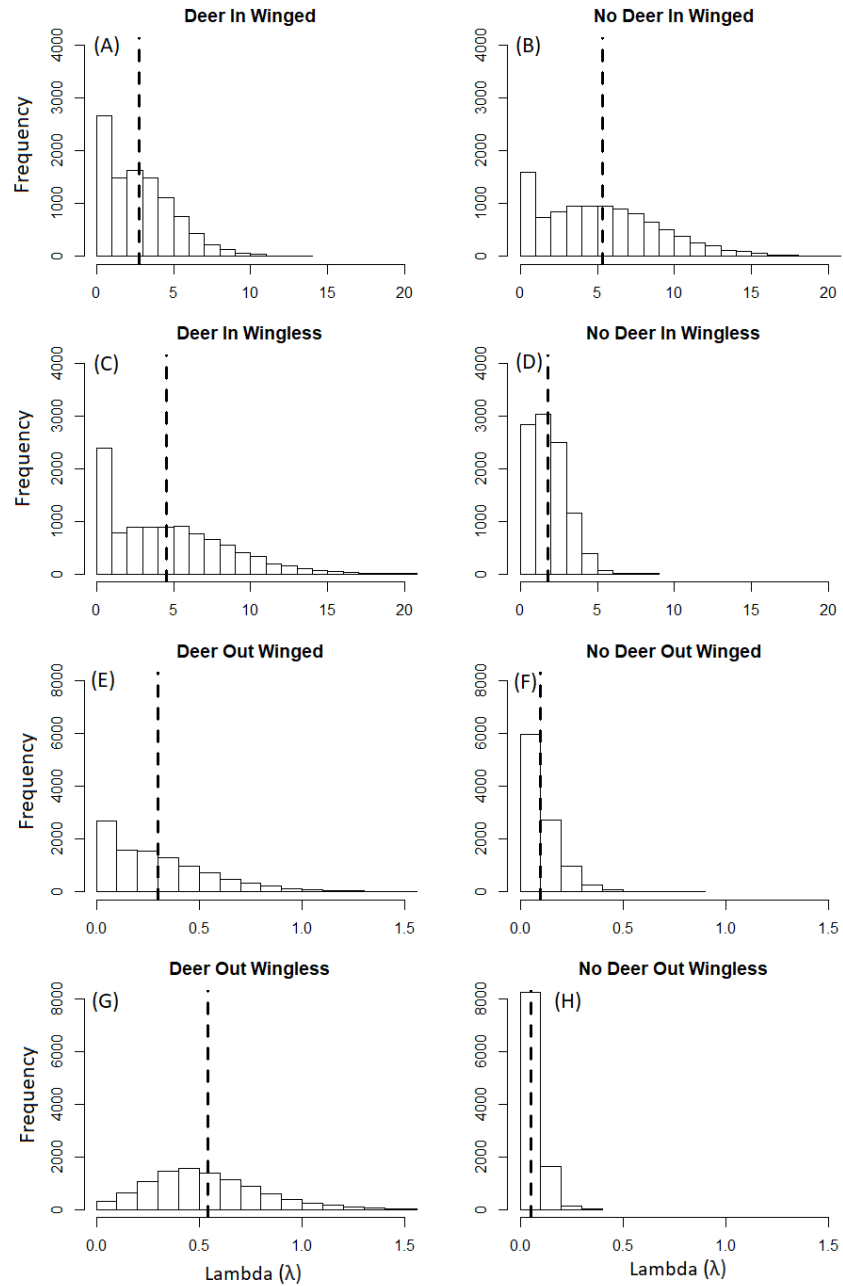
### **14.2 Estimating Number of Florets from Inflorescence Volume**

Regression equation for estimating the number of florets produced per plant by inflorescence volume,  $n = 167$ , using the 2013-2014 exclosure data on all surviving plants in May 2014 on Sidney Island. Inflorescence volume was estimated as an ellipsoid ( $V = (4/3)*abc$ , where  $a$  is the distance from the midpoint to the top of the inflorescence, and  $b$  and  $c$  are the distance from the midpoint to the side of the inflorescence)

*Predicted # Florets*

$$\begin{aligned} &= \exp(3.0305 - 0.1343(\text{deer} = \text{present}) + 0.1778(\text{fruit} = \text{wingless}) \\ &\quad - 0.1476(\text{deer} = \text{absent}, \text{fruit} = \text{wingless}) + 0.3391(\text{LogInflV}) + 0.0994 \\ &\quad * (\text{logInflV})(\text{deer} = \text{absent}) + 0.0365 * (\text{logInflV})(\text{fruit} = \text{wingless}) \\ &\quad - 0.1297 * (\text{LogInflV})(\text{deer} = \text{absent})(\text{fruit} = \text{wingless}) \end{aligned}$$

## Appendix 15: Distributions of Predicted Population Growth Rates ( $\lambda$ ) on Sidney Island (Chapter 3)



**Figure A15.1** Distributions of predicted population growth rates ( $\lambda$ ) inside (A-D) and outside (E-H) enclosures on Sidney Island (Chapter 3) for historically exposed (deer) and naïve (no deer) populations bearing winged and wingless fruits. Vertical lines represent mean predicted population growth rates ( $\lambda$ ).

## Appendix 16: Sampling Locations and Fraction of Plants Bearing Either Fruit Phenotype in Populations Sown in Totem Field (Chapter 4)

**Table A16.1** Locations of 20 source populations collected in 2005 and planted into the 2006-07 common garden protected from ungulate browsers in Totem Field, UBC (Chapter 4), percentage of plants in native populations bearing wingless fruits, and the number of families collected from each by fruit phenotype (see Methods).

Population	UTM (N, E)	% Plants with Wingless Fruits	# of Fruits (wingless, winged)
<b>Historically Exposed (With Deer)</b>			
Coal Island	5393202, 471444	100%	30, 0
Georgeson	5410177, 482611	85%	11, 11
Moresby Island	5397061, 477525	98%	11, 11
Piers Island	5394805, 469211	90%	22, 22
Prevost Island	5409749, 470845	99%	44, 0
<b>Historically Naïve (Without Deer)</b>			
Anniversary Island	5407800, 486683	32%	11, 11
Blunden Island	5399056, 487524	5%	7, 18
Brackman Island	5396218, 471657	22%	12, 11
Bright Island	5407567, 474053	20%	21, 22
Canoe Cove	5392250, 470176	28%	22, 22
Clive Island	5394341, 470151	4%	7, 15
East Chanel Island	5405424, 472016	1%	0, 44
West Chanel Island	5405333, 471703	1%	0, 44
Hawkins Islets	5409656, 472856	1%	22, 22
Owl Island	5408240, 470681	9%	22, 22
Middle Pellow Island	5396969, 473650	7%	22, 22
West Pellow Island	5396937, 473687	3%	11, 11
Reay Island	5392410, 475741	3%	22, 22
Rubly Island	5390401, 476998	14%	22, 22
Sallas Rocks	5381383, 478589	5%	0, 44

**Table A16.2 Locations of 17 source populations collected in 2006 and planted into the 2006-07 common garden protected from ungulate browsers in Totem Field, UBC (Chapter 4), percentage of plants in native populations bearing wingless fruits, and the number of families collected from each by fruit phenotype (see Methods).**

<b>Population</b>	<b>UTM (N, E)</b>	<b>% Plants with Wingless Fruits</b>	<b>Families (wingless, winged)</b>
<b>Historically Exposed (With Deer)</b>			
Georgeson	5410177, 482611	85%	7, 5
Little Samuel Island	5408604, 484248	80%	7, 5
Moresby Island	5397061, 477525	98%	10, 0
Crow's Nest (Salt Spring Island)	5403824, 466848	94%	10, 2
<b>Historically Naïve (Without Deer)</b>			
North Ada Island	5460015, 420562	3%	4, 3
South Ada Island	5459805, 420425	17%	3, 4
Anniversary Island	5407800, 486683	32%	4, 8
Belle Island	5408776, 484579	50%	5, 7
Blunden Island	5399056, 487524	5%	0, 12
Brackman Island	5396218, 471657	22%	1, 11
Clive Island	5394341, 470151	4%	0, 12
East Dock Island	5391034, 473657	3%	1, 7
West Dock Island	5390929, 473644	4%	0, 10
East Pellow Island	5397012, 473572	2%	2, 8
West Pellow Island	5396937, 473687	3%	0, 12
Ruth Island	5463745, 411342	5%	0, 10
Shell Island	5390933, 472504	3%	3, 8

**Table A16.3 Locations of 21 source populations collected in 2015 and planted into the 2015-16 common garden protected from ungulate browsers in Totem Field, UBC (Chapter 4), percentage of plants in native populations bearing wingless fruits, and the number of families collected from each by fruit phenotype (see Methods).**

<b>Population</b>	<b>UTM (N, E)</b>	<b>% Plants with Wingless Fruits</b>	<b>Families (wingless, winged)</b>
<b>Historically Exposed (With Deer)</b>			
Dean Park (Vancouver Island)	5384977, 467621	93%	6, 6
Galiano Island	5420788, 463331	54%	6, 7
Mayne Island	5407867, 480821	93%	7, 5
Moresby Island	5397061, 477525	98%	6, 6
Pender Island	5401676, 478716	94%	6, 6
Piers Island	5394805, 469211	90%	6, 6
Prevost Island	5409749, 470845	99%	6, 6
AVNR (Salt Spring Island)	5403861, 465986	93%	6, 6
Sansum Narrows (Salt Spring Island)	5401924, 458954	87%	8, 4
Schooner Cove	5459915, 417255	56%	9, 3
<b>Historically Naïve (Without Deer)</b>			
Canoe Cove	5392250, 470176	28%	6, 6
Chades Island	5398192, 472230	3%	6, 6
Chanel Islands	5405333, 471703	1%	5, 7
Clive Island	5394341, 470151	4%	6, 6
Grace Islet	5411069, 463791	2%	2, 10
Isabella Island	5397411, 468333	3%	0, 12
Musgrave Island	5399003, 460040	1%	6, 6
Owl Island	5408240, 470681	9%	6, 6
Port Washington Island	5406547, 476287	1%	1, 11
Shell Island	5390933, 472504	3%	3, 9
South Winchelsea Island	5460311, 421567	7%	3, 9

## Appendix 17: ANOVA Results for Plant Height in the Totem Field Common Gardens

### (Chapter 4)

Table A17.1 ANOVA results for the model predicting plant height at day 55 in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Intercept	1	36.36	< <b>0.0001</b>
Browsing History	1	35.21	< <b>0.0001</b>
Fruit Phenotype of Sown Fruit	1	26.17	< <b>0.0001</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Sown Fruit	1	0.60	0.44

Table A17.2 Variance accounted for by random effects variables in the model predicting plant height at day 55 in the Totem Field common gardens (Chapter 4).

Random Effects Variable	Variance	SD
Garden Year	$8.5 \times 10^{-3}$	$9.2 \times 10^{-2}$
Garden Year/Bed ID	$7.5 \times 10^{-3}$	$8.6 \times 10^{-2}$
Population	0.13	0.36
Residual	0.49	$6.0 \times 10^{-3}$



**Table A17.3 ANOVA results for the model predicting plant height at day 119 in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	71.92	<b>&lt;0.0001</b>
Browsing History	1	61.08	<b>&lt;0.0001</b>
Fruit Phenotype of Sown Fruit	1	24.72	<b>&lt;0.0001</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Sown Fruit	1	3.32	0.07

**Table A17.4 Variance accounted for by random effects variables in the model predicting plant height at day 119 in the Totem Field common gardens (Chapter 4).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Garden Year	$9.4 \times 10^{-3}$	$9.7 \times 10^{-2}$
Garden Year/Bed ID	$5.6 \times 10^{-3}$	$7.5 \times 10^{-2}$
Population	$3.9 \times 10^{-2}$	0.20
Residual	0.39	$4.7 \times 10^{-3}$

**Table A17.5 ANOVA results for the model predicting plant height at day 192 in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	979.47	<b>&lt;0.0001</b>
Browsing History	1	56.88	<b>&lt;0.0001</b>
Fruit Phenotype of Sown Fruit	1	51.52	<b>&lt;0.0001</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Sown Fruit	1	4.65	<b>0.03</b>

**Table A17.6 Variance accounted for by random effects variables in the model predicting plant height at day 192 in the Totem Field common gardens (Chapter 4).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Garden Year	$2.4 \times 10^{-3}$	$4.9 \times 10^{-2}$
Garden Year/Bed ID	$4.9 \times 10^{-3}$	$6.9 \times 10^{-2}$
Population	$8.4 \times 10^{-2}$	0.29
Residual	0.41	$5.0 \times 10^{-2}$

**Table A17.7 ANOVA results for the model predicting plant height in April in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	191.88	<b>&lt;0.0001</b>
Browsing History	1	17.87	<b>&lt;0.0001</b>
Fruit Phenotype of Sown Fruit	1	19.03	<b>&lt;0.0001</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Sown Fruit	1	0.01	0.92

**Table A17.8 Variance accounted for by random effects variables in the model predicting plant height in April in the Totem Field common gardens (Chapter 4).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Garden Year	0.16	0.39
Garden Year/Bed ID	$1.4 \times 10^{-3}$	$3.7 \times 10^{-2}$
Population	$5.9 \times 10^{-2}$	0.24
Residual	0.36	$4.4 \times 10^{-3}$

**Table A17.9 ANOVA results for the model predicting plant height in May in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	650.50	<b>&lt;0.0001</b>
Browsing History	1	20.51	<b>&lt;0.0001</b>
Fruit Phenotype of Sown Fruit	1	10.83	<b>0.001</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Sown Fruit	1	0.53	0.47

**Table A17.10 Variance accounted for by random effects variables in the model predicting plant height in May in the Totem Field common gardens (Chapter 4).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Garden Year	$4.8 \times 10^{-2}$	0.22
Garden Year/Bed ID	$4.2 \times 10^{-3}$	$6.5 \times 10^{-2}$
Population	$3.4 \times 10^{-2}$	$6.5 \times 10^{-2}$
Residual	0.36	$4.3 \times 10^{-3}$

## Appendix 18: ANOVA Results for Growth Form (H:W Ratio) in the Totem Field Common Gardens (Chapter 4)

Table A18.1 ANOVA results for the model predicting growth form (measured as the height to width ratio, H:W ratio, natural log transformed) at day 55 in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Intercept	1	65.10	<b>&lt;0.0001</b>
Browsing History	1	24.72	<b>&lt;0.0001</b>
Fruit Phenotype of Sown Fruit	1	0.13	0.72
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Sown Fruit	1	0.94	0.33

Table A18.2 Variance accounted for by random effects variables in the model predicting growth form (measured as the height to width ratio, H:W ratio) at day 55 in the Totem Field common gardens (Chapter 4).

Random Effects Variable	Variance	SD
Garden Year	$1.8 \times 10^{-2}$	0.13
Garden Year/Bed ID	$3.0 \times 10^{-3}$	$5.5 \times 10^{-2}$
Population	$7.6 \times 10^{-2}$	0.28
Residual	0.46	$5.6 \times 10^{-3}$

**Table A18.3 ANOVA results for the model predicting growth form (measured as the height to width ratio, H:W ratio, natural log transformed) at day 119 in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	569.84	<b>&lt;0.0001</b>
Browsing History	1	9.20	<b>0.002</b>
Fruit Phenotype of Sown Fruit	1	2.05	0.15
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Sown Fruit	1	1.10	0.29

**Table A18.4 Variance accounted for by random effects variables in the model predicting growth form (measured as the height to width ratio, H:W ratio) at day 119 in the Totem Field common gardens (Chapter 4).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Garden Year	$3.8 \times 10^{-3}$	$6.2 \times 10^{-2}$
Garden Year/Bed ID	$7.0 \times 10^{-3}$	$8.4 \times 10^{-2}$
Population	$1.4 \times 10^{-2}$	0.12
Residual	0.35	$4.3 \times 10^{-3}$

**Table A18.5 ANOVA results for the model predicting growth form (measured as the height to width ratio, H:W ratio, natural log transformed) at day 192 in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	0.85	0.36
Browsing History	1	80.35	<b>&lt;0.0001</b>
Fruit Phenotype of Sown Fruit	1	5.61	<b>0.02</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Sown Fruit	1	1.02	0.31

**Table A18.6 Variance accounted for by random effects variables in the model predicting growth form (measured as the height to width ratio, H:W ratio) at day 192 in the Totem Field common gardens (Chapter 4).**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Garden Year	$5.4 \times 10^{-2}$	0.23
Garden Year/Bed ID	$8.1 \times 10^{-3}$	$9.0 \times 10^{-2}$
Population	$2.1 \times 10^{-2}$	0.15
Residual	0.27	$3.3 \times 10^{-3}$

## Appendix 19: ANOVA Results for the Total Number of Branches in the Totem Field

### Common Gardens (Chapter 4)

Table A19.1 ANOVA results for the model predicting the total number of branches (natural log transformed) in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Intercept	1	247.22	< <b>0.0001</b>
Browsing History	1	0.11	0.74
Fruit Phenotype of Surviving Plant	1	12.00	< <b>0.001</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Surviving Plant	1	4.99	<b>0.03</b>

Table A19.2 Variance accounted for by random effects variables in the model predicting the total number of branches (natural log transformed) in the Totem Field common gardens (Chapter 4).

Random Effects Variable	Variance	SD
Garden Year	0.04	0.21
Garden Year/Bed ID	0.02	0.14
Population	0.05	0.22
Residual	0.91	0.01



## Appendix 20: ANOVA Results for the Number of Branches Below 10 cm Height in the Totem Field Common Gardens (Chapter 4)

Table A20.1 ANOVA results for the model predicting the number of branches below 10 cm of height (natural log transformed) in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Intercept	1	610.39	< <b>0.0001</b>
Browsing History	1	37.09	< <b>0.0001</b>
Fruit Phenotype of Surviving Plant	1	9.24	<b>0.002</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Surviving Plant	1	6.93	<b>0.008</b>

Table A20.2 Variance accounted for by random effects variables in the model predicting the number of branches below 10 cm of height (natural log transformed) in the Totem Field common gardens (Chapter 4).

Random Effects Variable	Variance	SD
Garden Year	$2.0 \times 10^{-3}$	$4.5 \times 10^{-2}$
Garden Year/Bed ID	$5.3 \times 10^{-3}$	$7.3 \times 10^{-2}$
Population	$4.6 \times 10^{-2}$	0.21
Residual	0.77	$9.4 \times 10^{-3}$

## Appendix 21: ANOVA Results for Flowering Phenology in the Totem Field Common

### Gardens (Chapter 4)

Table A21.1 ANOVA results for the model predicting flowering phenology in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Browsing History	2	117.32	< <b>0.0001</b>
Fruit Phenotype of Surviving Plant	2	75.65	< <b>0.0001</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Surviving Plant	2	19.27	< <b>0.0001</b>

## Appendix 22: ANOVA Results for Fecundity Relative to Neighbour Composition in the Totem Field Common Gardens (Chapter 4)

Table A22.1 ANOVA results for the model predicting fecundity (number of florets) relative to neighbour composition in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Browsing History	1	99.49	< <b>0.0001</b>
Fruit Phenotype of Surviving Plant	1	77.60	< <b>0.0001</b>
Proportion of Neighbours from Historically Exposed Populations	1	18.17	< <b>0.0001</b>
Number of Living Neighbours	1	3.77	0.05
Mean Height of Neighbouring Plants	1	0.48	0.49
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Surviving Plant	1	467.61	< <b>0.0001</b>
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	1	2.85	0.09
Number of Living Neighbours * Mean Height of Neighbouring Plants	1	5.70	<b>0.02</b>

Table A22.2 Variance accounted for by random effects in the model predicting fecundity (number of florets) relative to neighbour composition in the Totem Field common gardens (Chapter 4).

Random Effects Variable	Variance	SD
Bed ID	81.39	9.02
Population	$1.1 \times 10^{-2}$	0.11
Population/Family	$5.5 \times 10^{-2}$	0.23

**Table A22.3 Beta coefficients ( $\beta$ ) for each term in the model predicting fecundity (number of florets) relative to neighbour composition in the Totem Field common gardens (Chapter 4), including independent variables and those nested in other variables, using Type III tests. Estimates are with a Poisson distribution and a log link.**

<b>Fixed Effects Variable</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>z-value</b>	<b>p-value</b>
Intercept	-1.80	7.90	-0.23	0.82
Browsing History: Historically Naïve	0.58	0.060	9.72	< 0.0001
Fruit Phenotype of Surviving Plant: Wingless	0.16	0.02	6.59	< 0.0001
Proportion of Neighbours from Historically Exposed Populations	0.20	0.05	4.19	< 0.0001
Number of Living Neighbours	-0.02	0.01	-1.64	0.10
Mean Height of Neighbouring Plants	0.001	0.00	1.00	0.32
Browsing History: Historically Naïve * Fruit Phenotype of Surviving Plant: Wingless	-0.80	0.04	-21.62	< 0.0001
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	-0.02	0.01	-1.69	0.09
Number of Living Neighbours * Mean Height of Neighbouring Plants	0.00	0.00	2.39	0.02

## Appendix 23: ANOVA Results for Plant Height Relative to Neighbour Composition in the Totem Field Common Gardens (Chapter 4)

**Table A23.1 ANOVA results for the model predicting plant height (cm) relative to neighbour composition in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.**

<b>Fixed Effects Variable or Interaction</b>	<b>Df</b>	<b><math>\chi^2</math></b>	<b>p-value</b>
<b>Fixed Effects Variable</b>			
Intercept	1	26.53	< <b>0.0001</b>
Browsing History	1	31.48	< <b>0.0001</b>
Fruit Phenotype of Surviving Plant	1	0.23	0.63
Proportion of Neighbours from Historically Exposed Populations	1	2.19	0.14
Number of Living Neighbours	1	6.36	<b>0.01</b>
Mean Height of Neighbouring Plants	1	3.64	0.06
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Surviving Plant	1	6.23	<b>0.01</b>
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	1	0.01	0.93
Number of Living Neighbours * Mean Height of Neighbouring Plants	1	7.71	<b>0.005</b>

**Table A23.2 Variance accounted for by random effects in the model predicting plant height (cm) relative to neighbour composition in the Totem Field common gardens (Chapter 4), including independent variables and those nested in other variables.**

<b>Random Effects Variable</b>	<b>Variance</b>	<b>SD</b>
Garden Year	83.85	9.16
Garden Year/Bed ID	1.53	1.24
Population	60.82	7.80
Population/Family	35.92	5.99
Residual	14.09	0.22

**Table A23.3 Beta coefficients ( $\beta$ ) for each term in the model for plant height (cm) relative to neighbour composition in the Totem Field common gardens (Chapter 4), including independent variables and those nested in other variables.**

<b>Fixed Effects Variable</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>z-value</b>	<b>p-value</b>
Intercept	40.88	7.94	5.15	< 0.0001
Browsing History: Historically Naïve	16.82	3.00	5.61	< 0.0001
Fruit Phenotype of Surviving Plant: Wingless	0.65	1.35	0.48	0.63
Proportion of Neighbours from Historically Exposed Populations	4.93	3.33	1.48	0.14
Number of Living Neighbours	-2.00	0.79	-2.52	0.01
Mean Height of Neighbouring Plants	0.11	0.06	1.91	0.06
Browsing History: Historically Naïve * Fruit Phenotype of Surviving Plant: Wingless	-4.29	1.72	-2.50	0.01
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	-0.07	0.73	-0.09	0.93
Number of Living Neighbours * Mean Height of Neighbouring Plants	0.03	0.01	2.78	0.01

## Appendix 24: ANOVA Results for Growth Form (H:W Ratio) Relative to Neighbour

### Composition in the Totem Field Common Gardens (Chapter 4)

Table A24.1 ANOVA results for the model predicting growth form (measured as the height to width ratio, H:W ratio; natural log transformed) relative to neighbour composition in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Intercept	1	12.26	< <b>0.001</b>
Browsing History	1	59.49	< <b>0.0001</b>
Fruit Phenotype of Surviving Plant	1	3.60	0.06
Proportion of Neighbours from Historically Exposed Populations	1	0.63	0.43
Number of Living Neighbours	1	0.10	0.75
Mean Height of Neighbouring Plants	1	1.13	0.29
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Surviving Plant	1	0.10	0.75
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	1	0.06	0.81
Number of Living Neighbours * Mean Height of Neighbouring Plants	1	3.18	0.07

Table A24.2 Variance accounted for by random effects in the model predicting for growth form (measured as the height to width ratio, H:W ratio) relative to neighbour composition in the Totem Field common gardens (Chapter 4).

Random Effects Variable	Variance	SD
Garden Year	$7.5 \times 10^{-2}$	0.27
Garden Year/Bed ID	$7.9 \times 10^{-3}$	$8.9 \times 10^{-2}$
Population	$2.5 \times 10^{-2}$	0.16
Population/Family	$9.7 \times 10^{-3}$	$9.9 \times 10^{-2}$
Residual	0.23	$3.8 \times 10^{-3}$

**Table A24.3 Beta coefficients ( $\beta$ ) for each term in the model for growth form (H:W Ratio; natural log transformed) relative to neighbour composition in the Totem Field common gardens (Chapter 4), including independent variables and those nested in other variables.**

<b>Fixed Effects Variable</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>z-value</b>	<b>p-value</b>
Intercept	-0.74	0.21	-3.50	< 0.001
Browsing History: Historically Naïve	0.45	0.06	7.71	< 0.0001
Fruit Phenotype of Surviving Plant: Wingless	-0.04	0.02	-1.90	0.06
Proportion of Neighbours from Historically Exposed Populations	-0.04	0.06	-0.80	0.43
Number of Living Neighbours	-0.00	0.01	-0.32	0.75
Mean Height of Neighbouring Plants	0.00	0.00	1.06	0.29
Browsing History: Historically Naïve * Fruit Phenotype of Surviving Plant: Wingless	-0.00	0.03	-0.32	0.75
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	0.00	0.01	0.24	0.81
Number of Living Neighbours * Mean Height of Neighbouring Plants	0.00	0.00	1.78	0.07



## Appendix 25: ANOVA Results for Total Number of Branches Relative to Neighbour

### Composition in the Totem Field Common Gardens (Chapter 4)

Table A25.1 ANOVA results for the model predicting the total number of branches relative to neighbour composition in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Intercept	1	152.12	< <b>0.0001</b>
Browsing History	1	0.21	0.64
Fruit Phenotype of Surviving Plant	1	0.27	0.60
Proportion of Neighbours from Historically Exposed Populations	1	3.32	0.07
Number of Living Neighbours	1	84.96	< <b>0.0001</b>
Mean Height of Neighbouring Plants	1	4.00	<b>0.045</b>
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Surviving Plant	1	18.49	< <b>0.0001</b>
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	1	7.37	<b>0.007</b>
Number of Living Neighbours * Mean Height of Neighbouring Plants	1	22.93	< <b>0.0001</b>

Table A25.2 Variance accounted for by random effects in the model predicting the total number of branches relative to neighbour composition in the Totem Field common gardens (Chapter 4).

Random Effects Variable	Variance	SD
Garden Year	$8.9 \times 10^{-2}$	0.30
Garden Year/Bed ID	$3.5 \times 10^{-2}$	0.19
Population	0.12	0.35

**Table A25.3 Beta coefficients ( $\beta$ ) for each term in the model for the total number of branches relative to neighbour composition in the Totem Field common gardens (Chapter 4), including independent variables and those nested in other variables. Estimates are with a Poisson distribution and a log link.**

<b>Fixed Effects Variable</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>z-value</b>	<b>p-value</b>
Intercept	3.07	0.25	12.33	< 0.0001
Browsing History: Historically Naïve	0.05	0.12	0.46	0.64
Fruit Phenotype of Surviving Plant: Wingless	-0.01	0.03	-0.52	0.60
Proportion of Neighbours from Historically Exposed Populations	0.12	0.07	1.82	0.07
Number of Living Neighbours	-0.15	0.02	-9.22	< 0.0001
Mean Height of Neighbouring Plants	-0.002	0.001	-2.00	0.05
Browsing History: Historically Naïve * Fruit Phenotype of Surviving Plant: Wingless	-0.14	0.03	-4.30	< 0.0001
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	0.04	0.01	2.71	0.01
Number of Living Neighbours * Mean Height of Neighbouring Plants	0.001	0.00	4.79	< 0.0001

## Appendix 26: ANOVA Results for the Number of Branches Below 10 cm Relative to Neighbour Composition in the Totem Field Common Gardens (Chapter 4)

Table A26.1 ANOVA results for the model predicting the number of branches below 10 cm of height relative to neighbour composition in the Totem Field common gardens (Chapter 4), including Wald's Chi-Square and p-values for fixed effect variables and interactions between variables, using Type III tests. Bold p-values denote statistical significance.

Fixed Effects Variable or Interaction	Df	$\chi^2$	p-value
<b>Fixed Effects Variable</b>			
Intercept	1	238.41	< <b>0.0001</b>
Browsing History	1	30.53	< <b>0.0001</b>
Fruit Phenotype of Surviving Plant	1	0.86	0.35
Proportion of Neighbours from Historically Exposed Populations	1	2.78	0.10
Number of Living Neighbours	1	6.51	<b>0.01</b>
Mean Height of Neighbouring Plants	1	0.17	0.68
<b>Two-way Interactions of Fixed Effects</b>			
Browsing History* Fruit Phenotype of Surviving Plant	1	1.20	0.27
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	1	0.72	0.39
Number of Living Neighbours * Mean Height of Neighbouring Plants	1	0.04	0.83

Table A26.2 Variance accounted for by random effects in the model predicting the number of branches below 10 cm of height relative to neighbour composition in the Totem Field common gardens (Chapter 4).

Random Effects Variable	Variance	SD
Garden Year	$1.2 \times 10^{-7}$	$3.6 \times 10^{-4}$
Garden Year/Bed ID	$2.3 \times 10^{-2}$	0.15
Population	$6.2 \times 10^{-2}$	0.25
Population/Family	0.19	0.44

**Table A26.3 Beta coefficients ( $\beta$ ) for each term in the model for the number of branches below 10 cm of height relative to neighbour composition in the Totem Field common gardens (Chapter 4), including independent variables and those nested in other variables. Estimates are with a Poisson distribution and a log link.**

<b>Fixed Effects Variable</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>z-value</b>	<b>p-value</b>
Intercept	2.32	0.15	15.44	< 0.0001
Browsing History: Historically Naïve	-0.57	0.10	-5.53	< 0.0001
Fruit Phenotype of Surviving Plant: Wingless	-0.04	0.04	-0.93	0.36
Proportion of Neighbours from Historically Exposed Populations	0.17	0.10	1.67	0.10
Number of Living Neighbours	-0.07	0.03	-2.55	0.01
Mean Height of Neighbouring Plants	-0.00	0.00	-0.41	0.68
Browsing History: Historically Naïve * Fruit Phenotype of Surviving Plant: Wingless	-0.06	0.06	-1.10	0.27
Proportion of Neighbours from Historically Exposed Populations * Number of Living Neighbours	0.02	0.02	0.85	0.40
Number of Living Neighbours * Mean Height of Neighbouring Plants	-0.00	0.00	-0.21	0.83

## Appendix 27: Calculations for the Estimated Number of Generations for Morphological Change

$$N_{gen} = [((\mu_1 - \mu_2) / \mu_2) * 100] / \text{evolvability}$$

$N_{gen}$ : number of generations;  $\mu_1$ : mean value observed for plants from historically exposed or naïve populations;  $\mu_2$ : mean value observed in the opposite selective environment

### I. Plant Height Day 192:

$\mu_{naïve} = 2.16 \text{ cm}$ ,  $\mu_{exposed} = 1.44 \text{ cm}$ ,  $\text{evolvability} = 2.83$

- a. Number of generations from mean value historically exposed to naïve

$$((1.44 \text{ cm} - 2.16 \text{ cm}) / 2.16 \text{ cm}) * 100 / 2.83 = \mathbf{12 \text{ generations}}$$

- b. Number of generations from mean value historically naïve to exposed

$$((2.16 \text{ cm} - 1.44 \text{ cm}) / 1.44 \text{ cm}) * 100 / 2.83 = \mathbf{18 \text{ generations}}$$

### II. Growth Form (H:W Ratio) at Day 192:

$\mu_{naïve} = 0.59$ ,  $\mu_{exposed} = 0.25$ ,  $\text{evolvability} = 30.11$

- a. Number of generations from mean value historically exposed to naïve

$$((0.25 - 0.59) / 0.59) * 100 / 30.11 = \mathbf{2 \text{ generations}}$$

- b. Number of generations from mean value historically naïve to exposed

$$((0.59 - 0.25) / 0.25) * 100 / 30.11 = \mathbf{5 \text{ generations}}$$

### III. Number of Branches Below 10 cm Height:

$$\mu_{\text{naive}} = 4.73, \mu_{\text{exposed}} = 8.32, \text{evolvability} = 7.79$$

- a. Number of generations from mean value historically exposed to naïve

$$((8.32 - 4.73) / 4.73) * 100 / 7.79 = \mathbf{10 \text{ generations}}$$

- b. Number of generations from mean value historically naïve to exposed

$$((4.73 - 8.32) / 8.32) * 100 / 7.79 = \mathbf{6 \text{ generations}}$$