Potential impact of Nootka lupine invasion on pollinator communities in Iceland

Jonathan Willow

Faculty of Life and Environmental Sciences
University of Iceland
Potential impact of Nootka lupine invasion on pollinator communities in Iceland

Jonathan Willow

60 ECTS thesis submitted in partial fulfillment of a Magister Scientiarum degree in Environment and Natural Resources

Advisors
Mariana Tamayo
Magnús H. Jóhannsson

Faculty of Life and Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
Reykjavik, May 2016
Potential impact of Nootka lupine invasion on pollinator communities in Iceland
60 ECTS thesis submitted in partial fulfillment of a Magister Scientiarum degree in Environment and Natural Resources

Copyright © 2016 Jonathan Willow
All rights reserved

Faculty of Life and Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
Sæmundargata 2
101, Reykjavik
Iceland

Telephone: 525 4000

Bibliographic information:

Printing: Háskólaprent
Reykjavik, Iceland, May 2016
Abstract

Declines in abundance and diversity of pollinating insects are widely documented throughout Europe. Invasive alien plant establishment is one of the numerous factors threatening pollinator communities. Throughout much of Iceland, the alien plant Nootka lupine (Lupinus nootkatensis) has established competitive colonies that have replaced native flowering plants. The reduction of flowering plant diversity associated with the spread of Nootka lupine could severely impact pollinators that are well-adapted to foraging on native flowering plants. The present study aimed to investigate how pollinator communities may be affected by the spread of Nootka lupine. It was expected that pollinator communities observed foraging on native flowering plants would be more diverse than those foraging on Nootka lupine. From June to August 2015, insects were collected from the flowers of Nootka lupine and native flowering plants in the heath adjacent to Lake Vifilsstaðavatn, in Heiðmörk, a conservation area in southwest Iceland. Specimens were later identified, and pollinator communities of Nootka lupine and native heath wildflowers were analyzed. Data gathered in this study suggests that Nootka lupine cannot sufficiently serve as a supplemental- and alternative food resource for Iceland’s insect pollinators. A number of Iceland’s pollinating taxa, including Iceland’s only native bee species, the heath bumblebee (Bombus jonellus), are at risk of severe population declines if Nootka lupine continues to replace native flowering plants throughout Iceland. Conservation of floral resources for insect pollinators should include both restoration and preservation of native wildflower communities, and eradication and control efforts to replace invasive plant communities with native species.
# Table of Contents

List of Figures ........................................................................................................ vi

Acknowledgements ..................................................................................................... ix

1 Pollinator conservation research in high latitude ecosystems ............................... 1
   1.1 Introduction ........................................................................................................ 1
   1.2 Flies .................................................................................................................. 1
   1.3 Resource Use .................................................................................................... 2
   1.4 Climate Change ............................................................................................... 3
   1.5 Plant Invasion and Range Expansion .............................................................. 4
   1.6 Ecological Restoration and Enhancement ...................................................... 4
   1.7 Conclusions ..................................................................................................... 6

2 Potential impact of Nootka lupine invasion on pollinator communities in Iceland ........................................................................................................ 7
   2.1 Introduction ....................................................................................................... 7
   2.2 Methods .......................................................................................................... 8
   2.3 Results ............................................................................................................. 9
   2.4 Discussion ....................................................................................................... 13

References ................................................................................................................ 19
List of Figures

Figure 1: Percent of individuals for each insect family encountered on native wildflowers and Nootka lupine in Heiðmörk.................................................................10
Figure 2: Number of individuals collected for the six most common insect families encountered on both native wildflowers and Nootka lupine in Heiðmörk..............11
Figure 3: Number of individuals collected for each bee species encountered on both native wildflowers and Nootka lupine in Heiðmörk.................................................................12
List of Tables

Table 1: Number of individuals collected for each insect family encountered on native wildflowers and Nootka lupine in Heiðmörk.................................................................9
Table 2: Number of individuals collected for each bee species encountered on both native wildflowers and Nootka lupine in Heiðmörk.................................................................12
Acknowledgements

I give immense thanks to my academic supervisor Mariana Tamayo for her guidance through this entire process. I also extend much thanks to my co-advisor Magnús H. Jóhannsson and my examiner Kristján Kristjánsson for their valuable advice; as well as Ólafur Patrick Ólafsson for generously providing me with laboratory space, and Victor Pajuelo Madrigal for his expertise in using ArcGIS.

The greatest thanks goes to my parents Marty and Barb for sharing the nature experience with me from the time I was born, and for 31 years of love and encouragement. Finally, I give special thanks to Cranberry Lake Biological Station.
1 Pollinator conservation research in high latitude ecosystems

1.1 Introduction

The loss and degradation of habitats caused by human activities appears to be the dominant threat to global biodiversity (Vié et al., 2009). At high latitudes such as arctic regions, although human-induced habitat loss is of great concern, the principle threat is climate change, as climate change synergistically exacerbates other threats, resulting in major ecological changes within high latitude ecosystems (Bennett et al., 2015). Among the major ecological changes further impacted by climate change are declines in inhabitable area for high latitude species (e.g., Franzén & Öckinger, 2012) and the potential for plant species invasion and dispersal into these ecosystems (e.g., Myers-Smith et al., 2011). Organisms at high latitudes must cope with seasonality, unpredictable physical conditions, and the stress associated with these environmental conditions; and they may be living closer to their physiological limits, possibly preventing them from being able to cope with additional human-induced stress (e.g., pollution) (Gabrielsen, 2014) However, research on the thermoregulatory capabilities of arctic bumblebee species from Alaska and Ellesmere Island revealed that the arctic bumble bee (Bombus polaris) has significantly higher abdominal temperatures than other bumblebee species in the arctic, and all bumblebee species from Alaska and Ellesmere Island have higher abdominal temperatures than temperate bumblebee species from Maine and Vermont, USA (Heinrich & Vogt, 1993). Additionally, low temperatures can delay recovery from disturbances, making high latitude ecosystems more vulnerable (Bennett et al., 2015).

Although recent studies have investigated the effects of adverse changes in arctic ecosystems on numerous taxa (e.g., Bennett et al., 2015; Laidre et al., 2015), insect pollinator communities at high latitudes have received relatively little attention in this regard. The aim of this chapter is to provide a cohesive review of insect pollinator research, and the ecological factors affecting insect pollinator communities, in high latitude ecosystems. Additionally, potential future research avenues, regarding the effects of climate change, alien plants, and ecological restoration, are discussed. Chapter 2 will present a study examining insect pollinator communities in southwest Iceland.

1.2 Flies

Research has shown that flies (Diptera) are important pollinators, especially in high latitudes (e.g., Kevan, 1970, 1972; Brown & McNeil, 2009). Observations in the high arctic, both of flies visiting multiple inflorescences on each plant visited (Kevan, 1970), and of a high proportion of captured flies carrying pollen (Kevan, 1972), highlight the need for pollinator studies in arctic and other high latitude regions to include flies. In these
regions, the role of flies as pollinators is likely further increased due to their high numbers (Kevan, 1972; Corbet & Danks, 1973; Lindegaard & Jónasson, 1979). In Ellesmere Island, Canada, more than 24 species of flies in ten families (Chironomidae, Empididae, Syrphidae, Muscidae, Calliphoridae, Sciaridae, Culicidae, Tachinidae, Agromyzidae, and Tipulidae) were observed carrying pollen (Kevan, 1972). In this study, 77% of all flower-visiting chironomids collected were carrying pollen, and they were by far the most abundant insect family collected from inflorescences. The second most abundant dipteran family collected was Empididae, of which 86% were carrying pollen. Furthermore, 85% of all muscids collected were carrying pollen. Researchers also observed that the positions in which flies forage nectar make pollen-transfer extremely likely (Kevan, 1972). Additionally, two of the primary pollinators of cloudberry (Rubus chamaemorus) in northern Quebec are the dipteran families Syrphidae and Muscidae, suggesting that habitat management encouraging healthy fly populations is critical for maximizing yields of cloudberry (Brown & McNeil, 2009).

Habitat management actions for promoting dipteran pollinator populations should include ensuring that there are abundant resources to support all life-stages of fly species in a given region. Future research in high latitude ecosystems should investigate the significance of different larval- and adult food resources for the maintenance of pollinating fly populations. Up-to-date analyses, regarding the role of various dipteran taxa in high latitude plant-pollinator networks, is necessary if we are to understand these networks in a changing environment.

### 1.3 Resource Use

A few studies have investigated resource use by insect pollinators at high latitudes (e.g., Kevan, 1972; Prŷs-Jones et al., 1981). For example, research in Ellesmere Island revealed plant-pollinator relationships and levels of pollinator dependency for 12 high arctic plant taxa. Results indicated that the flowering plant species most frequently visited by insect pollinators in this region are completely- or partially dependent on them for seed-set. Purple saxifrage (Saxifraga oppositifolia), northern white mountain avens (Dryas integrifolia), and arctic willow (Salix arctica) were among the most common flowering plants in the study region, and were pollinated primarily by flies, although partially dependent on both flies and bumblebees for maximum seed-set. Meanwhile, arctic lousewort (Pedicularis arctica) and capitate lousewort (P. capitata) were dependent on bumblebees for seed-set.

Other studies in Canada’s Northwest Territories and Ellesmere Island indicate that the arctic bumblebee (B. polaris) establishes colonies in abandoned lemming nests (Milliron & Oliver, 1966; Richards, 1973), as well as in snow bunting nests (Kukal & Pattie, 1988). Research has revealed that, in northern Quebec, cloudberry is pollinated mainly by four families of insect pollinators, namely the dipteran families Syrphidae and Muscidae, and the bee families Halictidae and Apidae (Brown & McNeil, 2009). In Iceland, the distribution, plant visitation, and forage significance has been studied for the heath bumblebee (B. jonellus) and garden bumblebee (B. hortorum). While heath bumblebees mostly were observed foraging among native wildflower species with short
corollas, and collected from all regions of Iceland, garden bumblebees were generally observed foraging on alien plants with longer corollas, and observed only in- and around Reykjavík, southwest Iceland (Prýs-Jones et al., 1981).

There remain data gaps regarding floral- and nesting resource-use by numerous important pollinator taxa in high latitude ecosystems. A future research avenue of high importance for pollinator conservation is to investigate resource use (e.g., foraging, nesting) with respect to a broad range of high latitude insect pollinator taxa. These studies should be conducted across all high latitude regions.

1.4 Climate Change

Climate warming has led in some cases to potentially beneficial habitat changes for some pollinators in arctic regions, such as in Padjelanta National Park in northern Sweden, where there has been a 65% reduction in glacial area over 110 years, and an increase in mountain birch forest. However, it is believed that these benefits are only temporary, and pollinator species dependent on high alpine habitats are threatened by climate warming in the arctic and other high latitude areas, as their inhabitable area (i.e. food- and nesting resources) is declining (Franzén & Öckinger, 2012). The loss of insect pollinators typically results from the loss of their required foraging, nesting, and overwintering resources (Potts et al., 2010). Indeed, modelling of plant-pollinator data from Greenland has indicated that the loss of pollinators from the plant-pollinator network is highly correlated with the loss of plants from the network (Pradal et al., 2009).

Future snow-cover scenarios in high latitudes are very uncertain, and predictions range from deeper, more prolonged snow cover, to reduced depths- and earlier melting of snow (Cooper et al., 2011). Research on white arctic mountain heather (Cassiope tetragona), an important food source for insect pollinators (Kevan, 1972), demonstrated that experimentally-increased snow depth resulted in significantly reduced growth of this plant, most likely as a result of shorter growing season and delayed phenology (Morgner, 2010). However, studies on the effects of snow depth on the abundance of flowers and growth of nine other common arctic plants in Svalbard showed that responses to changes in snow depth vary and are species-specific (Semenchuk et al., 2013; Rumpf et al., 2014).

Research investigating how various snow regimes affect different flowering plants in high latitudes may be very useful for developing predictive models of arctic plant community change. In order to understand how changes in snow regimes might affect insect pollinator communities in the long-term, research into the effects on flowering, phenology, and growth should be conducted for a much broader range of flowering plant species in high latitudes. Additionally, up-to-date observational studies examining the roles of different flowering plant species within high latitude plant-pollinator networks should be conducted, as this would help guide predictive model development and conservation management.
1.5 Plant Invasion and Range Expansion

Increases in biomass, cover, and abundance of shrubs have been documented in many high latitude tundra ecosystems in the past century. These encroachments are primarily of alder in northern Alaska, alder and willow in western arctic Canada, dwarf willow and evergreen shrub species in the Canadian high arctic, birch in northern Quebec, and willow in arctic Russia (Myers-Smith et al., 2011). In Svalbard, the number of locations with the high latitude subspecies of the dwarf evergreen shrub crowberry (*Empetrum nigrum* ssp. *hermaphroditum*) is noticeably increasing. Moreover, indigenous people of the Russian- and Canadian arctic are observing increases in shrub cover within their territories (Myers-Smith et al., 2011). This phenomenon is thought to be mostly catalyzed by climate-driven range expansions, and it will likely result in a declining of habitat for numerous plant species, particularly tundra grassland specialists (Bennett et al., 2015), and subsequently any insect pollinators dependent upon these plant species. The degree of impact will depend on the rate and degree of climate change, as well as the dispersal abilities of these shrub species (Boelman et al., 2015). Pollen records suggest that alder, birch, and willow species were more widespread across mid- and high arctic ecosystems during warmer and wetter periods after the last glacial maximum, suggesting that shrub species are well adapted for colonizing or becoming more abundant in tundra ecosystems when growing conditions are favorable (Myers-Smith et al., 2011). In addition to shrub encroachment, species invasions resulting directly from human introductions are likely to increase in high latitude ecosystems, in part due to increases in tourism and shipping (Ware et al., 2012, 2014).

The effects of different invasive or range-expanding plant species on insect pollinator communities in these ecosystems needs to be investigated. Knowledge of how various incoming plant species affect these ecosystems will allow optimum prioritization of conservation needs. It is often difficult to differentiate between human-induced plant invasion and climate-driven range expansion (Bennett et al., 2015). In either case, investigating the potential impacts of various incoming plant species on native wildflower- and pollinator communities should provide valuable information for modelling future changes in vegetation and the plant-pollinator network. Investigating the use of plant species immigrating into high latitude ecosystems as resources (i.e., foraging, nesting, and overwintering sites) for pollinators, as well as the rate at which these plant species replace native wildflower communities, will be critical for understanding the potential impacts of these immigrating plant species on the regional plant-pollinator networks.

1.6 Ecological Restoration and Enhancement

The potential for restoration and creation of pollinator habitat to enhance pollinator populations needs to be studied in high latitude ecosystems. However, ecological restoration in high latitudes has innate difficulties, as low temperatures in these environments can delay recovery from disturbance (Bennett et al., 2015), and succession is slow, requiring tens to hundreds of years (Cargill & Chapin, 1987; Harper & Kershaw, 1997; Forbes et al., 2001). Research indicates that adding fine textured- and organic matter
accelerates soil and plant community development (Cargill & Chapin, 1987; Wong, 2003; Naeth & Wilkinson, 2014), and that without the addition of plant propagules and organic matter, restoration of highly disturbed sites in the arctic will not occur (Cargill & Chapin, 1987; Forbes et al., 2001; Naeth & Wilkinson, 2014). Results of different reclamation treatments in Iceland showed that total plant cover was significantly higher in seeded and fertilized areas than in control plots, especially when biological crusts (i.e., mosses and lichens) were included in analyses (Gretarsdottir et al., 2004). In this study, long-term seeding and fertilization were beneficial for the formation of persistent plant cover that promotes plant colonization (Gretarsdottir et al., 2004). In addition, tundra plant community stability and resilience may rely on mosses and lichens, as they regulate surface temperature and water availability, and are important for succession by benefitting plant seeds and seedlings in tundra surface layers (Naeth & Wilkinson, 2014). Future restoration ecology studies should aim to develop methods to quicken the successional process in a way that fosters rich, diverse, and resilient wildflower communities that benefit plant-pollinator networks.

Hagen (2002) examined the restoration potential of 12 native arctic species from Svalbard by studying the germination ability of seeds and bulbils, and the rooting ability of cuttings. Responses of each species differed among the species. Bulbils of alpine bistort (Bistorta vivipara) showed the highest germination rate, while seeds of a wood-rush species (Luzula arcuata ssp. confusa), mountain sorrel (Oxyria digyna), and Svalbard poppy (Papaver dahlianum) also germinated well. In contrast, the lowest germination response was observed in mountain avens (D. octopetala) (Hagen, 2002). In the experiments with cuttings, species that rooted well included dwarf willow (Salix herbacea), polar willow (S. polaris), kinnikinnick (Arctostaphylos uva-ursi), crowberry (E. nigrum ssp. hermaphroditum), and lingonberry (Vaccinium vitis-idaea), while species showing the weakest rooting included mountain avens and white arctic mountain heather (C. tetragona). These results indicate several species’ potential for use in ecological restoration, and Hagen’s (2002) study should inspire future research to test different methods of propagating native forage plants that are important for insect pollinators in other high latitude regions. Additionally, future studies regarding the ability of propagated plants to survive, grow, and reproduce in situ will be crucial for determining the suitability of different plant species for restoration endeavors (Hagen, 2002). Results from these types of studies would be very useful for restoration practitioners working to promote pollinator habitat in different high latitude ecosystems.

Creating pollinator habitat in urban environments should be a priority too, particularly due to the negative effects of urban development on resources important for insect pollinators, such as forage and nesting sites (McIntyre & Hostetler, 2001; Banaszak-Cibicka, 2012; Deguines et al., 2012). Research has shown reduced diversity and species richness of pollinators with urbanization (McIntyre & Hostetler, 2001; Matteson et al., 2008; Ahrné et al., 2009; Hernandez et al., 2009; Kearns & Oliveras, 2009; Bates et al., 2011; Baldock et al., 2015). For example, a study of the hover fly and bee community in and around Birmingham, England, showed that rural sites host significantly greater abundance and species richness of pollinators (Bates et al., 2011). Urban environments can, however, provide resources for pollinators (McFrederick & LeBuhn, 2006; Hopwood, 2008; Osborne et al., 2008; Larson et al., 2014; Potter & LeBuhn, 2015; Hausmann et al.,
2016). A recent study in Ontario, Canada revealed a positive relationship between pollinator abundance and the proportion of urban garden area planted with native flowering plants (Fukase & Simons, 2016). This positive relationship was present when all pollinators were accounted for, as well as when bumblebees, honey bees, megachilid- and andrenid bees, and vespid wasps were analyzed separately. Interestingly, garden area did not have a significant effect. A positive relationship was, however, present between flowering plant density and pollinator abundance (Fukase & Simons, 2016). Research in high latitudes should compare insect pollinator communities of urban areas with those of surrounding landscapes. Furthermore, urban studies in high latitudes should attempt to create habitats rich with pollinator resources, and analyze the use of these resources by local pollinator communities. Such studies are relatively inexpensive and may represent great contributions to biodiversity conservation in high latitudes.

1.7 Conclusions

This chapter has provided a review of research conducted in high latitudes, regarding insect pollinators and issues surrounding the resources on which they depend. In addition, potential research avenues relevant to the conservation of pollinator communities in arctic- and other high latitude ecosystems have been presented here. Investigations into the role of flies as pollinators in high latitude ecosystems indicate that pollinator research and conservation management in these regions need to consider dipteran communities. Studies regarding resource use of the broad pollinator community in high latitudes have typically been conducted in northern Canada (e.g., Kevan, 1972; Brown & McNeil, 2009), and there is a need to extend and conduct these types of studies throughout the arctic and other high latitude regions. Research investigating the roles of different plant- and insect species within plant-pollinator networks in high latitude regions, combined with studies on the potential effects of climate change on different flowering plant species in the north, is crucial in order to develop accurate predictive models of plant-pollinator networks, and will be valuable for effective and holistic conservation management. Increases in biomass, cover, and abundance of shrubs in high latitude tundra ecosystems will likely result in declines of numerous plant species, as well as the pollinators that rely on them. Investigating the effects of how different invasive- and range expanding plants may affect high latitude plant-pollinator networks will also help guide conservation management in these regions.

With regard to ecological restoration in arctic- and other high latitude ecosystems, methods to quicken successional processes for the benefit of native wildflower communities should be studied. Additionally, studies testing various propagation methods for native plant species relevant to pollinator conservation in northern regions (e.g., Hagen, 2002) need to be carried out to provide region-specific guidance for restoration actions across the north. Lastly, as urban development negatively impacts pollinator habitat, and since these environments are capable of providing valuable habitat for pollinator communities, attempts should be made to enhance pollinator resources in high latitude urban environments, and subsequently analyze the impacts that these enhancements have on pollinator communities.
2 Potential impact of Nootka lupine invasion on pollinator communities in Iceland

2.1 Introduction

Declines in abundance and diversity of pollinating insects are widely documented throughout Europe (e.g., Maes & Van Dyck, 2001; Biesmeijer et al., 2006; Kosior et al., 2007; Fox, 2013). Research indicates that 9.2% of bee species in Europe, for which there are sufficient data (only 43.3% of Europe’s bee species), are threatened with extinction (Nieto et al., 2014). Bees and other pollinating animals have a vital function in the maintenance of wild- and agricultural plant communities. Globally, it is estimated that 87.5% of all flowering plant species are pollinated by animals (Ollerton et al., 2011), and approximately one-third of all human food benefits from this ecosystem service (Wratten et al., 2012). The loss of pollinators from a community may not be easily reversed, and it could have serious impacts on birds, spiders, and other predators of pollinators (Allen-Wardell et al., 1998).

Loss of pollinators primarily occurs as a result of habitat loss and degradation, typically by the conversion- and homogenization of land and the associated loss of foraging, nesting, and overwintering sites, as well as the application of agrochemicals that can decrease food resource availability for pollinators or have lethal effects on the insects themselves (Kosior et al., 2007; Potts et al., 2010). Another anthropogenic threat to pollinators, particularly bees, is the translocation of alien bees, which not only increases the risk of pathogen spread, but can also negatively affect genetic diversity as a result of interbreeding with endemic populations, leading to the extinction of local sub-species (Potts et al., 2010).

Invasive plants are another factor threatening pollinator communities. The establishment of invasive plants can lead to habitat loss for pollinators by aggressively competing with native plants for abiotic (water, nutrients, light, and space) and biotic (e.g., pollination services) resources (Stout & Morales, 2009). However, the effects of plant invasions on pollinator communities have been shown to vary within different communities (Traveset & Richardson, 2006; Bjerknes et al., 2007; Stout & Morales, 2009). A study near Kraków, Poland revealed greater abundance and species richness of bees, butterflies, and hover flies in meadows that were not invaded by alien goldenrods (Solidago canadensis and S. gigantea), compared to invaded meadows (Moron et al., 2009). Additionally, research in open dune habitat in Michigan, USA, revealed that insect visitation to flowers of the threatened plant Pitcher’s thistle (Cirsium pitcheri) was 3.2 times greater in plots where the invasive plant baby’s breath (Gypsophila paniculata) had
been removed, compared to invaded plots (Baskett et al., 2011). On the other hand, the same study revealed significantly greater abundances of halictid bees and hover flies in sites invaded by baby’s breath, compared to uninvaded sites (Baskett et al., 2011). Also, research in Sweden revealed that pollinator visitation to two native plants, common bird’s-foot trefoil (Lotus corniculatus) and clammy campion (Lychnis viscaria), was higher for plants adjacent to invasive Russell lupine (Lupinus polyphyllus) plants, compared to plants that were 200 m away from the closest Russell lupine plant (Jakobsson et al., 2015), indicating an attraction to both native and invasive plants. These results were partially attributed to Russell lupine’s showy flowers on tall shoots, which presents an attractive visible cue to pollinators. Similarly, in coastal Mediterranean shrubland habitat in northeastern Spain, the invasive plants Elands sourfig (Carpobrotus affine acinaciformis) and erect prickly pear (Opuntia stricta) have larger flowers than any of the co-occurring native plants, and they significantly attract a greater number of pollinator species, and have more pollinator visitations, than any native plant in the area (Bartomeus et al., 2008). In addition, research in Japan revealed a larger number of pollinator visits to an invasive dandelion (Taraxacum officinale), compared to a native dandelion (T. japonicum), possibly as a result of the invasive dandelion’s larger flower size and higher production of nectar (Kandori et al., 2009). Although numerous studies have investigated the effects of invasive plants on insect pollinators, to the author’s knowledge there is a lack of research regarding these relationships at high latitudes.

In Iceland, the distribution, plant visitation, and forage significance has been studied for the heath bumblebee (Bombus jonellus) and garden bumblebee (B. hortorum). The heath bumblebee was observed visiting an invasive alien plant, Nootka lupine (Lupinus nootkatensis), and researchers suggested that Nootka lupine was a mildly-significant source of pollen for the heath bumblebee (Prŷs-Jones et al., 1981). The dramatic changes in vegetation that have taken place over the last few decades, particularly with respect to Nootka lupine’s distribution (Magnússon, 2010), combined with the lack of published research on the broader pollinator community, begs an analysis of plant-pollinator relationships in Iceland, especially regarding Nootka lupine. The present study aims to provide a descriptive comparison of how pollinator communities differ between Nootka lupine and the native flowering plants in heath habitat in Iceland. In addition, the study will guide and prioritize future research regarding insect pollinators and invasive plants, as well as enhance our knowledge of plant-pollinator interactions, in high latitude areas such as Iceland. Finally, the findings of this study will give an indication of whether or not Nootka lupine can sufficiently serve as a supplemental- and alternative food resource for Iceland’s insect pollinators, in the event that Nootka lupine continues to replace native flowering plant communities throughout Iceland.

2.2 Methods

All sampling was conducted within a 0.58 km² area of heath habitat adjacent to Lake Vífillstaðavatn, in Heiðmörk, a conservation area in southwest Iceland. Here, the flowering plant network is represented by a mosaic of dense Nootka lupine patches and patches of native flowering plants, consisting of both woody and herbaceous flora.
Sampling took place under full sun and in low-wind conditions, in order to maximize insect pollinator activity. Insects were collected during the summer of 2015, from June 21 to August 3, during the flowering period of Nootka lupine.

The sampling methodology consisted of timed meanderings (Goff et al., 1982) within Nootka lupine patches and adjacent patches of native heath wildflowers. Each timed meander was 30 minutes in length, and each 30-minute survey focused on either Nootka lupine or native heath wildflowers. On each day of sampling, equal time was spent collecting insects in both of these flowering-plant-community categories, and the flowering-plant community in which sampling took place changed after each 30-minute sampling segment. Overall, sampling took place on 9 different days, with a total of 64 surveys being conducted (32 within native heath wildflowers and 32 within Nootka lupine).

During sampling, if an insect was found to be in contact with a reproductive structure within a flower, the insect was then considered to be a potential pollinator, and subsequently collected and killed in a jar containing a cotton ball soaked with 100% acetone. After each day of sampling, the insects collected were preserved in 80% ethanol.

In the laboratory, most insects were identified to family, except for bees which were identified to species. Because the samples were inadvertently pooled in the laboratory, only descriptive comparisons regarding taxonomic richness and abundance were made between Nootka lupine and native heath wildflowers.

### 2.3 Results

Overall, 767 individual insect pollinators, representing 24 insect families (Table 1; Fig. 1), were counted. These insects encompassed the orders Diptera, Hymenoptera, Trichoptera, Lepidoptera, and Coleoptera. The majority of insects, 647 individuals (84% of collected insects), occurred on native heath wildflowers and included 22 taxonomic families. In contrast, only 120 individuals (16% of collected insects) were found on Nootka lupine, representing 12 taxonomic families. The most commonly observed insects were from the bee family Apidae, followed by the dipteran families Bibionidae, Fanniidae, Muscidae, Chironomidae, and Syrphidae (Table 1; Fig. 2).

<table>
<thead>
<tr>
<th>Insect Family</th>
<th>collected from native wildflowers</th>
<th>collected from <em>Lupinus nootkatensis</em> flowers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apidae</td>
<td>237</td>
<td>40</td>
</tr>
<tr>
<td>Bibionidae</td>
<td>112</td>
<td>6</td>
</tr>
<tr>
<td>Fanniidae</td>
<td>94</td>
<td>2</td>
</tr>
<tr>
<td>Muscidae</td>
<td>68</td>
<td>12</td>
</tr>
<tr>
<td>Syrphidae</td>
<td>49</td>
<td>7</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>48</td>
<td>32</td>
</tr>
<tr>
<td>Limnephilidae</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Pteromalidae</td>
<td>6</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 1: Number of individuals collected for each insect family encountered on native wildflowers and Nootka lupine in Heiðmörk.
<table>
<thead>
<tr>
<th>Insect family</th>
<th>Collected from native wildflowers</th>
<th>Collected from Lupinus nootkatensis flowers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chrysomelidae</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Geometridae</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Simuliidae</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Braconidae</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Sciaridae</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Tenthredinidae</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Eulophidae</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Vespidae</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Ditomyiidae</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Phoridae</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Tipulidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Lonchopteridae</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Dolichopodidae</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Empididae</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Lauxaniidae</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Acartophthalmidae</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>647</td>
<td>120</td>
</tr>
</tbody>
</table>

Figure 1: Percent of individuals for each insect family encountered on native wildflowers and Nootka lupine in Heiðmörk.
Figure 2: Number of individuals collected for the six most common insect families encountered on both native wildflowers and Nootka lupine in Heiðmörk.

On native heath wildflowers, the most abundant insect families were Apidae (237), Bibionidae (112), Fanniidae (94), Muscidae (68), Syrphidae (49), and Chironomidae (48) (Table 1; Fig. 2). In contrast, the most common insect families on Nootka lupine were Apidae (40), Chironomidae (32), Muscidae (12), Lauxaniidae (11), Syrphidae (7), and Bibionidae (6) (Table 1). Interestingly, members of the dipteran families Lauxaniidae and Acartophthalmidae were only observed on Nootka lupine. However, insects from the dipteran families Simuliidae, Sciaridae, Ditomyiidae, Phoridae, Lonchopteridae, Dolichopodidae, and Empididae only occurred on native heath wildflowers. Similarly, insects from the parasitoid wasp families Pteromalidae, Braconidae, and Eulophidae, and the wasp families Tenthredinidae and Vespidae, were only detected on native heath wildflowers.

Five bee species from the family Apidae were found on both Nootka lupine and native heath wildflowers (Table 2; Fig. 3). Four of the five species were bumblebees (B. jonellus, B. lucorum, B. hypnorum, and B. hortorum), while the fifth species was the honeybee (Apis mellifera). The heath bumblebee (B. jonellus) was primarily found on native heath wildflowers (139 individuals) rather than Nootka lupine (5 individuals). All other bee species were also more common on native heath wildflowers, except for the garden bumblebee (B. hortorum) which was similar on both plant communities.
Table 2: Number of individuals collected for each bee species encountered on both native wildflowers and Nootka lupine in Heiðmörk.

<table>
<thead>
<tr>
<th>Bee Genus</th>
<th>collected from native wildflowers</th>
<th>collected from <em>Lupinus nootkatensis</em> flowers</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bombus jonellus</em></td>
<td>139</td>
<td>5</td>
</tr>
<tr>
<td><em>Bombus lucorum</em></td>
<td>47</td>
<td>28</td>
</tr>
<tr>
<td><em>Bombus hypnorum</em></td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td><em>Bombus hortorum</em></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Apis mellifera</em></td>
<td>43</td>
<td>5</td>
</tr>
</tbody>
</table>

Figure 3: Number of individuals collected for each bee species encountered on both native wildflowers and Nootka lupine in Heiðmörk.

Other insects were also found on both native heath wildflowers and Nootka lupine, and they included the families Limnephilidae (Trichoptera), Geometridae (Lepidoptera), Chrysomelidae (Coleoptera), and Tipulidae (Diptera).

There was no standardized data collection regarding the number of pollinator visits received by each species of native heath wildflower. However, during the sampling period, it was clearly noticed that bumblebees were collected most frequently on the flowers of wood crane’s-bill (*Geranium sylvaticum*), wild thyme (*Thymus praecox* subsp. *arcticus*), and water avens (*Geum rivale*) during their respective flowering periods. Members of multiple dipteran families (e.g., Fanniidae, Muscidae) were frequently collected from the flowers of buttercups (*Ranunculus* spp.).
2.4 Discussion

The results of this study reveal clear differences in insect pollinator communities between the invasive flowering plant Nootka lupine and native flowering plants in heath habitat in Iceland. The community of insect pollinators on native heath wildflowers was almost twice as taxonomically-rich as that of Nootka lupine. These results, and their implications, are similar to that of Moron et al. (2009), and different from those of Bartomeus et al. (2008) and Kandori et al. (2009). The results this study suggest that, given the rapid spread of Nootka lupine throughout Iceland (see Magnússon, 2010), both insect pollinator diversity and abundance are likely to decrease over time, and plant and animal communities that are dependent on these pollinators will likely be negatively impacted.

Only one bee species, the heath bumblebee (*B. jonellus*), is considered native to Iceland; and this species was detected during this study. The white-tailed bumblebee (*B. lucorum*), the tree bumblebee (*B. hypnorum*), and the garden bumblebee (*B. hortorum*) are considered alien to Iceland. These bumblebee species most likely came to Iceland hibernating in cargo, and honeybees (*A. mellifera*) were imported to Iceland in the early 1900s; and the first attempt to breed honeybees occurred in 1936 (K. Kristjánsson, Reykjavík University, personal communication, March 7, 2016). All bee species detected in this study were more common on native heath wildflowers than Nootka lupine, with the exception of the garden bumblebee which was similar on both plant communities. Moron et al. (2009) also discovered a significantly greater abundance of bees, as well as significantly greater bee species richness and diversity, in uninvaded wildflower patches. It has been suggested that Nootka lupine is a mildly-significant source of pollen for the heath bumblebee (Prŷs-Jones et al., 1981). However, the results of this study suggest that Nootka lupine may have negligible value as a forage resource for the heath bumblebee, as only five of the 144 heath bumblebees were collected on Nootka lupine. Moreover, this research shows the importance of the native heath wildflower community to both native- and alien bee pollinators. An additional possible reason for the small number of heath bumblebees observed using Nootka lupine relates to a possible competitive exclusion due to the frequent presence of a larger bumblebee species, the white-tailed bumblebee, in Nootka lupine stands. Twenty-eight individuals (much more than for any other bee species in this study) of the white-tailed bumblebee were collected from Nootka lupine inflorescences. The infrequent observations of any other bee species in Nootka lupine stands may be due in part to aggressive territorial behavior by white-tailed bumblebees. To further explore the significance of Nootka lupine and native wildflowers as sources of pollen for the heath bumblebee, the occurrence of heath bumblebees on different flowering plants should be studied throughout the heath bumblebee’s Icelandic distributional range, including areas where the white-tailed bumblebee is not present. Additionally, research should analyze pollen loads from the corbiculae of heath bumblebees, in order to analyze this species’ use of Nootka lupine and different native wildflowers with greater accuracy.

Bumblebees (*Bombus* spp.) are of especially high conservation interest. They have evolved behaviors (e.g., pollen-gathering, buzz pollination), morphological structures (branched body hairs well-adapted for collecting- and retaining pollen), and endothermic capabilities, that make them well-adapted for transporting large amounts of pollen (De Luca & Vallejo-Marín, 2013; Heinrich & Vogt, 1993). The heath bumblebee, as the only
bee species native to Iceland, is an ideal focal bee species for pollinator conservation in Iceland. With that in mind, the great difference in the number of observations of the heath bumblebee, between Nootka lupine and native heath wildflowers (28 times more heath bumblebees observed on native heath wildflowers), is of great concern. The results of this study indicate that the heath bumblebee may rely on native heath wildflowers for foraging habitat.

So far, studies in Iceland on pollinator diversity and communities have focused on bumblebee species (e.g. Prŷs-Jones et al., 1981). This study indicates that other important insect pollinators seem to have a clear preference for native heath wildflowers over Nootka lupine. For example, hover flies (Syrphidae) are the most widely studied dipterans with respect to pollination, and their importance as pollinators is widely-acknowledged (Larson et al., 2001). This study also confirms the relevance of hover flies as pollinators in Icelandic heath habitat, as they were the sixth most abundant family collected. In addition, results indicate that hover flies are important pollinators of native plant communities in Iceland, as they were seven times more numerous on native heath wildflowers than on Nootka lupine.

Pollinator conservation studies, when discussing flies, often focus only on members of the family Syrphidae, despite the evidence that non-syrphid flies are important pollinators, especially in high latitudes (e.g., Kevan, 1970, 1972; Brown & McNeil, 2009). Research on Ellesmere Island, Canada, revealed high percentages of individuals within numerous dipteran taxa carrying pollen grains (Kevan, 1972). Furthermore, Kevan (1972) concluded that the positions in which dipterans forage nectar suggest that the transfer of pollen is extremely likely. Additionally, recent research analyzing pollen loads in temperate ecosystems estimated that 84% of the pollen carried by flies was carried by non-syrphid flies (Orford et al., 2015). In high latitudes, the role of flies as pollinators is likely further increased due to their high numbers (Kevan, 1972; Corbet & Danks, 1973; Lindeggaard & Jónasson, 1979). These results challenge the ongoing idea that syrphids are the only group of flies that are of significance to pollination studies. In this study, non-syrphid flies were also common pollinators, representing 50% of insects detected, and 87% of flies detected. A very striking preference towards native heath wildflowers was seen, with regard to the dipteran families Bibionidae, Fanniidae, and Muscidae. Members of these three families have previously been shown to be efficient pollen vectors from tropical to arctic and alpine regions (Johnson & Steiner, 1994; Larson et al., 2001; Goldblatt et al., 2005; Brown & McNeil, 2009). Overall, this study also highlights the importance of non-syrphid Diptera as pollinators within native heath wildflower communities in Iceland.

Of the 767 insects identified in this study, 80 were member of the dipteran family Chironomidae (non-biting midges). Though they were observed to be in contact with floral reproductive structures, their effectiveness as pollinators is unknown. It has been suggested that, as they may often only visit one inflorescence within their short life-span, they may not be significant as pollinators (Larson et al., 2001). However, research on Ellesmere Island, Canada revealed that 77% of all flower-visiting midges collected were carrying pollen, and they were by far the most abundant insect family collected from inflorescences (Kevan, 1972). The abundance of midges, especially in northern ecosystems, such as Iceland’s Lake Mývatn (Lindegaard & Jónasson, 1979), also begs further inquiry into their role in pollination.
Floral morphology may influence whether a particular insect visits an inflorescence. In an alpine Chilean study, the pollinator assemblage and number of visits to an invasive dandelion (*T. officinale*) was similar to that of two native wildflower species also of the Family Asteraceae (*Hypochaeris thrincioides* and *Perezia carthamoides*). These results were partially attributed to the similar floral morphologies between these plant species (Muñoz & Cavieres, 2008). Here in Iceland, it was observed that the floral morphologies of the native heath wildflowers were dissimilar to that of Nootka lupine, possibly accounting in part for the differences in plant visitation. Nootka lupine flowers require a slight amount of pressure (e.g., a bumblebee landing) upon the lower “wing” pedals, in order for the flower’s “keel”, which holds the stamens, to be exposed. This can limit pollen-access to situations where the keel has been exposed, though sometimes insects can be observed to have partially entered through the opening between the lower wing pedals.

In order for pollinator populations to persist, all ecological requirements must be available within flight range (Westrich, 1996; Steffan-Dewenter et al., 2002; Steffan-Dewenter, 2003). Additionally, habitats providing seasonal successions of forage plants allow more-diverse pollinator assemblages (Fussell & Corbet, 1992; Corbet, 1995). The flight range of species of conservation interest must be considered as well. Research with bees has shown body size to correlate with flight range, i.e. larger bees having a larger flight range (van Nieuwstadt & Iraheta, 1996; Gathmann & Tscharntke, 2002; Greenleaf et al., 2007). Therefore, resource utilization occurs at different spatial scales depending on bee size (Kremen et al., 2007; Ockinger & Smith, 2007; Winfree et al., 2009). The abundance of small bees is impacted by landscape parameters at smaller spatial scales, with the same pattern existing for medium-sized and large-sized bees respectively (Tscheulin et al., 2011). In the absence of coordinated eradication and control measures for Nootka lupine, combined with native plant restoration efforts, native wildflower communities will likely become smaller, more fragmented, and exist farther apart, thus hindering the conservation of insect pollinators in Iceland. Indeed, studies have found positive correlations between habitat connectivity and both abundance- and species richness of bees (Steffan-Dewenter, 2003; Gonçalves et al., 2014). Future research in Iceland should study the responses of pollinator communities to increases in floral resource connectivity. In addition, restoration efforts should be implemented in a way that the critical ecosystem service of pollination, as well as genetic exchange of both plants and pollinators, is maintained at all relevant spatial scales.

The idea of alternative stable states suggests that a sufficiently large perturbation, when applied to an ecological variable (e.g., food resource availability), can cause an ecological community to shift from one state of equilibrium to another (Beisner et al., 2003). Indeed, research on the impact of habitat loss on pollinators suggests a threshold beyond which habitat loss inevitably would lead to the collapse of the plant-pollinator network (Fortuna & Bascompte, 2006). In Greenland, plant-pollinator models show a positive correlation between the loss of pollinators and the loss of plants within the network (Pradal et al., 2009). Furthermore, a study in Great Britain and the Netherlands revealed that plant species that rely on declining pollinators have themselves declined (Biesmeijer et al., 2006). If Nootka lupine continues to replace native flowering plant communities throughout Iceland, then the native plant community’s mutualistic insect partners will likely also undergo population declines. This represents a positive-feedback
cycle, with the end result potentially being an ecological shift from a state where plant-pollinator mutualisms sustain themselves, to a state where numerous plant-pollinator mutualisms are lost.

Efforts to simultaneously eradicate and control Nootka lupine and restore native vegetation must be considered, if pollinator conservation efforts are to be successful. Herbicide application has had good results for the eradication of yellow bush lupine (*L. arboreus*), which has become a pest in New Zealand. Increases in graminoid cover were observed following herbicide treatment of yellow bush lupine (the herbicide Versatil™ was used due to its effectiveness, at low concentrations, on legumes) (Konlechner et al., 2015). These increases in graminoids were likely due to a rapid increase in soil productivity may explain these increases, as large amounts of nitrogen in forms available to plants are released during the decay of lupine species (Maron & Connors, 1996), and also because graminoids tend to respond particularly well to nutrient enhancement (Hobbs & Huenneke, 1992). Thus, future research on Nootka lupine eradication and control, and pollinator habitat restoration, in Iceland, should incorporate legume-targeting herbicide treatments, and encouraging the growth of native wildflowers and native graminoids.

Urban areas, especially Reykjavík, are of particular importance for restoration, as they have most-likely lost a disproportionately large percentage of their pollinator habitat (i.e., foraging, nesting, and overwintering sites). Educational programs intended to promote urban gardening with native wildflowers, and increase awareness of the value of native wildflowers and pollinators, would help to reduce importations of alien plants (Stout & Morales, 2009), and benefit pollinators.

To maximize the benefit for pollinator conservation in urban and wild areas, restoration efforts should encourage native flowering plant communities that provide food resources for pollinators throughout the growing season, in order to support diverse pollinator communities. Simultaneously, the heath bumblebee and other native pollinators should be the target-group for such initiatives. Thus, research determining the significance of different native wildflower species, regarding the provision of forage resources, would provide valuable information for the conservation of individual pollinator taxa (e.g., Prŷs-Jones et al., 1981). Additionally, future research in Iceland should study the responses of pollinator communities to the restoration of different native plant communities.

Bumble Bee Watch (Bumble Bee Watch, 2016a) is a citizen science project led by the Xerces Society (2016a), an organization based in the United States. The project allows individuals to upload photos of bumblebees, with identifications verified by experts. This project helps scientists determine the status and conservation needs of bumblebee species, and helps locate rare- or endangered populations of bumblebees. In addition to increasing peoples’ knowledge of bumblebee ecology and conservation efforts, the project helps citizen scientists connect with each other (Bumble Bee Watch, 2016b). Additionally, the Great Sunflower Project (Great Sunflower Project, 2016), a nationwide citizen science effort in the United States, has been helping to establish baseline information on pollinator services and critical resources for insect pollinators, and identifying areas of conservation concern. The project encourages people throughout the United States to collect data on insect pollinators in their yards, gardens, parks, and schools (Xerces Society, 2016b). In the Great Sunflower Project, individual citizen scientists count pollinator visitations to individual wildflowers, also recording the type of plant, type of pollinators visiting the
Pollinator conservation in Iceland would benefit from programs analogous to Bumble Bee Watch and the Great Sunflower Project, as it would engage the public in pollinator conservation efforts, and provide scientists with useful data for understanding the conservation needs of insect pollinators throughout Iceland.

The data gathered from this study suggest that Nootka lupine cannot sufficiently serve as a supplemental- and alternative food resource for Iceland’s insect pollinators. Thus, a number of Iceland’s insect pollinators, including Iceland’s only native bee species, the heath bumblebee, are at risk of declining due to the spread of Nootka lupine around the country. Conservation of floral resources for insect pollinators should include both restoration- and preservation of native wildflower communities, and efforts to replace invasive plant populations (e.g., Nootka lupine, cow parsley (Anthriscus sylvestris)) with native plant populations. Promoting the conservation of the heath bumblebee will benefit other insect pollinators as well as native plant communities. However, in order to promote pollinator diversity, it is important to identify significant floral resources for other important pollinator taxa in Iceland. Aside from areas currently invaded by alien plants, pollinator habitat should be restored in urban areas, like Reykjavík, as well as encouraged throughout Iceland in a way that promotes pollinator resource connectivity.
References


Franzén M, Öckinger E (2012) Climate-driven changes in pollinator assemblages during the last 60 years in an Arctic mountain region in Northern Scandinavia. Journal of Insect Conservation 16:227-238.


Harper KA, Kershaw GP (1997) Soil characteristics of 48-year-old borrow pits and vehicle tracks in shrub tundra along the CANOL No. 1 pipeline corridor, Northwest Territories, Canada. *Arctic and Alpine Research* 29:105-111.


