Water into nectar:
The effects of seasonal drought on bumble bee and flowering plant communities

by

Andrew D. F. Simon
B.A.Sc., Quest University Canada, 2016

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

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in the School of Environmental Studies

University of Victoria

Supervisory Committee

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Abstract

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Habitat loss and climate change are major factors implicated in the decline of bumble bees worldwide. These factors may be particularly acute in regions subject to climatic extremes such as seasonal drought. Combining methods from pollinator research and phylogenetic community ecology, I investigated the impacts of seasonal drought on plant phenology and bumble bee community ecology across gradients of disturbance and soil moisture in a semi-arid ecosystem. Seasonal fluctuations in floral resources coincided with significant phylogenetic clustering in plant communities, with decreasing plant diversity observed under conditions of increasing drought stress. In the late season, modified wet areas supported higher floral resource availability and greater bumble bee abundances as compared to dry woodlands, though wetlands were also an important source of late season floral resources. Despite these local effects, however, the areal extent of natural *vs* modified matrix habitat accounted for the majority of variation in models explaining bumble bee abundances. Modified matrix habitat was negatively associated, and natural matrix habitat positively associated, with the occurrence of bumble bee workers in June and late-flying queens in July and August. Results provide insight into the temporal niche dynamics of entomophilous flowering plants in this system, and emphasize the importance of conserving natural habitat diversity in efforts to promote resilient plant-pollinator communities. This study also provides evidence for the local extinction of *Bombus occidentalis* Greene, 1858 and *Bombus suckleyi* Greene, 1860 from Galiano Island, BC, Canada, as well as the island's recent colonization by *Bombus vosnesenskii* Radoszkowski, 1862.

Bombus flavifrons **Cresson, 1863**
on *Limonium* Mill.
Photograph by Andrew Simon
August 14, 2018

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Acknowledgments

I first wish to acknowledge my supervisor, Brian Starzomski, and fellow colleagues in the Starzomski lab for making a home for this research in the School of Environmental Studies. Many thanks to Pascale Archibald, Daniel Kirkpatrick, and Kevin Toomer, who helped me persevere through an intensive field season. Hannah Marx introduced me to methods in phylogenetic community ecology, opening up unexpected new horizons for this research. Trevor Lantz provided deft critical feedback, substantially improving the articulation of my findings. And Lincoln Best provided vital mentorship in bumble bee taxonomy. This labour was also assisted by Mae Frank, Sable Gilmore, Scott Gilmore, Sarah Johnson and Marika van Reeuwyk—among so many other "beeple", to whom I extend my gratitude. Mark Webber is thanked for his wisdom and generosity, and ever-expanding lab space; Curtis Björk and Trevor Goward, for nurturing my love of plants, which led irrevocably toward a fascination with their pollinators; Joel Gibson and Claudia Copley, for their hospitality in the collections at the Royal BC Museum; and Heather Klassen, who provided me with enough data loggers to keep me busy for years to come. Thank you to the many members of the Galiano community for supporting my biodiversity research—especially Randy Bishop, Patrick Van Holderbeke, and the late Gloria Olson and her family. I would also like to acknowledge the Crystal Mountain Society, Islands Trust Conservancy, Galiano Club, Galiano Conservancy Association, Galiano Island Parks and Recreation Commission, Garry Oak Meadow Preservation Society, and Tapovan Sri Chinmoy Peace Park, for opening up lands for this research. Finally, I am grateful for the funding received from the BC Parks Living Lab program, the Ian McTaggart Cowan Professorship in the School of Environmental Studies at the University of Victoria, NSERC, and the Lorene Kennedy Graduate Bursaries.

Dedication

This thesis is dedicated to Lauren Magner, without whom I could never have made it this far, and with whom I am glad to continue on sharing in a love of nature and commitment to place—embraced by the many relationships that complete our life together on Galiano Island. In the future I imagine us marveling at the many plant–pollinator interactions to be appreciated in the diverse ecological communities we call home.

"Bee" **by Annette Shaw**

Chapter I.
General Introduction

Bumble bees (*Bombus* Latreille, 1802) are welcomed by many as joyful heralds of springtime. Even as I worked through the final revisions of this thesis, I was privy to numerous comments from friends and colleagues delighted to share their first annual reports of these charismatic pollinators: loyal associates of our earliest blooming flowering plants here on British Columbia's south coast. Indeed, if you wished to be the first to see a bumble bee in this part of the world, you might stake out Oregon grape (*Berberis aquifolium*), red-flowering currant (*Ribes sanguineum*), or hairy manzanita (*Arctostaphylos columbiana*) on a brisk February afternoon (cherry, rosemary, and grape hyacinth make good bumblebee-friendly alternatives in your garden). In the right sun-soaked setting, it wouldn't be long before you witnessed a black-bottomed (*Bombus melanopygus*), black-notched (*B. vancouverensis*) or Sitka bumble bee (*B. sitkensis*) queen making the rounds, busy establishing her colony in anticipation of the multitudes of plants yet to bloom.

Carpe tempus verni.—Bumble bees "seize the springtime" with an industriousness that ranks them among the world's most ecologically and economically important pollinators. Emerging during the cold, wet conditions of late winter, the bumble bee queen is a master of thermodynamics, conserving energy in all that she does. One can appreciate this principle on cool mornings by observing her slow, intent perusal of each inflorescence she visits, as energy is conserved when she walks, rather than flies, from one nectar source to the next (Heinrich 1979). She is a hefty animal, insulated by a coat of hair known to be shorter in species adapted to warm climates and longer in those adapted to cold (Peat et al. 2005). Her corbicula dusted yellow and heavy with pollen, her fat body swelling and honey stomach growing full—it is impressive to witness her muster the energy necessary to take flight on a blustery wind, a feat achieved with the help of the antifreeze in her blood and complex muscle contractions in her thorax (Heinrich 1979, Heinrich 1990). The queen unclasps her twofold set of wings and basks in the sunlight, going through a shivering warm-up routine using the same muscles that allow her to beat her wings at up to 200 beats per second (Kammer & Heinrich 1972). "*BZZZZZZZ!"*—She vibrates for a while, tossing flecks of pollen to the air. Then, clasping her wings, she takes off. Aloft, she will regulate the temperature of her muscles relative to the air by flying at different heights—preferring air at about 8–10°C for optimal conservation of energy (Richards 1973).

The bumble bee's early emergence and ability to fly in cold temperatures have long impressed naturalists, provoking enough curiosity to spur studies in bumble bee physiology, behaviour, ecology, and evolution. We now know that these abilities have evolved in Holarctic regions over the last 25 to 40 million years, as modern day lineages of the genus *Bombus* diversified through intermittent periods of glaciation, warming, and turnover of the plant communities with which they co-evolved (Condamine & Hines 2015). Yet as resilient as the bumble bee may be, having evolved through the vicissitudes of geological time, these facets of its natural history also speak to its vulnerability as a cold-adapted genus now threatened by the impacts of climate change.

Numerous factors have been implicated in the decline of *Bombus* over the last century, including the spread of pathogens and pesticides associated with industrial agricultural practices (Szabo et al. 2012, Sanchez-Bayo 2014). In the long view, however, there is mounting evidence to suggest that climate change will have more drastic consequences for many species in the genus (Kerr et al. 2015). Across the northern hemisphere, some species have undergone dramatic declines in recent decades, with ranges receding northward by nearly 300km in southern regions, and to higher elevations (Kerr et al. 2015, Biella et al. 2017). These findings are consistent with an understanding of the evolutionary history of the genus *Bombus*, as testified by convergent molecular and geological evidence showing strong correlations between global climatic shifts and prehistoric diversification and extinction events. In brief: throughout the course of their evolution, bumble bee species have undergone increased rates of extinction in times of climate warming, and diversification in times of cooling (Hines 2008, Condamine & Hines 2015). Their sensitivity to global warming makes them vulnerable to a number of factors, including restrictions in floral resource availability during periods of climatic stress such as drought (Thomson 2016).

Seasonal drought is a naturally recurring phenomenon in the southern Gulf Islands of British Columbia, Canada, yet is expected to become more extreme, and more extended, under future climate scenarios (Klassen et al. 2015). In this MSc thesis, I investigate the effects of seasonal drought on plant and pollinator communities in this system, with a focus on the genus *Bombus* as a model organism. This work is divided into three major chapters, as described below, book-ended by this general introduction and a concluding chapter.

In Chapter II, I begin with an exploration of the temporal and spatial dimensions of the bumble bee foraging landscape, analyzing plant community phenology across gradients of disturbance and soil moisture under conditions of seasonal drought. This chapter centres around the concept of the temporal niche: a phenomenon arising from functional trait diversity in plant communities, as fluctuating resources become partitioned by different plant functional types whose divergent life histories entail differing regimes of photosynthetic activity and resource uptake to support vegetation and reproduction. Because of the severe implications of drought for the vital activities of plants, competitive interactions are expected to be relatively brief and thus of limited importance to the structure and dynamics of plant communities in water-limited ecosystems (Kikvidze & Brooker 2009). Environmental filtering is therefore hypothesized to be the dominant community assembly process structuring flowering plant communities in these environments. Based on this hypothesis, I predicted that major flowering events would coincide with phylogenetic clustering in plant communities, with related plants of similar functional types blooming in response to local restrictions in soil moisture.

In Chapter III, I turn my attention to the bumble bees. Bumble bees are primitive social insects that follow an annual colony cycle, depending on both early and late season floral resources to ensure the establishment of colonies and the intergenerational survivability of reproductive queens (Williams et al. 2012, Rundlöf et al. 2014, Carvell et al. 2017). In semi-arid ecosystems, however, late season floral resources are restricted by seasonal drought. Research has found that modified environments such as gardens provide important late season refuges for bumble bees and other pollinators in these ecosystems (McFrederick & LeBuhn 2006, Wray & Elle 2015). Previous research has largely focused on fragmented landscapes, however, contrasting only one semi-natural habitat type with modified agricultural and urban environments. In this chapter, I consider the importance of habitat diversity more broadly, across gradients of disturbance and soil moisture, for bumble bee communities under conditions of drought stress.

Chapter IV draws my thesis to a close as I address the fate of *Bombus occidentalis* Greene, 1858 and *Bombus suckleyi* Greene, 1860, two bumble bees of conservation concern which had historically been reported, but are now considered locally extinct, from Galiano

Island. Finally, Chapter V serves as a general conclusion, drawing out some of the broader implications and limitations of my findings.

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***Bombus sitkensis* Nylander, 1848**
on *Berberis aquifolium* (Pursh) Nutt.
Photograph by Andrew Simon
March 21, 2020

"Everybody knows the burly, good-natured bumble-bee. Clothed in her lovely coat of fur, she is the life of the gay garden as well as of the modestly blooming wayside as she eagerly hums from flower to flower, diligently collecting nectar and pollen from the break to the close of day."

Frederick William Lambert Sladen – The Humble-Bee (1914)

Chapter II.
Phylogenetic restriction of plant invasion in drought-stressed environments: implications for plant–pollinator communities in semi-arid ecosystems

Bombus melanopygus **Nylander, 1848**
on *Rosa nutkana* C. Presl
Photograph by Andrew Simon
June 2, 2018

The third person plural voice is adopted in the following chapter, which has been prepared as an independent manuscript for publication.

Citation: Simon, A. D. F., H. E. Marx, and B. M. Starzomski. Phylogenetic restriction of plant invasion in drought-stressed environments: implications for plant-pollinator communities in semi-arid ecosystems. In prep.

Co-authorship statement: ADFS designed the study with support from BMS; field data were collected by ADFS; HEM constructed the phylogeny and assisted in the application of methods in phylogenetic community ecology; the manuscript was composed by ADFS with input from the entire author team.

Chapter II.

Phylogenetic restriction of plant invasion in drought-stressed environments: implications for plant–pollinator communities in semi-arid ecosystems

Abstract

Plant-pollinator community diversity has been found to decrease under conditions of drought stress, however research into the temporal dimensions of this phenomenon remains limited. In this study, we investigated the temporal niche dynamics of entomophilous plant communities in a semi-arid ecosystem, considering the implications of seasonal drought for the pollinator foraging landscape. Combining methods from pollinator research and phylogenetic community ecology, we tested the influence of environmental filtering over plant community phenology across gradients of disturbance and soil moisture. Critical seasonal fluctuations in floral resources, quantified by counts of flowering shoots, coincided with significant phylogenetic clustering in plant communities, with decreasing plant diversity observed under conditions of increasing drought stress. Exotic Asteraceae became increasingly pervasive across the landscape, occupying a late season temporal niche in drought-stressed environments. Results indicate that environmental filtering is the dominant assembly process structuring the temporal niche of plant communities in this water-limited ecosystem, at once illustrating how competing assembly processes may coincide and become confounded on different spatial and temporal scales. Based on these results, and trends seen elsewhere, a late season restriction in the overall diversity of plant-pollinator communities is likely to occur in this system under future climate scenarios.

Introduction

The availability of water is the primary factor limiting the growth and reproduction of land plants (Rosenzweig 1968, Silvertown et al. 2015). In semi-arid ecosystems, the regular occurrence of summer drought thus has a profound impact on plant phenology, strongly influencing plant-pollinator community interactions. With climate change these ecosystems are globally expected to undergo widespread shifts in precipitation patterns, with extreme winter rainfall variability and increasingly severe drought predicted under future scenarios (Tapiador et al. 2007, Pan et al. 2010, Spies et al. 2010, Bladé et al. 2011, Collins et al. 2013). Such changes are likely to influence both spatial and temporal dimensions of the foraging landscape, resulting in shifting abundances and relationships among plant and insect communities.

Increasing drought may cause reductions in floral resource availability, resulting in a lower proportion of flowers containing nectar, fewer flowers per inflorescence, and reduced floral richness in some communities (Phillips et al. 2018). Drought has also been found to advance flowering phenology among annual herbaceous plants (König et al. 2017), and to cause stress or reduced productivity among perennial shrubs (Pérez-Camacho et al. 2012). On the other hand, increasing winter precipitation may disproportionately benefit annual herbaceous communities, and, with warming temperatures, may extend the growing season, opening up new temporal niches for exotic species to occupy (Pérez-Camacho et al. 2012, Wolkovich & Cleland 2014, Ashbacher & Cleland 2015). Many of these effects depend on the variable response of annual and perennial plant functional types to drought stress, which has numerous direct and indirect consequences for pollinator ecology.

Annual and perennial plant functional types are generally considered to lie at two ends of an adaptation gradient to drought, based on their relative drought avoidance or drought tolerance respectively (Díaz et al. 2007, Pérez-Camacho et al. 2012). In semi-arid ecosystems, annuals tend to germinate during late autumn rains, concentrating primary productivity during the wettest phase of the year, and to flower in early spring, surviving periods of low soil moisture availability as seeds. Perennials, by contrast, generally maintain primary productivity longer, and flower later, drawing from the tail end of the wet season resource pulse and persisting through drought in vegetative form (Schwinning & Kelly 2013). Shallow-rooted annuals develop faster than perennials, gaining priority in acquiring resources (Dìaz et al. 2016, Westoby et al. 2002, Falster & Westoby 2003, Wright et al. 2004), whereas greater root length in perennials may provide competitive advantage in acquiring resources at deeper depths of the soil profile (Casper & Jackson 1997, Fargione & Tilman 2006, Fort, Cruz, & Jouany 2014).

Diversity among plant functional types can promote niche complementarity in ecological communities (Gross et al. 2007, Gubsch et al. 2011), partitioning resources both spatially and temporally, and thereby increasing the overall productivity throughout the year (Schwinning & Kelly 2013, Wolkovich & Cleland 2011, Wolkovich & Cleland 2014, Wagg et al. 2017). From the point of view of pollinators, then, the differing life history strategies of annuals and perennials may have important consequences, underlying critical seasonal fluctuations in floral resources throughout semi-arid ecosystems. Indeed, functional diversity among plants is known to correlate positively with functional diversity among pollinators, promoting the persistence of diverse plant communities (Fontaine et al. 2006, Papanikolaou et al. 2017). Yet overall species diversity in plant-pollinator communities has been shown to decline under conditions of drought (Hoiss et al. 2015). Understanding the differential response of annuals and perennials to critical resource fluctuations is therefore key to predicting future changes in these communities.

Temporal niches have been postulated as a phenomenon arising from functional trait diversity in plant communities, as fluctuating resources become partitioned by plant functional types whose divergent life histories entail differing regimes of photosynthetic activity and resource uptake to support vegetation and reproduction (Yachi & Loreau 1999, Ogle & Reynolds 2004, Schwinning & Kelly 2013). As noted by Schwinning and Kelly (2013), temporal niches arise as an inevitable outcome of functional trait diversity within communities, insofar as traits maximizing resource uptake under certain conditions may limit resource uptake at other times. Furthermore, all plant species have resource-mediated density limits, making their development differentially sensitive to resource fluctuations (Schwinning & Ehleringer 2001, Schwinning et al. 2004). Temporal niches are therefore expected to have important implications in the context of plant invasion theory, as changes in the timing and intensity of seasonal drought could open temporal windows of invasion opportunity, benefiting non-native species adapted to exploit changing environmental conditions at different times of year (Wolkovich & Cleland 2011, Wolkovich & Cleland 2014).

Researchers have predicted that the late season would not likely present opportunity for invasion in semi-arid ecosystems, as non-native species may not be as adapted to high levels of drought stress as compared to native species (Alpert et al. 2000, Wolkovich & Cleland 2014). This assumes that drought-tolerant native plants might competitively exclude less tolerant non-native plants, or that non-natives might not be as well adapted to drought-stressed environments. Because of the severe restrictions drought imposes on the vital activities of plants, however, competitive interactions are expected to be of relatively limited importance to the structure of plant communities in water-limited ecosystems (Kikvidze & Brooker 2009). Environmental filtering is therefore expected to prevail as the dominant mode of community assembly in these systems, with plant community composition determined primarily by local abiotic constraints. In this context, environmental filtering predicts that a late season temporal niche might become occupied by exotic species phylogenetically related to the native host community, assuming that drought tolerant functional traits are conserved within clades.

In this study, we investigated the effect of seasonal drought on the temporal niche dynamics of entomophilous flowering plants in a semi-arid ecosystem. We hypothesized that closely related native and exotic plants would tend to share similar life history, and that peak flowering events would therefore coincide with phylogenetic clustering in plant communities based on expected phenological responses of plant functional types to limitations in soil moisture availability. To test this hypothesis, we analyzed plant phenology as it varied over the course of the growing season, assessing spatial and temporal overlaps in the local niche breadth of native *vs* non-native plants across gradients of disturbance and soil moisture. In dry environments, we predicted that both annuals and perennials would tend to flower early in response to diminishing soil moisture. In wet environments, we predicted both delayed and prolonged flowering among perennials sustained by higher levels of soil moisture. Late flowering was generally expected to correlate with perenniality among related native and exotic plants across all site conditions. We also expected disturbance and drought stress to favour exotic species, increasing late season floral resource availability. Finally, we predicted that the phylogenetic relationships underlying these phenological patterns would reveal effects of environmental filtering, with temporal niches segregated based on similarities in community phylogenetic structure and life history among related native and exotic species.

Methods

Study area

Galiano Island lies in the rain shadow of the mountains of Vancouver Island and the Olympic Peninsula, in southern coastal British Columbia, Canada. This region is defined by its semi-arid climate, characterized by mild, wet winters and warm, dry summers (Klassen et al. 2015**).** The combined effects of low precipitation, warm temperatures, and a high number of sunshine hours result in an annual moisture deficit on Galiano Island from mid-June to early October, and near drought conditions across the island's most exposed aspects (Harrison 1994). These conditions are expected to become more extreme under projected climate change scenarios. Global climate change simulations and regional climate models suggest that increases in winter precipitation (0.5–1.0mm/day) and the intensity and duration of summer drought are likely, along with more complex temperature-precipitation interactions (Christensen et al. 2007, Pike et al. 2008, Salathé et al. 2008, Spies et al. 2010).

Sampling

We analyzed the phenological response of plant communities to seasonal drought using a 2x2 factorial study design contrasting four extreme site conditions of disturbance and soil moisture availability: 1) dry semi-natural environments (woodlands and rock outcrops); 2) wet semi-natural environments (wetlands); 3) dry modified environments (disturbed upland areas such as clear-cuts); and, 4) wet modified environments (rural areas including gardens, orchards and fields). We stratified site conditions based on available terrestrial ecosystem mapping data (Madrone 2008) and randomly distributed 2x15m belt transects throughout 6 sites per site condition (total 24 sites). Each site was allocated 6-8 transects, the number of transects scaled roughly in proportion to the area covered, with the aim of capturing variability in floral resource availability across the landscape. Counts of flowering shoots were recorded for each plant species at 1m intervals and used to estimate floral resource availability. Soil moisture was recorded at 5m intervals as volumetric water content (%VWC) using a Field Scout TDR probe. Sampling was conducted over five months, from April through August 2018. Two vernally wet sites, initially stratified as wet semi-natural sites, proved to have a soil moisture regime and vegetation community more characteristic of dry semi-natural sites, and had to be reclassified. This resulted in an imbalance in the study design, with 4 sites representing the wet semi-natural condition *vs* 8 sites representing the dry semi-natural condition.

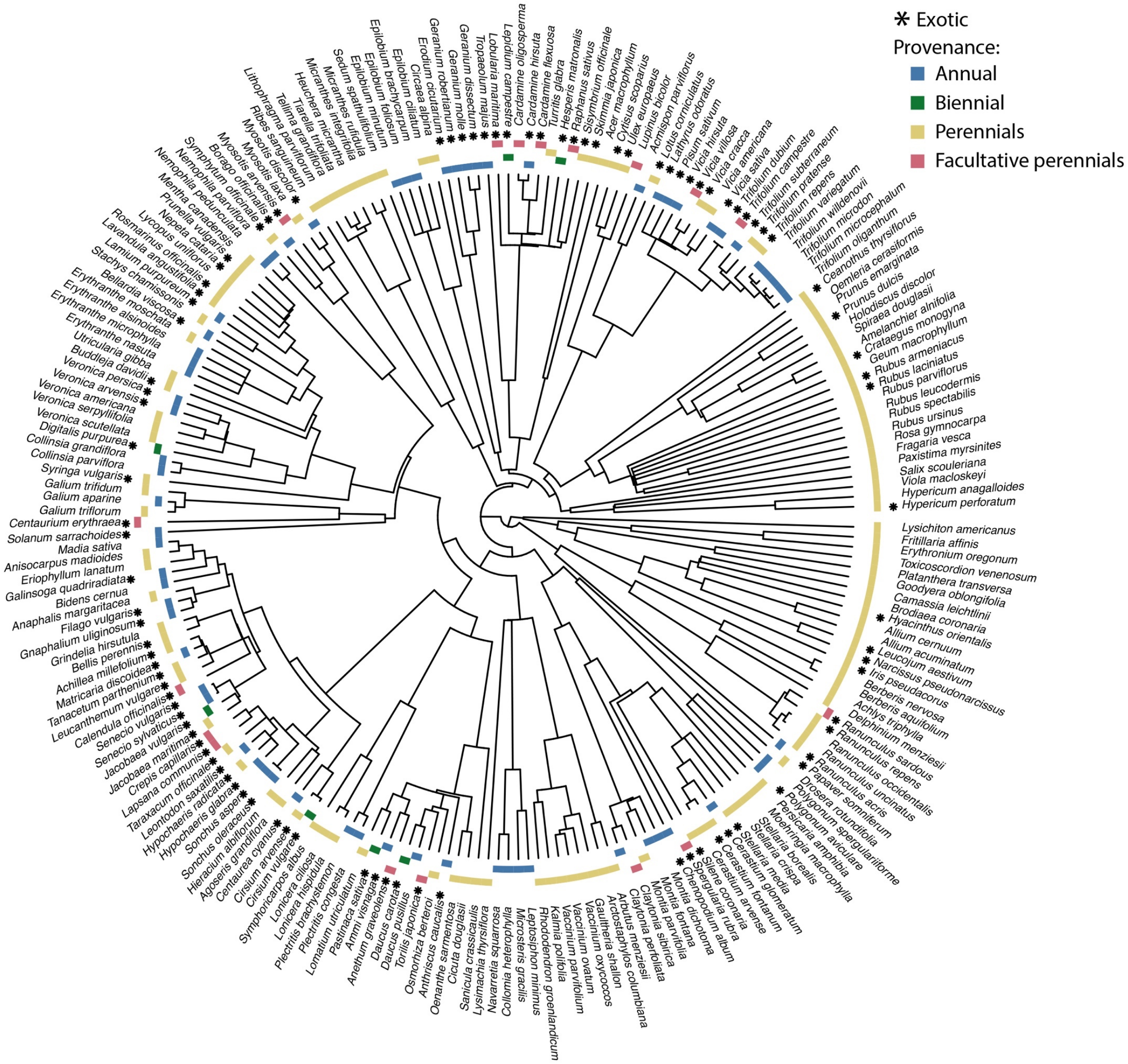

Figure 1. Phylogenetic relationships of entomophilous flowering plants observed on Galiano Island, showing provenance and life history of species.

Modelling

We assembled a phylogeny of seed plants known to Galiano Island based on a previously published robust species-level phylogeny of 353,185 seed plants derived from GenBank sequence data (Smith & Brown 2018). A total of 207 species of entomophilous flowering plants were sampled across sites, 173 of which were represented in the study area phylogeny. This subset of Galiano Island's study area phylogeny comprises the community phylogeny analyzed in this study (Fig.1). Species omitted from this phylogeny due to lack of sequence data do not demonstrate any taxonomic biases that could affect the results of this study.

We investigated phylogenetic patterns at two spatial scales. First, we pooled transects to assess patterns within each site condition for each sample period. Second, we assessed finer scale temporal patterns across the landscape within each transect for each sample period. To compare phylogenetic patterns between native *vs* exotic plant assemblages, we compared phylogenetic patterns for each group separately across each community and sample period. Interspecific phylogenetic distance matrices were used to calculate abundance-weighted mean pair-wise distance (MPD) and mean nearest taxon distance (MNTD) metrics for community and transect scale matrices. Whereas MPD is a measure of mean phylogenetic distance between all pairs of species in a sample, MNTD measures the average phylogenetic distance from each species to its closest relative. Both metrics are routinely used to test hypotheses about the mean relatedness of taxa within communities (Tucker et al. 2017).

To determine significance in the phylogenetic structure of community data, we compared observed phylogenetic metrics (MPD and MNTD) calculated for each subset of community data against a null model. The null model was generated by drawing random taxa from the study area phylogeny and randomly shuffling labels representing taxa across the tips of phylogenies generated based on each subset of community data, thereby randomizing assemblages while holding species richness and occurrence frequency constant (Kembel et al. 2010). Standardized effect sizes (z) resulting from null model tests were analysed for each sample period and site condition, to determine the significance of phylogenetic dispersion patterns in community data. Positive z values are associated with phylogenetic over-dispersion; negative values with phylogenetic clustering. The R packages ‘pez’ (Pearse et al. 2015) and ‘picante’ (Kembel et al. 2010) were used to implement community phylogenetic diversity analyses.

Transect-scale phylogenetic metrics were regressed against environmental variables with linear mixed effects models (LMM) using the R package ‘nlme’ (Pinheiro et al. 2019). Random slope-intercept models were fitted incorporating phylogenetic metrics as a response to log-transformed soil VWC and factors of disturbance (fixed effects), with transects nested within sites (random effects). Models failed to converge using mean pairwise distance, so mean nearest taxon distance was adopted for these analyses. To test differences in soil moisture availability between sites, random intercept LMMs were fitted using the same nested random effects structure, incorporating log transformed soil VWC as a response to site conditions as fixed effects (Pinheiro et al. 2019).

Finally, we fit negative binomial generalized linear mixed effects models (GLMMs) incorporating counts of flowering shoots as a response to site conditions (fixed effects) and transects nested within sites (random effects) to test differences in Floral Resource Availability (FRA) between site conditions. Seven outliers representing extremely high counts of flowering shoots among the exotic *Cytisus scoparius* (L.) Link (Scotch broom) prevented model convergence and had to be removed. Similar models were fitted for each site condition and sample period to test differences in the contributions of native *vs* exotic species to FRA, and to test differences in FRA contributed by different plant functional types within clades. These models were implemented using the R package ‘lme4’, and ‘glmmTMB’ in cases where zero-inflation proved problematic (Bates et al. 2015, Brooks et al. 2017). The best models were selected based on AIC test scores (R Core Team 2019), assuming ΔAIC of 2.0 as a threshold for model improvement (Burnham & Anderson 2002). Model effects are reported as Incidence Rate

Ratios (IRR), and as marginal R^2 values (variance explained by fixed effects) where appropriate. Marginal effects were calculated using ‘sjPlot’ (Lüdecke 2018). Statistical analyses were implemented in R Version 3.6.0 (R Core Team 2019).

Results

Onset of seasonal drought

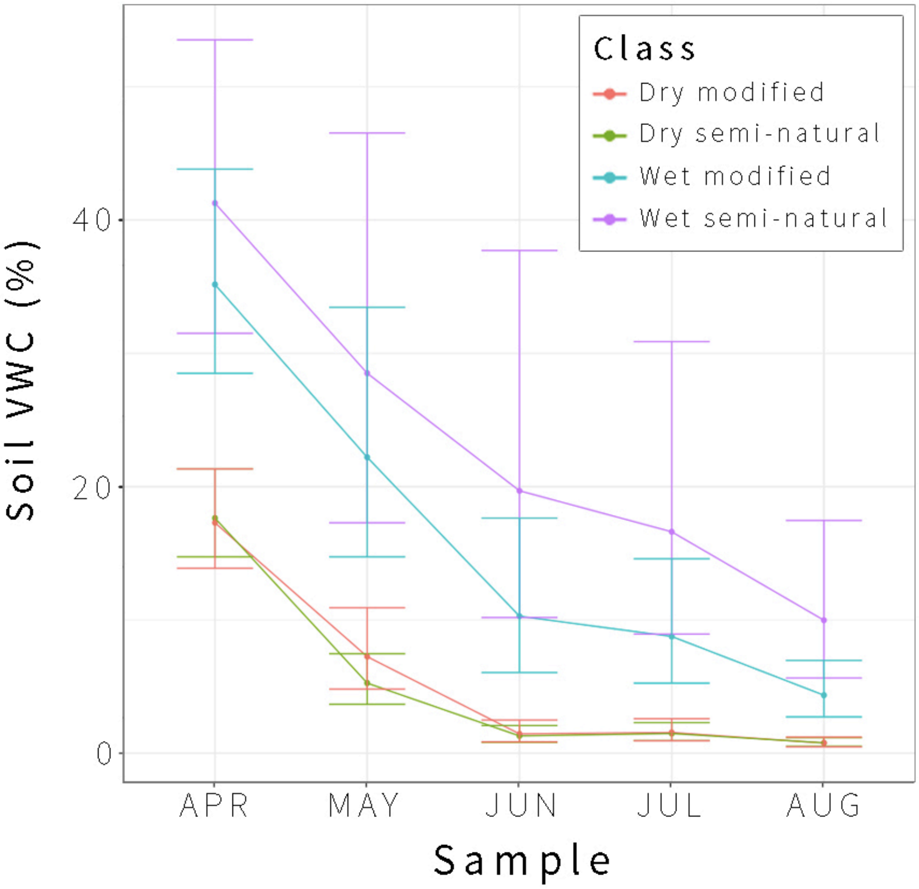

Figure 2. Mean soil moisture across each site class from April through August, shown with 95% confidence intervals (LMM estimates). Soil moisture was estimated as volumetric water content (%VWC), a ratio of water to soil (m^3/m^3), using a TDR probe. All differences in wet vs dry site conditions are significant at p=<0.001–0.001. Model formula: logSM ~ Class, random = ~1|Site/Transect (separate models fit for each sample period).

The onset of seasonal drought is exhibited by diminishing soil moisture across all site conditions (Fig.2). Dry semi-natural and dry modified sites declined to 1.5 ±1.5% VWC by June, with similarly low soil moisture conditions sustained throughout the rest of the growing season. Wet semi-natural sites sustained relatively high soil moisture, declining from 20.6 ±1.1% VWC in June to 10.6 ±1.2% VWC in August. Wet modified sites were comparatively dry yet significantly wetter than dry sites from June (10.9 ±1.5% VWC) until August (4.6 ±1.5% VWC).

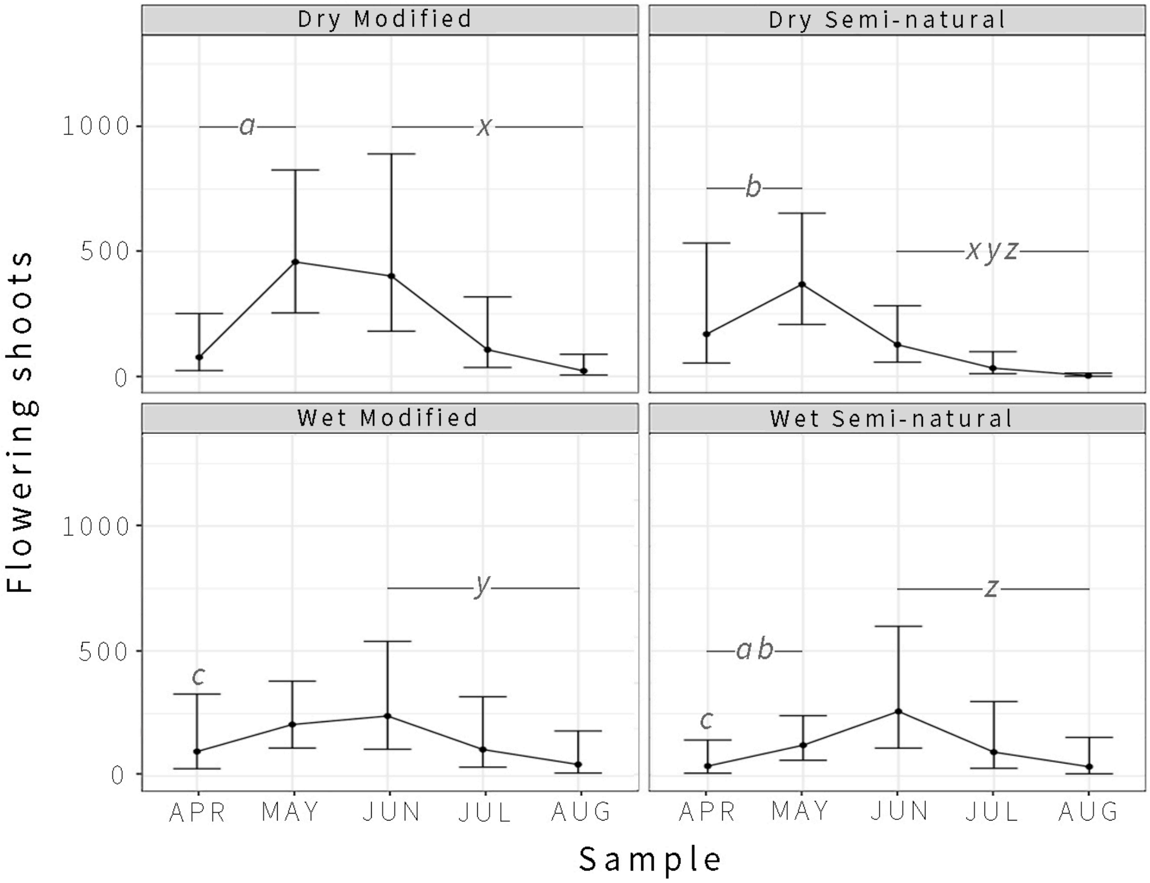

Figure 2. Mean Floral Resource Availability (FRA) across habitats and samples, with 95% confidence intervals (GLMM estimates). Significant differences between site conditions, both for independent samples and across sample ranges, are marked with letters (a is significantly different from a, b significantly different from b…). All differences significant at p=<0.001–0.02. Model formula: glmer.nb(Count ~ Class + (1|Site.ID) (separate models fit for each sample period).

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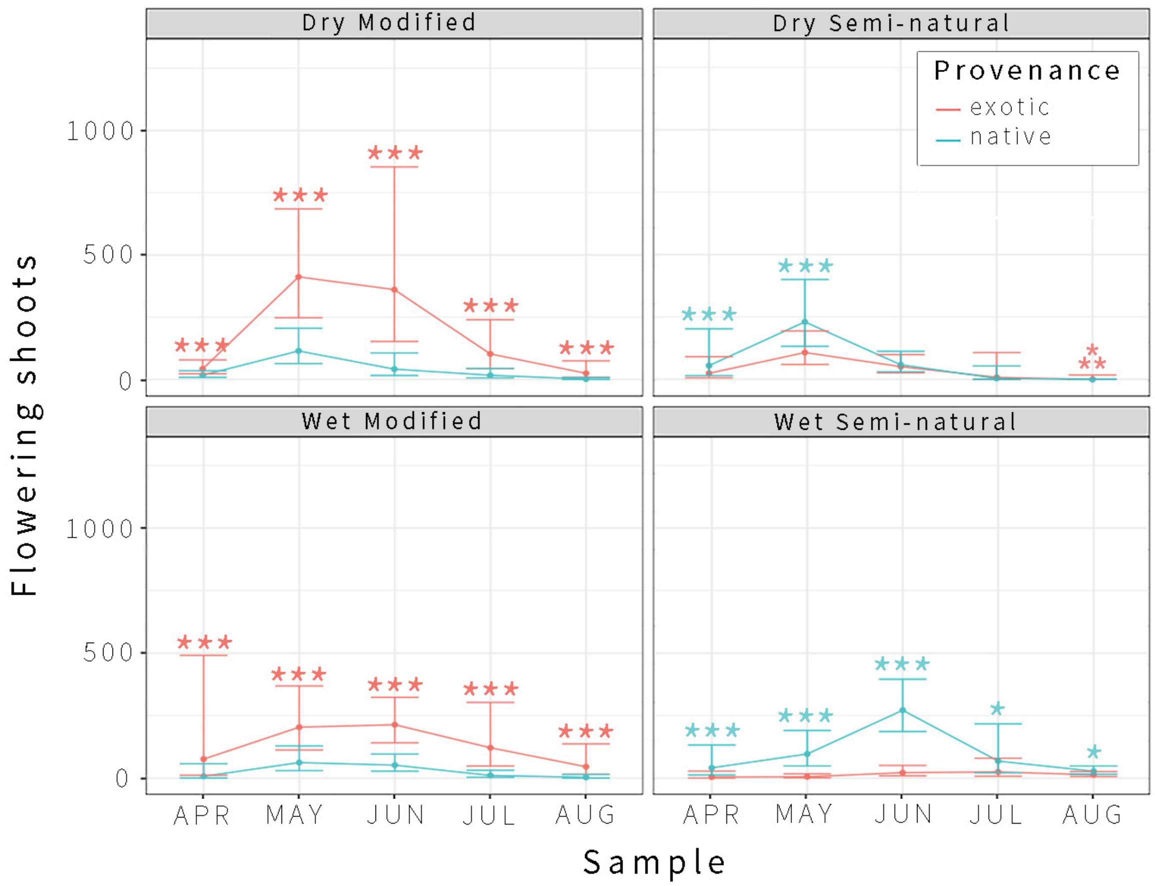

Figure 3. Mean FRA among native *vs* exotic plants across habitats and samples, with 95% confidence intervals (GLMM estimates). Asterisks indicate significant differences between native *vs* exotic FRA at * (*p*=<0.05) and *** (*p*=<0.001). ⁂ indicates significance could not be calculated because only exotic species are present. Model formula: glmer.nb(Count ~ Provenance + (1|Site) (separate models fit for each class and sample period).

Plant community phenology

Plant community phenology varied significantly across habitat types, resulting in distinct peaks and declines in Floral Resource Availability (FRA) over the course of the growing season (Fig.3). Soil moisture gradients were critical to these fluctuations, with FRA peaking early (in May) in dry semi-natural and dry modified habitats, supporting significantly more FRA than wet semi-natural habitats from April through May, and FRA peaking later (in June) in wet semi-natural and wet modified habitats. Both wet and disturbed conditions generally sustained FRA later into the season, with wet semi-natural, wet modified and dry modified habitats supporting significantly more FRA than dry semi-natural habitats from June through August. By August, significantly higher FRA was found in wet modified, wet semi-natural and dry modified habitats *vs* dry semi-natural environments, in rank order of abundance.

Disturbance was also a critical factor promoting FRA among exotic plants (Fig.4). The highest levels of FRA were found in dry modified environments in May and June, driven by the invasive Scotch broom (*Cytisus scoparius*). With decreasing soil moisture, FRA became increasingly concentrated among exotics, with significantly higher FRA found among exotic *vs* native plants overall from June through August. By August, FRA was greatest among exotic plants in most environments, with FRA among native plants diminishing to less than a quarter of the FRA found among exotics ($IRR_{FRA.EXO.}=0.23_{FRA.NAT.}$, p=<0.001), and FRA sampled exclusively among exotics in dry semi-natural habitats. Wet semi-natural habitats, by contrast, sustained significantly higher levels of FRA among native plants throughout the growing season ($IRR_{FRA.NAT.}=2.53_{FRA.EXO.}$, $p=0.05$).

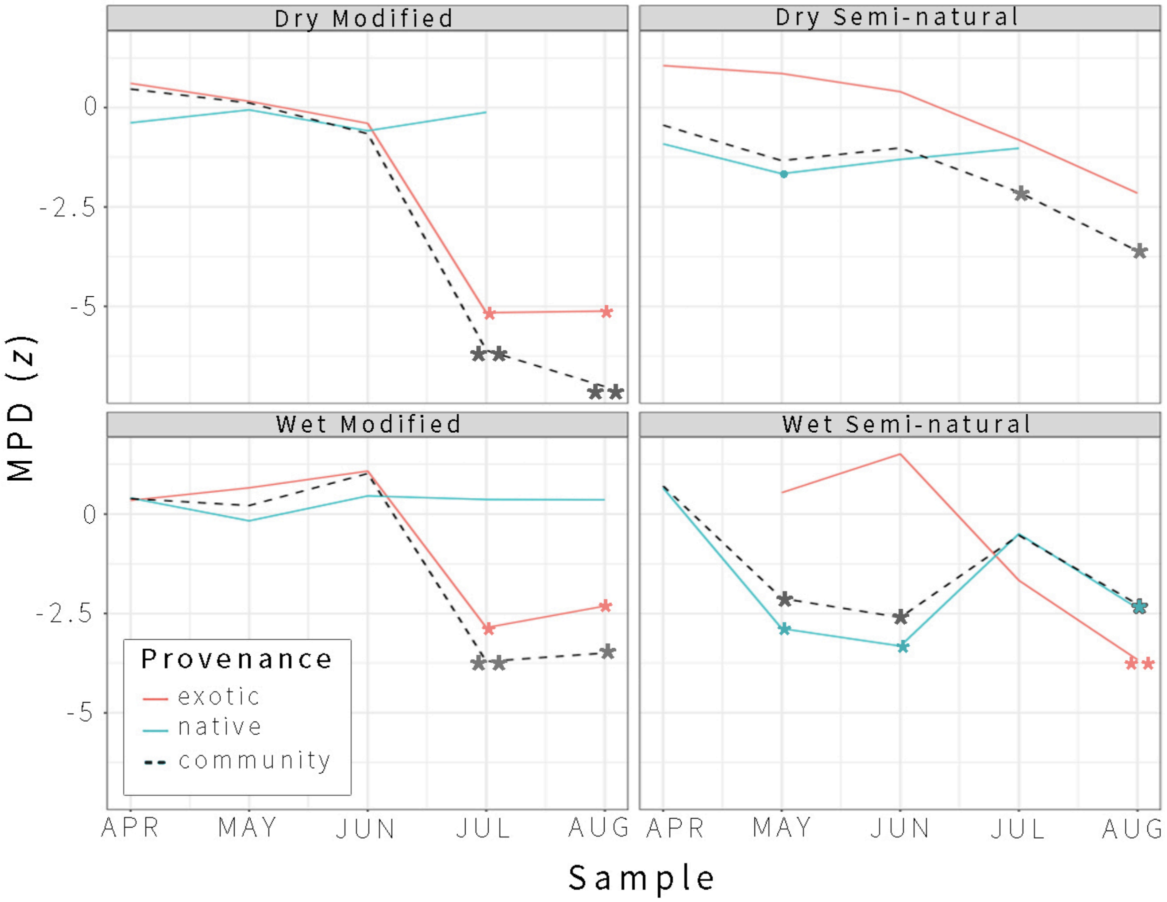

Figure 4. Standardized effect size of Mean Pairwise Distance (MPD *z*) calculated for native and exotic plant assemblages across site conditions and samples; negative values indicate increasingly clustered plant assemblages. Significance indicated at * (*p*=<0.05), and ** (*p*=<0.01); ⁂ indicates that significance could not be calculated, because only exotic species were present. A bullet (•) marks a near-significant clustering event (*p*=0.056).

Spatial and temporal niche dynamics

We found patterns of phylogenetic clustering in plant community phenology at multiple scales, from the community to the transect level, which coincided with major flowering events across the landscape. Here, we provide an overview of these patterns, with a focus on significant clustering seen at the community scale (Fig.5). Approximately 90% of the FRA sampled during this study was found among 12 orders of flowering plants (Table 1). Major flowering events coincided with significant clustering among dominant plant families in these clades, representing overlaps in the temporal niche breadth of related native and exotic plant species within different site conditions.

In May, peak flowering in dry semi-natural environments coincided with near significant clustering among native plants (z= -1.7162413, p=0.056), with FRA concentrated among members of the Boraginaceae, Caryophyllaceae, Montiaceae, Phrymaceae, Plantaginaceae, Lamiaceae, and Fabaceae. While community-level clustering in May was near significant only among native species, significantly clustered transects included related native and exotic plants, the majority of which were herbaceous annuals. However, there was marked divergence in life history between native and exotic Fabaceae, with the invasive perennial shrubs Scotch broom and gorse (*Ulex europaeus*) blooming among related native and exotic annual herbs—especially in disturbed environments.

Peak flowering in wet semi-natural environments coincided with significant clustering among native perennial Ericaceae and Primulaceae in May (z= -2.7192367, p=0.02) and June (z = -2.5618528, p=0.04). Few exotic species flowered in wet semi-natural environments throughout the early and midseason. However, by August, significant clustering was found among exotic biennial and perennial herbs in the Asteraceae in this site condition, as well as among native perennial herbs in the Lamiaceae and Plantaginaceae.

By the late season, the landscape was dominated by the Asteraceae. Across all site conditions, significant clustering coincided with high mean FRA in this plant family, including both native and exotic species, with the highest degree of clustering exhibited in dry modified environs in August (z= -7.2641540, p=< 0.01). Through July and August, within the Asteraceae, perennial herbs were the most diverse PFT, flowering most abundantly across the landscape; annuals, biennials, and pauciennials comprised relatively marginal FRA within this family. In dry semi-natural environments, the only plants flowering in August were exotic members of the Asteraceae: the herbaceous biennial bull thistle (*Cirsium vulgare*) and herbaceous perennial hairy cat's-ear (*Hypochaeris radicata*). Figure 4 provides an overview of the relative abundance of PFTs across site conditions (see Appendix B for detailed analysis of the proportional representation of PFTs within families.)

Table 1. Mean observed soil Volumetric Water Content (%VWC), with standard errors, and mean Floral Resource Availability (FRA) for plant orders exhibiting significant clustering in transects (GLMM estimates). Orders are summarized by family, species richness (native:exotic), their overall (%) contributions to FRA across the landscape, and the number of transects (*n*) within which taxa are clustered. The timing of significant clustering events in transects, and families implicated, are marked with an asterisk *. Two asterisks ** indicate significant clustering at the community level. Mean observed soil VWC reflects the temporal and spatial niche breadth of each clade, with higher values associated with early flowering phenology and wetter environs, and lower levels associated with late phenology and drier environs. See Appendix B for more details.

						Mean FRA				
Order	Family	N:E	% FRA	*n*	%VWC	April	May	June	July	August
Asterales	Asteraceae*	12:26	18	133	4.6 ±0.9	*15	14	*52	**54	**76
Boraginales	Boraginaceae*	3:4	6	8	10.3 ±2.3	*6	*60	*12	4	<1
Brassicales	Brassicaceae* Tropaeolaceae*	2:12	3	7	20.7 ±5	*45	*7	*2	2	<1
Caryophyllales	Caryophyllaceae* Droseraceae Montiaceae* Plumbaginaceae Polygonaceae*	12:7	6	12	10.6 ±2.3	*30	*33	*13	6	<1
Dipsacales	Caprifoliaceae*	5:0	3	1	4.9 ±2.2	2	5	*5	1	
Ericales	Ericaceae* Polemoniaceae Primulaceae*	13:0	8	10	8.0 ±1.8	4	**12	**19	8	<1
Fabales	Fabaceae*	9:14	29	36	6.4 ±1.3	2	*83	*55	*5	*<1
Geraniales	Geraniaceae*	0:5	1	5	7.0 ±1.5	2	*17	*12	3	<1
Lamiales	Phrymaceae* Plantaginaceae* Lamiaceae* Lentibulariaceae* Orobanchaceae* Scrophulariaceae*	16:18	7	21	10.3 ±2.3	*18	*41	*23	*12	**2
Liliales	Liliaceae* Melanthiaceae	3:2	<1	1	12.7 ±5.1	*2	3	1	<1	
Myrtales	Onagraceae*	7:0	<1	2	5.4 ±1.7		*4	3	2	<1
Rosales	Crassulaceae Grossulariaceae Rhamnaceae Rosaceae*	15:10	8	5	6.6 ±1.5	6	*37	*27	*6	1

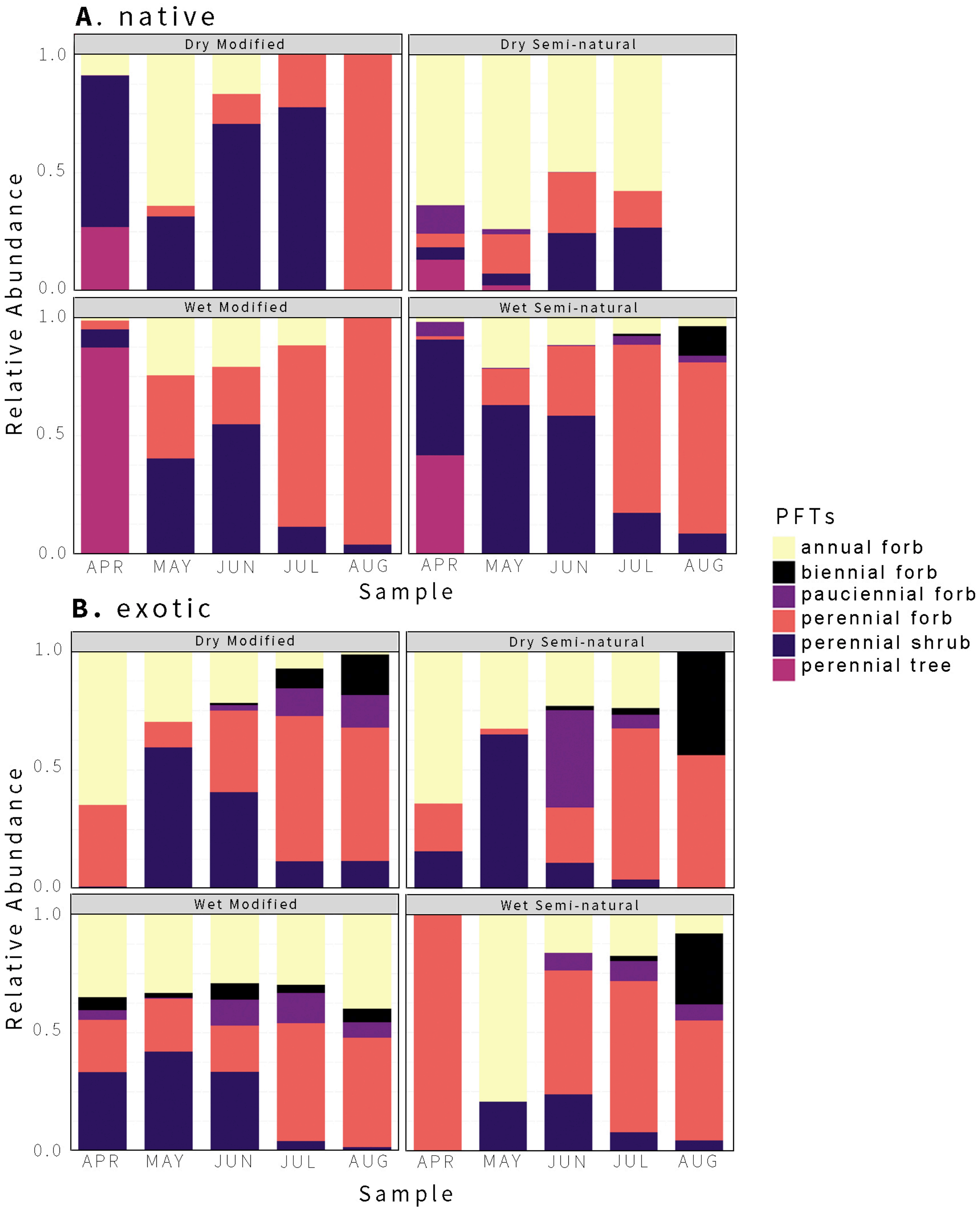

Figure 5. Proportional floral resource availability by plant functional type, contrasting (**A**) native and (**B**) exotic plants, for each sample and site condition.

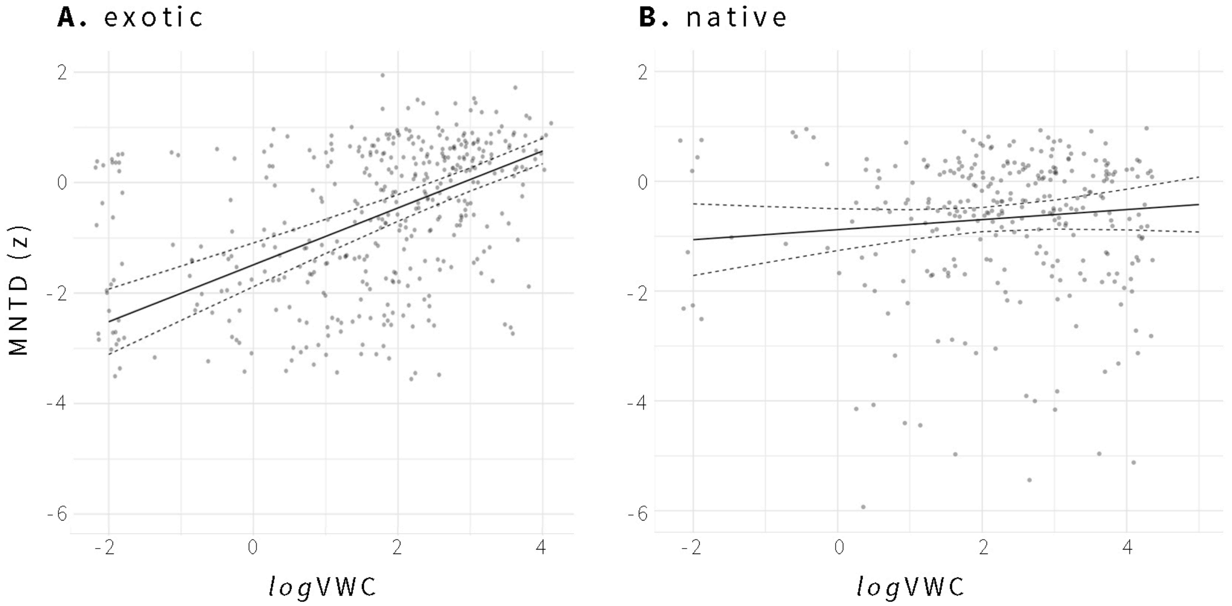

Figure 6. Standardized effect size of the phylogenetic metric mean nearest taxon distance (MNTD), calculated for transects, regressed against log transformed soil volumetric water content (logVWC) (GLMM). Model formula: lme(MNTD.z ~ logVWC, random = ~1 + logSM |Site/Transect).

Relationship between phylogenetic patterns and environmental variables

Regressing the standardized effect size (*z*) of observed transect-level MNTD against *log*VWC showed significant phylogenetic clustering among exotic plants as a function of diminishing soil moisture (Fig.7). This relationship is significant when all taxa are pooled, including both native and non-native species ($IRR_{log\text{VWC}}$=0.30, CI=0.19–0.42, *p*=<0.001, R_2=0.131), yet is strongest when the exotic cohort of flowering plants is isolated ($IRR_{log\text{VWC}}$=0.52, CI =0.41–0.62, *p*=<0.001, R_2=0.256). The Asteraceae are largely responsible for this effect, as a highly diverse family that flowered prolifically throughout the late season (Table 1). The Fabaceae also contributed to the effect, however, because this family is represented by a high diversity of early- and late-blooming species spanning both dry and wet environments, the effect is comparatively muted, with significant clustering occurring across low and high soil moisture conditions (Table 1).

The relationship between phylogenetic clustering and soil moisture availability was not found when native plants were isolated for modelling (IRR_{logVWC}=0.09, CI =-0.06–0.24, *p*=0.24, marginal R_2=0.004). This is explained by the broad niche breadth of dominant families of native plants, which bloom widely across the soil moisture gradient (*e.g.,* Ericaceae, represented by *Arbutus* and *Arctostaphylos* in dry environs, *Gaultheria, Lysimachia* and *Vaccinium* in mesic to moist environs, and *Kalmia, Rhododendron, Vaccinium* and *Lysimachia* in wet environs, Appendix B). Disturbance was not a significant predictor of phylogenetic clustering in models, though it remained a significant factor predicting the abundance of exotic species on the landscape, with greater FRA among exotics under high ($IRR_{H.DIST.}$=$3.31_{L.DIST.}$, *p*=<0.001) and moderate levels of disturbance ($IRR_{M.DIST.}$=$1.8_{L.DIST.}$, *p*=0.02), as compared with conditions of low disturbance. Disturbed site conditions also exhibited greater community-level clustering than undisturbed site conditions in the late season (Fig.5).

Discussion

Environmental filtering is a widespread process driving patterns of functional niche occupancy across plant communities (Li et al. 2018). Our results provide evidence for the spatial and temporal dimensions of this process in a semi-arid ecosystem, consistent with a growing body of empirical evidence demonstrating the physiological basis of eco-hydrological niche segregation (Araya et al. 2011, Schwinning & Kelly 2013, Silvertown et al. 2015). As reported for other semi-arid ecosystems (*e.g.,* Pérez-Camacho et al. 2012, Schwinning & Kelly 2013), we found that the relative drought avoidance of annuals and drought tolerance of perennials was reflected in the phenological response of plant communities to local fluctuations in soil moisture. Annuals tended to bloom early, especially in dry environments. Perennials were less restricted in their phenology, blooming early, but also later and longer into the growing season, especially in wet environments. Life history was to a large extent conserved within dominant plant families, which tended to exhibit similar phenology depending on local site conditions, occupying distinct temporal niches across soil moisture gradients. These dynamics reflect the principles of phylogenetic niche conservatism, as major flowering events coincided with clustering among related plants sharing similar life history and inferred environmental tolerances.

Eco-evolutionary theory predicts these nested spatial and temporal patterns, as taxa are regionally expected to be filtered into habitats based on the phylogenetic distribution of adaptive traits, and then to further segregate into niches based on competing processes of habitat filtering *vs* competition among similar species at the community scale (Webb et al. 2002). In this water-limited system, soil moisture regimes are recognized as the primary (spatial) niche axis around which habitat filtration acts, with communities of dry-adapted plants establishing in moisture-shedding sites and wet-adapted plants establishing in moisture-receiving sites (MacKinnon et al. 1992, Klassen et al. 2015). Within communities, a secondary (temporal) niche axis may be recognized in seasonal fluctuations of soil moisture availability. Under this schema, soil moisture availability locally varies through time, placing abiotic constraints on the phenology of plant communities. Depending on the differential response of plant functional types to these changing conditions, plants become segregated into temporal niches (*e.g.,* Araya et al. 2011, Schwinning & Kelly 2013). To the extent that life history is conserved within clades, these temporal niches are defined by patterns of phylogenetic clustering.

Environmental filtering was the dominant community assembly process reflected in the phylogenetic structure of temporal niches, with significant clustering coinciding with major flowering events. However, there were instances of divergence in plant functional types within families, which in some cases suggests effects of limiting similarity (*e.g.,* Gause 1932, MacArthur & Levins 1967, Mayfield & Levine 2010). For example, the exotic perennial shrubs *Cytisus scoparius* and *Ulex europaeus* bloomed alongside related annual herbaceous Fabaceae within dry site conditions, a community structure that could facilitate more efficient community water use (Rodriguez-Iturbe et al. 1999, Schwinning & Kelly 2013). In other cases divergence in plant functional types coincided with temporal and spatial niche segregation of related families—as, for example, among the Lamiales, which bloomed early in dry semi-natural environments, mostly as annual herbaceous species in the Phrymaceae and Plantaginaceae, and later as perennial herbaceous Lamiaceae and Plantaginaceae, predominantly in wet semi-natural environments. Similarly, members of the Fabaceae bloomed early, primarily as annuals in dry semi-natural environs, and later as perennials (*e.g., Trifolium repens* L.) in wet modified environs. These patterns suggest that though environmental filtering was a dominant process it did not necessarily preclude effects of limiting similarity in these systems. More importantly, however, they illustrate how competing community assembly processes may sometimes coincide, or become confounded, on different spatial and temporal scales.

Previous research in this region by Marx et al. (2016) revealed evidence for both phylogenetic similarity (environmental filtering) and functional trait distinctiveness (limiting similarity) as factors important to the success of invading plant species in this semi-arid island archipelago. On small islands the authors found that non-native plants tended to be more phylogenetically and functionally similar to the native host community, suggesting that, at this scale, environmental filtering due to strong abiotic pressures was the dominant community assembly process. Yet as island size increased, landscapes became more heterogenous, resulting in increasingly complex abiotic and biotic interactions, with related native and non-native species exhibiting greater disparity in functional traits (Marx et al. 2016). Our study provides further insight into this archipelago scale analysis, demonstrating how habitat diversity at the scale of an island can confound effects of environmental filtering and limiting similarity observed at larger spatial scales, which may not be clear unless temporal niche dynamics are analyzed.

Phylogenetic restriction of plant invasion under conditions of drought stress

A high diversity of plants flowered in the early season in this system, when soil moisture levels were highest. However, diversity declined as a function of decreasing soil moisture. The late season temporal niche was dominated by both native and exotic members of the Asteraceae. Significant clustering coincided with high floral resource availability, particularly among late-flowering exotic members of the family, driving the effect of increasing phylogenetic clustering under conditions of increasing drought stress.

Dispersal by wind, summer flowering, and long-flowering are traits known to contribute to invasion success in semi-arid ecosystems (Lloret et al. 2005), and are typical of regionally occurring members of the Asteraceae (Funk et al. 2009). As predicted, native and non-native members of this family shared the same late season phenology, though both cohorts were highly diverse in life history, represented across the spectrum of plant functional types. These results indicate that traits other than life history are likely associated with drought tolerance in the Asteraceae, such as the high levels of fructan concentrated as primary storage carbohydrates in this clade (Livingston et al. 2009). That said, annuals were most abundant in disturbed environments where certain species (*e.g., Senecio sylvaticus* L.) are known to be constrained as early successional species within a limited time-space niche (West & Chilcote 1968). Yet within dry and wet semi-natural environments, where exotic members of the family may rightly be considered invasive, non-native Asteraceae were represented predominately by biennials and perennials.

In this study, the late flowering of exotic biennial and perennial Asteraceae (*e.g., Cirsium, Hypochaeris*, *Senecio*) in both dry and wet semi-natural environments suggests that, within this clade, perennial life history is an adaptive trait supporting plant invasion in undisturbed drought-stressed environment. These findings provide counter-evidence to predictions that late season drought might limit invasion probabilities under conditions of drought stress (Alpert et al. 2000, Wolkovich & Cleland 2014), suggesting that life history may be a predictor of invasion success in the late season, especially insofar as life history traits are shared among related native and exotic drought-tolerant species. While this observational study only shows correlations between plant community phenology and seasonal fluctuations in soil moisture during one year of field work, patterns are consistent with the literature and robust beyond the duration of this study (Simon 2020, unpublished data). Future research should consider a more robust suite of quantitative functional traits in relation to soil moisture gradients, to resolve a better understanding of temporal niche dynamics in this system.

Figure 7. *Hypochaeris radicata* blooming prolifically across slopes host to a diverse community of native annual herbaceous species. November 3, 2019, Galiano Island, BC, Canada.

Implications for plant-pollinator communities

Phylogenetic clustering among dominant clades of flowering plants coincided with major flowering events in this system, underlying dramatic seasonal fluctuations in floral resource availability across the foraging landscape. These patterns are consistent with what might be expected given the effects of environmental filtering in water-limited environments, and have important ecological implications for the future of plant-pollinator communities in these systems.

In the absence of major anthropogenic disturbance events, soil moisture gradients were likely crucial in shaping plant-pollinator interactions across the foraging landscapes of the past, particularly for insects having annual colony cycles such as bumble bees (*Bombus* spp.) which depend on the availability of floral resources throughout the early and late season (Williams et al. 2012, Rundlöf et al. 2014). However, since the mid 1800s, disturbances associated with European colonization have altered these ecosystems, with changing predator-prey dynamics resulting in increased deer browsing pressures, and land conversion resulting in habitat loss and the introduction of a high diversity of exotic plants (Martin et al. 2011, Marx et al. 2016). Promoted by disturbance, exotic plants now contribute a significant proportion of floral resources in this system. Research has suggested that urban gardens and agricultural systems supporting a diversity of mass-flowering plants in the late season may be more important than "unimproved" semi-natural habitats in sustaining bee species under conditions of drought (Wray & Elle 2015). However, the results of this study show that the phylogenetic restriction of plant invasion in drought-stressed environments has resulted in a concentration of late season floral resources among exotic Asteraceae. The proliferation of this clade may have had numerous consequences for plant-pollinator networks historically, potentially benefiting generalist pollinator species, or conversely favouring specialists with narrower foraging requirements (Minckley et al. 2013, Thomson 2016).

Based on the patterns documented in this study, several predictions can be made concerning the temporal niche dynamics of these communities under future climate scenarios. Given forecasted increases in the intensity and severity of drought, drought-tolerant families such as the Asteraceae are likely to expand in this system, especially with increasing anthropogenic disturbance. Members of this family, such as *Hypochaeris radicata*, have been observed blooming late in dry semi-natural environments, well after the period of summer drought (Fig.8). Hence, this species, which is capable of vegetative reproduction (Doi et al. 2006), might also be expected to benefit from priority effects (Wolkovich & Cleland 2014).

Similar exotic perennials may be expected to increase in abundance under favourable winter moisture regimes, which could result in competitive exclusion of annual herbaceous species. Furthermore, in this study, wetlands were host to a low diversity of exotic (entomophilous) plants yet hosted several exotic biennial and perennial Asteraceae in the late season, particularly on the drier margins of these habitats. Given this pattern, microtopographic rises in wetlands may become increasingly prone to invasion with increasing drought stress. This effect, coinciding with the restricting effects of drought stress on native perennial shrub communities (Pérez-Camacho et al. 2012), could lead to shifts in the quantity and quality of floral resources in these environments. All of the above changes could result in decreasing diversity and overall changes in the composition of plant-pollinator communities, calling on ecologists and land managers to monitor the temporal niche dynamics of drought-stressed environments.

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Chapter III.

Bumble bee (*Bombus* spp.) community response to seasonal drought in a semi-arid island ecosystem (Hymenoptera: Apidae)

***Bombus mixtus* Cresson, 1878**
on *Rubus armeniacus* Focke
Photograph by Kevin Toomer
June 1, 2018

The third person plural voice is adopted in the following chapter, which has been prepared as an independent manuscript for publication.

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Chapter III.
Bumble bee (*Bombus* spp.) community response to seasonal drought in a semi-arid ecosystem (Hymenoptera: Apidae)

Abstract

Habitat loss threatens to exacerbate climate change impacts on pollinator communities, particularly in semi-arid ecosystems where late season floral resources are limited by seasonal drought. Yet while gardens have been found to supplement floral resources in semi-arid urban landscapes, less is known about the role of natural habitat diversity in sustaining late season floral resource availability. We investigated the importance of habitat diversity for bumble bees in a semi-arid ecosystem by observing flowering plant and bumble bee community response to seasonal drought across gradients of disturbance and soil moisture. Additionally, we tested the relative importance of natural *vs* modified matrix habitat for bumble bees in a landscape that remains relatively intact ecologically compared to those typically studied in pollinator research. In the late season we found that modified wet areas supported higher floral resource availability, and greater bumble bee worker abundances, as compared to dry semi-natural environments. Wetlands also supported higher levels of late season floral resources, and greater abundances of bumble bee workers, though the latter effect was not significant. Despite higher levels of late season floral resources in modified wet environments, modified matrix habitat was negatively associated, and natural matrix positively associated, with workers in June and late-flying queens in July and August. *Bombus vosnesenskii* Radoszkowski, 1862 was found to be most prevalent in disturbed habitats, consistent with trends seen elsewhere in the literature. The results of this study emphasize the importance of conserving natural habitat diversity in efforts to promote the resilience of pollinator communities.

Introduction

Climate change has been implicated in the worldwide decline of bumble bees (*Bombus* Latreille, 1802) as temperature and precipitation begin to exceed the historically observed tolerances of species, and some species ranges recede to higher latitudes and elevations (Kerr et al. 2015, Biella et al. 2017, Soroye et al. 2020). Numerous anthropogenic stressors, including habitat fragmentation and industrial agriculture, also threaten to exacerbate these effects (Szabo et al. 2012, Sanchez-Bayo & Goka 2014, Shackelford et al. 2018). In semi-arid ecosystems, climate change portends increasingly extreme winter precipitation events, and more intense, prolonged seasonal drought—factors likely to broadly affect species ranges and interspecific dynamics (Dale et al. 2001, Hansen et al. 2001, Salathé et al. 2008, Spies et al. 2010). These changes may have numerous direct and indirect consequences for bumble bees and the plant communities upon which they depend (Minckley et al. 2013, Straka & Starzomski 2014, Hoiss et al. 2015, Thomson 2016).

Increasing drought may cause reductions in floral resources supporting pollinators, resulting in a lower proportion of flowers containing nectar, fewer flowers per inflorescence, and reduced floral richness in some communities (Phillips et al. 2018). Drought has also been found to advance flowering phenology among annual herbaceous plants (König et al. 2017), and to cause stress or reduced productivity among perennial shrubs (Pérez-Camacho et al. 2012). In turn, overall species diversity in plant-pollinator communities has been found to decline under conditions of drought stress (Hoiss et al. 2015). These effects could potentially benefit generalist pollinators such as bumble bees, or, conversely, promote specialists with narrower foraging requirements (Minckley et al. 2013). Drought has moreover been found to exacerbate effects of interspecific competition between honeybees (*Apis mellifera*) and bumble bees, reducing the foraging and reproductive success of native bumble bee populations (Thomson 2016).

Bumble bees are central place foragers limited by the availability of both nesting and foraging habitat. Compositionally diverse landscapes offering a mosaic of herbaceous and forested habitats are known to promote the availability of foraging and nesting resources, and in turn, greater bumble bee abundances (McFrederick & LeBuhn 2006, Kennedy et al. 2013, Jha et al. 2013, Wray & Elle 2015). From the bumble bee perspective, beneficial habitat diversity might include semi-natural woodlands and wetlands, as well as gardens and utility rights-of-way (Morón et al. 2014, Hill & Bartromeus 2016, Vickruck et al. 2019). Indeed, researchers have suggested that urban gardens and agricultural systems supporting a diversity of mass-flowering plants in the late season may be more important than "unimproved" semi-natural habitats in sustaining bumble bees, particularly in drought-prone environments (McFrederick & Lebuhn 2006, Heard et al. 2007, Wray & Elle 2015).

Research has tended to contrast agricultural and urban habitats with only one alternative semi-natural habitat type—generally in the context of highly fragmented landscapes (*e.g.*, Heard et al. 2007, Moroń et al. 2014, Wray & Elle 2015, Hill & Bartromeus 2016). Landscape heterogeneity, however, gives rise to a gradient of environments which may provide important foraging habitat over the course of the growing season. While gardens provide important late season foraging habitat in urban landscapes, natural habitats such as wetlands may also support late season floral resources and thereby serve a similar function in more ecologically intact environments. Certain bumble bee species may also be favoured by semi-natural habitats, while others exhibit greater affinities for disturbed areas. On the northwest coast of North America, for example, *Bombus vosnesenkskii* Radoszkowski, 1862 (yellow-headed bumble bee) has expanded its range in recent decades, becoming a dominant species in urban environments, where other species, such as *Bombus occidentalis* Greene, 1858 (western bumble bee) and *Bombus sitkensis* Nylander, 1848 (Sitka bumble bee), have been observed to decline (McFrederick & LeBuhn 2006, Colla & Ratti 2010).

We investigated the importance of habitat diversity for bumble bees in a semi-arid ecosystem, by observing flowering plant and bumble bee community response to seasonal drought across gradients of disturbance and soil moisture. We predicted that dry semi-natural habitats such as woodlands would host less floral resources and, in turn, fewer bumble bee workers than other habitat types during seasonal drought. Conversely, we predicted that modified wet habitats such as gardens, and wet semi-natural habitats such as wetlands, would support greater floral resources, and, in turn, greater worker abundances in the late season. Disturbance was predicted to promote late season floral resource availability among exotic plant species, with bumble bee workers expected to persist longer in disturbed environments both wet and dry. We also tested whether surrounding natural and modified matrix habitat influenced bumble bee abundances at the site level. Finally, we tested whether different habitat types favoured certain species, with *Bombus vosnesenskii* expected to be more prominent in disturbed environments.

Methods

Study area

Galiano Island lies in the rain shadow of the mountains of Vancouver Island and the Olympic Peninsula, in southern coastal British Columbia, Canada. This region is defined by its semi-arid climate, characterized by mild, wet winters and warm, dry summers (Klassen et al. 2015). The combined effects of low precipitation, warm temperatures, and a high number of sunshine hours result in an annual moisture deficit on Galiano Island from mid-June to early October, resulting in near drought conditions across the island's most exposed aspects (Harrison 1994). Global climate change simulations and regional climate models suggest that increases in winter precipitation (0.5–1.0mm/day) and the intensity and duration of summer drought are likely, along with more complex temperature-precipitation interactions (Christensen et al. 2007, Pike et al. 2008, Salathé et al. 2008, Spies et al. 2010).

Galiano Island is relatively intact ecologically, with about 24% of its land base conserved in protected areas, and a high percentage of forest cover, hosting vegetation communities typical of the Coastal Douglas-fir Biogeoclimatic Zone (Madrone 2008). Aside from some limited forestry, only ~11% of the landscape has been converted for present day human use (Madrone 2008, Shackelford et al. 2018). This study area thus presents a contrast with the fragmented environments previously studied by pollinator researchers in semi-arid ecosystems (*e.g.,* McFederick & LeBuhn 2005, Wray and Elle 2015).

Sampling

This study was based on a 2x2 factorial study design contrasting four extreme conditions of disturbance and soil moisture availability: 1) dry semi-natural environments (woodland and associated rock outcrop communities); 2) wet semi-natural environments (wetlands); 3) dry modified environments (disturbed upland areas such as clear-cuts and hydro-line corridors); and, 4) wet modified environments (gardens, orchards and fields). We selected sites representative of each condition based on available terrestrial ecosystem mapping data (Madrone 2008), randomly distributing 2x15m belt transects throughout 6 sites per site condition (total 24 sites) to estimate floral resource availability. Each site was allocated 6–8 transects, the number of transects scaled roughly in proportion to the area covered, with the aim of capturing variability in floral resources across the landscape. Counts of flowering shoots were estimated for each plant species at 1m intervals and soil moisture recorded at 5m intervals as volumetric water content (%VWC) using a Field Scout TDR probe. Sampling was conducted monthly over the course of 5 x 11-day sampling periods, from April through August, 2018.

To sample bumble bees, three blue vane traps (Stephen & Rao 2005) were placed at roughly equidistant intervals across each site. Traps were positioned to ensure their visibility given surrounding vegetation and landscape features, and to minimize public interference. Bumble bees captured by blue vane traps were pooled into one sample per site, resulting in 24 x 5 (120) samples divided into the four habitat types. Unfortunately, public interference in one dry semi-natural site resulted in the loss of a sample in May (n = 120 - 1 = 119). Furthermore, two vernally wet meadow sites initially stratified as wet semi-natural sites based on high levels of early season soil moisture proved to have a soil moisture regime and vegetation community more characteristic of dry semi-natural sites. These sites had to be reclassified, resulting in an imbalanced study design, with 4 sites representing the wet semi-natural condition *vs* 8 sites representing the dry semi-natural condition (Chapter II).

Terrestrial ecosystem mapping data were used to obtain estimates of land cover falling within a 500m buffer around each site, orienting around polygon centroids, including natural, modified, and forested matrix habitat. Additional environmental data were collected along transects, including estimates of canopy cover, slope, moss cover, coarse woody debris, and bare soil.

Modelling

Linear mixed effects models (LMMs) were fitted incorporating log-transformed soil volumetric water content (*logVWC*) as a response to contrasting habitat types (fixed effects), with transects nested within sites (random effects). To test differences in floral resource availability between habitat types, we fit negative binomial generalized linear mixed effects models (GLMMs) incorporating counts of flowering shoots as a response to contrasting habitat types (fixed effects) and transects nested within sites (random effects). Seven outliers representing extremely high counts of flowering shoots among the exotic *Cytisus scoparius* (L.) Link (Scotch broom) prevented model convergence and had to be removed. Negative binomial generalized linear mixed effects models (GLMMs) were also fitted to test differences in bumble bee abundances (counts) across habitats and sample periods, with habitat types incorporated as fixed effects and sites included as random effects. Additional environmental variables such as proportions of natural and modified matrix, forest cover, slope and moss cover were also included as predictors in models.

We tested differences in the total count of bumble bees sampled between habitat types for each sample period separately. Because our focus was on whether certain habitat types supported prolonged foraging under conditions of drought stress, we concentrated primarily on bumble bee worker abundances as a proxy for bumble bee foraging activity, though differences were also considered among drones and queens—especially late-flying queens, whose presence in the environment may be considered a proxy for the reproductive success of colonies. We fitted GLMs to test differences in the abundances of bumble bees within isolated sample periods. We also considered species abundances as a response to habitats and other environmental variables, both across sample periods (GLMMs) and within sample periods (GLMs). LMMs were implemented using the R package ‘nlme’ (Pinheiro et al. 2019); GLMs were implemented using the R package ‘MASS’ (Venables & Ripley 2002); and GLMMs implemented using ‘lme4’, and ‘glmmTMB’ in cases where zero-inflation proved problematic (Bates et al. 2015, Brooks et al. 2017). The best models were selected based on AIC test scores (R Core Team 2019), assuming ΔAIC of 2.0 as a threshold for model improvement (Burnham & Anderson 2002). Model effects are reported as Incidence Rate Ratios (IRR), and as marginal R^2 values (variance explained by fixed effects) where appropriate. Marginal effects were calculated using ‘sjPlot’ (Lüdecke 2018). Statistical analyses were implemented in R Version 3.6.0 (R Core Team 2019).

Results

Onset of seasonal drought

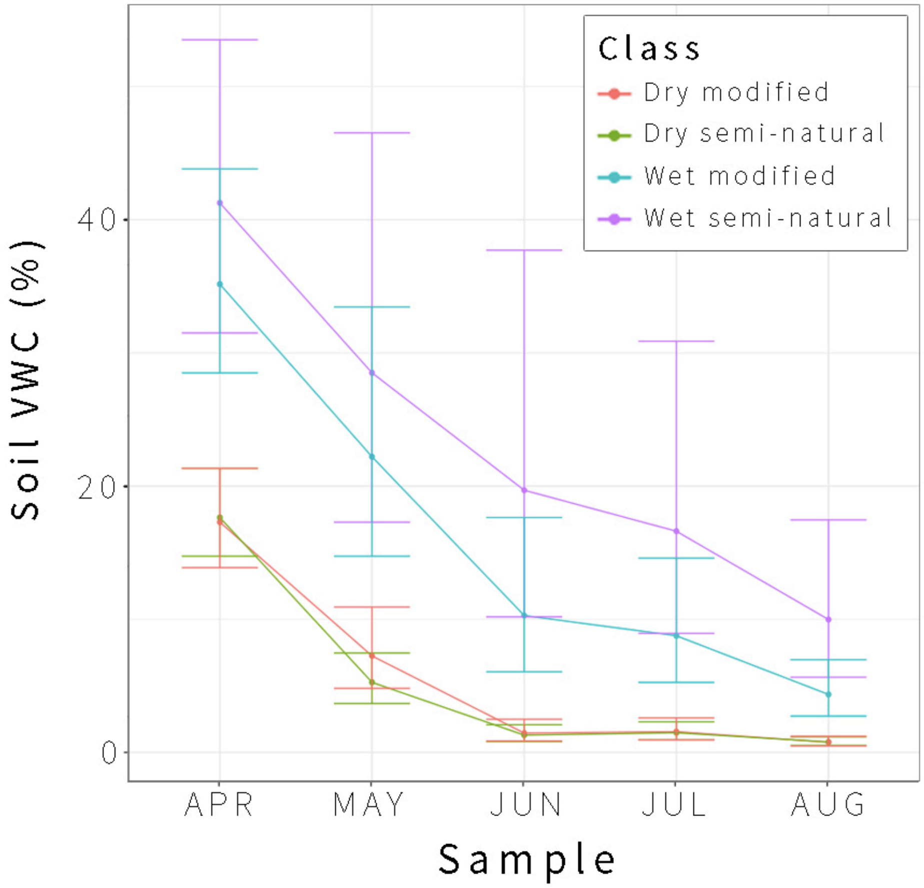

Figure 8. Mean soil moisture across each site class from April through August, shown with 95% confidence intervals (LMM estimates). Soil moisture was estimated as volumetric water content (%VWC), a ratio of water to soil (m^3/m^3), using a TDR probe. All differences in wet vs dry site conditions are significant at p=<0.001–0.001. Model formula: logSM ~ Class, random = ~1|Site/Transect (separate models fit for each sample period).

The onset of seasonal drought is exhibited by diminishing soil moisture across all habitats (Fig.9). Dry semi-natural and dry modified sites declined to 1.5 ±1.5% VWC by June, and had similarly low soil moisture conditions throughout the rest of the growing season. Wet semi-natural sites sustained relatively high soil moisture, declining from 20.6 ±1.1% VWC in June to

10.6 ±1.2% VWC in August. Wet modified sites were comparatively dry yet significantly wetter than dry sites from June (10.9 ±1.5% VWC) until August (4.6 ±1.5% VWC).

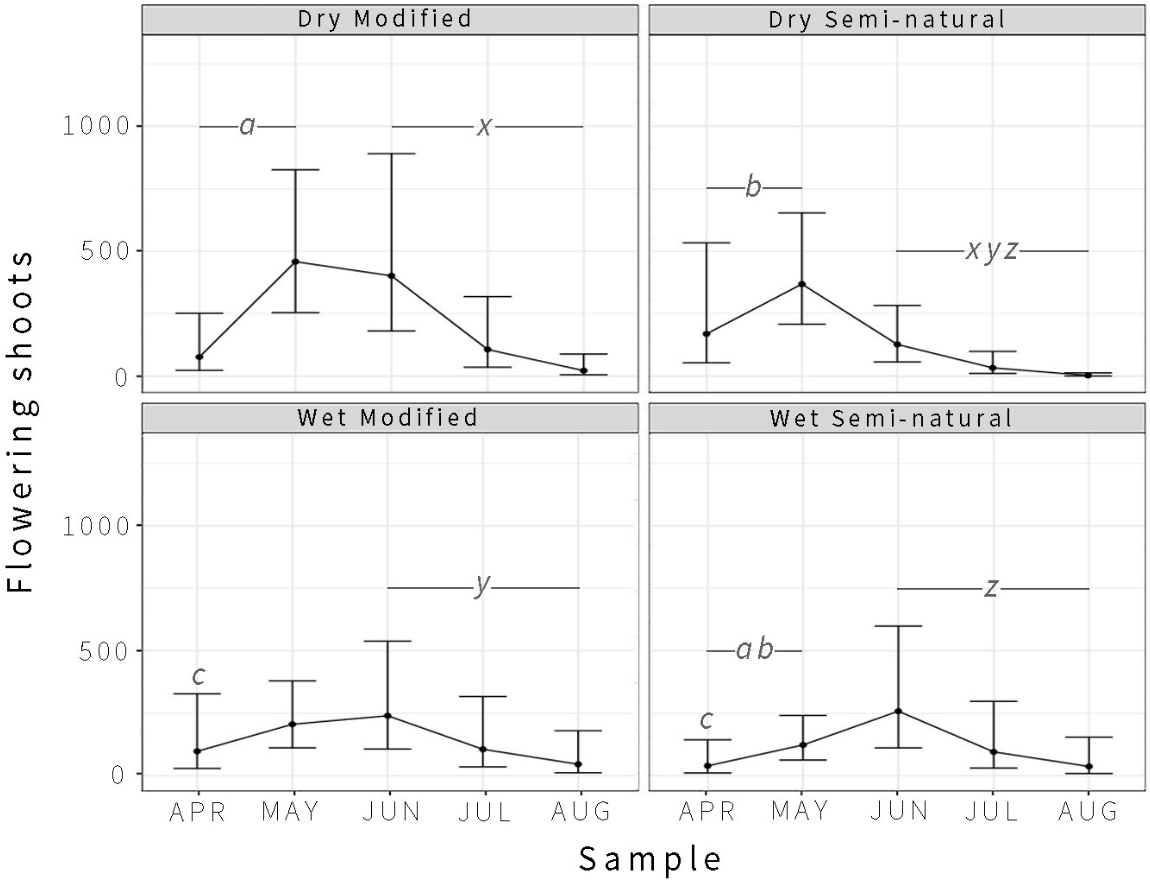

Figure 9. Mean Floral Resource Availability (FRA) across habitats and samples, with 95% confidence intervals (GLMM estimates). Significant differences between site conditions, both for independent samples and across sample ranges, are marked with letters (*a* is significantly different from *a*, *b* significantly different from *b*…). All differences significant at *p*=<0.001–0.02. Model formula: glmer.nb(Count ~ Class + (1|Site.ID) (separate models fit for each sample period).

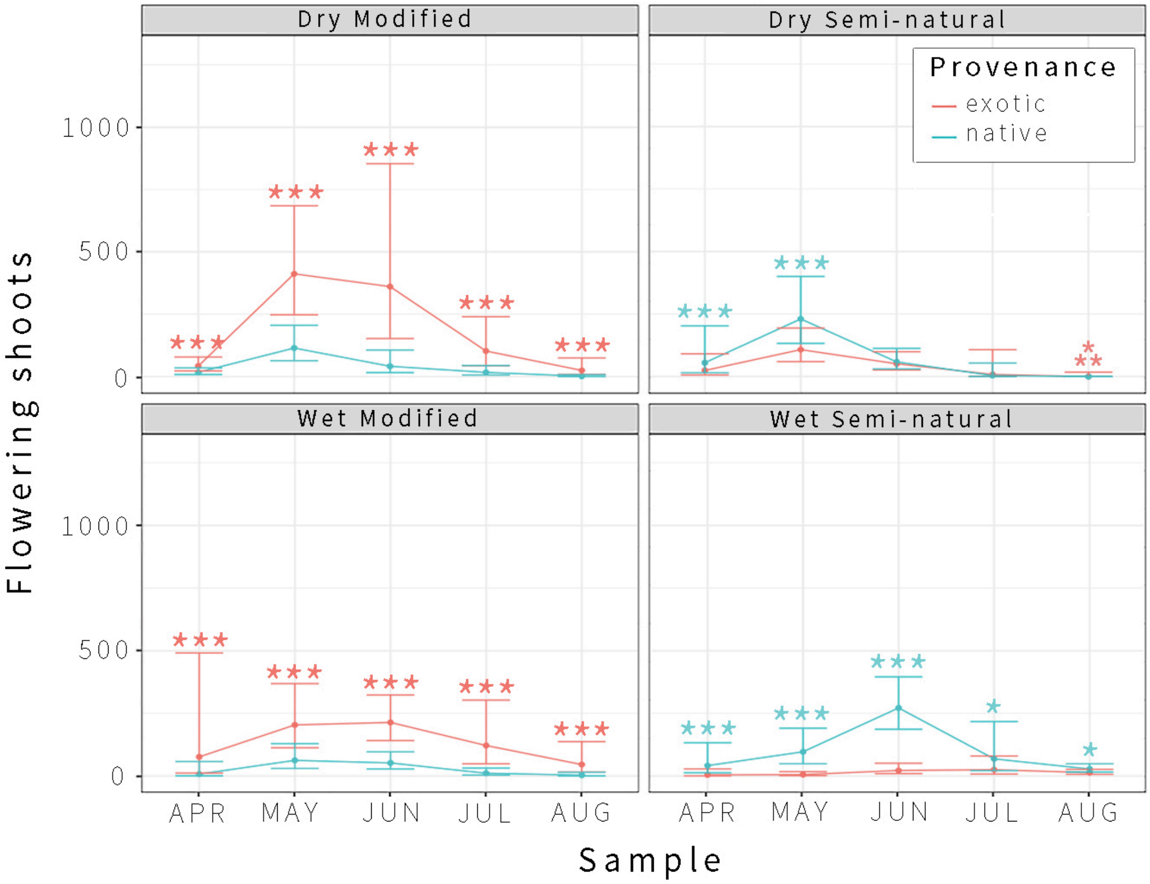

Figure 10. Mean FRA among native *vs* exotic plants across habitats and samples, with 95% confidence intervals (GLMM estimates). Asterisks indicate significant differences between native *vs* exotic FRA at * (p=<0.05) and *** (p=<0.001). ⁂ indicates significance could not be calculated because only exotic species are present. Model formula: glmer.nb(Count ~ Provenance + (1|Site) (separate models fit for each class and sample period).

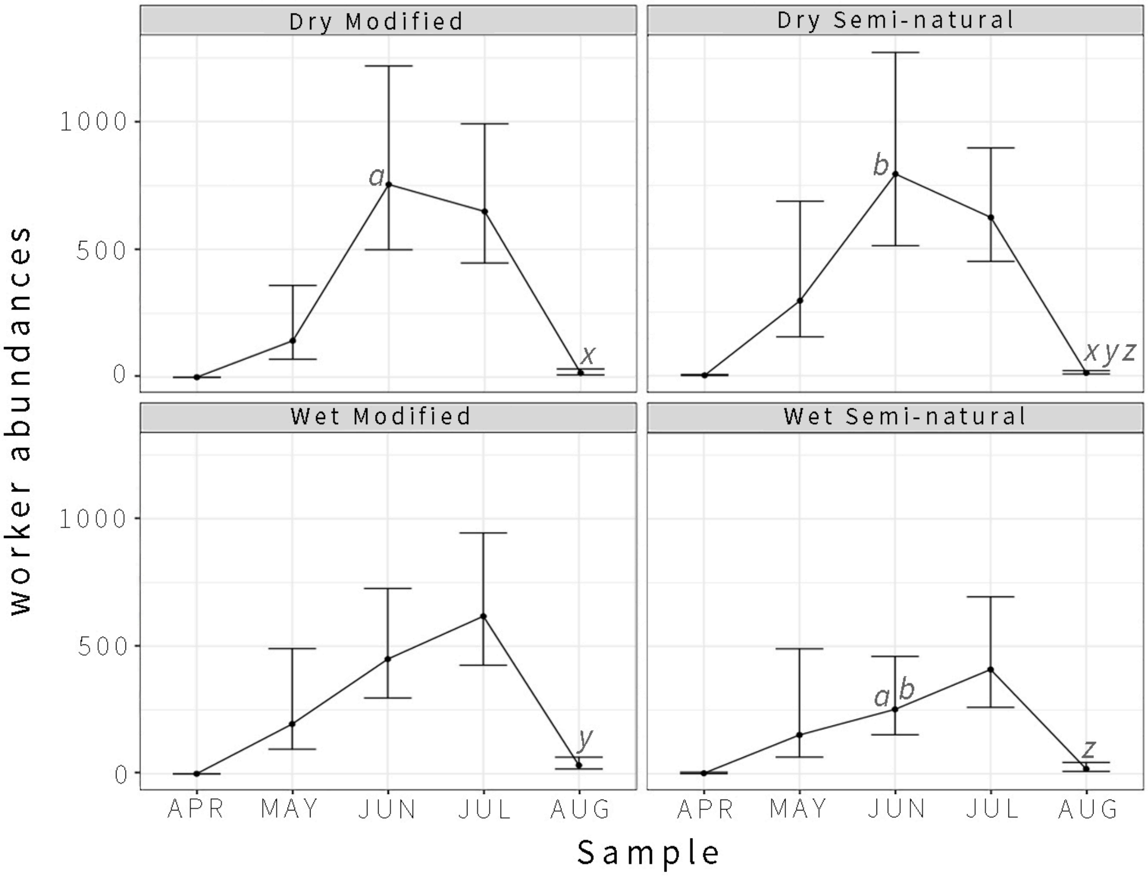

Figure 11. Mean bumble bee worker abundances across habitats and samples, with 95% confidence intervals (GLM estimates). Significant differences between site conditions are marked with letters (a is significantly different from a, b significantly different from b…). All differences significant at p=<0.01. For model predictions of bumble bee worker abundances in August, see Figure 13. Model formula: glm.nb(Bombus ~ Class) (separate models fit for each sample period).

The foraging landscape

Plant community phenology varied significantly across habitat types, resulting in distinct peaks and declines in Floral Resource Availability (FRA) over the course of the growing season (Fig.3). In dry semi-natural and dry modified habitats, FRA peaked early (in May), supporting significantly more FRA than wet semi-natural habitats from April through May. In wet semi-natural and wet modified habitats, FRA peaked later (in June). Both wet and disturbed conditions sustained FRA later into the season, with wet semi-natural, wet modified and dry modified habitats supporting significantly more FRA than dry semi-natural habitats from June through August. By August, significantly higher FRA was found in wet modified, wet semi-natural and dry modified habitats *vs* dry semi-natural environments, in rank order of abundance.

Disturbance was also a critical factor promoting Floral Resource Availability among exotic plants (Fig.4). The highest levels of FRA were found in dry modified environments in May and June, driven by the invasive *Cytisus scoparius* (L.) Link (Scotch broom). With decreasing soil moisture, FRA became increasingly concentrated among exotics, with significantly higher FRA found among exotic *vs* native plants overall from June through August. By August, exotic species pervaded most environments, with FRA among native plants diminishing to less than a quarter of the FRA found among exotics ($IRR_{FRA.EXO.}=0.23_{FRA.NAT.}$, p=<0.001), and FRA exclusively found among exotics in dry semi-natural habitats. Wet semi-natural habitats, by contrast, sustained significantly higher levels of FRA among native plants throughout the growing season ($IRR_{FRA.NAT.}=2.53_{FRA.EXO.}$, $p=0.05$).

Bumble bee abundances

There was no significant difference in bumble bee worker abundances among habitats from April through May as colonies were getting established. However, by the month of June, dry modified and dry semi-natural habitats hosted significantly more bumble bee workers than wet semi-natural habitats (Fig.12). In July bumble bee abundances declined in dry modified and semi-natural habitats, which continued to sustain similar bumble bee abundances. Meanwhile bumble bee abundances peaked in wet semi-natural and modified environments. However, no significant differences in bumble bee abundances were detected between habitats during this sample period. Finally, workers declined dramatically across all habitats by August (Fig.13). During this sampling period, wet modified habitats supported significantly more workers than dry semi-natural habitats ($IRR_{WET.M.}=3.07_{DRY.N.}$, $p=0.008$), which supported the fewest workers. Wet semi-natural and dry modified habitats also supported more workers than dry semi-natural habitats in August, though these differences were not significant (Fig.13).

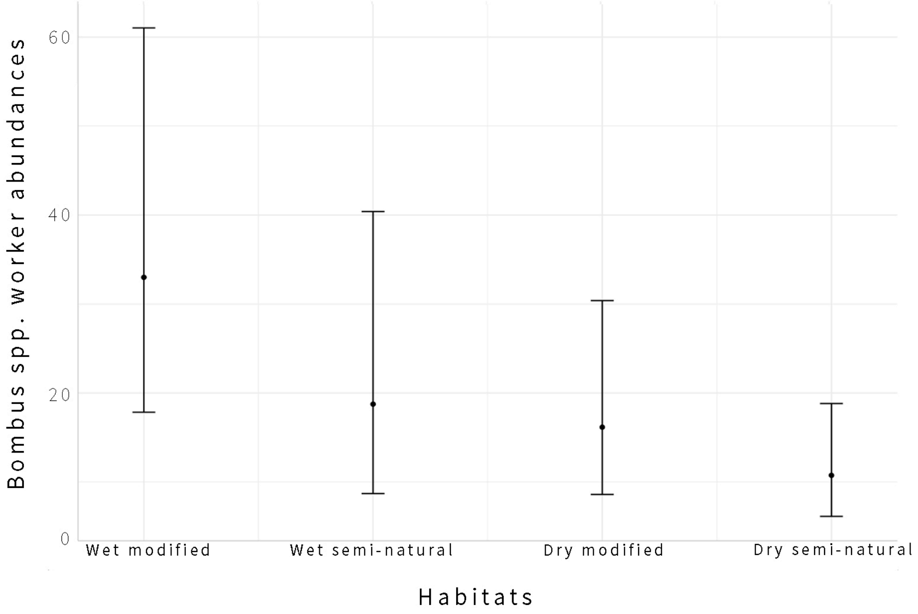

Figure 12. Mean worker abundances across habitat types in August, with 95% confidence intervals (GLM estimates). Model formula: glm.nb(Bombus ~ Class).

Environmental predictors of bumble bees across the landscape

In addition to floral resources, we tested the response of bumble bees across all habitats and sample periods, as well as the response of discrete species and castes, against several geospatial parameters and environmental variables known to be associated with foraging and nesting resources (Table 2). Table 3 summarizes important predictors of bumble bee abundances across the landscape.

Floral Resource Availability (FRA) was the only significant predictor of bumble bee abundances across all habitat types (Table 3). Although FRA was not a significant predictor of workers across all sample periods, FRA was a significant predictor of workers in May. Additionally, FRA was a significant predictor of late-flying queens (in July and August). Natural matrix habitat was a significant predictor of workers in June, and a significant predictor of late-flying queens. Conversely, modified matrix habitat was a significant negative predictor of workers in June, and a significant negative predictor of late-flying queens. No other terms were statistically important or otherwise improved model AIC scores in these analyses.

Table 2. Environmental variability across habitats. Mean and standard deviation are reported for: floral resource availability (counts of flowering shoots per 15x2m transect, averaged per site); land cover of sites within a 500m radius: natural area, and modified area (ha); and, site environmental parameters: slope, canopy cover, moss cover and coarse woody debris cover (%).

Habitat	FRA	Natural matrix	Modified matrix	Slope	Canopy cover	Moss cover	CWD cover
Dry modified	46 ±40	39.2 ±7.9	38.2 ±8.6	18 ±7	19 ±14	15 ±6	9 ±4
Dry semi-natural	26 ±31	41.7 ±20.1	14.4 ±10.9	51 ±22	55 ±19	23 ±11	10 ±5
Wet modified	39 ±29	43.8 ±12.5	34.0 ±12.7	8 ±3	18 ±12	4 ±4	2 ±4
Wet semi-natural	41 ±59	63.4 ±4.2	14.9 ±12.7	9 ±4	36 ±12	8 ±10	13 ±3

Species-specific responses

Six bumble bee species (*Bombus flavifrons* Cresson, 1863; *Bombus melanopygus* Nylander, 1848; *Bombus mixtus* Cresson, 1878; *Bombus sitkensis*; *Bombus vancouverensis* Cresson, 1878; and *B. vosnesenskii*) were captured in blue vane traps during this study, all of which were present throughout all four habitat types. Floral resource availability was a significant predictor of all bumble bee species abundances except *Bombus flavifrons*. Additional environmental variables were significant predictors of the abundances of *B. sitkensis* and *B. vosnesenskii* in particular.

Bombus sitkensis was a moderately abundant bumble bee species, sampled with ~60% the frequency of the most abundant species, *B. vancouverensis*, across all habitats ($\text{IRR}_{\text{B.SIT.}}=0.59_{\text{B.VAN.}}$, p=<0.001). *Bombus sitkensis* was significantly more abundant in wet semi-natural habitats *vs* dry modified habitats ($\text{IRR}_{\text{WET.N.}}=1.74_{\text{DRY.M.}}$, p=0.022) where this species was least abundant. Mean FRA was also a significant term predicting abundances of *B. sitkensis* (Table 3).

Bombus vosnesenskii was the least abundant bumble bee species sampled in this study—less than a third as abundant as *B. vancouverensis* ($\text{IRR}_{\text{B.VOS.}}=0.28_{\text{B.VAN.}}$, p = <0.001). This species occurred with greater frequency in dry modified habitats *vs* wet semi-natural habitats ($\text{IRR}_{\text{DRY.M}}=3.51_{\text{WET.N.}}$, p=<0.001), which hosted the fewest individuals of this species. Wet modified habitats also hosted significantly more *B. vosnesenskii* individuals than wet semi-natural habitats ($\text{IRR}_{\text{WET.M.}}=2.49_{\text{WET.N.}}$, p=0.046). Additionally, mean slope and FRA were significant predictors in the top model explaining *Bombus vosnesenskii*'s abundances in the environment (Table 3).

Table 3. Environmental predictors of bumble bee species abundances, summarized for top models. Model summaries include Incidence Rate Ratios, with 95% confidence intervals, and random effects variance for predictors of bumble bee abundances generally, as well as for a set of castes and species for which model terms proved significant (or otherwise improved model AIC scores). For GLMMs, R^2 values are presented as marginal values, adjusted based on random effects variances. For GLMs, pseudo (Nagelkerke) R^2 values are presented for significant terms.

Predictor	Model	Response	IRR	CI	*p*	σ^2	$\tau_{00\ \text{Site.ID}}$	ICC	*n* obs	R^2
Mean.FRA	GLMM*i*	*Bombus* spp.	1.28	1.05 – 1.56	0.015	1.04	0.04	0.04	301	0.062
	GLMM*ii*	*B. sitkensis*	1.17	1.04 – 1.33	0.012	0.80	0.00	—	115	0.063
	GLMM*iii*	*B. vosnesenskii*	1.46	1.27 – 1.67	<0.01	0.46	0.00	—	85	0.472
	GLMM*iv,v*	late-flying queens	1.28	1.11 – 1.48	0.001	0.30	0.05	0.13	48	0.231
	GLM*a*	workers (May)	1.78	0.97 – 3.27	0.021	—	—	—	23	0.298
Mean.slope	GLMM*iii*	*B. vosnesenskii*	1.51	1.16 – 1.96	0.002	0.46	0.00	—	85	0.472
Natural.matrix	GLMM*iv*	late-flying queens	1.27	1.05 – 1.53	0.013	0.30	0.05	0.13	48	0.231
	GLM*b*	workers (June)	5.24	1.50 –16.57	0.006	—	—	—	24	0.690
Modified.matrix	GLMM*v*	late-flying queens	0.79	0.65 – 0.95	0.013	0.30	0.05	0.13	48	0.231
	GLM*c*	workers (June)	0.19	0.06 – 0.67	0.006	—	—	—	24	0.690
Forest.matrix	GLMM*vi*	late-flying queens	1.27	1.05 – 1.52	0.011	0.31	0.03	0.09	48	0.231

Discussion

This study investigated the importance of habitat diversity in providing early and late season Floral Resource Availability (FRA) for bumble bees in a semi-arid ecosystem. As predicted, we found that disturbance and soil moisture were both critical factors influencing seasonal fluctuations in FRA across the foraging landscape, each habitat type exhibiting distinct peaks and declines in the floral resources available to support pollinators through the growing season. Early season FRA peaked in dry semi-natural and dry modified habitats, whereas late season FRA peaked and was sustained longer in wet modified and wet semi-natural habitats from June through August, as seasonal drought set into this system. Disturbance also promoted late season

FRA in modified habitats, which was concentrated among exotic plants, whereas in wetlands native plants supported the highest levels of FRA throughout the growing season.

Bumble bee abundances correlated with variability in Floral Resource Availability across habitats to a limited degree, with significant relationships found in only in a few cases. Floral resources were lowest in wet semi-natural habitats throughout the early season, and these habitats supported significantly fewer workers than other habitats by June. In contrast, FRA and bumble bee abundances were highest in dry modified and dry semi-natural habitats in this sample period. By August wet modified habitats such as gardens hosted significantly more workers than dry semi-natural habitats. Wetlands also hosted nearly twice as many workers than dry habitats in August, though this difference was not significant. However, the quality of matrix habitat proved to be the strongest predictor of bumble bee occurrences on the landscape, explaining the majority of variation in bumble bee response in most models.

These results partly accord with previous findings emphasizing the role of modified environments in promoting bumble bee foraging habitat—particularly late season foraging habitat in semi-arid ecosystems (McFrederick & Lebuhn 2006, Heard et al. 2007, Wray & Elle 2015, Hill & Bartromeus 2016). However, we also found evidence that semi-natural habitat diversity—and natural matrix habitat more broadly—was important for bumble bees. In our study, worker abundances in dry semi-natural habitats were comparable to those found in dry disturbed habitats throughout the growing season, despite higher levels of late season floral resources in the latter environments. Furthermore, late season declines in worker abundances in dry semi-natural habitats were not as severe as seen within more impacted ecosystems, such as the fragmented oak savannahs of the nearby Saanich Peninsula on Vancouver Island.

In this system, Wray and Elle (2015) found pollinator diversity and abundance (including bumble bees) to decline sharply in dry woodlands from June through August, tracking closely with decreasing floral resources—except where surrounding urban matrix habitat supplemented diminishing floral resources in these environments. We found a different pattern: high numbers of bumble bee workers were sustained in dry semi-natural habitats through June and July, despite a dramatic decline in floral resources. Modified matrix habitat, moreover, was negatively associated, and natural matrix habitat positively associated, with worker abundances in June, and with late-flying (reproductive) queens in August. Bumble bees thus appeared to be resilient to local declines in floral resources, with workers (in June) and late-flying queens occurring in greater numbers in sites surrounded by natural matrix habitat independent of variation in local site conditions. Thus, while in fragmented urban landscapes gardens may play an important role supplementing late season floral resources, our results suggest that in more intact ecosystems modified matrix habitat may be less important.

Bumble bees are known to forage at great distances, depending on resources available in the environment (Heinrich 1979, Darvill et al. 2004, Knight et al. 2005, Hagen et al. 2011, Jha & Kremen 2013). Documented foraging ranges vary significantly—from 1.5 km (Osborne et al. 2008) to as far as 11.6 km (Rao & Strange 2012). Given these ranges, colonies might be sustained in resource-poor patches providing sufficient resources are available in surrounding matrix habitat. The differences between our findings and those of Wray and Elle (2015) may be attributable to the contrasting quality of matrix habitat between study areas, given the less impacted state of Galiano's ecosystems which likely support more nesting and foraging resources than fragmented urban and agricultural landscapes. Galiano Island's ecosystems remain relatively intact, with ~11% of the landscape converted for present day human use

(Madrone 2008). In contrast, on the Saanich Peninsula less than 5% of the ecosystem remains in its natural state (MacDougall et al. 2004, Shackelford et al. 2019).

Wetlands as refuges for bumble bees during late season drought?

While recent research has found wetlands to be important for pollinators in agricultural landscapes (Vickruck et al. 2019), our study did not support the hypothesis that wetlands provide important foraging habitat for bumble bees in this semi-arid ecosystem. Through the early season, Floral Resource Availability remained significantly lower in wetlands than other habitats, and wetlands were host to correspondingly low numbers of workers. Bumble bee nesting density is known to be directly related to floral abundances, especially early season FRA (Knight et al. 2009, Williams et al. 2012), which may have resulted in decreased bumble bee workers abundances in these habitats. Yet it is also possible that wetlands are generally less habitable to ground-dwelling bumble bees than drier, upland habitats. Wet conditions have been observed to hamper bumble bee colony development (Harder 1986), and pollinator nesting is also known to be positively associated with moderately sloped upland habitats (Potts et al. 2005, Wray & Elle 2015). Hence wetlands may be avoided by nesting queens, resulting in a lower density of colonies in these environments. In wetlands, worker abundances peaked in July—one month after FRA reached its peak—which suggests a lag in the productivity of local colonies. This pattern is also apparent across other habitat types, with worker abundances climaxing in the months following peak flowering events.

Wetlands nevertheless supported greater Floral Resource Availability than dry semi-natural habitats in the late season. Moreover, in contrast to all other habitats, where exotic plants became increasingly prevalent, wetland FRA was found chiefly among native plants.

Considering the foraging distances traveled by bumble bees, these findings indicate that semi-natural habitat diversity remains important for pollinators, insofar as dry and wet semi-natural habitats support the availability of both early and late season floral resources in semi-arid ecosystems.

In the absence of major anthropogenic disturbance events, soil moisture gradients were likely crucial in shaping plant-pollinator interactions across the foraging landscapes of the past—particularly for insects having annual colony cycles such as bumble bees, which depend on the availability of both early and late season floral resources (Williams et al. 2012, Rundlöf et al. 2014). Since the mid 1800s, however, disturbances associated with European colonization have altered these ecosystems, with changing predator-prey dynamics resulting in increased deer browsing pressures, and land conversion resulting in natural habitat loss and the introduction of a high diversity of exotic plants (Martin et al. 2011, Marx et al. 2016). Promoted by disturbance, exotic plants now contribute to a significant proportion of floral resources in this system. These disturbed conditions may favour certain bumble bee species over others, contributing to modern day shifts in plant-pollinator community dynamics (McFrederick & LeBuhn 2006, Fraser et al. 2012, Cole et al. 2019).

Bumble bee community dynamics

This study revealed significant patterns in the distribution of *Bombus vosnesenskii* and *B. sitkensis* that are interesting to note in light of previous research suggesting competitive interactions between these species (McFrederick & LeBuhn 2006). We found *Bombus vosnesenskii* to be most abundant in dry upland environments, where *B. sitkensis* was least abundant, whereas *Bombus sitkensis* was most abundant in wetlands, where *B. vosnesenskii* was least abundant. In British Columbia, *Bombus vosnesenskii* has undergone significant and rapid range expansion since 2000, demonstrating an impressive capacity for colonization (Fraser et al. 2012). This species is now dominant in urban environments throughout western North America, where its abundance is correlated with reduced bumble bee species richness, having a particularly negative association with *B. sitkensis* (McFrederick & LeBuhn 2006, Cole et al. 2019). Because both species are subterranean nesters, researchers speculate that this negative relationship may be due to competition for nesting habitat (McFrederick & LeBuhn 2006). To the extent that *Bombus vosnesenksii* demonstrated a preference for disturbed upland environs on Galiano Island, it may be that *B. sitkensis* has found a haven in lowland habitats where it is less subject to competition with *B. vosnesenskii*. On the other hand, although *Bombus sitkensis* was widespread throughout all habitats sampled in this study, the effect of apparent competition between these species could be confounded by opposing habitat preferences.

Despite its capacity for colonization, *Bombus vosnesenskii* was the least abundant bumble bee sampled on Galiano Island in 2018. Its preference for disturbed environments may be limiting its establishment on this relatively forested island. In California, researchers have noted that this species is not as abundant in less fragmented environments, suggesting a threshold of urbanization that must be crossed to bring about this species' dominance (McFrederick & LeBuhn 2006). The sparse occurrence of *Bombus vosnesenskii* on Galiano Island—a rural island that remains relatively intact ecologically—supports this hypothesis. However, this pattern may also be due to a recent colonization event, as this species has only expanded its range over the last couple decades (Fraser et al. 2012) and was not previously known from Galiano Island's historical record (Simon 2020, pers. observation).

Conclusions

Habitat loss and fragmentation are major threats to terrestrial biodiversity worldwide (Rogan & Lacher 2018). Conservation thus depends on both protecting intact ecosystems and ensuring quality matrix habitat to buffer against the stress of habitat destruction (Franklin & Lindenmayer 2009). Significant fluctuations in floral resources were observed across this semi-arid island ecosystem, with each habitat exhibiting distinct peaks and declines in floral resources. Yet although gardens supported more late season floral resources for workers, bumble bees continued to persist in resource-poor patches of the landscape, and were in some cases negatively influenced by modified matrix habitat. Thus, while previous research has identified urban centres as critical sources of late season floral resources in semi-arid ecosystems (McFrederick & LeBuhn 2006, Wray & Elle 2015), the results of this study suggest natural matrix habitat may be more important in less fragmented landscapes.

Compositionally rich landscapes hosting floral resources through both the early and late season are known to be critical to ensure the intergenerational survival of bumble bees (Knight et al. 2009, Williams et al. 2012, Carvell et al. 2017). Although this study was limited to one year of sampling, results largely accord with phenological patterns previously documented for plant-pollinator communities in this system (*e.g.,* Wray & Elle 2015). In this semi-arid ecosystem, natural habitat diversity emergent across the soil moisture gradient, from woodlands to wetlands, supported floral resources throughout the growing season. Our results thus underline an important lesson for pollinator conservation in the face of climate change and increasing habitat destruction. Across fragmented urban and agricultural landscapes, restoration interventions may be required to promote the foraging habitat necessary to foster diverse pollinator communities. However, such measures are of secondary importance to conservation in the context of more intact natural ecosystems. Where possible, the conservation of natural habitat diversity—across the spectrum of dry to wet habitat types—can help sustain floral resources throughout the year, and should be prioritized in efforts to foster the resilience of pollinators on the landscape.

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Chapter IV.

Evidence of bumble bee species extirpation and colonization: a note concerning *Bombus occidentalis*, *B. suckleyi*, and *B. vosnesenskii* (Hymenoptera: Apidae) from Galiano Island, British Columbia, Canada

Bombus vosnesenskii **Radoszkowski, 1862**
on *Ulex europaeus* L.
Photograph by Katie Kushneryk
May 4, 2019

The third person plural voice is adopted in the following chapter, which has been prepared as an independent manuscript for publication.

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Chapter IV.
Evidence of bumble bee species extirpation and colonization: a note concerning *Bombus occidentalis, B. suckleyi,* and *B. vosnesenskii* (Hymenoptera: Apidae) from Galiano Island, British Columbia, Canada

Abstract

Two bumble bee species—*Bombus occidentalis* Greene, 1858 and *Bombus suckleyi* Greene, 1860—are presumed extirpated from Galiano Island, BC, Canada, based on comparison of historical and current species occurrence data, including data from intensive sampling using blue vane traps. The decline of *Bombus occidentalis* in western North America has long been observed in many areas, yet to our knowledge this is the first probable case of its local extinction. Results suggest that an additional species, *Bombus vosnesenskii* Radoszkowski, 1862*,* which has been expanding its range in the wake of the decline of *Bombus occidentalis*, may be a recent arrival on Galiano Island. Elsewhere in the region *Bombus vosnesenskii* has become a dominant species, particularly in urban environments. However, it is the least abundant species on this largely forested island. Community analysis also suggests possible competitive interactions between *Bombus sitkensis* Nylander, 1848 and *Bombus vosnesenskii* that are consistent with trends previously reported in the literature. Potential factors contributing to this likely case of bumble bee extirpation and subsequent colonization are discussed in the context of Galiano Island's historical land use and ecology. In conclusion, we assess the potential for citizen science to aid in the detection of species extirpation via comparison of historical biological specimen collections and contemporary crowd-sourced biodiversity data.

Introduction

Worldwide, bumble bees face increasing threats associated with climate and anthropogenic landscape change, which have resulted in population declines and species range restrictions (Szabo et al. 2012, Sanchez-Bayo & Goka 2014, Kerr et al. 2015, Biella et al. 2017, Soroye et al. 2020). In western North America, *Bombus occidentalis* Greene, 1858 is a well-established case of widespread species decline resulting in its near extirpation from coastal regions (Colla & Ratti 2010). The decline of *Bombus occidentalis* has largely been attributed to pathogens associated with commercial rearing of bumble bees in industrial agricultural settings, including the parasitic fungus *Nosema bombi* (Rao & Stephen 2007, Otterstatter & Thomson 2008, Colla & Ratti 2010, Graystock et al. 2016).

With the decline of *Bombus occidentalis,* another bumble bee species—*Bombus vosnesenskii*—has undergone significant range expansion in western British Columbia (Fraser et al. 2012). Research indicates that this species has come to occupy the niche left vacant by *Bombus occidentalis*, showing high potential for colonization, particularly in urban environments where its dominance is associated with declines among other species (McFrederick & LeBuhn 2006, Fraser et al. 2012, Cole et al. 2019).

Here we present evidence for the likely local extinction of *Bombus occidentalis* and its associated parasite *Bombus suckleyi* Greene, 1860 from Galiano Island, BC, Canada, based on the analysis of: i) historical species occurrence data; ii) data collected through intensive, systematic sampling conducted in 2018 using blue vane traps; and, iii) recent observations on the citizen science platform iNaturalist. Community data provide further insight into bumble bee population dynamics, suggesting possible competitive interactions between *Bombus sitkensis* and *Bombus vosnesenskii*—the latter of which appears to have only recently colonized Galiano

Island. Set against the backdrop of Galiano Island's land use history, these findings present clues regarding the historical cause of *Bombus occidentalis'* decline, as well as insight into the ecology of *Bombus vosnesenskii*.

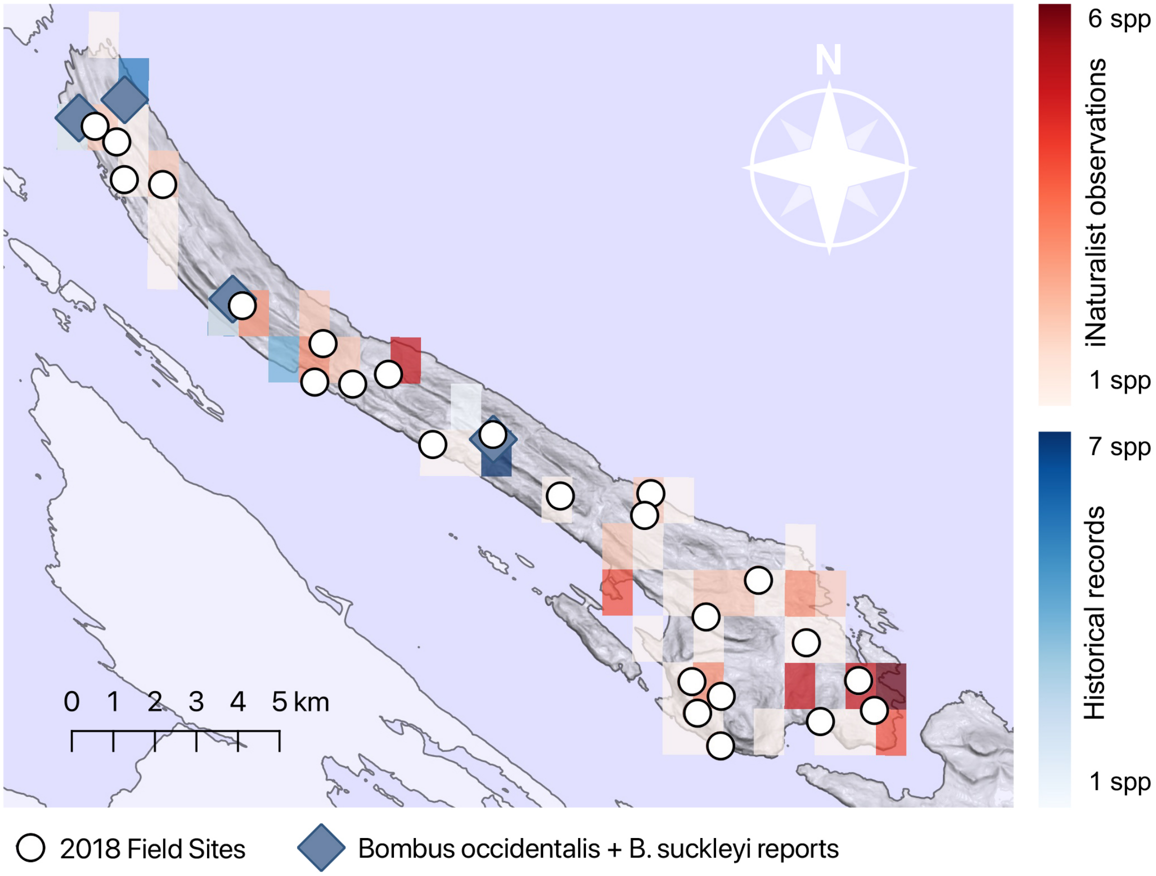

Figure 13. Heat map of bumble bee species occurrence data, including historical records (1970–2010) and recent iNaturalist observations (2014–2019). The six species presently known to Galiano Island were widespread in 2018, occurring in samples from all 24 field sites. Grid scale = 0.01°; at this latitude, each cell represents ~82 ha.

Study area and methods

Galiano Island lies in the rain shadow of the mountains of Vancouver Island and the Olympic Peninsula, in southern coastal British Columbia, Canada. This region is defined by its semi-arid climate, characterized by mild, wet winters and warm, dry summers (Klassen et al. 2015).

Galiano remains relatively intact ecologically, with about 24% of its land base conserved in protected areas and a high percentage of forest cover. Today only ~11% of the landscape has been converted for active human use, including rural development and limited small-scale agriculture (Madrone 2008), though forestry and cumulative land use effects have altered habitats as throughout the rest of British Columbia (Shackelford et al. 2018).

We sampled bumble bees as part of a study investigating the role of soil moisture availability and disturbance in moderating the impact of seasonal drought on plant-pollinator community dynamics (Chapter III). Bumble bees were collected using blue vane traps (Stephen & Rao 2005) systematically distributed across the landscape in a 2x2 factorial study design contrasting dry vs wet, and disturbed vs undisturbed, site conditions. Site conditions were stratified using terrestrial ecosystem mapping data (Madrone 2008). Sampling was conducted over five sample periods, from April through August, across 24 field sites, resulting in 119 samples (120 less one sample compromised due to human interference) representing 47,896 individuals. Bumble bees were identified following Williams et al. (2014). Historical species occurrence data (n = 71) were derived from collections held at the UBC Beaty Biodiversity Museum and Royal British Columbia Museum, which were systematically reviewed for this study. No other Galiano Island bumble bee collections exist as far as the authors are aware. Additional observational data (n = 121) were collected using the online citizen science platform iNaturalist. The distribution of historical and contemporary species occurrence data are presented in Figure 14.

Historical and contemporary species occurrence data were analyzed using rarefaction methods implemented using the function ‘specaccum’ in ‘vegan’, R package v.2.5–5 (Oksanen et al. 2019, R Core Team 2019), to estimate species richness in historical and contemporary communities (Fig.15). We then compared rarefaction curves with null model tests using the R package 'rareNMtests' v.1.1 (Cayuela & Gotelli 2014) to test differences in historical and contemporary assemblages, and also to validate the results of rarefaction based on iNaturalist observations against the results of intense systematic sampling. To do this we followed the null model test procedure outlined in Cayuela et al. (2015). Bumble bees collected by blue vane traps were pooled and treated as individuals (n = 47,896) for comparison with individual-based rarefaction curves generated based on historical and iNaturalist data using null model tests.

Results and discussion

Seven bumble bee species are historically reported for Galiano Island, represented by 71 specimens in research collections: 1) *Bombus flavifrons* Cresson, 1863; 2) *Bombus melanopygus* Nylander, 1848; 3) *Bombus mixtus* Cresson, 1878; 4) *Bombus occidentalis*; 5) *Bombus sitkensis* Nylander, 1848; 6) *Bombus suckleyi*; and 7) *Bombus vancouverensis* Cresson, 1878[1]. Of the seven species collected from 1970–2010, only five have since been detected. *Bombus occidentalis* and *Bombus suckleyi* have not been seen since 1990 and 1975 respectively. An additional species, *Bombus vosnesenskii,* was reported locally for the first time in 2017 based on an iNaturalist observation,[2] and subsequently confirmed through blue vane sampling. These findings coincide with regional trends documenting the historical decline of *Bombus occidentalis* (Colla & Ratti 2010), and the subsequent expansion of *Bombus vosnesenskii* in British Columbia (Fraser et al. 2012). Six species are now known to occur on Galiano Island (Fig.15, Table 4).

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[1] Previously reported as *Bombus bifarius* (Cresson, 1878), this taxon is now recognized as *Bombus vancouverensis vancouverensis* Cresson, 1878, an overlooked subspecies endemic to the Georgia Depression and Puget Sound (Ghisbain et al. 2020).

[2] https://www.inaturalist.org/observations/6412054

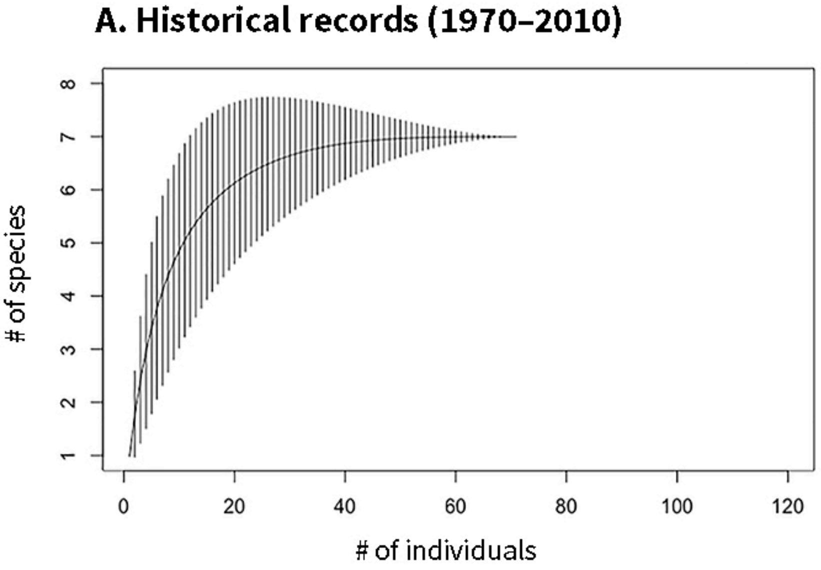
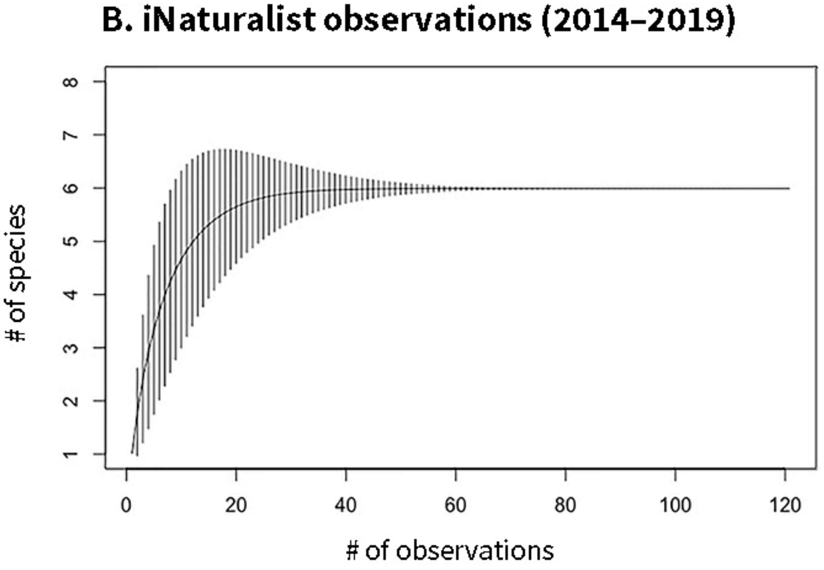
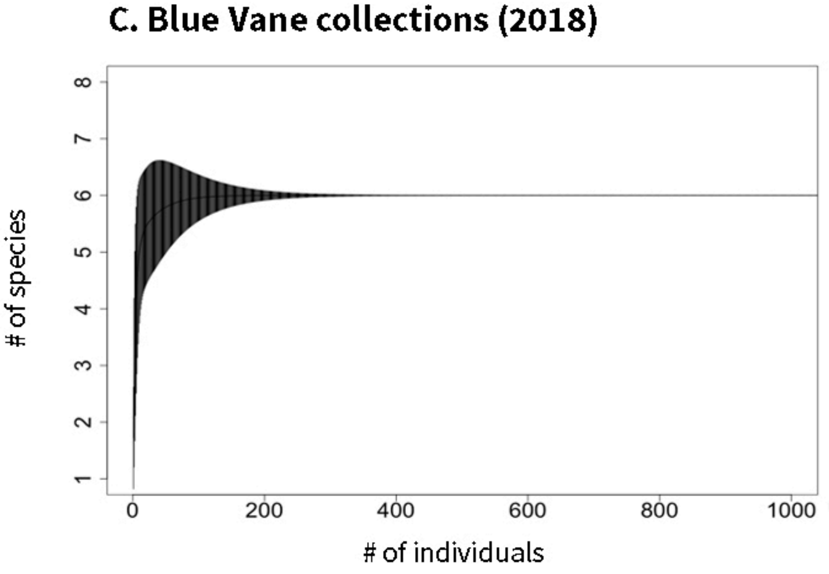


Figure 14. A. Individual-based rarefaction of historical records (1970–2010, *n*=71), with 95% confidence intervals. Rarefaction curve reaches an asymptote at 69 iterations, estimating species richness at 7 spp.



B. Individual-based rarefaction of iNaturalist observations (2014–2019, *n*=121), with 95% confidence intervals. Rarefaction curve reaches an asymptote at 79 iterations, estimating species richness at 6 spp.



C. Individual-based rarefaction of samples from intensive blue vane trap sampling regime (*n* =47,896), with 95% confidence intervals. Rarefaction curve reaches an asymptote at 460 iterations, estimating species richness at 6 spp.

Species accumulation curves generated based on all sources of bumble bee community data reached their asymptote, predicting 7 species in the historical record and 6 species based on both sources of contemporary data (Fig.15). Null model tests of rarefaction curves based on both sources of contemporary data against the curve generated from historical data showed that the past community assemblage significantly differed from the present day community (*p*=0.005). Null model tests comparing rarefaction of iNaturalist community data against rarefaction of data obtained through systematic sampling confirmed that samples were randomly drawn from the same underlying assemblage (*p*=0.16). These tests, combined with the results of rarefaction shown in Figure 15, demonstrate that survey efforts based on intensive systematic sampling and iNaturalist observations were both sufficient to estimate the richness of the contemporary bumble bee community.

Because historical collection efforts are spatially limited in extent, individual-based rarefaction of historical biological specimen data could be spatially biased. However, recent work has shown individual-based rarefaction to be preferable to spatially explicit rarefaction in order to control for differences in random sampling effort (Osazuwa-Peters et al. 2018). Moreover, recent sampling across a broad spectrum of habitat diversity revealed that bumble bee species were widespread on Galiano Island (Chapter III). Species occurred throughout all habitats, and community composition overall was relatively even across the landscape, though two species varied significantly in abundance between habitats (Table 5). Bumble bees are known to have broad foraging ranges—from 1.5 km (Osborne et al. 2008) to as far as 11.6 km (Rao & Strange 2012)—and were thus likely pervasive throughout the extent of this relatively small island (27.5 km in length and 1.6 km at its narrowest point). Although it cannot be ruled out entirely, we reason that spatial autocorrelation is not likely to have been a significant source of bias in historical collection efforts, further justifying individual-based rarefaction as an approach to comparing historical and contemporary species occurrence data in this study.

Table 4. Counts and proportional abundances of bumble bee species represented by: i) net-collected vouchered specimens (net); ii) iNaturalist observations (iNat); and, iii) individuals captured in blue vane traps (BVs). Sampling area is roughly estimated based on the spatial extent of sampling within 82 ha grid cells (Fig.14). Taxa are abbreviated: *Bombus flavifrons* (*B.flav*.), *B. melanolpygus* (*B.mel*.), *B. mixtus* (*B.mix*.)*, B. sitkensis* (*B.sit*.), *B. vancouverensis* (*B.van*.), and *B. vosnsenskii* (*B.vos*.).

Sample Period	Area (ha)	Method	Species	Individuals	*B.flav.*	*B.mel.*	*B.mix.*	*B.occ.*	*B.sit.*	*B.suc.*	*B.van.*	*B.vos.*
1970–2010	492	net	7	71	4	26	5	9	7	3	11	
					(0.13)	(0.42)	(0.05)	(0.16)	(0.13)	(0.05)	(0.11)	
2014–2019	3,444	iNat	6	121	22	15	11		13		46	14
					(0.18)	(0.12)	(0.09)		(0.11)		(0.38)	(0.12)
2018	1,968	BVs	6	47,896	5,636	5,298	6,990		7,357		21,868	747
					(0.12)	(0.11)	(0.14)		(0.15)		(0.46)	(0.02)

The disappearance of *Bombus occidentalis* and *B. suckleyi* from Galiano Island is interesting to note in light of the known parasitic relationship between these species. The cuckoo bumble bee, *Bombus suckleyi,* has been documented breeding in colonies of *B. occidentalis* (Thorp et al. 1983), and is not known to associate with any other species reported for Galiano Island. It thus appears to have vanished as an obligate parasite along with its host. Other potential sources of environmental stress on Galiano historically include apiculture and reforestation, the latter of which may have resulted in loss of open foraging habitat, which may have increased the effect of other stressors in the environment. Low genetic diversity in this insular population of *B. occidentalis* may have also placed it at risk (Lozier et al. 2011).

Given trends seen elsewhere (*e.g.,* the case of *B. vosnesenskii's* range expansion in western British Columbia), shifts in community composition are to be expected in the wake of local extirpation events. Interestingly, however, whereas *B. vosnesenskii* has become dominant in many urban environments (McFrederick & LeBuhn 2006, Cole et al. 2019), we found it to occur relatively infrequently across Galiano's forested landscape (Table 5). *Bombus vosnesenskii* abundances were greatest in disturbed upland habitats, which supported significantly more individuals vs wet lowland habitats (Chapter III). These findings suggest that this species may be having a difficult time getting established on this largely forested island. Researchers have previously suggested a threshold of urbanization that must be crossed before *B. vosnesenskii* assumes prominence in a community (McFrederick & LeBuhn 2006). However it is also possible that low numbers of *B. vosnesenskii* are indicative of a recent colonization event on Galiano Island.

Potential competitive interactions between *Bombus vosnesenskii* and *B. sitkensis* were also noted in this study. We found *B. sitkensis* to be significantly less abundant in dry modified environments where *B. vosnesenskii* was most prevalent; conversely, *B. sitkensis* was most abundant in lowland habitats where *B. vosnesenskii* was least common (Table 5). These findings coincide with previous research finding that the dominance of *B. vosnesenskii* correlated with declines in bumble bee species richness, having a particularly negative effect on *B. sitkensis* (McFrederick & LeBuhn 2006, Cole et al. 2019). Because both *B. sitkensis* and *B. vosnesenskii* are subterranean nesters, researchers speculate that this negative relationship may be due to competition for nesting habitat (McFrederick & LeBuhn 2006). To the extent that *B. vosnesenskii* abundances were positively correlated with sloped terrain in this study, it may be that *B. sitkensis* has found a haven in lowland habitats where it is less subject to competition with *B. vosnesenskii*. However, it is also possible that this apparent competitive interaction is confounded by opposing habitat preferences of the two species.

Table 5. Bumble bee community composition across habitat types, based on intensive blue vane sampling from April through August 2018. Proportional abundances of species are relatively even across habitats, with the exception of *Bombus sitkensis* and *B. vosnesenskii,* the abundances of which were found to be significantly different between habitats marked with * (Chapter III). Taxa are abbreviated: *Bombus flavifrons* (*B.flav*.), *B. melanolpygus* (*B.mel*.), *B. mixtus* (*B.mix*.), *B. sitkensis* (*B.sit*.), *B. vancouverensis* (*B.van*.), and *B. vosnsenskii* (*B.vos*.).

Habitat Type	Sites	Samples	*B.flav.*	*B.mel.*	*B.mix.*	*B.sit.*	*B.van.*	*B.vos.*
Dry semi-natural (woodlands, outcrops, coastal meadows)	8	39	0.13	0.12	0.13	0.15	0.45	0.02
Dry modified (clear cuts, hydro-line corridors, *etc*.)	6	30	0.08	0.12	0.14	0.09*	0.54	0.03*
Wet semi-natural (wetlands)	4	20	0.12	0.08	0.17	0.26*	0.36	<0.01*
Wet modified (orchards, gardens, fields, *etc*.)	6	30	0.13	0.11	0.17	0.17	0.42	0.01

Conclusions

Baseline data for many insect groups, including bumble bees, are highly deficient. As a result, important pollinator species may undergo dramatic declines unnoticed (Buchmann & Nabhan 1996). Where baseline data are available, however, adequate search effort can detect critical changes in the composition of insect communities. Our study demonstrates the efficacy of two forms of search effort in detecting the probable local extinction of *Bombus occidentalis* and *B. suckleyi* from Galiano, and the subsequent colonization of the island by *B. vosnesenskii*.

Blue vane traps are effective in sampling large insects such as bumble bees (Stephen & Rao 2005) yet they can also result in high mortality. Our findings show that bumble bee surveys may not necessarily need to be so intensive, depending on the size of the species pool and the area under study. In this study, iNaturalist observations crowd-sourced over five years produced a reliable estimate of local species richness, comparable to the estimate obtained through systematic sampling using blue vane traps.

Because bumble bee species were pervasive in the environment, we could have confidence that past and present search efforts were likely not subject to serious spatial bias. Most taxonomic groups are not so ubiquitous, however. These considerations place important caveats on these results, indicating that iNaturalist might be harnessed to detect changes in local community composition in cases where: a) adequate historical baseline data are available; b) the study area and species pool of the target taxonomic group is relatively small; and, c) spatial autocorrelation of species occurrences is considered unproblematic. Further inventory work combining methods to sample bumble bees on different spatial scales is warranted to determine the reliability of citizen science-based data to support such inferences.

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Chapter V.
General Conclusion

***Bombus vancouverensis* Cresson, 1878**
on *Collinsia parviflora* Lindl.
Photograph by Andrew Simon
April 14, 2017

Habitat loss and climate change are two major factors implicated in the decline of bumble bees worldwide. In this study, I investigated the effects of seasonal drought on plant phenology and bumble bee community ecology in the semi-arid ecosystem of the southern Gulf Islands of British Columbia, Canada. This system proved ideal in both its climate and land use history, providing the critical gradients of soil moisture and disturbance necessary to test my hypotheses. Yet the process of thinking along these gradients ran much deeper than expected as I reflected on the vital importance of water for plant physiology, and for ecosystem dynamics more generally. My field work thus led me to think more critically about the latent dimensions of my research question, which later unfolded to become a central part of this thesis. I was grateful to collaborate with Hannah Marx in this investigation, which allowed me to take a novel approach integrating methods from pollinator research with phylogenetic community ecology. As a result, this research proved to be of general interest not only from the perspective of pollinator ecology but also in the context of eco-evolutionary and plant invasion theory, particularly as it applies to water-limited ecosystems. In this concluding chapter I reflect on some of the principal outcomes of this research, drawing out the broader implications and limitations of my findings.

From the outset it should be acknowledged that this was an observational study. Yet although the results are correlational, they are consistent with a growing body of rigorous empirical evidence demonstrating a) the physiological basis of eco-hydrological niche segregation in plant communities; and, b) the importance of compositionally rich landscapes for the intergenerational survival of bumble colonies. These patterns may be further investigated through experimental approaches to test underlying causal mechanisms or processes.

This thesis begins with a well-established biological premise: that the availability of water is the primary factor limiting the growth and reproduction of land plants (Rosenzweig 1968, Silvertown et al. 2015). In semi-arid ecosystems, the regular occurrence of summer drought may thus be expected to have a profound impact on plant phenology, strongly influencing plant-pollinator community interactions. As reported for other semi-arid ecosystems (*e.g.,* Pérez-Camacho et al. 2012, Schwinning & Kelly 2013), I found that the relative drought avoidance of annuals and the drought tolerance of perennials played an important role influencing plant community phenology in response to local fluctuations in soil moisture. Life history was to a large extent conserved within dominant plant families, which tended to exhibit similar phenology depending on local site conditions, occupying distinct temporal niches emergent across soil moisture gradients. Major flowering events thus coincided with significant phylogenetic clustering in plant communities, with decreasing plant diversity observed under conditions of increasing drought stress.

Considered alongside other studies in phylogenetic community ecology, this study was novel in forging a link between the abstractions of eco-evolutionary theory and ecologically significant effects in the context of the pollinator foraging landscape. Furthermore, I was able to test a hypothesis in plant invasion theory concerning the temporal niche dynamics of semi-arid environments: that due to high levels of drought stress, the late season temporal niche would not be subject to invasion (Alpert et al. 2000, Wolkovich & Cleland 2014). My results revealed an overlap in the temporal niche breadth of related native and exotic flowering plants in the family Asteraceae, which flowered late under conditions of low soil moisture—hence falsifying the aforementioned prediction, while emphasizing the importance of the role of environmental filtering over plant invasion dynamics in this system. This study also revealed some of the ways in which habitat diversity can confound phylogenetic patterns observed at larger spatial scales. Patterns in the phylogeny and life history of flowering plants emerged in their phenological response to local fluctuations of soil moisture in this system, which would not have become apparent without analyzing the temporal dimensions of these communities. Further research is required to understand how environmental filtering affects the process of invasion both spatially and temporally, to shape the phylogenetic structure of plant communities.

Despite being limited to a single field season, other data gathered from my experience in this system assures me that the phenological patterns analyzed in this study are robust. Further research involving experimental manipulation of variables such as temperature and soil moisture availability, and a more rigorous analysis of quantitative functional traits, would serve to test some of the underlying assumptions of the theory applied in this study.

In Chapter III, I examined the importance of habitat diversity for bumble bees. Of particular interest was the role of soil moisture and disturbance in promoting late season floral resource availability. Consistent with other studies in water-limited systems, I found gardens locally supported higher late season floral resources and greater bumble bee worker abundances as compared to dry woodlands. At larger spatial scales, however, modified wet environments had a negative influence on bumble bee abundances. Modified matrix habitat was negatively associated with bumble bee workers in June and late-flying queens in July and August, independent of local variability in floral resources. On the other hand, more workers (in June) and late-flying queens occurred in areas surrounded with more natural habitat matrix. Workers proved resilient to late season declines in floral resources, persisting in dry woodland habitats despite dramatic declines in floral resources in these environments. These findings, in contrast to the results of research focusing on more fragmented landscapes, suggests this resiliency must depend to a certain extent on ecosystem integrity, in terms of the availability of foraging and nesting resources.

In urban landscapes gardens have been found to play an important role supplementing declines in late season floral resources within dry parklands and fragmented oak communities (McFrederick & LeBuhn 2006, Wray & Elle 2015). However, the results of my research suggested that natural matrix habitat buffered against local effects of diminishing floral abundances in similar dry habitats, while modified matrix habitat was negatively associated with bumble bee abundances. Furthermore, woodlands and wetlands supported floral resources from the early to late season, thus emphasizing the importance of natural habitat diversity for bumble bees and other pollinators in supporting floral resources throughout the year. Hence, while in fragmented urban landscapes gardens may play an important role supplementing late season floral resources, the results of my research suggest that in more intact ecosystems modified areas may be less important. These findings present an important counter-narrative to studies focusing on more fragmented landscapes, which I hope may serve to encourage further research into the dynamics of more ecologically intact systems. Pollinator ecology can surely benefit from more research outside the realm of urban and agricultural systems, even if some of the greatest effects out there are anthropogenic!

One of the challenges facing ecologists in the field of pollinator ecology concerns the use of proxy indicators to infer foraging and nesting behaviour. In this study, the abundance of workers was considered as a proxy of foraging activity, and the abundance of late-flying queens interpreted as a proxy of the reproductive success of colonies. However, it is not always clear whether the presence of a worker might relate to locally available floral resources, or whether it might be more closely related to the overall density of colonies in an area. Similarly, the presence of a late-flying queen is likely closely related to the fecundity of nearby colonies. Yet given the extensive foraging range of bumble bees (Rao & Strange 2012, Williams et al. 2014), her presence could also signal her attraction to resources further afield, in areas remote from her native colony. While these proxy indicators are often assumed as the basis for interpreting the results of observational studies in pollinator ecology, a certain amount of uncertainty necessarily attends these interpretations. With that said, progress is being made through the use of molecular techniques to measure the intergenerational survival of bumble bee colonies (*e.g.,* Carvell et al. 2017). These methods have improved upon the rigour of traditional approaches to pollinator ecology, lending further support to observational studies showing the importance compositionally rich landscapes for bumble bees.

In Chapter IV of this thesis I address a topic that partly motivated my research to begin with: the plight of *Bombus occidentalis* Greene, 1858 and *Bombus suckleyi* Greene, 1860*,* both species of conservation concern that were found to have disappeared from Galiano Island based on intensive, systematic sampling in 2018. Here I consider the reliability of different forms of contemporary data used to infer changes in the composition of Galiano's bumble bee community with reference to the historical baseline. In this study, iNaturalist observations crowd-sourced over the course of five years produced a reliable estimate of local species richness comparable to the estimate obtained through systematic search efforts using blue vane traps. Because bumble bee species were pervasive in the environment, we could have confidence that past and present search efforts were likely not subject to serious spatial bias. Most taxonomic groups are not so ubiquitous, however. The small size of the study area and local bumble bee species pool placed additional caveats on these findings. In summary, the results of this study indicated that iNaturalist can potentially be harnessed to detect changes in local community composition providing that: a) adequate historical baseline data are available; b) the study area and species pool of the target taxonomic group is relatively small; and, c) spatial autocorrelation of species occurrences is considered unproblematic. I hope that this note helps to spur further inventory work combining sampling methods on different spatial scales, to address the reliability of citizen science-based data to support such inferences. May the bumble bees that lost their lives in my research be honoured with this work.

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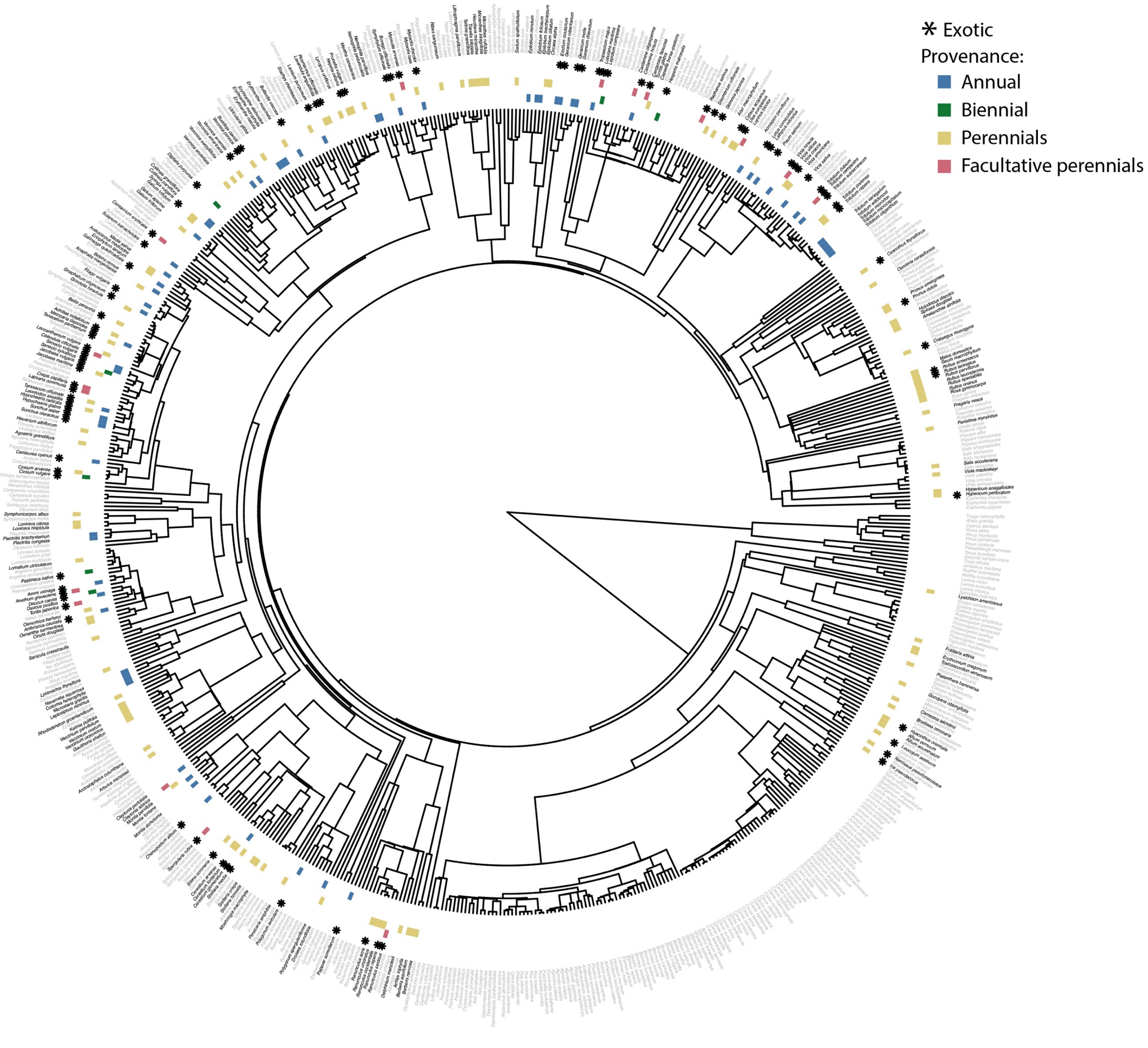
Appendix A. Phylogeny of Galiano Island seed plants



Study Area Phylogeny. Phylogeny of seed plants known to Galiano Island based on a robust phylogeny of 353,185 seed plants derived from GenBank by Smith & Brown (2018). Of the 717 seed plants recorded in the flora of Galiano Island, 645 species were represented in the reference phylogeny, which were pruned to create this study area phylogeny. Entomophilous flowering plants analyzed in Chapter II are identified in bold, with labels showing provenance and life history of species.

Appendix B. Proportional representation of Plant Functional Types

The following tables summarize proportional floral resource availability among different plant functional types (PFTs) for the dominant plant families sampled over the course of this study. Plant orders are presented alphabetically, grouped by site condition, and species listed by provenance and plant functional type. Significant phylogenetic clustering at the community scale is indicated by three asterisks ⁂; two asterisks ** indicate significant clustering at the transect scale; one asterisk * indicates that plants cooccurred with related species within the same site though they did not cluster within the same transect. The following tables represent >90% of the FRA sampled during this research.

Apiales

(Apiacaee)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Daucus pusillus*			<0.01		
native	perennial herbs	*Lomatium utriculatum* *Osmorhiza berteroi* *Sanicula crassicaulis*	1.00	1.00	<0.01**		
exotic	pauciennials	*Torilis japonica*			0.99**		

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Osmorhiza berteroi*		1.00			
exotic	biennials	*Daucus carota*					1.00
exotic	pauciennials	*Torilis japonica*			1.00		

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Cicuta douglasii* *Oenanthe sarmentosa* *Osmorhiza berteroi* *Sanicula crassicaulis*		1.00	1.00	1.00	

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Osmorhiza berteroi* *Sanicula crassicaulis*	1.00	0.39**	0.16		
exotic	annuals	*Ammi visnaga* *Anthriscus caucalis*		0.61**	0.84		1.00
exotic	biennials	*Daucus carota* *Pastinaca sativa*		<0.01		0.50	
exotic	pauciennials	*Anethum graveolens* *Torilis japonica*				0.50	

Asterales

(Asteracae)

Dry semi-natural							
Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Madia gracilis* *Madia sativa*			0.16**	0.16⁂	
native	perennial herbs	*Achillea borealis* *Agoseris grandiflora* *Anisocarpus madioides* *Eriophyllum lanatum* *Gamochaeta ustulata* *Grindelia hirsutula* *Hieracium albiflorum*		0.18	0.35**	0.07⁂	
exotic	annuals	*Centaurea cyanus* *Hypochaeris glabra* *Senecio sylvaticus*		0.66	0.03**	0.05⁂	
exotic	biennials	*Cirsium vulgare*				0.03⁂	0.46⁂
exotic	perennial herbs	*Hypochaeris radicata* *Leucanthemum vulgare* *Mycelis muralis* *Taraxacum* sp.	1.00	0.16	0.45**	0.65⁂	0.54⁂
exotic	pauciennials	*Crepis capillaris* *Sonchus oleraceus*			0.01**	0.04⁂	

Dry modified							
Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Anaphalis margaritacea* *Gamochaeta ustulata*				<0.01⁂	0.01⁂
exotic	annuals	*Filago vulgaris* *Leontodon saxatilis* *Senecio sylvaticus* *Senecio vulgaris* *Sonchus asper*	0.04		0.01**	0.04⁂	<0.01⁂
exotic	biennials	*Cirsium vulgare* *Jacobaea vulgaris*				0.05⁂	0.19⁂
exotic	perennial herbs	*Bellis perennis* *Cirsium arvense* *Hypochaeris radicata* *Jacobaea maritima* *Leucanthemum x superbum* *Leucanthemum vulgare* *Mycelis muralis* *Sonchus arvensis* *Taraxacum* sp.	0.96**	1.00	0.98**	0.66⁂	0.56⁂
exotic	pauciennials	*Crepis capillaris*			<0.01**	0.25⁂	0.23⁂

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Bidens cernua*					0.01⁂
native	perennial herbs	*Anaphalis margaritacea*				<0.01⁂	0.02⁂
exotic	annuals	*Senecio sylvaticus* *Sonchus asper*			0.24**	0.15⁂	0.06⁂
exotic	biennials	*Cirsium vulgare* *Jacobaea vulgaris*				0.03⁂	0.30⁂
exotic	perennial herbs	*Cirsium arvense* *Hypochaeris radicata* *Mycelis muralis* *Taraxacum* sp.	1.00		0.52	0.73⁂	0.52⁂
exotic	pauciennials	*Crepis capillaris* *Lapsana communis*			0.24	0.09⁂	0.08⁂

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Symphyotrichum chilense*			<0.01*		0.10**
exotic	annuals	*Centaurea cyanus* *Galinsoga quadriradiata* *Gnaphalium uliginosum* *Leontodon saxatilis* *Matricaria discoidea* *Senecio sylvaticus* *Senecio vulgaris* *Sonchus asper*	<0.01**		<0.01**	0.11⁂	0.24⁂
exotic	biennials	*Cirsium vulgare* *Jacobaea vulgaris*				<0.01⁂	0.02⁂
exotic	perennial herbs	*Achillea millefolium* *Bellis perennis* *Cirsium arvense* *Hypochaeris radicata* *Leucanthemum x superbum* *Leucanthemum vulgare* *Mycelis muralis* *Sonchus arvensis* *Tanacetum parthenium* *Taraxacum* sp.	0.99**	0.99	0.96**	0.70⁂	0.49⁂
exotic	pauciennials	*Calendula officinalis* *Crepis capillaris* *Lapsana communis* *Sonchus oleraceus*	<0.01**	0.01	0.03	0.19⁂	0.15⁂

Boraginales

(Boraginaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Nemophila parviflora* *Nemophila pedunculata*	1.0**	0.22**	0.11		
exotic	annuals	*Myosotis discolor*		0.78**	0.89		

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Nemophila parviflora*	1.0	0.16**	0.24**		
exotic	annuals	*Myosotis discolor*		0.84**	0.53**		
exotic	pauciennials	*Myosotis arvensis*			0.23**	1.0	

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Nemophila parviflora*	1.0	0.86	0.08		
native	perennial herbs	*Myosotis laxa*			0.92	1.0	1.0
exotic	annuals	*Myosotis discolor*		0.14			

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Nemophila parviflora*	1.0	0.10	0.02**	<0.01	
native	perennial herbs	*Myosotis laxa*			<0.01**	<0.01	0.05
exotic	annuals	*Borago officinalis* *Myosotis discolor*		0.89	0.97**	0.97	0.95
exotic	perennial herbs	*Symphytum officinale*		0.01	0.01	0.02	

Brassicales

(Brassicaceae, Tropaeolaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Turritis glabra*		0.06			
native	pauciennials	*Cardamine oligosperma*	0.50**				
exotic	annuals	*Cardamine hirsuta*	0.50**	0.94	1.00		

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
native	pauciennials	*Cardamine oligosperma*	<0.01				
exotic	annuals	*Cardamine hirsuta* *Draba verna* *Sisymbrium officinale*	0.99**				

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	pauciennials	*Cardamine oligosperma*	1.00				

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
exotic	annuals	*Capsella bursa-pastoris* *Cardamine hirsuta* *Draba verna* *Eruca sativa* *Sisymbrium officinale* *Tropaeolum majus*	0.82**	0.50**	0.03	0.52*	0.68
exotic	biennials	*Brassica* sp. *Hesperis matronalis* *Lepidium campestre*	0.10**	0.49**	0.32**	0.30	0.32
exotic	pauciennials	*Cardamine flexuosa* *Lobularia maritima* *Raphanus sativus*	0.08**	0.01	0.65**	0.18	

Caryophyllales

(Caryophyllaceae, Droseraceae, Montiaceae, Plumbaginaceae, Polygonaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Claytonia exigua* *Claytonia perfoliata* *Claytonia rubra* *Polygonum spergulariiforme*	0.94**	0.67**		0.03	
native	perennial herbs	*Cerastium arvense* *Moehringia macrophylla* *Montia parvifolia*	<0.01**	0.21**	0.47**		
exotic	annuals	*Cerastium glomeratum*	<0.01	0.06**			
exotic	perennial herbs	*Silene coronaria* *Stellaria media*	0.05**	0.06**	0.53**	0.97	

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Claytonia perfoliata* *Claytonia rubra*	0.58	0.85**	0.01		
exotic	annuals	*Cerastium glomeratum*	0.12	0.10**	0.11**		
exotic	perennial herbs	*Cerastium fontanum* *Silene coronaria* *Stellaria media*	0.30	0.05**	0.88**	0.98	
exotic	pauciennials	*Spergularia rubra*				0.02	

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Drosera rotundifolia* *Stellaria borealis*		0.97	0.96	0.88	0.75

		Stellaria crispa					
native	pauciennials	*Claytonia sibirica*		0.03	0.01	0.12	
exotic	perennial herbs	*Cerastium fontanum*			0.03		0.25

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Claytonia perfoliata*	0.01	0.02			
native	perennial herbs	*Persicaria amphibia*				0.01	
exotic	annuals	*Cerastium glomeratum* *Polygonum aviculare*	0.02	0.88**	0.19**	0.69	0.05
exotic	perennial herbs	*Cerastium fontanum* *Limonium* sp. *Silene coronaria* *Stellaria media*	0.97	0.10**	0.81**	0.30	0.95

Dipsacales

(Caprifoliaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Plectritis brachystemon* *Plectritis congesta*	1.00	0.99	0.31**	0.67	
native	perennial shrubs	*Lonicera ciliosa* *Lonicera hispidula* *Symphoricarpos albus*		0.01	0.69**	0.33	

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Lonicera hispidula*			1.00	1.00	

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Symphoricarpos albus*			1.00		

Ericales

(Ericaceae, Primulaceae, Polemoniaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Collomia heterophylla* *Leptosiphon minimus* *Microsteris gracilis*		0.19	<0.01		
native	perennial herbs	*Lysimachia latifolia*		<0.01	<0.01		
native	perennial shrubs	*Arctostaphylos columbiana* *Gaultheria shallon* *Vaccinium ovatum*	1.00	0.63**	0.99**	1.00	

native	perennial trees	*Arbutus menziesii*		0.18**			

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial shrubs	*Arctostaphylos columbiana* *Gaultheria shallon* *Vaccinium ovatum* *Vaccinium parvifolium*	1.00	1.00	1.00**	1.00	

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Lysimachia europaea* *Lysimachia thyrsiflora*		<0.01⁂	<0.01⁂		
native	perennial shrubs	*Gaultheria shallon* *Kalmia polifolia* *Rhododendron groenlandicum* *Vaccinium ovatum* *Vaccinium oxycoccos* *Vaccinium parvifolium*	1.00	0.99⁂	0.99⁂	1.00	1.00

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial shrubs	*Gaultheria shallon*			1.00	1.00	

Fabales

(Fabaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Acmispon parviflorus* *Trifolium microcephalum* *Trifolium microdon* *Trifolium oliganthum* *Trifolium variegatum* *Trifolium willdenovii*	0.09	0.41**	0.29		
native	perennial herbs	*Vicia americana*			<0.01		
native	pauciennials	*Lupinus bicolor* *Lupinus polycarpus*		0.04**	<0.01		
exotic	annuals	*Trifolium dubium* *Vicia hirsuta* *Vicia sativa*		0.01**	0.06		
exotic	perennial shrubs	*Cytisus scoparius*	0.91	0.54**	0.64		

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
exotic	annuals	*Trifolium dubium*		0.08**	0.21**	0.31**	

		Trifolium subterraneum *Vicia hirsuta* *Vicia sativa*					
exotic	perennial herbs	*Trifolium pratense*			<0.01**	0.08**	0.75
exotic	perennial shrubs	*Cytisus scoparius* *Ulex europaeus*		0.92**	0.79**	0.61**	0.25
exotic	pauciennials	*Trifolium campestre*			<0.01**		

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
exotic	annuals	*Vicia sativa*		0.46	0.84	0.07	
exotic	perennial herbs	*Vicia cracca*				0.93	
exotic	perennial shrubs	*Cytisus scoparius*		0.54	0.16		

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
exotic	annuals	*Lathyrus odoratus* *Pisum sativum* *Trifolium dubium* *Trifolium subterraneum* *Vicia hirsuta* *Vicia sativa*		0.54	0.77**	0.02**	
exotic	perennial herbs	*Lotus corniculatus* *Trifolium pretense* *Trifolium repens*			0.08**	0.91**	0.99**
exotic	perennial shrubs	*Cytisus scoparius*		0.46	0.14*		
exotic	pauciennials	*Vicia villosa*			0.01	0.07**	<0.01**

Geraniales

(Geraniaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
exotic	annuals	*Erodium cicutarium* *Geranium dissectum* *Geranium molle*	1.00	1.00**	1.00	1.00	

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
exotic	annuals	*Geranium dissectum* *Geranium molle* *Geranium robertianum*	1.00	1.00	1.00**	1.00	1.00

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
exotic	annuals	*Geranium dissectum* *Geranium molle*		0.95	1.00*	1.00	
exotic	perennial shrubs	*Rosmarinus officinalis*		0.05			

Lamiales

(Phrymaceae, Plantaginaceae, Lamiaceae, Lentibulariaceae, Orobanchaceae, Scrophulariaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Aphyllon purpureum* *Collinsia grandiflora* *Collinsia parviflora* *Erythranthe alsinoides* *Erythranthe microphylla* *Erythranthe nasuta*	0.98**	0.70**	0.86	0.58	
native	perennial herbs	*Castilleja hispida* *Clinopodium douglasii*	<0.01	0.01	0.11		
exotic	annuals	*Lamium purpureum* *Veronica arvensis*	0.01**	0.29**	0.01		
exotic	biennials	*Digitalis purpurea*			0.02	0.01	
exotic	perennial herbs	*Prunella vulgaris*				0.41	

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Erythranthe alsinoides*	0.04				
native	perennial herbs	*Clinopodium douglasii*			0.45*	0.38**	
exotic	annuals	*Bellardia viscosa* *Lamium purpureum* *Veronica arvensis* *Veronica persica*	0.96**	1.00	0.06*	<0.01**	
exotic	biennials	*Digitalis purpurea*			0.48*	0.09**	
exotic	perennial herbs	*Prunella vulgaris*			0.01	0.27**	0.49
exotic	perennial shrubs	*Buddleja davidii* *Lavandula angustifolia*				0.26**	0.51

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Lycopus uniflorus* *Mentha canadensis* *Stachys chamissonis* *Utricularia gibba* *Veronica americana* *Veronica scutellata*			1.00	0.95	0.99***

exotic	annuals	*Lamium purpureum* *Veronica arvensis*		1.00			
exotic	perennial herbs	*Prunella vulgaris*				0.05	0.01**

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Clinopodium douglasii* *Erythranthe moschata* *Stachys chamissonis* *Veronica americana* *Veronica scutellata* *Veronica serpyllifolia*	0.04**	0.26	0.31**	0.16**	0.03
exotic	annuals	*Lamium hybridum* *Lamium purpureum* *Veronica arvensis*	0.96**	0.59**	0.08	0.04	
exotic	biennials	*Digitalis purpurea*			0.26	0.02*	
exotic	perennial herbs	*Agastache* sp. *Mentha* sp. *Mentha x piperita* *Monarda* sp. *Nepata cataria* *Origanum* sp. *Prunella vulgaris* *Salvia* sp.			0.35	0.78**	0.97**
exotic	perennial shrubs	*Syringa vulgaris*		0.15			

Liliales

(Liliaceae, Melanthiaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Erythronium oregonum* *Fritillaria affinis* *Toxicoscordion venenosum*	1.00**	1.00	1.00		

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
exotic	perennial herbs	*Tulipa* sp. *Lilium* sp.	1.00			1.00	

Myrtales

(Onagraceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	annuals	*Clarkia amoena* *Epilobium brachycarpum* *Epilobium foliosum* *Epilobium minutum*		1.00**	1.00	1.00	

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Circaea alpina*			1.00		

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Circaea alpina* *Epilobium ciliatum*			1.00	1.00	1.00

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Circaea alpina* *Chamaenerion angustifolium* *Epilobium ciliatum*			1.00	1.00	1.00

Rosales

(Crassulaceae, Grossulariaceae, Rhamnaceae, Rosaceae)

Dry semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Fragaria vesca* *Sedum spathulifolium*		0.85	0.34		
native	perennial shrubs	*Amelanchier alnifolia* *Holodiscus discolor* *Prunus emarginata* *Rosa gymnocarpa* *Rubus ursinus*		0.15	0.65		
exotic	perennial shrubs	*Rubus armeniacus*			0.01	1.00	

Dry modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Fragaria vesca* *Geum macrophyllum*		0.03	0.01*	<0.01**	
native	perennial shrubs	*Holodiscus discolor* *Ribes sanguineum* *Rubus leucodermis* *Rubus ursinus*	1.00	0.97	0.90*	0.13	
exotic	perennial shrubs	*Rubus armeniacus*			0.09	0.87**	1.00

		Rubus laciniatus					

Wet semi-natural

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Fragaria vesca* *Geum macrophyllum*	0.03	0.02	0.03		
native	perennial shrubs	*Oemleria cerasiformis* *Rubus leucodermis* *Rubus spectabilis* *Rubus ursinus* *Spiraea douglasii*	0.97	0.98	0.92	0.69	0.68
exotic	perennial shrubs	*Rubus armeniacus* *Rubus laciniatus*			0.05*	0.31	0.32

Wet modified

Provenance	PFT	Taxa	April	May	June	July	August
native	perennial herbs	*Fragaria vesca* *Geum macrophyllum*		<0.01	<0.01**	0.01**	
native	perennial shrubs	*Rosa gymnocarpa* *Rosa nutkana* *Rubus parviflorus* *Rubus spectabilis* *Rubus ursinus* *Spiraea douglasii*	0.11	0.12**	0.11	0.07	0.17
exotic	perennial herbs	*Fragaria* sp. *Fragaria vesca*	<0.01	0.04	<0.01**		
exotic	perennial shrubs	*Ceanothus thyrsiflorus* *Crataegus monogyna* *Rubus armeniacus* *Rubus laciniatus* *Rubus* sp.	0.87	0.73**	0.88**	0.92**	0.83
exotic	perennial tree	*Malus x domestica* *Prunus dulcis* *Prunus* sp. *Pyrus* sp.	0.02	0.11**			