ARCTIC ARTHROPOD COMMUNITIES IN HABITATS OF DIFFERING SHRUB ABUNDANCE

by

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ABSTRACT

ARCTIC ARTHROPOD COMMUNITIES IN HABITATS OF DIFFERING SHRUB ABUNDANCE

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Recent global warming, which has been severe in the Arctic, has caused advancement in the timing of snowmelt and expansion of shrubs into open tundra. Such an altered climate may directly and indirectly (via effects on vegetation) affect arctic arthropod populations. I conducted research at four sites in the vicinity of the Arctic Long Term Ecological Research (LTER) site at Toolik Field Station in northern Alaska in the summers of 2010 and 2011 to determine how vegetation and environmental variables affect arthropod abundance, diversity, and phenology (the timing of life history events) in habitats of differing shrub abundance.

Shrub-dominated habitats in the Arctic have been shown to capture snow and delay the timing of snow melt, increase light attenuation through increases in canopy cover, and increase structural complexity compared with tundra with low or no shrub abundance. Arthropod abundance, diversity and community composition are known to be strongly influenced by the physical structure of the environment, and the phenology of arctic arthropods has been linked to the timing of snow melt. Consequently, I hypothesized that sites dominated by shrubs create a different habitat than open tundra vegetation and that this would alter arthropod community composition, patterns of abundance, and the phenology of arthropods. Shrub-dominated habitats were found to differ from open tundra habitats in several structural complexity measurements, having greater maximum shrub height, branch complexity, and foliar canopy cover during the period of maximum leaf out; this response was driven by two of the sites that had the tallest shrubs in the study. Additionally, snow melt was delayed in shrub-dominated habitats on average by 4 days, and a corresponding trend toward greater thawing degree days (TDD, more days above freezing) was found in open tundra habitat in 2011. Pitfall traps captured significantly more arthropods in shrub plots than open tundra plots, the most dramatic difference occurring in the most southern site. Furthermore, taxonomic richness and diversity were significantly greater in shrub plots than open tundra plots. Patterns of abundance within the five most abundant arthropod orders were found to differ, with spiders (Order: Araneae) more abundant in open tundra habitats and true bugs (Order: Hemiptera), flies (Order: Diptera), and wasps and bees (Order: Hymenoptera) more abundant in shrub-dominated habitats. Arthropod phenology was earlier in open tundra habitats, and phenological patterns differed among arthropod orders, most likely due to taxa-specific differences in timing of resources, opportunities for reproduction, and life history traits. Using a regression approach to assess variation across all the sites and vegetation types, few strong correlations were found between vegetation and environmental variables and the abundance and phenology of arthropods, although shrub height seemed to be important for the overall abundance of arthropods and the timing of snow melt and TDD were important for determining phenological patterns of arthropods. However, only certain orders showed significant correlations with the timing of snow melt and TDD, with earlier snow melt and higher TDD causing beetles (Order: Coleoptera) and Hymenoptera to reach their median activity level earlier in the season, respectively.

As climate warming continues to increase over the coming decades, and with further shrub expansion and alteration in the timing of snow melt likely to occur, increases in arthropod abundance, richness, and diversity and a delay in arthropod phenology associated with shrub-

dominated habitat may have important ecological effects in arctic food webs since arthropods are a major food source for migratory songbirds. Furthermore, climate change is going to impact arthropod taxa differently, modifying their contribution to arthropod-related ecological processes, including decomposition and trophic interactions, in which they play an important role in the Arctic.

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CHAPTER 1

INTRODUCTION

1.1 Climate Change in the Arctic

Global mean surface temperatures are on the rise. As of 2007, eleven out of the previous twelve years ranked in the top 12 warmest years on record since 1850 (Trenberth et al. (IPCC) 2007). The Intergovernmental Panel on Climate Change (IPCC) determined that warming is greatest at northern latitudes, given that average arctic temperatures have been increasing at almost twice the rate of the rest of the world in the past 100 years (Trenberth et al. (IPCC) 2007). From the mid-19th to the mid-20th century, the Arctic warmed to the highest temperatures in 400 years, based on data from lake and marine sediment, ice cores, and tree ring records (Overpeck et al. 1997). Average annual temperatures in the Arctic have increased by 2 to 3°C since the 1950s (ACIA 2005). This disproportionate increase in temperature is especially evident in arctic Alaska, where average surface air temperature has increased approximately 1.5°C between 1961 and 2004 (Chapin et al. 2005); other studies have supported this observation (Overpeck et al. 1997, Serreze et al. 2000, ACIA 2005, Hinzman et al. 2005). Not only have average temperatures increased over the past several decades in the Arctic, but records have shown advancement in the timing of snowmelt (Dye 2002, Hinzman et al. 2005, Høye et al. 2007a), lengthening of the growing season (Myneni et al. 1997, Keyser et al. 2000) and substantial thawing of permafrost (ACIA 2005).

Changes in vegetation, particularly the expansion of deciduous shrubs in the Arctic, have been detected through comparison of historical and contemporary photographic imagery in Alaska (Sturm et al. 2001a) and other arctic regions (Tape et al. 2006, Myers-Smith et al. 2011). Satellite imagery has indicated an increase in the Normalized Difference Vegetation Index (NDVI, a measure of the abundance of photosynthetically active vegetation [Rouse et al.

1974]) over much of the Arctic (Slayback et al. 2003, Jia et al. 2003, Stow et al. 2003, 2007). Myneni et al. (1997) showed that photosynthetic activity of vegetation in northern high latitudes increased from 1981 to 1991 which suggested an increase in vegetation growth and a lengthening of the growing season. Furthermore, dynamic vegetation modeling of responses to climate warming has predicted increases in shrubs at the expense of other plant functional groups (Epstein et al. 2000). Experimental studies have corroborated these results. For example, Walker et al. (2006) demonstrated that experimental warming of 1-3°C led to a decrease in species diversity of plants initially, where mosses and lichens became less abundant and vascular plants, particularly deciduous shrubs, increased in growth and abundance.

Climate change is likely to intensify in the future. General circulation models used in the Arctic Climate Impact Assessment (2005) project additional warming of approximately 4 to 5°C by 2080. Additionally, climate change projections predict increases in precipitation, thawing of permafrost, and possible increases in the amount and magnitude of storms in some regions of the Arctic (ACIA 2005). Other models have corroborated the evidence put forth by the ACIA, projecting increases in temperature and precipitation in the future for arctic regions of the world (Kattenberg et al. 1996, Christensen et al. (IPCC) 2007). Further increases in temperature in the Arctic are likely to lead to further advancement in the timing of snow melt and subsequent lengthening of the growing season.

1.2 Arctic Environment and Arthropods

Although the Arctic has experienced recent warming, it is still a harsh environment for invertebrate organisms. As a result of the severe conditions experienced, biological diversity in the Arctic is low compared with temperate and tropical regions of the world (Strathdee and Bale 1998), although estimates of arthropod species richness are as high as 2,200 for the North American Arctic alone (Danks 1981, 1990). Arctic climates challenge arthropods in a variety of ways and severity of the environment is thought to be the limiting factor of whether or not a particular species is found in a given climatic zone (Danks 1999).

Arctic arthropods deal with extremely cold winter temperatures and periods of continuous dark through three main overwintering strategies: freeze avoidance, freeze tolerance, and desiccation (Ávila-Jiménez et al. 2010, Bale and Hayward 2010). In order to deal with the short, cool summer growing season, arthropods possess either rapid development and produce a complete reproductive cycle in one year, or delayed development where successive life cycle stages overwinter for more than one year (Strathdee and Bale 1998). Behavioral thermoregulation, melanistic coloration, hairiness and other adaptations allow arthropods to deal with short term unpredictability of weather events such as freezing (even in the summer) as well as considerable year to year variability (Danks 1999, Danks 2004, Ávila-Jiménez et al. 2010).

As climate change is thought to have significant impacts on the above factors, and since arthropods are sensitive to spring and summer temperatures and are known to integrate the effects of climate variables over prolonged periods (Danks 1992, Strathdee and Bale 1998, Bale et al. 2002), arthropods can be used as indicators of environmental change. Climate change will affect arctic arthropod species differently depending on life cycle, physiology, microhabitat, and other factors. For instance, Bale et al. (1996) believe that since above-ground habitats are likely to be enhanced more than the soil environment, arthropods with flexible life cycles that can exploit above-ground microclimate advantages are likely to increase in abundance relative to arthropods with rigid life cycles that lack the ability to quickly respond to such changes. Corresponding changes in arthropod populations will likely have impacts on organisms that interact with them and with many ecological processes. Arctic arthropods interact with other trophic levels in a variety of ways and perform many biological roles including decomposition, predation and other activities (Danks 1981, Danks 1992). Many arctic arthropods are detritivores that depend on dung or carrion of vertebrate animals in order to survive; others function as herbivores or are important pollinators (Danks 1981; Kevan 1972, 1973; Kevan and Baker 1983). Additionally, arthropods interact with other members of their phylum, acting as parasitoids, predators, prey, ectoparasites, and nest parasites (Danks 1981). Arthropods also have significant interactions with higher trophic levels, for example, acting as ectoparasities of birds and mammals. Migratory birds, including passerines and shorebirds, heavily utilize arthropods as a food source, especially during the growth of fledglings (Custer and Pitelka 1977, 1978; Seastedt and Maclean 1979). Not only do arctic birds prey on arthropods, fish also use them as a food source, predominantly arthropod groups which have aquatic forms (Danks 1981).

1.3 Overall Objective

The majority of organismal studies done in the Arctic to understand responses to climate change have been on plants. Few studies have been conducted on animal populations, especially invertebrate populations. With my research, I hope to further knowledge of arctic ecosystems and the important place of arthropods in the Arctic. The overall goal of my research is:

Characterize arthropod communities in shrub-dominated and open tundra habitats to determine if there are differences in arthropod abundance, taxonomic richness and diversity, phenology (the timing of life history events), and community composition due to vegetation and/or abiotic variables.

1.4 Shrub Vegetation Creates a Different Habitat than Open Tundra Vegetation

As stated earlier, warming in the Arctic has led to the expansion of deciduous shrubs into open tundra (Chapin et al. 1995, Sturm et al. 2001a, Tape et al. 2006). Brubaker et al. (1995) demonstrated that paleoclimate records also indicated similar shrub expansion during previous Holocene warming events. Shrub expansion into open tundra is likely to create a different habitat for many organisms, vastly impacting their ecology.

A meta-analysis of standardized warming experiments across the tundra biome demonstrated that warming increased shrub dominance and canopy height, decreased cover of lichens and mosses, and decreased plant species diversity over a two year period (Walker et al. 2006). Furthermore, Chapin et al. (1995) demonstrated experimentally that increased temperatures, nutrient levels, and light attenuation altered biomass, aboveground production, species richness and composition of tundra plant communities. Specifically, deciduous shrubs outcompeted other plants through more efficient nutrient use and increased shading of understory plants leading to the decline of mosses, lichens, forbs and other non-shrub species after a nine year period. Other studies have supported the findings that long-term manipulations of soil nutrients, used to simulate temperature-related increases in nutrient mineralization (Rustad et al. 2001), show increased shrub abundance and decreases in the spatial and temporal heterogeneity of tundra vegetation communities, both structurally and compositionally (Bret-Harte et al. 2001, Shaver et al. 2001). Alterations in the composition and abundance of plant species will have important effects on ecosystem processes in the Arctic, as well as on organisms at all trophic levels (Eviner and Chapin 2003). Deciduous shrub-dominated plant communities tend to have higher NDVI values than other tundra communities because deciduous shrubs have higher canopy leaf area compared to other plant species (Riedel et al. 2005a,b; Blok et al. 2011). There is a large body of literature that illustrates the importance of biophysical habitat structure on the distribution of various faunal species (e.g., MacArthur and MacArthur 1961, Murdoch et al. 1972, Lawton 1983, Garnder et al. 1995), therefore, changes in the biophysical habitat structure in the arctic tundra, through increases in shrub canopy cover, stature, and branch abundance are likely to impact many species, not only arthropods.

Increased shading via greater deciduous shrub canopy cover will likely reduce the temperature at ground surface, affecting arthropod groups whose activity has been linked strongly to ground surface temperatures (Høye and Forchhammer 2008b). For example, wolf spiders (Family: Lycosidae) bask in sunlight to warm the egg sacs attached to their abdomen (Humphrey 1974). A decline in solar radiation reaching the ground surface is likely to reduce the abundance and activity of wolf spiders, a common family in the Arctic.

Many studies have shown that more abundant and larger shrub vegetation trap snow more effectively than shorter non-shrub vegetation and suffer less loss due to sublimation, particularly the tallest and densest shrubs often associated with water tracks (a hillsope drainage feature with intermittent water flow) or riparian areas (McFadden et al. 2001, Sturm et al. 2001b). Deeper snow delays the timing of snow melt up to two weeks, reducing the length of the growing season (Borner et al. 2008). Although a reduction in growing season length is possible in shrub dominated habitats, these same areas may also see an increase in snow melt runoff and correspondingly higher summer soil moisture levels, a factor important for many arthropod species (McFadden et al. 2001, Sturm et al. 2001b). Additionally, increased soil temperatures in winter through the insulating effects of snow may produce conditions more favorable for further shrub growth as well as ameliorating conditions for arthropod overwintering (Sturm et al. 2001b, Bale and Hayward 2010). However, delay in the timing of snow melt will likely have a negative impact on the phenology of arctic arthropods, which has been strongly linked to the timing of snow melt (Høye et al. 2007a, Høye and Forchhammer 2008a).

Based on this information I hypothesize that:

H1: Shrub vegetation creates a different habitat for arthropods than open tundra vegetation.

P1.1 Shrub vegetation has greater maximum shrub height, greater branch complexity, and higher NDVI values than open tundra vegetation.

P1.2 Shrub vegetation delays the timing of snow melt, reduces accumulated daily mean temperatures above freezing (thawing degree days, TDD), and has lower temperature at ground surface relative to open tundra vegetation.

1.5 Arthropod Communities Differ Between Shrub and Open Tundra Vegetation

Plant communities have strong influence on the physical structure of the environment, and therefore, are likely to impact the distributions and interactions of many different types of organisms, especially arthropods (Lawton 1983, McCoy and Bell 1991). The "habitat heterogeneity hypothesis" assumes that more structurally complex habitats provide more niches, and therefore increase species diversity (Tews et al. 2004). I suggest that vegetation has significant impacts on arthropod abundance, diversity and composition, an example of bottom-up control, where the abundance and diversity of lower trophic levels controls the diversity and abundance of higher trophic levels (Hunter and Price 1992, Siemann 1998, Siemann et al. 1998). A positive effect of the physical structure of the vegetation on animal species diversity has been demonstrated in many studies (MacArthur and MacArthur 1961, Murdoch et al. 1972, Lawton 1983, Gardner et al. 1995). As stated above, I hypothesize that shrub dominated plant communities provide a different habitat than open tundra (non-shrub dominated) communities, most likely due to differences in structural complexity of the vegetation.

Structural complexity (or plant architecture), as used in my research, refers to the variation in vertical structure within a habitat (August 1983) and is described by several vegetation variables including measures of shrub height, foliar canopy cover, and branch abundance. Plant architecture is a term that was originally proposed by Lawton and Schroder (1977) to describe plant structural attributes, so that plants having greater structural complexity permit greater niche diversity and hence greater arthropod abundance and species diversity. The two main components of plant architecture are the size and variety of above-ground parts. Lawton (1983) separated the existing theoretical explanations for the influence of plant architecture on herbivorous insect species diversity into two broad hypotheses. The "size per se hypothesis" states that larger plants are more likely to be colonized by arthropods, and consequently support larger populations and greater diversity. The "resource diversity hypothesis" predicts that plants with a greater variety of structural variables or resource types (sites for resting, sexual display, oviposition, or feeding) support a greater abundance and diversity of arthropods (Lawton 1983). A further elaboration on this hypothesis was discussed by Brose (2003) and was labeled the "microhabitat specialization hypothesis." The "microhabitat specialization hypothesis" states that the potential for horizontal and vertical zonation of insects, specifically herbivores and their associated predators, due to the spatial heterogeneity in plant resources and microhabitat specialization of some insects (MacLean and Hodkinson 1980, MacLean 1983), is particularly enhanced for architecturally complex plants like shrubs and could play an important role in arthropod faunal diversity through increases in microsite availability (Uetz 1991, Lawton 1983). Furthermore, changes in vegetation structure are likely to affect the vulnerability of prey species to their natural enemies: birds, predatory insects, parasitoids, spiders and so on. Many authors have discussed this idea, termed the "enemy-free space hypothesis" (Price et al. 1980, Lawton and Strong 1981, Lawton 1983, Brose 2003). It is reasonable to suggest that, on average, there will be more ways and more places to take refuge from predators on an architecturally complex plant than on a simple one (Lawton 1983). While many studies have focused on the impact of plant architecture on herbivorous insects, other studies have shown correlations between the structural complexity of a habitat and the abundance, diversity and community composition of various groups of arthropods, including spiders (Halaj et al. 1998, Rypstra et al. 1999, Høye and Lobo 2007, Bowden and Buddle 2010), beetles (Dennis et al. 1998, Brose 2003, Lassau et al. 2005), true bugs [Hemiptera] (Brown et al. 1992, Dennis et al. 1998), butterflies (Haysom and Coulson 1998), and wasps (Lassau and Hochuli 2005).

While numerous studies have shown correlations between habitat structural complexity and the abundance and diversity of arthropods, this may not be the case for all arthropod groups. In particular, spiders present an interesting case. Many studies have linked the importance of habitat architecture to spider community composition and distribution of individual species (Uetz 1991, Halaj et al. 1998, Rypstra et al. 1999, Langellotto and Denno 2004, Høye and Lobo 2007, Bowden and Buddle 2010); however, increases in structure and canopy cover that decrease the amount of solar radiation reaching the ground surface may negatively impact surface active spider populations that rely on sunlight to behaviorally thermoregulate (Humphreys 1974, Muff et al. 2009). Furthermore, the surface of the soil and vegetation heat up when exposed to solar radiation, leading to temperatures greater than ambient air temperature, an outcome especially important in areas with reduced canopy cover. Many arthropods, in addition to cursorial spiders, are known to gain heat through basking and other activities (Danks 2004, 2006), therefore, microhabitat selection and behavioral thermoregulation that facilitate heat gain in arctic arthropods may be more important than vegetation structure to the abundance and diversity of some arthropod groups.

Based on this information, I hypothesize that:

H2: Arthropod communities differ between shrub and open tundra vegetation.

P2.1 Shrub vegetation has higher arthropod abundance than open tundra vegetation.

P2.2 Shrub vegetation has higher taxonomic richness and diversity of arthropods relative to open tundra vegetation.

P2.3 Shrub and open tundra vegetation have different arthropod community composition.

1.6 Arthropod Abundance and Phenology and the Significance of Snow Melt and TDD

Recent records in the Arctic have shown advancement in the timing of snowmelt (Dye 2002, Hinzman et al. 2005, Høye et al. 2007a). This is important since the timing of life history events, or phenology, of many organisms has been linked to the timing of snow melt in the Arctic (Høye et al. 2007a). In particular, the timing of emergence of many arthropods, both surface active and flying, is closely related to the timing of snow melt (Høye et al. 2007a, Høye and Forchhammer 2008a). Certain arthropod groups may be strongly affected by any changes in the timing of snow melt. For example, arthropods that are active immediately after snow starts to melt, including *Culiseta* mosquitoes (Frohne 1954, 1956), spiders (Wingfield et al.

2004), psyllids (Hodkinson et al. 1979), chironomids (Danks and Oliver 1972, Danks 1981) and beetles (Kaufmann 1969, 1971), are likely to have highly altered patterns of abundance and activity as shifts in the timing of snow melt occur in the Arctic. Alternatively, variability in the timing of snow melt may have impacts on arthropod orders, such as Lepidoptera and Hymenoptera, which generally appear later in the season (Høye and Forchhammer 2008a). For instance, butterflies are highly dependent on flowers; changes in the timing of snow melt that alter the abundance and phenology of flowers (Høye et al. 2007a,b) may cause mismatches in plant-pollinator interactions. Moreover, parasitoid wasps are highly dependent on the presence of host species and changes in the timing of snow melt that alter host or parasite phenology will likely affect host-parasite interactions. Earlier spring snow melt may also lead to increases in the abundance of some arthropods. For instance, a longer growing season and earlier snow melt have been associated with larger body size in some arctic spider species, particularly in females (Høye et al. 2009, Høye and Hammel 2010). Larger females tend to have greater reproductive output which may increase the overall abundance of organisms in a habitat (Simpson 1993).

The activity of arthropods has been most significantly related to temperature and solar radiation (a proxy for ground surface temperature) (Høye and Forchhammer 2008b). Thus, thawing degree days (TDD), a measurement of accumulated mean daily temperature above freezing, will likely be correlated with the overall seasonal abundance of arthropods. For example, Hodkinson et al. (1996) found that the biomass of chironomid flies (midges) was significantly greater in 1993 (a warmer year) than in 1992 (a colder year). This suggests that the cumulative degree days above freezing had a significant impact on the abundance of midges in high Arctic Svalbard. Earlier snow melt and higher TDD are likely to lead to earlier occurrence of arthropods and perhaps greater abundance over the season, an outcome that suggests a greater contribution to arthropod-related ecological processes (Høye and Forchhammer 2008b).

Based on this information, I hypothesize that:

H3: The phenology and abundance of arthropods are correlated with the beginning of the growing season, measured by timing of snowmelt and accumulated mean daily temperature above freezing (thawing degree days, TDD).

P3.1 Phenological patterns differ among arthropod orders.

P3.2 Earlier snow melt and higher thawing degree days cause arthropods to reach their median activity level earlier in the season.

P3.3 Earlier snow melt and higher thawing degree days result in higher arthropod abundance over the season.

CHAPTER 2

METHODS

2.1 Study Area

Research was based at the Arctic Long Term Ecological Research (LTER) site at Toolik Field Station (TLFS) in the northern foothills of the Brooks Range, Alaska, USA (68°38´ N, 149°34´ W, elevation 760 m). Average annual precipitation ranges from 200-300 mm with approximately 50% as snow, and mean summer temperature is 10°C. Four research sites were included in the study (Figure 2.1). The most southern site, Roche Mountonee (ROMO), is located approximately 32 km southeast of Toolik Lake in the Atigun River Valley, just north of the Atigun Pass. This site is one of the first locations where migratory birds arrive north of the Brooks Range. It is characterized by open tussock tundra and areas of substantial riparian shrub cover. The second site, TLFS, is located near the outlet of Toolik Lake and is characterized by open tussock tundra and areas of sparse shrub cover. Located approximately 11km east of Toolik Lake is the third site, Imnavait Creek (IMVT). This site is characterized by open tussock tundra and areas of sparse shrub cover in a water track. The final and most northern site, Sag River-Department of Transportation camp (SDOT), is approximately 31 km northeast of Toolik Lake. It is characterized by open tussock tundra with areas of tall and dense riparian shrub cover. All four sites are low arctic zone habitats.

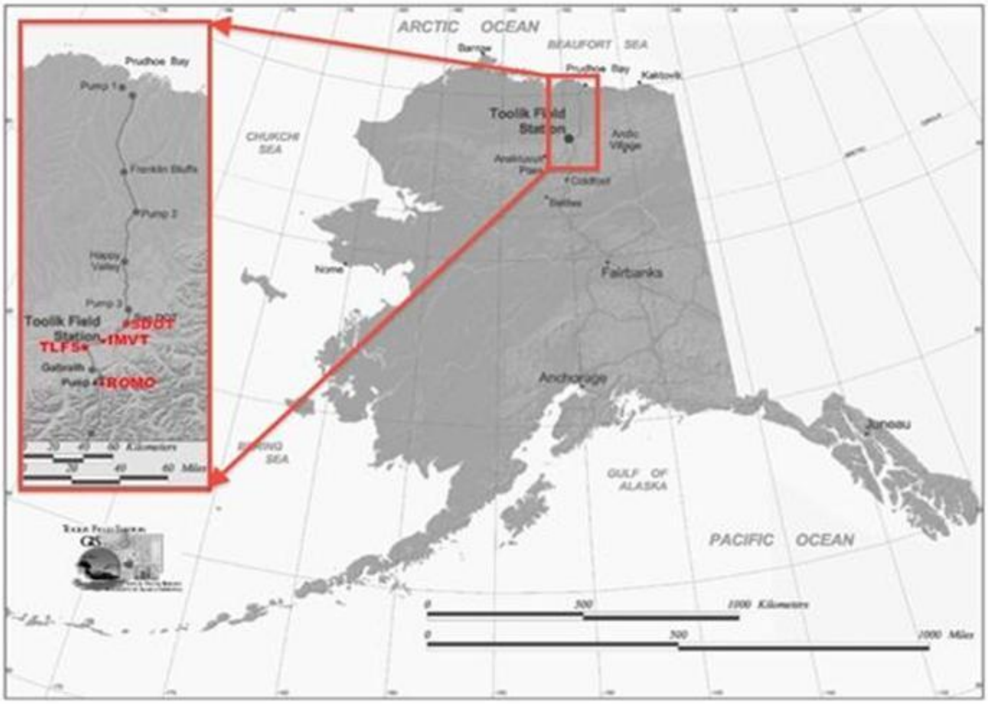

Figure 2.1 Map of Alaska and the North Slope (inset) showing the location of the four study sites.

2.2 Arthropod Sampling

At each of the four sites, two 10,000 m^2 plots were established in May and June 2010: an open tundra plot (no or low shrub abundance) and a shrub plot (moderate to high shrub abundance). Within each plot, two 100 meter replicate transects were established. Arthropod abundance was measured via pitfall traps (Fichter 1941, Normant 1987) because of the ability of pitfall traps to collect in a consistent and repeatable manner (Bowden and Buddle 2010). Ten pitfall traps were placed at 10 meter intervals along the two 100 meter transects located in the shrub and open tundra plots in order to sample arthropods (for a total of 40 traps per site). Pitfall traps consisted of a plastic drinking cup (~7.5 cm diameter × 10 cm deep) buried in the ground with the lip of the cup flush with the ground or vegetation surface. Each trap was filled with approximately 2 cm of a 50:50 mixture of water and ethanol to preserve specimens until the sample was retrieved. Pitfall trapping was conducted over the period 29 May – 17 July in 2010 and 21 May – 30 July in 2011, with start date at each site depending on timing of snowmelt. In general the arthropod data from 2011 were the subject of all analyses because of the longer sample period and finer taxonomic resolution; 2010 data were also analyzed and results were similar, but I only report total arthropod abundance for comparison with 2011. Sampling occurred once per week at all sites with traps being collected after a 48 hour period. Traps were occasionally lost as a result of wildlife disturbance or human error. Arthropod specimens were stored in 70% ethanol and identified to class, order or family, except for Acari (mites) and Collembola (springtails). These soil microarthropods were not counted and were excluded from analysis.

2.3 Environmental Data

In 2011, temperature at ground surface within shrub and open tundra plots was measured hourly using Thermochron® iButton® temperature data loggers (Maxim Dallas Semiconductor DS1921G-F5#, Sunnyvale, California, USA). In order to determine variation in microclimate between shrub and open tundra vegetation, Thermochron® iButtons® were mounted in a vertical array on a PVC pipe staked into the ground (Danby and Hik 2007, Lewkowicz 2008). The arrays had data loggers situated at 0, 5, 15, 25, 50, 75, and 100 cm above the ground surface at ROMO (open tundra plot), SDOT (open tundra plot), IMVT and TLFS, while additional data loggers placed at 150 and 200 cm were used in shrub plots at ROMO and SDOT. Two arrays were placed in each vegetation type and were oriented northward to prevent direct sun exposure to the iButton® data loggers. Mean, minimum, and maximum daily temperatures over the growing season were calculated for this study using ground surface temperature measurements only.

In 2011, snow free dates were derived from quadrat level photos. Snow free date was defined as the date when 50% of the quadrats along a transect were free of snow cover (Høye and Forchhammer 2008). However, due to infrequent observations of the timing of snow melt at each site, date of snowmelt in each plot was estimated as the date of 50% snow cover by interpolation between the latest observation where snow cover was above 50% and the earliest observation where snow cover was below 50% (Høye et al. 2007a Supplemental). In some cases snowmelt occurred prior to our initial observations and we used three days prior to the first observation when snow melt was greater than 50% as date of snowmelt. Snow melt was calculated at the transect level, therefore only 16 sampling points were available for statistical analysis.

Thawing degree days (TDD), a measurement of accumulated mean daily temperature above freezing since the day of snow melt, was calculated by averaging the daily contribution of all hourly air temperature measurements above zero where subzero recordings were set to zero since arthropod activity does not vary once temperature drops below freezing (Høye and Forchhammer 2008b, Tulp and Schekkerman 2008). TDD was calculated using iButton® data logger ground surface temperature data. Similar to snowmelt, TDD was assessed at the transect level; therefore, only 16 sampling points were available for statistical analysis.

2.4 Vegetation Data

Ten quadrats (1m × 1m) were established along each 100 meter transect at 10 meter intervals. All vegetation data were measured by other field workers as part of the larger NSF-funded project, including Heather Greaves, Jennie McLaren, Carol Moulton, and Shannan Sweet. Percent cover data were collected for most quadrats during the week of 19 July 2010, but two transects were sampled on 21 July 2011. Within each quadrat, percent cover was visually estimated for mosses, lichens, litter, and individual vascular plant species (only the total cover of vascular species is reported here). Species richness was estimated for each vegetation type and site from percent cover measurements. Branch complexity was measured using a modified point frame method (Boelman et al. 2011). A graduated dowel was placed vertically at 10 cm intervals along the inside edge of each quadrat and the number of branches that touched the dowel was recorded along with the height increment in which the branch occurred. Branch complexity was calculated as the mean number of hits per quadrat over all 10 dowel insertions. Branch complexity was measured before shrub leaf out in shrub plots during the week of 7 June 2010 and open tundra plots on 4 and 7 June 2011. Maximum shrub height was determined by measuring the height of the tallest shrub in each quadrat. At each plot, weekly quadrat-level spectral radiance measurements were recorded throughout the 2010 (made by Greaves) and 2011 (made by Sweet) field seasons with a field portable spectroradiometer (FieldSpec3, Analytical Spectral Devices, Boulder, CO, USA). From these canopy reflectance measurements, the highest normalized difference vegetation index (NDVI) value (peak-NDVI) was calculated to determine the period of maximum leaf-out (Boelman et al. 2011). NDVI is indicative of the abundance of photosynthetically active vegetation (Rouse et al. 1974) and is used in this study to capture variation in foliar canopy cover.

2.5 Arthropod Phenological Data

To characterize the phenology of arctic arthropods, I estimated the date when 50% of the total seasonal catch of arthropods was reached (termed date50) for each plot and site (Corbet and Danks 1973, Høye and Forchhammer 2008a). Date50 was interpolated between the last date when less than 50% of the total capture was reached and the first date when more than 50% of the total capture was reached by taking the average of the corresponding Julian days (Høye et al. 2007a), and was calculated for all arthropods as a community as well as separately for the five most abundant arthropod orders captured (Araneae, Coleoptera, Hemipter, Hymenoptera, and Diptera).

2.6 Arthropod Diversity

I calculated Shannon's Diversity Index using data for all taxa found. Shannon's Diversity Index (*H*) (Shannon 1948) was calculated using the following equation:

$$H = -\sum_{i=1}^{S} p_i * (\ln * p_i)$$

With S = number of taxa present in a sample (taxa richness) and p_i = the proportion of individuals made up of the *i*th taxa.

2.7 Statistical Analysis

2.7.1 Hypothesis 1

In order to test for differences in vegetation and environmental variables between sites and vegetation types, two-way analysis of variance (ANOVA) was conducted with site and vegetation type as the main effects. Data were not normal, so log transformation was used for most of the variables, although arcsin square root transformation was used for percent cover and NDVI. Scheffe's test was used as a conservative method for testing pairwise comparisons.

PCA was performed using eight different vegetation variables (maximum shrub height, branch complexity, peak NDVI, species richness, and percent cover moss, litter, lichen, and vascular plants) at each site and vegetation type in order to parse out any underlying structure in the vegetation data. PCA was used as a dimension reduction technique to condense a data set of many variables to a new data set of fewer orthogonal variables (McGarigal et al. 2000). Varimax rotation of the component axes was performed during the analysis to provide the set of orthogonal axes that best explains the maximum variance in the original data (McGarigal et al. 2000). In order to meet assumptions of PCA, all variables were transformed to improve normality. Although not all transformations produced data that were normally distributed, transformations did improve normality, hence transformed data were used for purposes of the final analysis.

2.7.2 Hypothesis 2

To analyze total arthropod abundance, I calculated the total number of arthropods caught in each trap across the entire season in shrub and open tundra vegetation at all four sample sites and performed a two-way ANOVA with site and vegetation type as the main effects for 2010. Data were log-transformed and analyses were performed using transformed data if normality was improved. Scheffe's test was used for pair wise comparisons as it is a relatively conservative test. The 2011 arthropod abundance data were analyzed as a Poisson Distribution with PROC GLM with a log-link function in SAS to account for the overdispersion in the data: site and vegetation type were used the main effects and their interaction was also tested. Contrasts were specified to determine if abundance differed between vegetation types within a site. Analyses were conducted on each year separately because of the different lengths of the two field seasons. All subsequent analyses were conducted for 2011 data only. The abundance of the five major orders of arthropods captured (Araneae, Coleoptera, Hemiptera, Hymenoptera, and Diptera) was also analyzed separately using a Poisson Distribution as described above for total arthropod abundance.

Multiple regression analysis using stepwise regression techniques was performed to determine the impact of vegetation variables on the abundance of all arthropods. This method is useful in trying to identify predictor variables that have the largest statistical contribution explaining the variance in the dependent variable. Moreover, multiple regression analysis using stepwise regression techniques was performed to determine the impact of vegetation variables on the abundance of the five major arthropod orders separately.

To analyze taxonomic richness and Shannon's Diversity Index across the entire season in shrub and open tundra vegetation across all four sample sites, two-way ANOVA was performed with site and vegetation type as the main effects. Data were log-transformed and analyses were performed using transformed data if normality was improved. In order to deal with not meeting assumptions of normality, Scheffe's test was used for pairwise comparisons as it is a relatively conservative test.

Principle components analysis (PCA) was used to analyze arthropod community composition. PCA was performed on 22 arthropod taxa in order to parse out any underlying structure in the arthropod data. All taxa that made up greater than 1% of the total capture were retained as variables in the analysis, while those falling under 1% were eliminated. A variety of data transformations were attempted to improve normality of the data set. The transformations did not significantly improve the normality of the data set and the results of the PCA did not change in any substantive way, therefore I retained the untransformed data for purposes of the final analysis. Additionally, no rotation of the component axes was performed during the analysis because the unrotated components provided the set of orthogonal axes that best explained the maximum variance in the original data. Since PCA was used purely for descriptive purposes, rigorous concern over meeting statistical assumptions regarding the raw data was not warranted (McGarigal et al. 2000).

2.7.3 Hypothesis 3

The average date when 50% of the seasonal capture was reached (date50) of the five major orders of arthropods captured was analyzed using a three-way ANOVA, with site, vegetation type, and taxon as main effects. These analyses were performed to determine if there were any differences in phenological patterns among orders in shrub and open tundra habitats.

In order to analyze correlations between thawing degree days and snow melt date with arthropod abundance and phenology (all arthropods as well as the five most abundant orders), multiple regression analysis using stepwise regression techniques were performed.

CHAPTER 3

RESULTS

A total of 9,149 individuals were trapped during the 2010 field season from 31 May – 17 July (Appendix Table 1a). Pitfall sampling occurred over 7 weeks for a total of 1,120 pitfall trap samples. Of those 1,120, 7 were lost due to natural disturbance and human error. This amounts to a loss of <1% (0.63%) of the total samples. A total of 8 small mammals were accidentally caught in pitfalls traps in 2010; 5 voles and 3 shrews. The earliest dates of a complete sample at each site (when all pitfall traps were snow free and collected a sample) were 31 May, 4 June, 5 June and 5 June for ROMO, IMVT, SDOT and TLFS respectively. Plots were established after snow melt, therefore, all pitfall traps within a plot and site were placed on the same date and recorded the same number of samples.

A total of 10,498 individuals were trapped during the 2011 field season from 21 May – 30 July (Appendix Table 1b). Pitfall sampling occurred over 10 weeks for a total of 1,588 pitfall trap samples. Of those 1,588, only 10 were lost due to natural disturbance and human error. This amounts to a loss of <1% (0.63%) of the total samples. A total of 8 small mammals were accidentally caught in pitfalls traps in 2011; 4 voles and 4 shrews. The earliest dates of a complete sample at each site (when all pitfall traps were snow free and collected a sample) were 6 June, 2 June, 10 June, and 3 June for ROMO, IMVT, SDOT, and TLFS respectively. Since each plot and site became snow free at different times, some traps were snow free earlier than others and sampling began prior to other traps within that plot or site.

In both 2010 and 2011, the most abundant orders captured were Araneae (spiders), Coleoptera (beetles), Hemiptera (true bugs), Hymenoptera (bees and wasps), and Diptera (flies).

3.1 Vegetation Characteristics

Significant effects of site ($F_{3,149}$=19.03; P<0.0001), vegetation type ($F_{1,149}$=102.44; P<0.0001), and a significant site*vegetation type interaction ($F_{3,149}$=18.50; P<0.0001) were found for maximum shrub height (Table 3.1). The significant interaction was driven by the much taller shrubs in shrub tundra compared with open tundra at SDOT and ROMO, while the two vegetation types supported mostly dwarf shrubs of similar mean height at IMVT and TLFS. Because of this, shrub vegetation had taller shrubs than open tundra vegetation. The tallest shrubs were found at SDOT and the average maximum shrub height was approximately 38 cm greater than at IMVT, which had the shortest shrubs.

Significant effects of site ($F_{3,148}$=26.26; P<0.0001), vegetation type ($F_{1,148}$=14.55; P=0.0002), and a significant site*vegetation type interaction ($F_{3,148}$=25.41; P<0.0001) were found for branch complexity (Table 3.1). The significant interaction was driven by the significantly greater branch complexity found within the open tundra plot compared with shrub plot at IMVT, while there was much greater branch complexity found within the shrub plots compared to open tundra at ROMO and SDOT. This latter pattern caused shrub vegetation to have greater branch complexity relative to open tundra vegetation. SDOT had the highest branch complexity, while ROMO had the lowest.

Significant effects of site ($F_{3,151}$=24.51; P<0.0001), vegetation type ($F_{1,151}$=47.06; P<0.0001), and a significant site*vegetation type interaction ($F_{3,151}$=9.00; P<0.0001) were found for peak-NDVI (Table 3.1). The significant interaction was driven by the similarity in peak-NDVI between vegetation types at ROMO, while the three remaining sites all had higher peak-NDVI values in shrub plots relative to open tundra plots. Because of this, shrub vegetation had a higher peak NDVI relative to open tundra vegetation. Analogous to branch complexity, peak-NDVI was the highest at SDOT and lowest at ROMO.

Plant species richness did not significantly differ among sites or vegetation types (Table 3.1).

I analyzed the percent cover of various groups of plants including mosses, lichens, litter, and vascular plants. Significant effects of site ($F_{3,151}$=2.73; P=0.05), vegetation type ($F_{1,151}$=6.23; P=0.01), and a significant site*vegetation type interaction ($F_{3,151}$=10.18; P<0.0001) were found for percent cover moss (Table 3.1). The significant interaction was driven by much greater moss cover in open tundra relative to shrub tundra at SDOT, while the three others sites all had similar moss cover within each vegetation type. Additionally, significant effects of site ($F_{3,151}$=6.88; P=0.0002), vegetation type ($F_{1,151}$=24.31; P<0.0001), and a significant site*vegetation type interaction ($F_{3,151}$=3.27; P=0.02) were found for percent cover litter (Table 3.1). The significant interaction was driven by a trend toward higher litter cover in shrub habitat compared with open tundra habitat at IMVT, whereas the other 3 sites showed a trend in the opposite direction. Overall, percent cover moss and percent cover litter were greater in open tundra habitat than shrub habitat. ROMO had the highest litter cover, but moss cover did not differ between sites.

A significant effect of site ($F_{3,151}$=17.32; P<0.0001) and a site*vegetation type interaction ($F_{3,151}$=5.96; P=0.0007) was found for percent cover lichen, although no significant effect of vegetation type was found (Table 3.1). Similar to percent cover moss, the significant interaction in lichen cover was driven by greater lichen cover in open tundra relative to shrub tundra at SDOT, while the three other sites all had similar lichen cover within each vegetation type. Percent cover lichen was highest at TLFS.

Significant effects of site ($F_{3,151}$=10.12; P<0.0001), vegetation type ($F_{1,151}$=15.39; P=0.0001), and a significant site*vegetation type interaction ($F_{3,151}$=20.41; P<0.0001) were found for percent cover of vascular plants (Table 3.1). The significant interaction was driven by significantly greater percent cover vascular plants in shrub tundra compared to open tundra at SDOT, while the three other sites showed similar vascular plant cover between vegetation types. Across all sites, vascular plant cover was greater in shrub-dominated habitat than open tundra habitat. SDOT had the highest vascular plant cover of the 4 sites.

Table 3.1 Vegetation date table with results from two-way ANOVA. Mean values are displayed for each variable in shrub and open tundra vegetation and at the site level (shaded columns). Means with shared letters within a row (for the site and the vegetation type*site interaction separately) are not significantly different at $p<0.05$.

	ROMO	ROMO	ROMO	TLFS	TLFS	TLFS	IMVT	IMVT	IMVT	SDOT	SDOT	SDOT
Variable	Shrub	Open	Site	Shrub	Open	Site	Shrub	Open	Site	Shrub	Open	Site
Maximum Shrub Height (cm)	86.3 (a)	13.3 (d)	49.8 (ab)	35 (b)	23.4 (bc)	29.5 (b)	21.8 (bcd)	15.9 (cd)	19 (c)	83.8 (a)	28.3 (b)	56.7 (a)
Branch Complexity (# of hits)	6 (cd)	2.4 (e)	4.2 (c)	13.6 (bc)	11.9 (bc)	12.7 (ab)	6.6 (d)	13.6 (b)	10.1 (b)	31.3 (a)	6.8 (cd)	19 (a)
Peak NDVI	0.6 (d)	0.6 (d)	0.6 (d)	0.7 (bc)	0.63 (d)	0.66 (b)	0.73 (b)	0.63 (d)	0.68 (b)	0.81 (a)	0.65 (cd)	0.73 (a)
Species Richness (per m^2)	12.2	11.2	11.7	12.3	13.2	12.7	12.6	13.9	13.2	12.8	10.1	11.5
% Cover Moss	18.78 (ab)	19.1 (ab)	19 (a)	19 (ab)	20.9 (ab)	20 (a)	18.5 (ab)	12.1 (bc)	15.3 (a)	7.3 (c)	25.4 (a)	16.3 (a)
% Cover Litter	10.8 (abc)	15.9 (a)	13.3 (a)	4 (c)	10.8 (abc)	7.4 (b)	10.2 (abc)	9.7 (abc)	9.9 (ab)	4.9 (bc)	12 (ab)	8.4 (b)
% Cover Lichen	5 (ab)	1.6 (bc)	3.3 (b)	7.2 (a)	7.5 (a)	7.4 (a)	1.4 (bc)	2.4 (ab)	1.9 (bc)	0.3 (c)	2.7 (b)	1.5 (c)
% Cover Vascular	56.5 (c)	61.7 (bc)	59.1 (c)	69.1 (bc)	59.8 (bc)	64.4 (bc)	69 (bc)	75.5 (b)	72.2 (ab)	87.5 (a)	55.4 (c)	71.5 (a)

Principle components analysis of the vegetation data produced three principle components that accounted for 71% of the variation, and all variables except species richness had loadings greater than 0.4 on one of the first two principle components (Table 3.2).

Table 3.2 Rotated component matrix showing component loadings of each variable on the three principle components and the total amount of variance explained following varimax rotation. Component loadings <0.4 are not shown.

	Component		
	1	2	3
Branch Complexity	0.764		
peak-NDVI	0.749	0.429	
Cover Litter	-0.745	0.422	
Max Shrub Height	0.621		
CoverMoss		-0.793	
Cover Lichen		-0.771	
Cover Vascular	0.648	0.651	
Plant Species Richness			0.971
% Variance Explained	31.97	25.904	13.306
Cumulative %	31.97	57.875	71.181

I plotted the loadings of each variable using the first two principle components (PC1 and PC2) as axes (Figure 3.1). PC1 represents a gradient of vascular plant growth, foliar canopy cover, shrub height and structural complexity (i.e. shrubbiness), while PC2 is negatively correlated with nonvascular ground cover (moss and lichen cover). Factor scores for PC1 and PC2 were plotted for all sample points and marked based on site and vegetation type. There was substantial overlap of sites and vegetation types; shrub plots tended to positively load on PC1 while open tundra plots tended to negatively load on PC1. There was also some separation based on SDOT shrub plots, indicative of variation in the vegetation present in this habitat (Figure 3.2).

3.2 Environmental Characteristics

Significant effects of site ($F_{3,8}$=7.41; P=0.01), and vegetation type ($F_{1,8}$=32.80; P=0.0004) were found for snow melt date (Table 3.3). In 2011, shrub vegetation was snow free approximately four days later than open tundra vegetation, and snow melt occurred significantly later at IMVT than either ROMO or SDOT. Although no significant effects were found for TDD, open tundra vegetation exhibited a trend toward greater TDD than shrub tundra that was marginally significant ($F_{1,7}$=4.93; P=0.06). Neither mean daily temperature nor maximum daily temperature varied across sites or vegetation type, however, a significant effect of site ($F_{3,7}$=7.99; P=0.01) and a site*vegetation type interaction ($F_{3,7}$=9.16; P=0.01) was found for minimum daily temperature(Table 3.3). The significant interaction was driven by an opposing trend in minimum temperature between vegetation types at IMVT, which showed a trend toward higher temperature in open tundra, whereas ROMO and SDOT showed a trend toward higher temperature in shrub tundra. Using pairwise comparisons, I found that ROMO was significantly warmer than TLFS, and SDOT and IMVT were intermediate between those two sites.

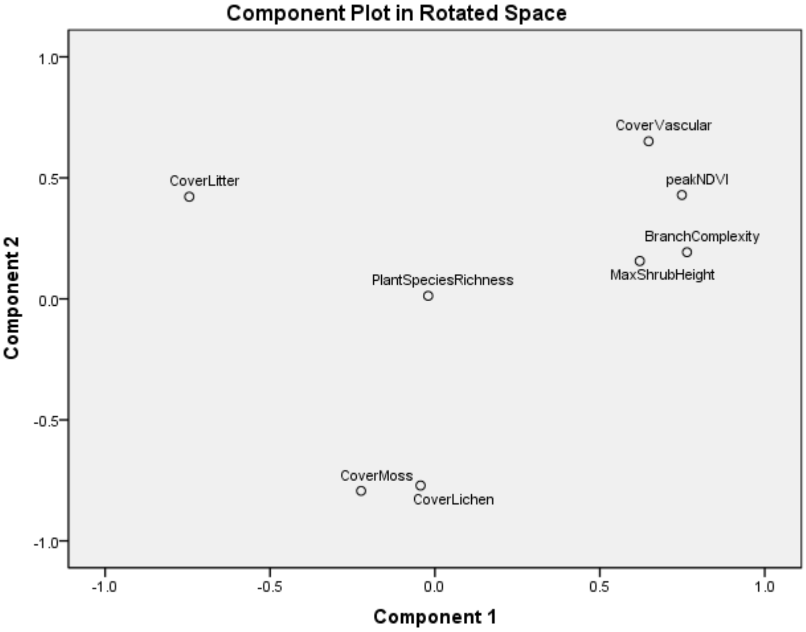

Figure 3.1 Results of each variable loading on the two main principle components produced from the PCA. See Table 3.2 for loading values and variance explained.

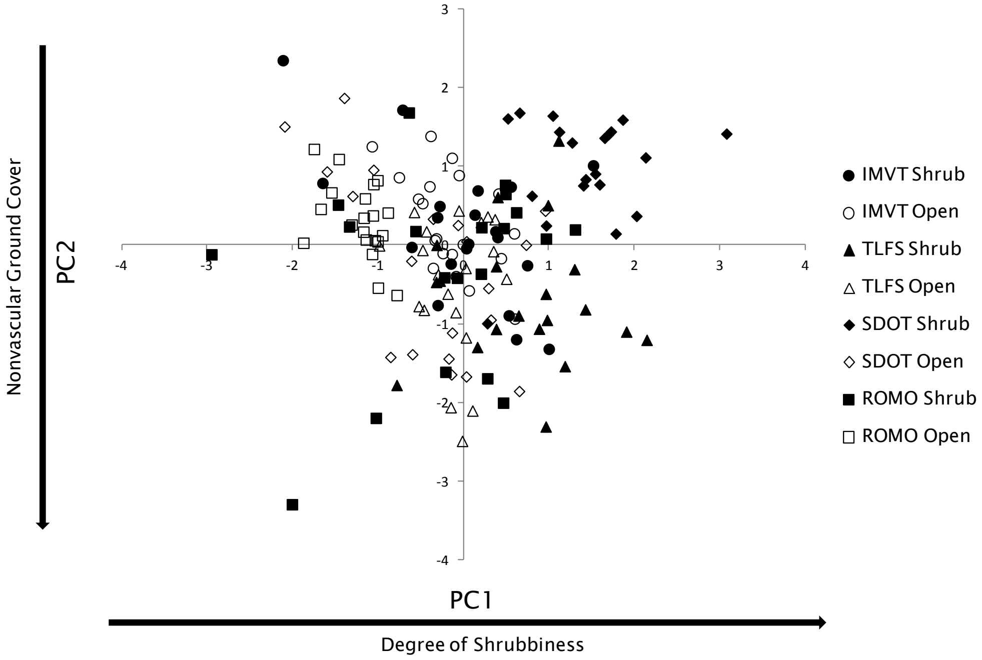

Figure 3.2 Regression factor scores for each sampling point on the first two principle components labeled by sample site and vegetation type. See Table 3.2 for loading values and variance explained.

Table 3.3 Environmental data table with results from two-way ANOVA. Mean values are displayed for each variable in shrub and open tundra vegetation and at the site level (shaded columns). Means with shared letters within a row (for site and the vegetation type*site interaction separately) are not significantly different at p<0.05.

	ROMO	ROMO	ROMO	TLFS	TLFS	TLFS	IMVT	IMVT	IMVT	SDOT	SDOT	SDOT
Variable	Shrub	Open	Site	Shrub	Open	Site	Shrub	Open	Site	Shrub	Open	Site
Snow Melt Date (Julian Day)	141.5	138	139.8 (b)	143.5	139	141.3 (ab)	146	141	143.5 (a)	140.8	138	139.4 (b)
TDD (°C)	668.3	687.1	677.7	607.7	702.6	655.1	576	759.6	667.8	668.5	724.6	696.6
Mean Daily Temperature (°C)	10.7	10.3	10.5	9.9	10.9	10.4	9.7	11.7	10.7	10.5	10.8	10.6
Maximum Daily Temperature (°C)	18.5	19.6	19.1	17.8	21.7	19.8	18.5	20.2	19.4	19.4	21.9	20.7
Minimum Daily Temperature (°C)	4.2 (a)	2.8 (ab)	3.5 (a)	2.1 (b)	1.8 (b)	1.9 (b)	2.2 (b)	3.8 (ab)	3 (ab)	2.8 (ab)	2.3 (b)	2.6 (ab)

3.3 Arthropod Abundance

In 2010, significant effects of site ($F_{3,152}$=23.79; P<0.0001), vegetation type ($F_{1,152}$=14.08; P=0.0002), and a significant site*vegetation type interaction ($F_{3,152}$=3.08; P=0.03) were found for total number of arthropods in each pitfall trap across sampling dates (Figure 3.3A). The significant interaction was driven by the significantly greater abundance found in shrub habitat compared to open tundra habitat at ROMO, while the three other sites had similar abundance of arthropods between vegetation types. This difference at ROMO as well as a similar trend at SDOT led to the overall pattern of greater arthropod abundance in shrub vegetation than open tundra vegetation. ROMO had significantly greater arthropod abundance than IMVT, TLFS, and SDOT, which were all statistically equivalent.

Similar to 2010, in 2011 there were significant effects of site (X^2_3 = 25.53; P<0.0001), vegetation type (X^2_1 = 6.87; P=0.009), and a significant site*vegetation type interaction (X^2_3 = 8.45; P=0.04) for total number of arthropods in each pitfall trap across sampling dates (Figure 3.3B). The significant interaction was driven by the significant difference in abundance between shrub and open tundra found at ROMO, SDOT, and IMVT, while TLFS had similar abundance of arthropods in both vegetation types. These differences caused arthropod abundance to be greater in shrub vegetation than open tundra vegetation. ROMO had the highest arthropod abundance while TLFS had the lowest abundance.

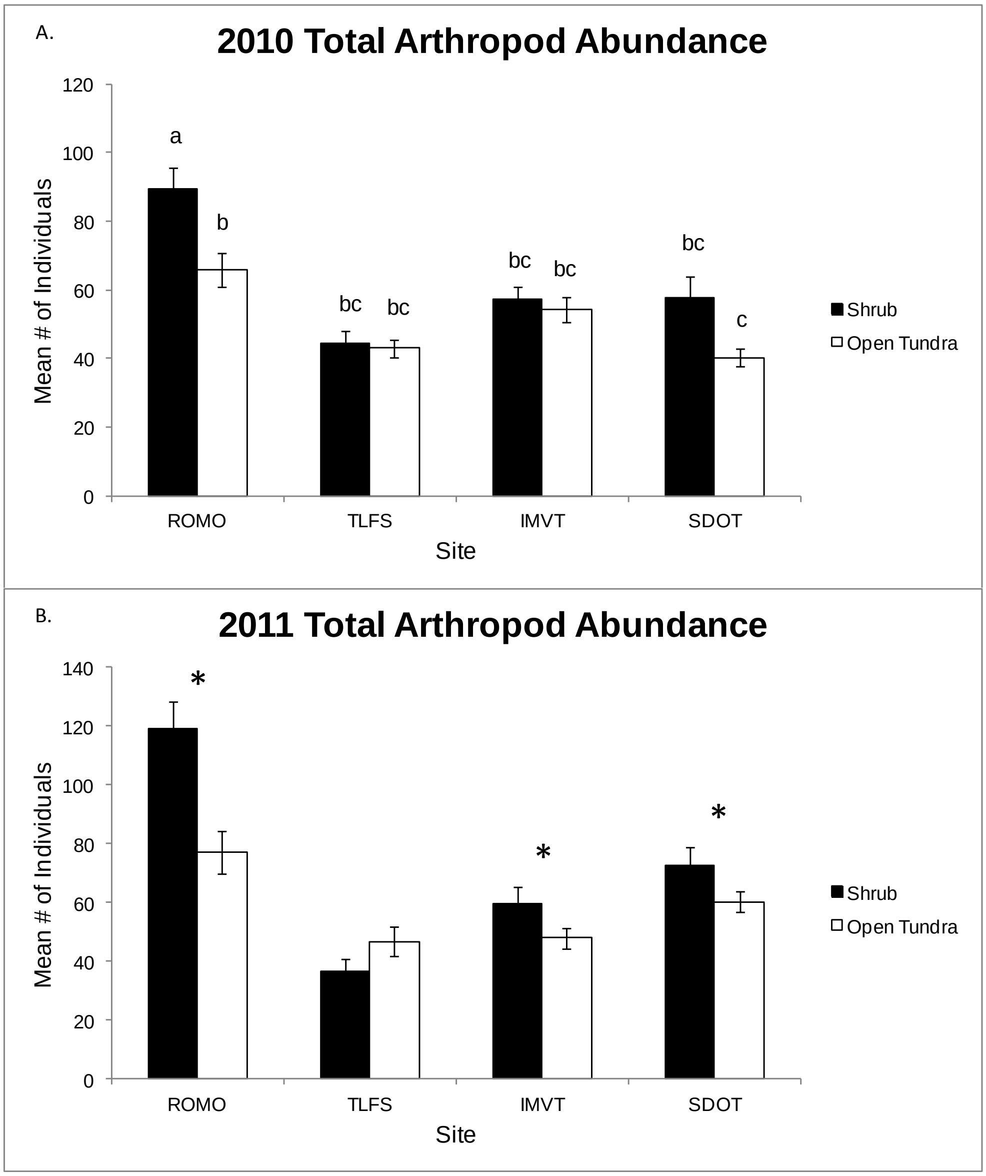

Figure 3.3 Mean number of arthropods (±SE) caught per pitfall trap in shrub and open tundra vegetation at four sites. (A) 2010 sampling. Mean values with the same letters are not significantly different at $p<0.05$. (B) 2011 sampling. Asterisks represent significant within site differences at $p<0.05$.

3.4 Arthropod Taxa Richness

Significant effects of site ($F_{3,152}$=32.46; P<0.0001), vegetation type ($F_{1,152}$=15.36; P=0.0001), and a significant site*vegetation type interaction ($F_{3,152}$=4.25; P=0.006) were found for taxonomic richness of arthropods in each trap across all sampling dates (Figure 3.4). The significant interaction was driven by the slight trend for greater taxonomic richness in open tundra compared to shrub at TLFS, while the three other sites all had trends toward greater richness in shrub-dominated habitat. This caused shrub plots to have higher taxonomic richness than open tundra plots. ROMO had significantly higher taxonomic richness than SDOT, while IMVT and TLFS had significantly lower richness than both ROMO and SDOT.

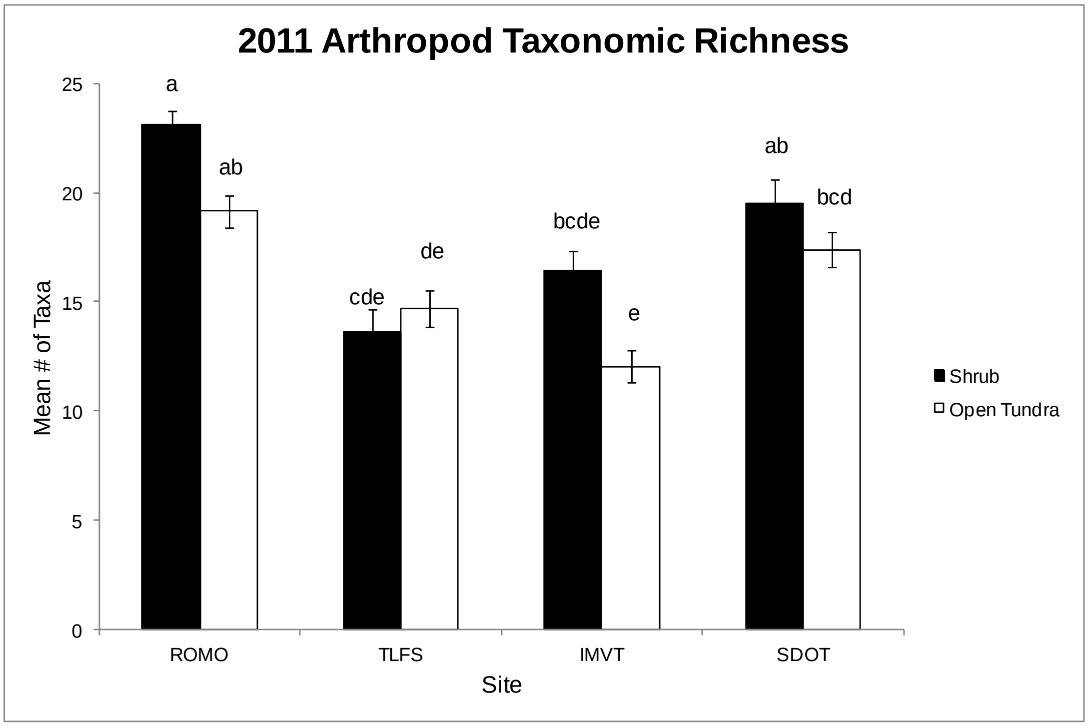

Figure 3.4 Mean number of taxa (±SE) caught per pitfall trap in 2011 in shrub and open tundra vegetation at four sites. Mean values with the same letters are not significantly different at *p*<0.05.

3.5 Shannon Diversity

Significant effects of site ($F_{3,152}$=5.80; P=0.0009), vegetation type ($F_{1,152}$=18.05; P<0.0001), and a significant site*vegetation type interaction ($F_{3,152}$=4.78; P=0.003) were found for Shannon diversity in each trap across sampling dates (Figure 3.5). The significant interaction was driven by the significant difference in diversity between vegetation types found at IMVT, whereas the other three sites had similar diversity indices between vegetation types. As with taxonomic richness, shrub plots had greater arthropod diversity than open tundra plots. ROMO and SDOT had the highest diversity while IMVT had the lowest diversity.

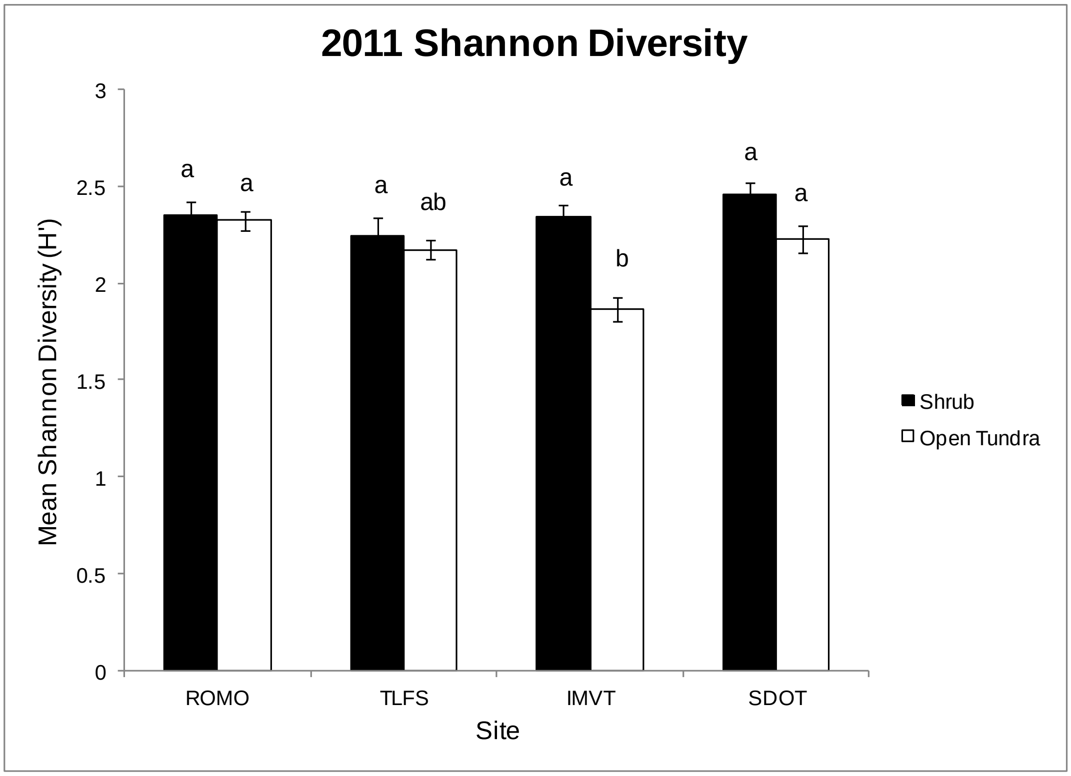

Figure 3.5 Mean Shannon Diversity Index (H) (±SE) calculated per pitfall trap in 2011 in shrub and open tundra vegetation at four sites. Mean values with the same letters are not significantly different at *p*<0.05.

3.6 Arthropod PCA

Principle components analysis was performed using the 22 arthropod families that each comprised >1% of the total arthropod capture over the entire season. Eight principle components were produced based on the original 22 families which accounted for 64.97% of the variation; only 3 components are shown (Table 3.4). The loadings for each family on the first two principle components (PC1 and PC2) were plotted (**Error! Reference source not found.**), and the explanation of variance by these two components was good (28%). Certain families seemed to be more strongly positively associated with PC1 such as Sciaridae, Miridae, Tipulidae, and Cicadellidae; while other families seemed to be more strongly positively associated with PC2 such as Gnaphosidae, Lycosidae, Carabidae, Delphacidae, and Empididae.

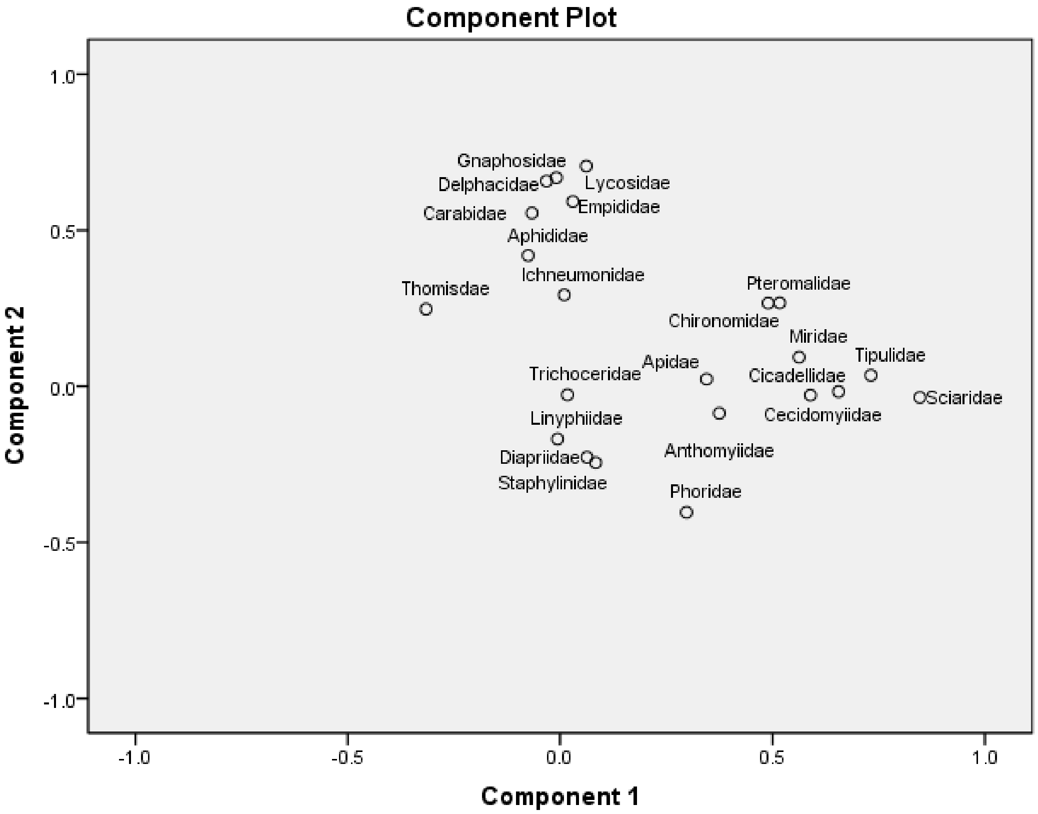

Figure 3.6 Loadings for each of the 22 arthropod taxa on the two main principle components produced from the PCA. See Table 3.4 for loading values and variance explained.

Table 3.4 Component matrix produced from PCA of 22 arthropod families showing component loadings of each family on the first three principle components and the total amount of variance explained. Component loadings <0.4 are not shown.

	Component		
	1	2	3
Sciaridae	0.847		
Tipulidae	0.731		
Cicadellidae	0.655		
Cecidomyiidae	0.589		
Miridae	0.563		
Pteromalidae	0.517		
Chironomidae	0.49		
Lycosidae		0.705	
Gnaphosidae		0.668	
Delphacidae		0.657	0.431
Empididae		0.592	
Carabidae		0.555	
Phoridae		0.404	
Diapriidae			0.762
Linyphiidae			0.651
Staphylinidae			0.638
Trichoceridae			
Ichneumonidae			
Aphididae		0.419	
Thomisae			
Anthomyiidae			
Apidae			
% of Variance Explained	15.119	12.834	9.524
Cumulative %	15.119	27.953	37.477

Additionally, I plotted the factor scores of the first two components for each sampling point and labeled the points based on site and plot/vegetation type (Figure 3.7). Communities from the three North Slope sites (TLFS, IMVT, and SDOT) had a significant amount of overlap, suggesting that arthropod community composition was similar at those three sites, whereas at ROMO, the lack of overlap suggests that there was different community composition within shrub and open tundra plots. PC1 seems to be separating ROMO from the other three sites based on the presence of a few particularly abundant families, including several fly families, a couple true bug families, and a parasitic wasp. PC2 seems to be separating out the shrub and open tundra arthropod communities based on the presence of a few particular families, including two spider families, a beetle, and a true bug, found in abundance at open tundra plots. Differences in shrub and open tundra arthropod communities found specifically at ROMO were likely driving the overall patterns observed.

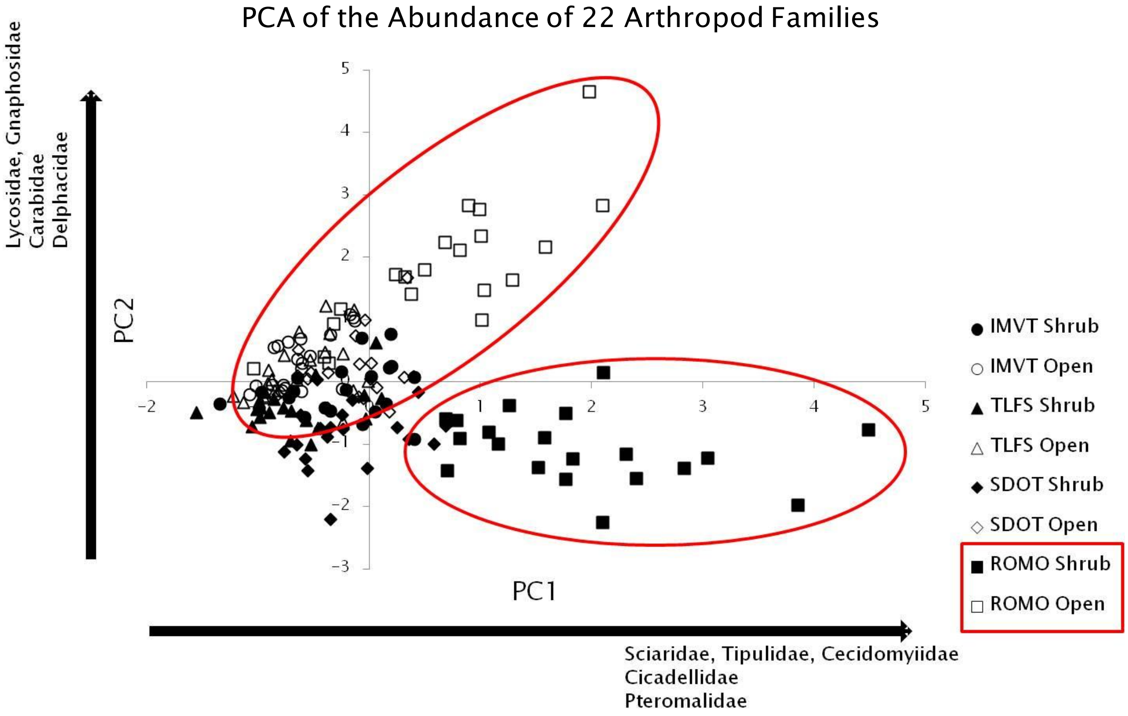

Figure 3.7 Regression factor scores for each trap based on the first two principle components labeled by site and vegetation type.

3.7 Individual Arthropod Order Abundance

Significant effects of site (X^2_3 = 18.53; P=0.0003) and vegetation type (X^2_1 = 21.71; P<0.0001) were found for total adult spider abundance (Araneae) in pitfall traps across sampling dates; there was no significant site*vegetation type interaction (Figure 3.8).

Consistent with expectations, spider abundance was higher in open tundra vegetation than in shrub vegetation. ROMO had higher abundance than TLFS but had similar abundance to SDOT and IMVT.

A significant effect of site (X^2_3 = 15.34; P=0.002) and a marginally significant site*vegetation type interaction (X^2_3 = 7.12; P=0.07) were found for beetle (Coleoptera) abundance, although there was no significant effect of vegetation type (Figure 3.9). The marginally significant interaction was driven by the significantly greater beetle abundance found in open tundra compared to shrub at IMVT, whereas the three other sites had no significant differences in beetle abundance between shrub and open tundra plots.

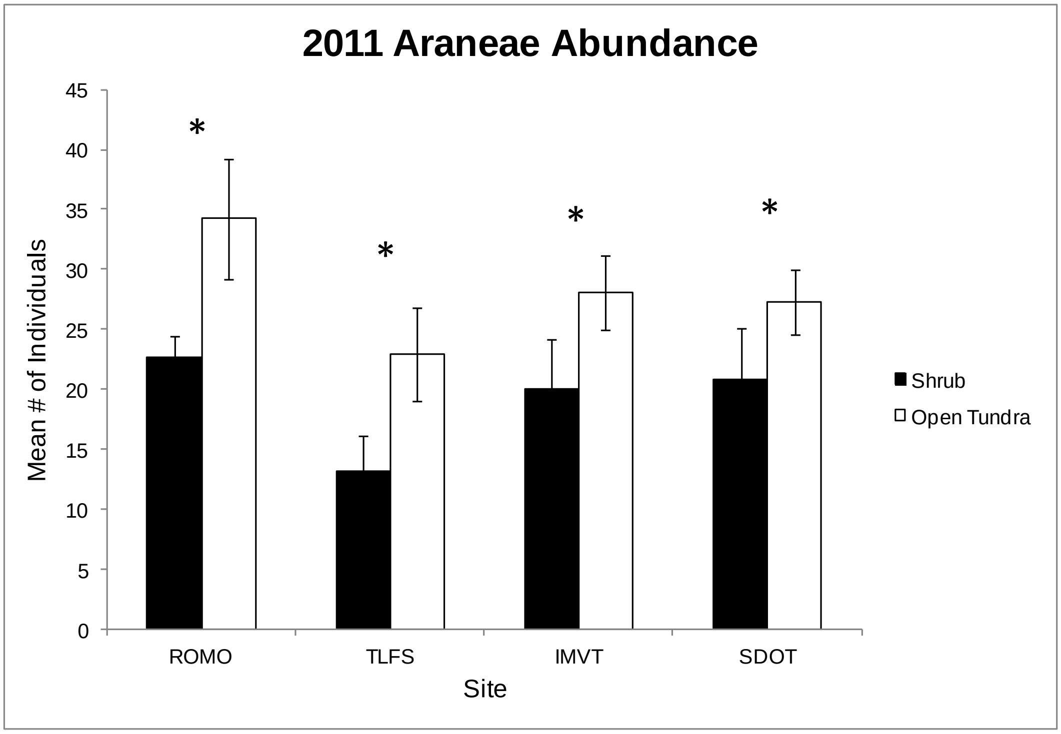

Figure 3.8 Mean number of spiders (±SE) caught per pitfall trap in 2011 in shrub and open tundra vegetation at four sites. Asterisks represent significant within site differences at $p<.05$.

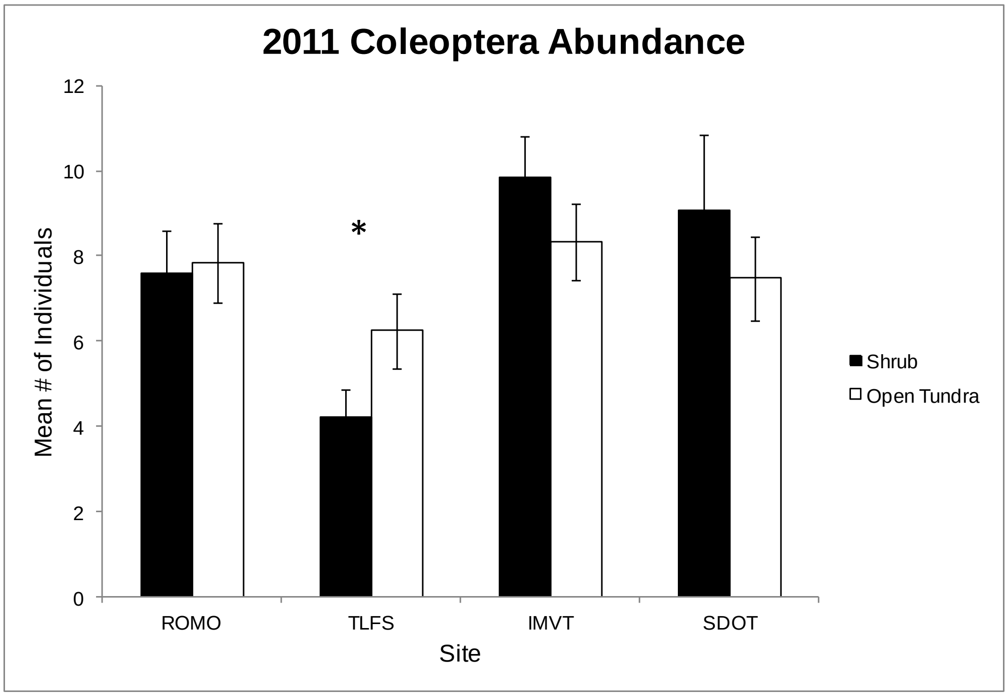

Figure 3.9 Mean number of beetles (±SE) caught per pitfall trap in 2011 in shrub and open tundra vegetation at four sites. Asterisks represent significant within site differences at *p*<.05.

Significant effects of site (X^2_3 = 24.05; P<0.0001), vegetation type (X^2_1 = 12.07; P=0.0005) and a significant site*vegetation type interaction (X^2_3 = 9.35; P=0.02) were found for total true bug (Hemiptera) abundance (Figure 3.10). The significant interaction was driven by the significantly greater true bug abundance found in shrub vegetation compared to open tundra vegetation at ROMO, IMVT, and SDOT, while TLFS showed no significant difference in true bug abundance between vegetation types. True bug abundance was significantly higher in shrub habitat relative to open tundra habitat. ROMO had the greatest true bug abundance, caused by the particularly high abundance of leafhoppers (Family: Cicadellidae), while TLFS had the lowest true bug abundance.

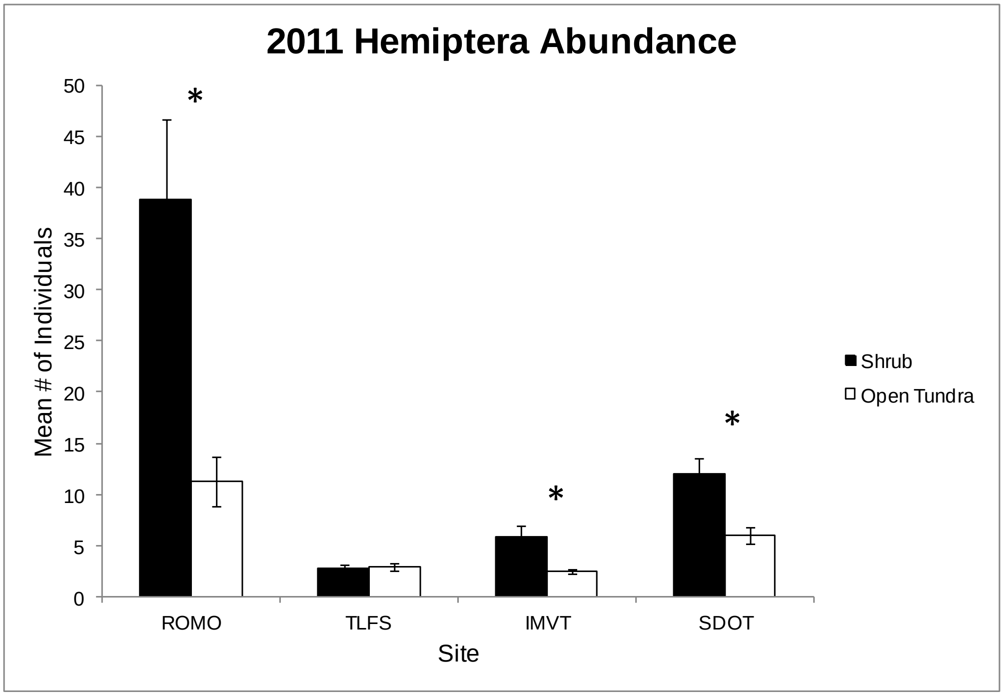

Figure 3.10 Mean number of true bugs (±SE) caught per pitfall trap in 2011 in shrub and open tundra vegetation at four sites. Asterisks represent significant within site differences at *p*<.05.

Significant effects of site (X^2_3 = 20.41; P=0.0001), vegetation type (X^2_1 = 12.09; P=0.0005), and a significant site*vegetation type interaction (X^2_3 = 12.09; P=0.0005) were found for total wasp and bee (Hymenoptera) abundance (Figure 3.11). The significant interaction was driven by the significantly greater wasp and bee abundance found in shrub vegetation relative to open tundra vegetation at ROMO and IMVT, whereas wasp and bee abundance did not significantly differ between vegetation types at TLFS and SDOT. Overall, wasp and bee abundance was significantly higher in shrub than open tundra habitat. ROMO had similar abundance to SDOT, but had greater wasp and bee abundance than IMVT and TLFS.

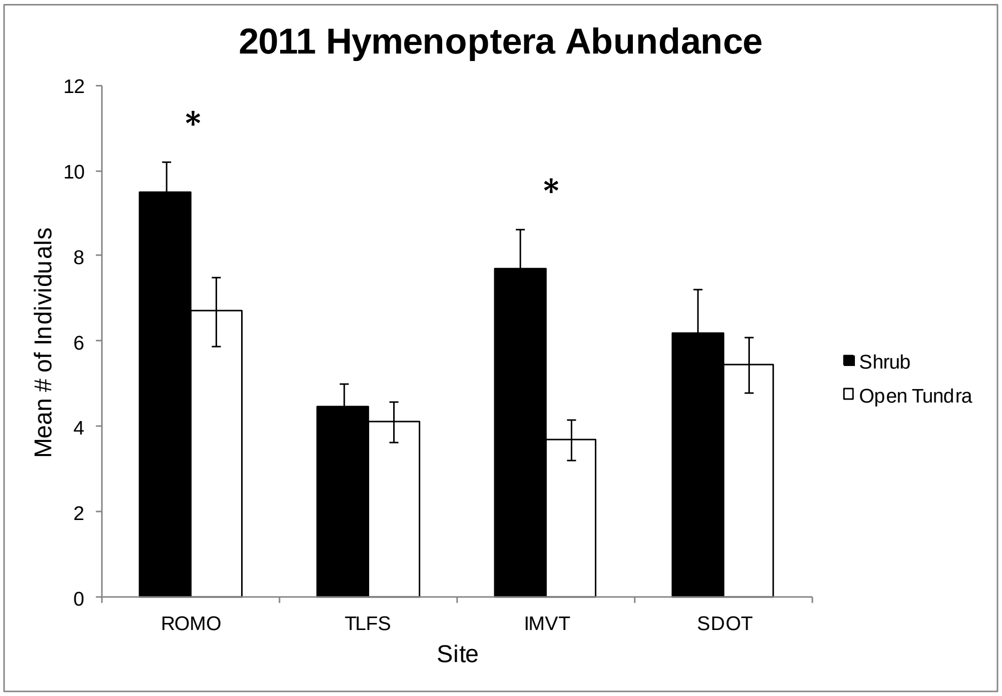

Figure 3.11 Mean number of wasps and bees (±SE) caught per pitfall trap in 2011 in shrub and open tundra vegetation at four sites. Asterisks represent significant within site differences at *p*<.05.

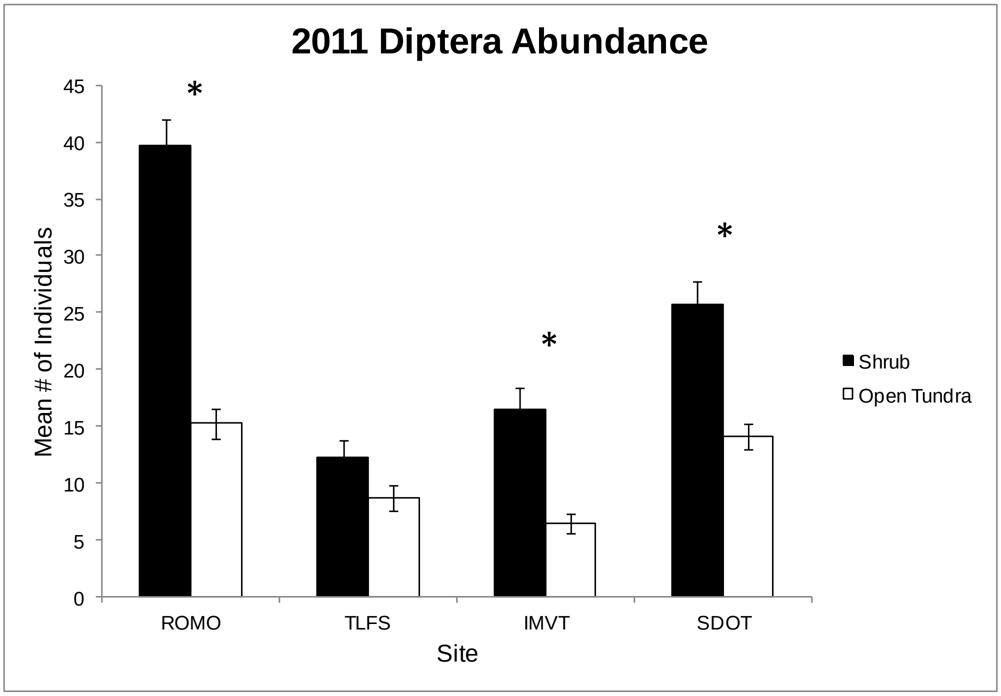

Figure 3.12 Mean number of flies (±SE) caught per pitfall trap in 2011 in shrub and open tundra vegetation at four sites. Asterisks represent significant within site differences at *p*<.05.

Significant effects of site (X^2_3 = 28.28; P<0.0001), vegetation type (X^2_1 = 23.62; P<0.0001) and a significant site*vegetation type interaction (X^2_3 = 10.15; P=0.02) were found for fly (Diptera) abundance (Figure 3.12). The significant interaction was driven by the significantly greater fly abundance found in shrub vegetation compared to open tundra vegetation at ROMO, IMVT, and SDOT, whereas there was no significant difference in fly abundance between vegetation types at TLFS. Fly abundance was significantly greater in shrub-dominated habitat than open tundra habitat. ROMO had similar abundance to SDOT but both had greater abundance of flies than IMVT and TLFS.

3.8 Arthropod Phenology

Significant effects of site ($F_{3,150}$=2.80; P=0.0423), vegetation type ($F_{1,150}$=10.36; P=0.0016) and a significant site*vegetation interaction ($F_{3,150}$=7.51; P<0.0001) were found for the average date50 of the entire arthropod community (Figure 3.13). The significant interaction was driven by the much later phenology in shrub compared to open tundra at SDOT, and the trend toward earlier phenology in shrub compared to open tundra at ROMO. Arthropods reached their median activity level on average five days earlier in open tundra habitat than in shrub-dominated habitat, except at ROMO. Furthermore, date50 at ROMO occurred significantly earlier than SDOT.

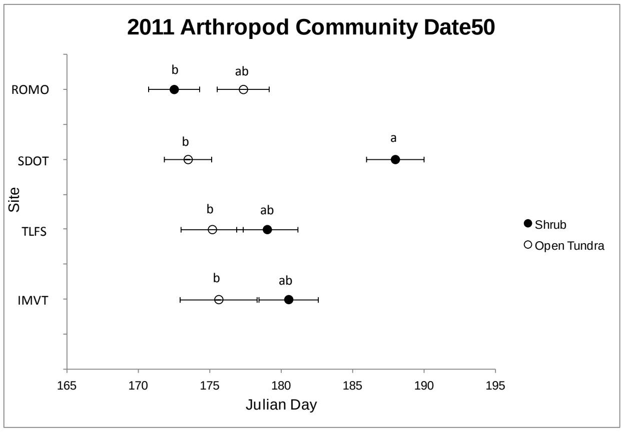

Figure 3.13 Average date50 (±SE) for all arthropods captured during the 2011 field season in shrub and open tundra vegetation at four sites. Mean values with the same letters are not statistically significant at *p*<.05.

Additionally, significant effects of vegetation type ($F_{3,729}$=14.87; P=0.0001), taxon ($F_{4,729}$=57.05; P<0.0001), site*vegetation type interaction ($F_{3,729}$=10.03; P<0.0001), site*taxon interaction ($F_{12,729}$=3.38; P<0.0001), vegetation type*taxon interaction ($F_{4,729}$=4.38; P=0.002), and site*vegetation type*taxon interaction ($F_{12,729}$=2.59; P=0.002), were found for date50 of the five major arthropod orders (Coleoptera, Diptera, Araneae, Hymenoptera, and Hemiptera) captured over the season (Figure 3.14 and Figure 3.15). The significant three way interaction was driven by taxa-specific variation within vegetation types and sites. For instance, Coleoptera, Diptera, and Hemiptera all showed a trend toward later phenology within shrub habitat at SDOT, whereas Araneae showed an opposite trend toward earlier phenology within shrub habitat at SDOT and seemed to occur earlier than any other order. Additionally, Hymenoptera showed no strong trend toward either vegetation type at SDOT. Overall, the analysis suggests that Araneae appeared first followed by Coleoptera which appeared significantly earlier than Hemiptera, Hymenoptera, and Diptera.

3.9 Multiple Regression Analysis with Arthropods and Vegetation Variables

For all multiple regression analyses, I only report results with models that had an R^2 greater than 0.10. In general, total arthropod abundance did not correlate well with the vegetation variables we measured, despite the differences I found among sites and vegetation types in the factorial analyses (described above). However, overall arthropod abundance was significantly positively correlated with maximum shrub height, although the variance explained by maximum shrub height was low (R^2 = 0.13; $F_{3,155}$ = 23.91; P<0.0001). In particular, fly abundance was significantly positively correlated with maximum shrub height and the amount of variance explained was good (R^2 = 0.25; $F_{3,155}$ = 52.64; P<0.0001). This may reflect the greater fly abundance in the sites with the tallest shrubs (ROMO and SDOT) that are essentially riparian areas. Beetle, spider, wasp and bee, and true bug abundance did not correlate well with any of the vegetation variables measured.

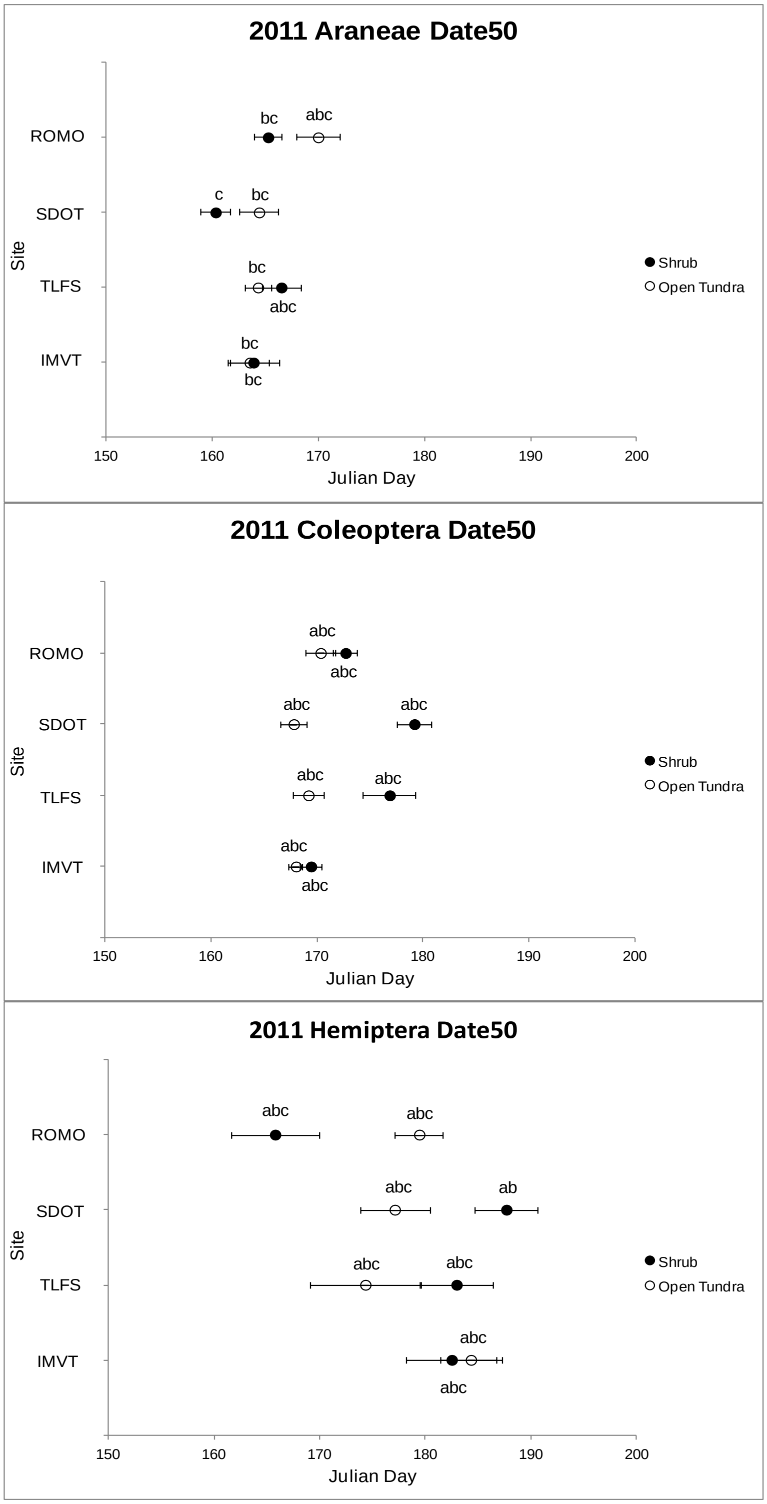

Figure 3.14 Average date50 (+-SE) for three major arthropod orders captured during the 2011 field season in shrub and open tundra vegetation at four sites. Mean values with the same letters are not statistically significant at *p*<.05.

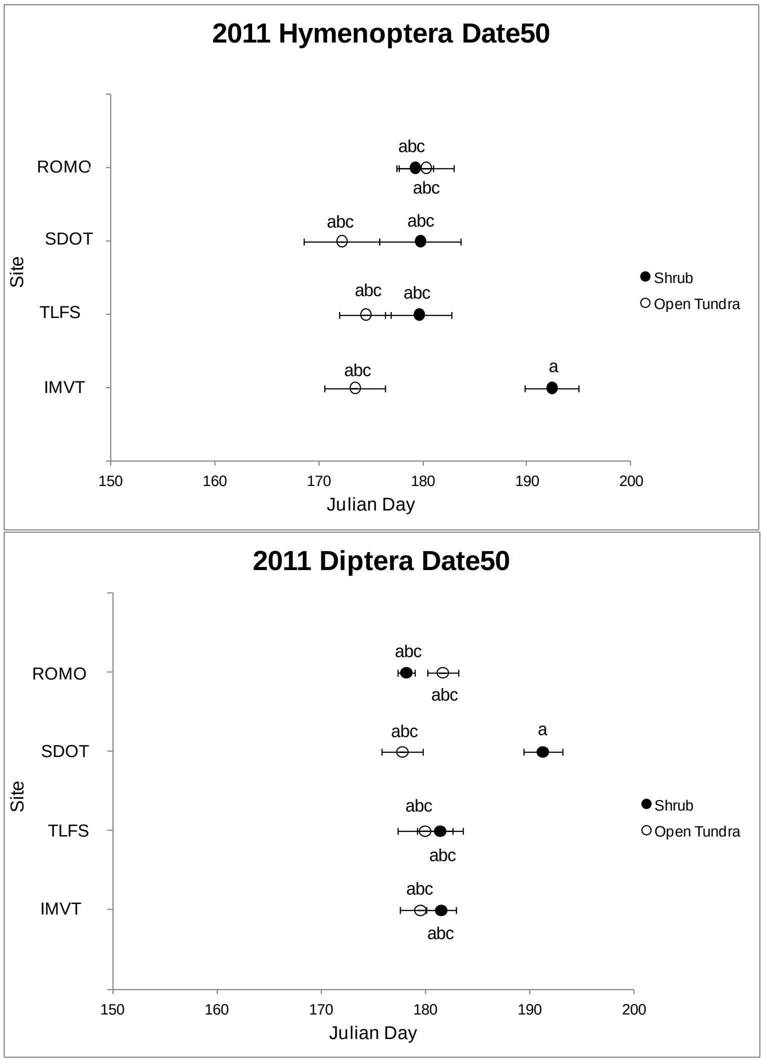

Figure 3.15 Average date50 (±SE) for two major arthropod orders captured during the 2011 field season in shrub and open tundra vegetation at four sites. Mean values with the same letters are not statistically significant at *p*<.05.

3.10 Multiple Regression Analysis with Arthropod Phenology and Environmental Variables

The phenology of spiders, flies, and true bugs, as well as the overall arthropod community, was not correlated with either TDD or snow melt date. Since TDD and snow melt were calculated at the transect level, we only had 16 points to use for this analysis. Because TDD and snow melt were correlated, we analyzed these using stepwise regression, assuming that only one variable would be a better predictor of phenology. The only orders that had significant correlations with either TDD or snow melt were beetles and wasps and bees.

Beetle phenology marginally negatively correlated with TDD ($R^2 = 0.23$; $F_{1,13} = 3.81$, $P = 0.07$). Higher TDD led to earlier phenology in beetles. Snow melt date was not correlated with beetle phenology.

Wasp and bee phenology was significantly positively correlated with snow melt date and the amount of variance explained by snow melt date was high ($R^2 = 0.48$; $F_{1,13} = 12.17$, $P = 0.004$). Earlier snow melt led to earlier phenology in wasps and bees. TDD was not correlated with wasp and bee phenology.

3.11 Multiple Regression analysis with Arthropod Abundance and Environmental Variables

The abundance of beetles, flies, true bugs, wasps and bees was not explained by either snow melt date or TDD. The only order that had a significant correlation with either TDD or snow melt was Araneae. The abundance of spiders was significantly negatively correlated with snow melt date and the amount of variance explained by snow melt date was good ($R^2 = 0.37$; $F_{1,13} = 7.61$, $P = 0.02$). Earlier snow melt increased the number of spiders captured. However, TDD was not correlated with spider abundance.

CHAPTER 4

DISCUSSION

4.1 Gradients of Shrubbiness Across Study Sites

Shrub and open tundra vegetation create a different habitat for arthropods both quantitatively and qualitatively, although there was substantial variation depending on location and other factors that affect plant species composition and thus habitat characteristics. For example, tall shrubs with high structural complexity were found at SDOT while ROMO also had tall shrubs but had the lowest branch complexity. At IMVT and TLFS shrubs were generally much shorter although they had intermediate values of branch complexity. In addition, shrubs at ROMO had the lowest foliar canopy cover, consistent with more open habitat and less dense vegetation, while shrubs at SDOT had the highest foliar canopy cover, consistent with more dense vegetation. The lower branch complexity and foliar canopy cover of shrubs at ROMO was correlated with the plant species present. The dominant shrub species at ROMO was *Salix alaxensis* (Alaska or feltleaf willow), one of the tallest shrubs on the North Slope, whereas at the other three sample sites the dominant shrub species was *Betula nana* (dwarf birch), a lower-stature, spreading shrub.

Greater differences in vegetation in shrub and open tundra habitats were found at ROMO and SDOT, whereas there was little difference between shrub and open tundra at IMVT and TLFS. ROMO and SDOT shrub plots were essentially both riparian and consisted of taller riparian shrubs, whereas TLFS was located near the outlet of Toolik Lake and consisted mainly of dwarf shrubs and IMVT consisted of more typical water track shrub vegetation (McNamara et al. 1999). Environmental characteristics associated with streams facilitate growth of species of shrubs that can attain greater heights because they can put down longer roots where the ground thaws more deeply; other abiotic variables can also affect the occurrence of particular shrub species.

The most southern site, ROMO, differed from the three North Slope sites. It was located in Atigun Valley and was subject to different environmental conditions during the growing season. For instance, minimum temperature at ground surface over the season was warmest at ROMO. Additionally, weather patterns could vary greatly at ROMO relative to the three other sites. For example, on rainy and foggy days across most of the North Slope, it could be sunny and clear within the Atigun valley at ROMO. Alternatively, there could be rain clouds within the valley while conditions across most of the North Slope and our remaining sites were clear and sunny. Furthermore, it is likely that other variables not measured, including soil moisture, would differ as well. This is likely to be important for many arctic arthropod species that are highly dependent on moisture conditions (Danks 2004). The substrate within the shrub plot at ROMO was generally much more rocky and higher in mineral content due to sediment deposition from the nearby river, which was unlike all other shrub and open tundra plots sampled. The differences in vegetation and environmental characteristics present at our sites, including plant species composition, shrub growth, and weather conditions, are likely to have effects on arctic arthropods which rely heavily on aspects of their habitat, particularly the microclimate created by vegetation and macroclimatic conditions.

4.2 Shrub and Open Tundra Vegetation Create Different Habitats for Arthropods

4.2.1 Shrub vegetation is more structurally complex than open tundra vegetation

Overall, shrub vegetation was found to create a different habitat than open tundra vegetation based on a combination of environmental and vegetation variables, supporting H1. Shrub vegetation was significantly taller, had greater branch complexity, and higher-peak NDVI values, indicative of greater foliar canopy cover, relative to open tundra vegetation although these differences were primarily found at SDOT and ROMO and did not occur at the other two sites where shrubs were shorter. Principle components analysis demonstrated that SDOT, the most northern site, had the highest degree of “shrubbiness” as it had the tallest shrubs, and highest values of branch complexity and foliar canopy cover. This is consistent with predictions and with other studies done on the impacts of increasing shrub dominance in the Arctic (Bret-Hart et al. 2001, Walker et al. 2006, Myers-Smith et al. 2011). However, plant species richness did not differ between habitat types. Other studies have demonstrated a decrease in plant species richness with experimentally increased shrub dominance (Chapin et al. 2005, Shaver et al. 2001, Walker et al. 2006). However, these studies were manipulative in nature, whereas my study was based on observation of the natural environment. Natural gradients of tundra plant species richness suggest that plant diversity can be greater in shrub habitats, but this usually depends on many environmental variables (Gough 2012).

The cover of mosses and litter was found to be greater in open tundra habitat, whereas vascular plant cover was greater in shrub habitat. Lichen cover did not significantly differ between vegetation types. Other studies on experimentally induced warming in the Arctic have shown that with increasing shrub dominance, the cover of mosses and lichens decline (Chapin et al. 1995, Walker et al. 2006, Elmendorf et al. 2012). Although I did not find any difference in lichen cover between shrub and open tundra vegetation, I did find that moss cover was greater in open tundra vegetation, which is consistent with prior studies. Litter cover was also greater in open tundra vegetation, although other studies have shown greater litter cover associated with increased deciduous shrubs (Myers-Smith et al. 2011).

4.2.2 Open tundra habitats are snow free earlier in the season than shrub dominated habitats

Shrub-dominated and open tundra habitats differed based on several environmental variables as well, confirming P1.2. The timing of snow melt in shrub plots was delayed relative to open tundra plots, and there was a trend toward greater thawing degree days in open tundra plots. These results support previous literature that has shown that deciduous shrubs capture snow more effectively, reduce losses due to sublimation, and delay the timing of snow melt (McFadden et al. 2001, Sturm et al. 2001b).

Though I predicted a difference in temperature at ground surface between vegetation types, the results of my data showed no significant difference between mean, maximum, and minimum temperature at ground surface in shrub and open tundra habitat. However, I did find a significant site*vegetation type interaction with minimum temperature. The interaction resulted from a trend toward higher temperature in open tundra compared to shrub at IMVT, whereas ROMO and SDOT showed a trend toward higher temperature in shrub habitat. The trend for higher temperature in open tundra at IMVT is consistent with expectations. Surprisingly, minimum temperatures were slightly higher in shrub plots at ROMO and SDOT, which was inconsistent with predictions. Prior studies have shown that increased canopy cover should increase light attenuation (Bret-Harte et al. 2001), and therefore, lower temperatures at ground surface. Perhaps increased canopy height and foliar canopy cover demonstrated by the results did not actually significantly lower the amount of light reaching the ground thereby causing no observable differences in temperature at ground surface. Also, a reduction in light may not have been of a large enough magnitude to cause significant changes in temperature at ground surface. Additionally, lack of a sufficient sample size could have prevented us from observing any actual differences in temperature since there were only two data loggers per vegetation type.

Although I did not find a significant difference in temperature between vegetation types, I did find that ROMO was significantly warmer than TLFS, and SDOT and IMVT were intermediate between those two sites. Future research would likely benefit from measuring winter temperatures within the soil or at ground surface, to determine if there were significant differences between shrub and open tundra habitats, and if these correlate with arthropod abundance during the summer.

4.3 Arthropod Communities Differ in Shrub and Open Tundra Habitats

4.3.1 Arthropods are more abundant in shrub vegetation than open tundra vegetation

Consistent with H2, arthropod abundance was significantly greater in shrub-dominated habitat than open tundra habitat over both years of sampling in all sites except TLFS. Greater overall abundance of arthropods in shrub habitat could be due to greater structural complexity, which other studies have found is significantly related to arthropod community composition, richness, and abundance (Lawton 1983, Dennis, et al. 1998, Brose 2003, Langelloto and Denno 2004, Lassau and Hochuli 2005, Høye and Lobo 2007, and many others). However, multiple regression analysis with the vegetation variables only demonstrated a significant positive correlation, although fairly weak, with maximum shrub height. Increases in shrub height may be responsible for increased vertical zonation among arthropods (Lawton 1983, Brose 2003). Additionally, taller shrubs could provide more resource sites for oviposition, feeding, refuge, and overall greater niche availability (Lawton 1983, Brose 2003).

As previously mentioned, site differences in arthropod abundance were also found and can be attributed to several possible factors. The most southern site, ROMO, had the highest arthropod abundance, and this site accounted for the largest difference in overall arthropod abundance between vegetation types. In 2011, TLFS had the lowest arthropod abundance of any site, and had a trend toward greater abundance in open tundra vegetation. The difference in arthropod abundance between ROMO and TLFS could be related to environmental differences between sites, since the activity and abundance of arthropods has been strongly linked to temperature (Høye and Forchhammer 2008b). Specifically, the significantly warmer minimum daily temperature at ROMO likely led to more arthropods being caught at ROMO relative to the other sites, particularly TLFS, which had the lowest arthropod abundance and lowest minimum temperature. It is also important to note that winter temperatures may be important for overwintering arthropods. Deciduous shrubs have been shown to hold more snow during the winter and increase snow depth (McFadden et al. 2001, Sturm et al. 2001b), which is likely to increase temperatures in the soil due to the insulating effect of snow (Sturm et al. 2005). Increases in winter soil temperatures may allow more arthropods to survive during the harsh winter (Bale and Hayward 2010). In addition, ROMO differed from the other sites in that it possessed much lower branch complexity, peak-NDVI, and percent cover vascular plants, and higher percent cover litter. As described above, it is likely that the difference in shrub species composition across sites is the primary cause of these vegetation and structural differences. Additionally, some arthropods may benefit from increased litter depth and complexity (Hurd and Fagan 1992, Rypstra et al. 1999, Langellotto and Denno 2004), and the movement of arthropods may be less hindered by somewhat sparsely branched shrubs (Lassau and Hochuli 2005), leading to larger arthropod capture numbers at ROMO.

4.3.2 Arthropod richness and diversity are higher in shrub vegetation than open tundra vegetation

Also consistent with my predictions, arthropod taxonomic richness and diversity were higher in shrub than open tundra plots, although these results differed among sites. The most southern site, ROMO, had the highest arthropod richness, while ROMO and SDOT had the highest diversity. Many studies have linked the richness and diversity of arthropods to the structural complexity of vegetation (Gardner et al. 1995, Haysom and Coulson 1998, Brose 2003, Lassau et al. 2005), which here was shown to be greater in shrub-dominated habitat relative to open tundra habitat. Similar to arthropod abundance, it is likely that other factors also played an important role in determining the richness and diversity of arthropods across sites and vegetation types.

4.3.3 Arthropod community composition differs between shrub and open tundra vegetation

Principle components analysis on 22 arthropod families captured over the 2011 season demonstrated that arthropod communities may differ between vegetation types, although the explanation of variance suggests that there was a great deal of overlap in community composition across sites and vegetation types. However, I did find that certain ground dwelling spiders and beetles were associated with open tundra habitat, while other groups such as several fly families, leafhoppers, and a parasitic wasp family were associated with shrub habitat. This pattern was strongly driven by arthropod community differences found at ROMO, which is expected based on the quantitative and qualitative differences between ROMO and the other sample sites. Muff et al. (2009) found that variables connected with light availability had a greater influence on spider communities than the type of ground vegetation. In addition, Pajunen et al. (1995) found that surface-active wolf spiders (Family: Lycosidae), were caught most in traps in warm, open habitats, whereas web-building spiders requiring suitable microhabitat structure for web construction were more strongly associated with structurally complex vegetation. Leafhoppers (Family: Cicadellidae) are exclusively herbivorous and feed on a variety of plants and previous work has shown that leafhopper assemblies are strongly affected by the structure of vegetation (Brown et al. 1992). More complex vegetation and greater vascular plant cover associated with shrub-dominated habitats are likely to benefit leafhoppers due to the larger food resource available as well as an increase in the spatial extent of a single plant. Additionally, leafhoppers that feed on birches and willows, two of the most abundant shrub species in arctic Alaska, are known to take advantage of the high nutritional value of the early spring growth (Hamilton and Whitcomb 2010).

4.3.4 Abundance patterns in shrub and open tundra vegetation are arthropod order specific and are correlated with various factors

Patterns of abundance differed among arthropod orders. In general, spiders were more abundant in open tundra habitat compared to shrub-dominated habitat. Although greater vegetation complexity has been shown to impact the abundance and diversity of spiders (Uetz 1991, Halaj et al. 1998, Rypstra et al. 1999, Bowden and Buddle 2010), many of these studies have looked at ground dwelling and web-weaving spiders together, and the latter are believed to rely on greater vegetation structure for web attachment. It is important to note that the majority of spiders caught in my pitfall traps were ground-dwelling hunting spiders of the family

Lycosidae (wolf spiders). Therefore, the low abundance of spiders associated with shrub-dominated habitat likely can be attributed to greater shrub height, branch complexity and foliar canopy cover in shrub compared to open tundra habitat, which has been shown to negatively impact the abundance of ground-dwelling spiders. Furthermore, wolf spiders are known to bask in sunlight and to behaviorally thermoregulate themselves as well as the egg sacs they carry attached to their abdomens (Humphrey 1974). Therefore, an increase in the amount of foliar canopy cover is likely to decrease the abundance of ground dwelling spiders through a reduction in light reaching the ground surface. The differences in amount of litter and foliar canopy cover in shrub and open tundra habitat could explain the greater abundance of spiders found in open tundra habitat. Other studies have supported this, showing that ground dwelling spiders generally prefer open canopy habitats (Pajunen et al. 1995, Muff et al. 2009). However, results from multiple regression analysis showed that spider abundance was not correlated with any of the vegetation variables measured even though spiders were more common in open tundra habitat. This may indicate that environmental variables may have a larger impact on spider abundance than vegetation variables. For instance, I found that spider abundance was significantly negatively correlated with snow melt date and the correlation was strong. Consistent with predictions, earlier snow melt led to a greater abundance of spiders over the growing season. A longer growing season and earlier snow melt have been associated with larger body size in some arctic spider species, particularly in females (Høye et al. 2009, Høye and Hammel 2010) and larger females tend to have greater reproductive output (Simpson 1993). Thus, it is reasonable to suggest that a longer growing season will lead to increased reproductive output and hence, increases in the abundance of spiders.

Beetle abundance did not differ between vegetation types. Other studies have shown that beetle abundance and diversity are influenced by the structural complexity of vegetation (Brose 2003), but this was not the case here as multiple regression analysis demonstrated that beetle abundance was not correlated with any of the vegetation variables measured. There is a diversity of trophic guilds within Coleoptera, which may have obscured patterns within particular groups. Additionally, the timing of snow melt and TDD were not correlated with beetle abundance, which may have been attributed to the tremendous variety of life cycles found in the order.

In contrast to spiders, the abundance of true bugs was significantly greater in shrub-dominated habitat than open tundra habitat. True bugs are predominantly phytophagous, that is, they feed on vegetation. Phytophagous insects are more likely to be present in more complex shrub vegetation that provides greater availability of resources for feeding, as well as more suitable sites for refuge, oviposition, and overwintering (Lawton 1983). Since greater vascular plant cover, branch complexity, shrub height and peak-NDVI were found in shrub-dominated habitat, this could provide insight into reasons why the abundance of true bugs was significantly greater in shrub relative to open tundra habitat, especially at ROMO where the abundance of true bugs was much greater than the other three sampling sites. However, after running a multiple regression analysis, no significant correlations were found with any of the vegetation variables measured. It is surprising that true bug abundance was not significantly correlated with any of the vegetation variables, as nearly all members of Hemiptera are phytophagous. Further research is needed to determine what habitat characteristics are most important in controlling patterns of abundance in this order.

Wasps and bees were also more abundant in shrub-dominated habitat. The abundance of wasps and bees may be highly dependent on host insects, since many wasps are parasitoids of other arthropods and the majority of Hymenoptera caught were parasitic. Although we did not collect data on specific hosts utilized by parasitic wasps, we did collect significant data on arthropod groups which may contain host organisms used by parasitic wasps such as true bugs and flies. Since fly abundance was positively correlated with shrub height, and since more flies and true bugs were found in shrub habitat than open tundra habitat, this could be a controlling factor for the abundance of wasps and bees, since many wasp species have highly specialized life histories and are host-specific (La Salle 1993). For example, PCA results showed that Miridae (plant bugs) and Cecidomyiidae (gall midges) are associated with shrub habitat, and Pteromalidae, a large family of parasitic wasps, are also associated with shrub habitat. More abundant host insects for the variety of parasitic wasps captured in my study may provide a larger resource base for enhanced reproductive success in parasitic Hymenoptera.

The abundance of flies was also significantly greater in shrub than open tundra habitat. Fly abundance was significantly positively correlated with maximum shrub height, and this correlation was strong. Greater shrub height could allow for more suitable locations for basking. Shrubs were tallest at ROMO and SDOT, which were the sites with the highest fly abundance. Many flies, especially mosquitoes (Hocking and Sharplin 1965), and arctic arthropods in general (Danks 2004) are known to bask to increase heat intake, and this should be easier on leaves and other plant structures that receive more direct light and are not shaded by other plants.

4.4 Arthropod Abundance and Phenology and the Significance of Snow Melt and TDD

4.4.1 Phenological patterns are arthropod order specific, differ in shrub and open tundra vegetation, and are correlated with various factors

Phenological patterns differed among arthropod orders and vegetation types. Spiders appeared first, followed by beetles, which appeared significantly earlier than true bugs, wasps and bees, and flies. Differences in the phenology of certain arthropod groups may be related to taxa-specific differences in the timing of resource availability and opportunities for reproduction (Høye and Forchhammer 2008a). Overall, arthropods appeared five days earlier in open tundra habitat than in shrub habitat except at ROMO where this pattern was reversed. The earlier phenology in shrub habitat at ROMO is largely due to the extraordinary number of leafhoppers (Family: Cicadellidae) captured early in the season prior to leaf out. In general, earlier snow melt in open tundra habitat was likely the reason for earlier arthropod phenology in open tundra habitat, since other studies have shown that arthropod phenology has been linked most strongly with the timing of snow melt (Høye et al. 2007a, Høye and Forchhammer 2008a). However, I found that the phenology of the overall arthropod community was not correlated with snow melt date or TDD. Infrequent observations of snow melt and weekly sampling of arthropods, rather than a more frequent daily sampling, may have prevented us from seeing significant patterns. Perhaps more frequent arthropod sampling and greater temporal resolution and precision in calculations of the timing of snow melt and TDD would have produced significant correlations between these variables and patterns of phenology and abundance for the entire arthropod community. Alternatively, there may be a difference between High and Low Arctic in terms of how tightly phenology is coupled to snow melt, since many prior studies that demonstrated a strong link between the timing of snow melt and arthropod phenology (Høye et al. 2007a, Høye and Forchhammer 2008a) were conducted in the High Arctic, whereas my sites were located in the Low Arctic.

I did find that the phenology of certain orders was significantly correlated with the timing of snow melt or TDD. For example, wasp and bee phenology was significantly positively correlated with snow melt date. Earlier snow melt produced earlier phenology of Hymenoptera. Additionally, there was a marginally significant negative correlation with beetle phenology and TDD. Higher TDD results in earlier phenology of Coleoptera. Spider, true bug, and fly phenology were not significantly correlated with either snow melt date or TDD.

Arthropod phenology is highly dependent on life cycle. For example, species with longer life cycles typically emerge early in the year in order to maximize time for feeding and reproduction during the short summer season (Danks 2007). Consequently, it is probable that rapidly developing insects will be less dependent on timing of snow melt and TDD while those with longer life cycles and slower development are likely to become active immediately after snow melt and therefore are likely to correlate with snow melt and/or TDD. Research has demonstrated that most Coleoptera develop slowly, have multi-annual life cycles, overwinter as larvae or adults, and become active soon after snow melts (Kaufmann 1971, Danks 1981, Danks 2006). Not surprisingly, greater thawing degree days, and possibly earlier snow melt, produced earlier appearance and activity of beetles. Rapid development is known to occur in a few families of Hymenoptera including small chalcidoids such as Mymaridae, Aphelinidae, and Pteromalidae (Danks 2006). It would be expected for these groups to be less correlated with snow melt or TDD. However, I found a significant positive correlation with Hymenoptera phenology and snow melt date. A possible explanation could be the relatively high proportion of Hymenoptera captured with longer life cycles, such as Apidae and Ichneumonidae (Danks 1981, 2006). Additionally, although many parasitic Hymenoptera develop rapidly, some species may develop more slowly, especially those with slowly developing hosts (Danks 2006).

Since life history can vary tremendously within orders, correlations with timing of snow melt and TDD may not have been found for Hemiptera, Diptera, and Araneae phenology due to the differential life cycles possessed by members of the same order. For example, some mosquitoes overwinter as eggs and emerge later in the season (*Aedes* spp.), while other species overwinter as inseminated adults that emerge immediately upon snow melt to feed and lay eggs (*Culiseta* spp.) (Frohne 1954, 1956). Perhaps by testing specific groups within orders with known and similar life histories, we may find significant correlations with environmental variables.

4.5 General Conclusions

Shrub-dominated habitats were found to differ in several measures of structural complexity of vegetation, having greater maximum shrub height, branch complexity, and peak-NDVI values than open tundra habitats. Additionally, snow melt was delayed in shrub habitat on average by 4 days and a trend toward greater thawing degree days (TDD) was found in open tundra habitat, providing support that shrub vegetation creates a different habitat for arthropods than open tundra vegetation. Consistent with predictions, pitfall trap sampling captured significantly more arthropods in shrub plots than open tundra plots. Additionally, taxonomic richness and taxonomic diversity were significantly greater in shrub plots than open tundra plots. Patterns of abundance within the five most abundant arthropod orders were found to differ between shrub and open tundra habitats. Few strong correlations were found with the vegetation and environmental variables on the abundance and phenology of arthropods, although shrub height seemed to be important for the overall abundance of arthropods as well as Diptera in particular.

Overall, arthropod phenology was earlier in open tundra habitat and differed among arthropod orders, most likely due to taxa-specific differences in timing of resources, opportunities for reproduction, and life history traits. Araneae appeared prior to all other orders, and they also were the most abundant order of arthropods captured throughout the growing season, likely due to the significant negative correlation between spider abundance and snow melt date. Arthropod phenology was correlated with the timing of snow melt and TDD, although only certain orders showed significant patterns, with earlier snow melt and higher TDD leading to earlier median activity levels in Coleoptera and Hymenoptera.

Although multiple regression analyses did not find many significant correlations between measures of vegetation characteristics, environmental variables, and arthropod abundance and phenology, differences were found between shrub-dominated and open tundra habitats in several of these measures, and further research may provide insight into the contributing factors that produced differences in arthropod abundance, richness, diversity, and phenology.

Future climate change predictions include increases in average air temperature, alterations in the timing of snow melt, and continued shrub expansion into open tundra (ACIA 2005, Hinzman et al. 2005, Sturm et al. 2005, IPCC 2007). Along with these vegetation and environmental changes, this research suggests that arthropod communities will change as well. Increases in shrub expansion are likely to cause increases in the abundance of arthropods, although some groups may decline, such as Araneae, which seem to prefer open tundra habitats. Additionally, increases in average temperature and alterations in the timing of snow melt are likely to impact the abundance and phenology of arthropods, some groups more than others.

Climate change is likely to affect other trophic levels directly through changes in their own habitat requirements, and indirectly through changes in their food source. For example, arthropods are an important food source for adults and developing offspring of migratory songbirds during the short summer growing season, and increases in shrub abundance are likely to directly affect birds by altering the availability of nesting habitat and refugia, and indirectly affect birds through changes in the availability of an abundant food source. It is also possible that trophic mismatches will occur with continued climate change. A trophic mismatch is a situation where the timing of life history events of two interdependent organisms does not match, and the consumer-resource link is broken (Stenseth and Mysterud 2002, Visser and Both 2005). Recently, multiple examples of this phenomenon have been documented (Visser et al. 1998, Visser and Both 2005, Parmesan 2006, Visser et al. 2006, Primack et al. 2009, Miller-Rushing et al. 2010), and as climate continues to change, trophic mismatches are likely to increase in occurrence and severity (Thackeray et al. 2010). If climate change alters arthropod phenology, peaks in insect abundance may occur before the time when the young of insectivorous birds require the most amount of food (Custer and Pitelka 1977, Visser et al. 1998), a situation that may have dramatic impacts on the reproductive success of migratory bird populations across the Arctic. Not only that, but taxa-specific alterations in arthropod abundance and phenological patterns will likely have impacts on plant-pollinator interactions (Høye and Forchhammer 2008a, Miller-Rushing et al. 2010), plant-herbivore interactions (Bale et al. 2002, Visser and Both 2005, van Asch et al. 2007, Torp et al. 2010), host-parasite interactions (Van Nouhuys and Lei 2004, Høye and Forchhammer 2008a, Vinstad et al. 2011), and predator-prey relationships (Høye et al. 2007a). Future research in these areas is needed to understand fully how current and future climate changes are altering the Arctic ecosystem.

APPENDIX A

ARTHROPOD IDENTIFICATION AND ABUNDANCE TABLE FOR 2010

		ROMO		TLFS		IMVT		SDOT		
Order or Phylum	Family or Group	Shrub	Open	Shrub	Open	Shrub	Open	Shrub	Open	Total
Coleoptera	Carabidae	133	98	47	83	244	261	53	66	985
	Staphylinidae	9	1	6	9	10	13	11	3	62
	Circulionidae	4	0	3	1	0	1	4	2	15
	Elateridae	26	1	1	20	1	0	2	18	69
	Coleoptera Larvae	5	6	2	2	1	4	5	1	26
	Unidentified Coleoptera	60	6	4	1	30	16	21	11	149
Hymenoptera	Apidae	4	5	25	59	33	39	27	26	218
	Formicidae	2	0	0	0	0	0	1	0	3
	Unidentified Hymenoptera	70	22	46	21	77	38	42	61	377
Araneae	Lycosidae	863	829	259	297	391	489	244	338	3710
	Linyphiidae	21	29	51	45	25	27	97	18	313
	Thomisidae	6	15	22	41	38	33	10	4	169
	Gnaphosidae	13	15	9	8	12	18	2	21	98
	Araneidae	0	2	9	3	10	6	1	1	32
	Clubionidae	9	10	4	5	5	4	1	10	48
	Unidentified Araneae	0	1	2	1	1	1	0	1	7
Diptera	Tipulidae	31	12	68	83	23	12	112	16	357
	Unidentified Diptera	312	198	264	114	187	61	383	155	1674
	Diptera Larvae	1	1	0	2	0	2	1	0	7
Hemiptera	Unidentified Hemiptera	199	51	52	17	21	23	116	43	522
Orthoptera	Acrididae	6	0	8	18	0	0	0	5	37
Lithobiomorpha	Lithobiidae	2	1	3	1	6	8	5	1	27
Lepidoptera	Unidentified Lepidoptera	3	3	2	4	5	1	2	2	22
	Lepidoptera Larvae	8	5	4	9	23	22	17	3	91

Gastropoda		2	9	11	5	22	4	34	4	91
Thysanoptera	Thripidae	1	8	1	15	5	5	1	0	36
Psocoptera		0	1	0	0	1	1	0	0	3
Neuroptera	Hemerobiidae	1	0	0	0	0	0	0	0	1
Total		1791	1329	903	864	1171	1089	1192	810	9149

APPENDIX B

ARTHROPOD IDENTIFICATION AND ABUNDANCE TABLE FOR 2011

		ROMO		TLFS		IMVT		SDOT		
Order or Phylum	Family or Group	Shrub	Open	Shrub	Open	Shrub	Open	Shrub	Open	Total
Coleoptera	Carabidae	70	136	48	89	136	128	59	93	759
	Staphylinidae	6	4	12	2	22	4	61	5	116
	Circulionidae	6	0	0	3	0	0	4	8	21
	Elateridae	13	0	3	28	1	2	2	24	73
	Leiodidae	20	2	0	0	4	1	1	1	29
	Coccinellidae	2	0	0	0	0	0	0	0	2
	Salpingidae	1	1	0	0	0	0	0	0	2
	Chrysomelidae	2	1	0	0	2	5	0	6	16
	Corylophidae	0	0	0	0	0	0	0	0	0
	Latridiidae	17	0	0	1	2	0	9	0	29
	Cucujidae	6	1	1	0	3	4	7	2	24
	Cleridae	0	1	0	0	0	0	0	0	1
	Cantharidae	1	4	2	0	0	0	0	0	7
	Scarabaeidae	0	1	0	0	0	0	0	0	1
	Tenebrionidae	0	0	0	0	10	0	0	0	10
	Coleoptera Larvae	7	0	0	0	2	2	2	0	13
	Unidentified Coleoptera	1	6	6	2	5	4	0	3	27
Hymenoptera	Apidae	57	20	28	23	17	25	21	28	219
	Formicidae	2	0	0	0	0	0	0	1	3
	Ichneumonidae	15	31	8	20	13	16	18	6	127
	Braconidae	3	5	2	1	0	0	4	1	16
	Vespidae	0	0	0	0	0	0	1	0	1

	Sphecidae	4	4	0	3	1	2	0	1	15
	Pteromalidae	66	31	18	13	40	12	11	26	217
	Encyrtidae	0	0	0	0	0	0	1	0	1
	Mymaridae	14	5	3	1	0	5	19	3	50
	Diapriidae	6	9	8	11	5	5	30	12	86
	Figitidae	1	9	0	1	2	0	0	2	15
	Halictidae	1	0	0	0	0	0	0	0	1
	Ceraphronidae	4	3	4	0	0	1	4	1	17
	Scelionidae	5	1	0	1	8	1	1	12	29
	Platygastridae	0	4	0	0	0	0	1	0	5
	Cimbicidae	0	0	0	1	0	0	0	0	1
	Eupelmidae	1	6	0	0	0	0	0	0	7
	Proctotrupidae	1	0	8	0	50	1	0	4	64
	Megaspilidae	1	2	0	1	0	0	2	0	6
	Cynipidae	0	0	0	0	0	0	1	0	1
	Aphelinidae	2	0	1	1	10	0	5	8	27
	Eulophidae	1	2	0	2	4	1	2	0	12
	Perilampidae	0	0	0	0	0	0	0	1	1
	Eurytomidae	0	0	0	0	0	0	0	2	2
	Tenthridinidae	1	0	0	0	2	0	0	0	3
	Tenthredinidae Larvae	0	0	2	0	0	0	0	0	2
	Other Hymenoptera Larvae	1	0	0	0	0	0	0	1	2
	Hymenoptera Pupa	0	0	3	0	2	1	3	0	9
	Unidentified Hymenoptera	4	2	0	0	0	0	0	0	6
Araneae	Lycosidae	352	458	146	287	239	368	221	423	2494
	Linyphiidae	7	14	14	18	12	19	56	16	156

	Thomisidae	2	15	12	10	14	21	3	10	87
	Gnaphosidae	9	26	4	6	5	7	4	21	82
	Araneidae	1	3	3	0	4	8	3	1	23
	Clubionidae	0	1	3	2	0	0	0	2	8
	Tetragnathidae	1	0	0	0	0	0	0	1	2
	Theridiidae	0	0	3	2	0	0	10	0	15
	Philodromidae	12	9	5	6	1	1	0	3	37
	Araneae Spiderlings	0	3	0	1	0	0	1	1	6
	Araneae Egg Sacs	33	116	63	105	120	121	116	55	729
	Unidentified Araneae	35	40	10	22	5	16	2	13	143
Diptera	Chironomidae	118	61	36	17	70	26	21	42	391
	Tipulidae	57	4	3	9	0	6	3	6	88
	Trichoceridae	10	6	16	23	10	7	18	25	115
	Sciaridae	363	79	94	55	107	24	165	96	983
	Empididae	15	72	1	0	7	1	6	2	104
	Cecidomyiidae	35	7	8	5	8	1	27	9	100
	Muscidae	10	5	3	2	1	2	14	6	43
	Ceratopogonidae	11	3	1	0	1	2	5	1	24
	Simuliidae	0	0	0	1	1	0	0	0	2
	Culicidae	8	5	6	0	4	1	3	2	29
	Anthomyiidae	38	3	9	9	11	10	8	24	112
	Scathophagidae	1	1	1	2	4	0	4	0	13

	Heleomyzidae	4	0	0	1	1	0	5	3	14
	Dolichopodidae	3	3	0	1	12	2	3	2	26
	Phoridae	92	25	50	25	69	25	184	36	506
	Chloropidae	7	6	6	7	6	3	8	9	52
	Agromyzidae	0	0	1	3	0	1	0	0	5
	Pipunculidae	0	2	0	0	0	0	0	2	4
	Carnidae	0	0	0	0	0	0	1	0	1
	Mycetophilidae	3	4	2	5	3	1	16	2	36
	Anisopodidae	14	2	0	0	0	0	0	0	16
	Bombyliidae	0	0	0	0	0	2	0	0	2
	Syrphidae	0	1	0	0	0	0	0	0	1
	Sciomyzidae	0	2	2	0	1	0	5	0	10
	Unidentified Acalyptrate Flies	6	14	2	4	12	5	7	7	57
	Diptera Larvae	0	0	3	4	1	4	10	8	30
Hemiptera	Psyllidae	1	4	2	3	14	1	4	0	29
	Miridae	111	2	3	0	0	0	21	0	137
	Nabidae	5	0	0	0	0	0	4	3	12
	Coreidae	2	0	0	0	0	0	0	0	2
	Tingidae	13	1	0	0	0	1	2	1	18
	Cicadellidae	618	64	26	18	69	38	174	60	1067
	Aphididae	8	97	9	21	22	2	8	28	195
	Delphacidae	8	67	2	4	3	0	16	15	115
	Saldidae	2	0	0	0	2	0	0	0	4
	Rhopalidae	1	0	0	1	0	0	1	1	4
	Fulgoridae	0	0	0	0	0	0	1	0	1

	Alydidae	0	0	1	1	0	0	0	0	2
	Pseudococcidae	2	0	0	1	1	0	2	0	6
	Unidentified Coccoidea	2	1	1	1	0	0	3	0	8
	Unidentified Hemiptera	5	0	0	0	0	0	3	1	9
Orthoptera	Acrididae	1	0	10	38	0	0	2	8	59
Lithobiomorpha	Lithobiidae	1	4	5	2	1	4	1	3	21
Lepidoptera	Gelechiidae	0	4	0	0	0	0	0	0	4
	Unidentified Lepidoptera	6	2	1	0	1	0	2	2	14
	Lepidoptera Larvae	2	6	3	8	9	8	3	3	42
Gastropoda		7	18	13	5	20	3	19	11	96
Thysanoptera	Thripidae	5	11	2	1	0	0	0	0	19
Psocoptera		0	0	0	0	1	0	1	0	2
Neuroptera	Hemerobiidae	0	0	0	0	1	0	1	0	2
Plecoptera	Nemouridae	0	0	1	0	0	0	0	0	1
Siphonaptera		0	0	0	0	0	0	8	0	8
Total		2389	1562	743	940	1214	961	1474	1215	10498

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BIOGRAPHICAL INFORMATION

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