ARTHROPOD FOOD WEBS IN ARCTIC TUNDRA: TROPHIC INTERACTIONS AND RESPONSES TO GLOBAL CHANGE

by

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Abstract

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Arctic ecosystems are undergoing rapid change. Terrestrial arctic arthropods (insects, spiders and others) are not only appreciably diverse, but also sensitive to their environment. As such, tundra arthropod communities and food webs could provide critical insight into the ecological consequences of global change in the Arctic. My dissertation examined the underpinnings of arthropod community and food web dynamics in arctic tundra. First, I explored how changes to plant production and plant community composition affect arthropod community composition, trophic structure and food web function. I also explored one key trophic interaction: cannibalism among wolf spiders, the most abundant terrestrial predator in most arctic systems. Last, I examined the effects of plant communities and weather on arthropod phenology and activity, key determinants of the rate and role of arthropod-mediated food web processes like predation, decomposition and pollination. Overall, my research reveals that arctic consumers are strongly limited by food availability well as weather conditions in the Arctic. Early springs, warmer temperatures, increased plant production and greater shrub dominance – key consequences of arctic global change—will affect the composition of arthropod communities and the ecological functions they perform.
Table of Contents

Acknowledgements...........................................................................................................iii

Abstract ............................................................................................................................... v

Chapter 1 Arctic Insects as Indicators of Environmental Change, 1992-2017 .......... 1
   Introduction .......................................................................................................................... 1
   Concepts and Methods ....................................................................................................... 2
      Community Composition ................................................................................................. 2
   Food Web Structure and Trophic Interactions ................................................................. 4
   Phenology and Physiology .............................................................................................. 7
   Authorship Information................................................................................................... 8

Chapter 2 Long-term nutrient addition alters consumer community composition but does not increase total biomass or abundance ......................... 9
   Abstract ............................................................................................................................ 10
   Introduction ....................................................................................................................... 11
   Materials and Methods .................................................................................................... 13
      Study system .................................................................................................................. 13
   Nutrient addition ............................................................................................................. 14
   Arthropod sampling and processing ............................................................................. 14
   Plant community response measures .......................................................................... 15
   Statistical Analysis ......................................................................................................... 15

Results .................................................................................................................................. 18
   Plant community ................................................................................................................ 18
   Arthropod abundance and biomass .............................................................................. 19
   Arthropod diversity ......................................................................................................... 21
   Arthropod community composition ............................................................................. 21
Discussion ........................................................................................................................................... 23

Fertilization did not increase total arthropod abundance or biomass......................... 23

Fertilization decreases plant diversity, but not arthropod richness ......................... 24

Fertilization alters both plant and arthropod community composition .................. 25

Conclusion ........................................................................................................................................... 26

Chapter 3 Linear responses of food web function to a gradient of nutrient enrichment ...................................................................................................................................................... 34

Abstract................................................................................................................................................ 35

Introduction .......................................................................................................................................... 35

Methods ............................................................................................................................................... 39

Study system and nutrient addition ....................................................................................... 39

Arthropod community responses: community composition and biomass ............... 40

Plant community responses: biomass, ANPP, C:N and community composition ................................................................. 41

Food web model .............................................................................................................................. 42

Statistical analysis ........................................................................................................................... 44

Results ............................................................................................................................................... 44

Plant community responses: biomass, C:N, ANPP and community composition ......................................................................................................................................................... 44

Arthropod community responses: biomass and community composition ............... 45

Food web model results ................................................................................................................... 46

Discussion .......................................................................................................................................... 48

Strikingly linear responses of insect food web, but not plants, to nutrient addition .............................................................................................................................................................................. 48

Weak herbivore effects on plant biomass intensified by nutrient addition .......... 50
<table>
<thead>
<tr>
<th>Chapter</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>93</td>
</tr>
<tr>
<td>Methods</td>
<td>97</td>
</tr>
<tr>
<td>Sampling design</td>
<td>97</td>
</tr>
<tr>
<td>Measures of plant canopy shading</td>
<td>98</td>
</tr>
<tr>
<td>Meteorological data collection and processing</td>
<td>98</td>
</tr>
<tr>
<td>Statistical analysis</td>
<td>100</td>
</tr>
<tr>
<td>Results</td>
<td>102</td>
</tr>
<tr>
<td>Descriptive results</td>
<td>102</td>
</tr>
<tr>
<td>Seasonal arthropod density trends in shrub and open habitats</td>
<td>103</td>
</tr>
<tr>
<td>Weather effects on arthropod activity across levels of shrub shading</td>
<td>103</td>
</tr>
<tr>
<td>Discussion</td>
<td>105</td>
</tr>
<tr>
<td>Shrub cover reduces early-season abundance of flies and beetles</td>
<td>105</td>
</tr>
<tr>
<td>Shrub shading and weather interact to affect arthropod activity</td>
<td>107</td>
</tr>
<tr>
<td>Thermal optima of arthropod activity exceed typical temperatures in arctic tundra</td>
<td>108</td>
</tr>
<tr>
<td>Conclusion</td>
<td>109</td>
</tr>
<tr>
<td>Chapter 6 Conclusions &amp; Future Directions</td>
<td>120</td>
</tr>
<tr>
<td>References</td>
<td>121</td>
</tr>
<tr>
<td>Biographical Information</td>
<td>142</td>
</tr>
</tbody>
</table>
Chapter 1

Arctic Insects as Indicators of Environmental Change, 1992-2017

Introduction

Twenty-five years ago this June, arctic entomologist Hugh Danks published a seminal review, “Arctic insects as indicators of environmental change” (Danks 1992). Danks’ central argument was that terrestrial insects, spiders and their relatives would be the proverbial canaries-in-the-coalmine of arctic global change, and would consequently yield an abundance of ecological insights—should we take the time to look. Hoping to guide the field towards significant discoveries, he proffered a list of eight potentially important “concepts and methods” that ranged the gamut of physiological, community and food web ecology.

Danks, with an expertise in insect cold hardiness, was acutely aware of the sensitivity of arctic arthropods to rising temperatures. And, as an avid taxonomist who compiled the authoritative species checklist of North American terrestrial arctic arthropods (Danks 1981), Danks had a special appreciation of the substantial diversity and trophic complexity of arctic arthropod food webs. Danks predicted that a warmer climate would trigger arthropod physiological responses that in turn would alter the phenology, distribution and relative abundance of arthropod taxa. Additionally, Danks argued that arthropod communities were a tool for tracking changes to complex trophic interactions and community dynamics on a tractable spatio-temporal scale.

At a time when most terrestrial arctic ecologists were concerned with plants and mammals, Danks’ argument was unique. Further, Danks’ focus on global warming was impressively timely: the first report by the Intergovernmental Panel on Climate Change (IPCC) was only two years old, and the severe ramifications of global warming for the
Arctic were just beginning to be understood. In the decades following Danks’ piece, the pace of ecological change in the Arctic was rapid. Temperatures rose at double the global rate of change, and ecosystem ecologists documented the transformation of arctic soils from global carbon sinks to sources of carbon dioxide (CO$_2$) via microbial respiration (Oechel et al. 1993, Euskirchen et al. 2012). Satellite imagery recorded rapid declines in arctic sea ice and increases in plant production across the tundra biome (Post et al. 2009). Scientists amassed long-term datasets, which offered insights into the consequences of earlier, warmer springs for plants, caribou and other mammals (Post et al. 2009).

Relative to these other fields, terrestrial arctic arthropod ecology developed much more slowly over these past two decades. Nevertheless, sufficient evidence has accrued over the years to evaluate the usefulness of Danks’ suggestions. Many of Danks’ predictions have proven to be prescient, while some topics he proposed have yet to be explored; meanwhile, ecologists have developed new fields of study with modern methods not available at the time of Danks’ article. Here I outline the ways in which my dissertation addresses a handful of Danks’ “concepts and methods,” and place my findings in the context of others.

Concepts and Methods

Community Composition

Insects are the most speciose group of terrestrial animals. The relatively species-poor arctic is no exception to the rule: at least 2,000 species of insects and spiders have been described from the Arctic, with at least as many yet to be discovered (Danks 1992). Danks proposed that the diversity of insect fauna offered unique potential to study compositional changes across spatial or temporal gradients of environmental severity,
i.e., temperature or resource limitation. This suggestion has proven to be fruitful: recent studies have shown that insect responses to climate change are idiosyncratic across species, even in those in the same taxonomic group, e.g. butterflies (Høye et al. 2014) and flies (Loboda et al. 2017), and have found that the effects of warming on spider assemblages can be stronger in wet than in dry habitat types (Bowden et al. 2015).

At the same time, arctic plant communities are changing: plants are becoming more productive and deciduous shrubs are becoming dominant in many tundra habitats (Tape et al. 2006, Myers-Smith et al. 2011, Tape et al. 2012). Thus, in addition to the direct effects of warming on tundra insect communities, warming could affect arthropod community composition via changes to plant production and community composition. Studies in natural gradients of shrub abundance have found that arthropod community composition in shrub tundra differs from that of open tussock tundra (Rich et al. 2013): shrub tundra harbors a greater abundance of flies, herbivores and web-building predators. Strong turnover can be detected even when shrub- and tussock-tundra plant communities are immediately adjacent to one another (Hansen et al. 2016), indicating that the filtering effects of shrub abundance on arthropod community composition are strong.

Increased soil nutrient availability (a result of greater microbial activity) is indicated as one of the proximate causes of tundra shrub encroachment (Myers-Smith et al. 2011). Supporting this mechanistic explanation, a handful of soil nutrient addition studies in moist acidic tussock tundra, a common plant community in arctic Alaska, have found that long-term additions of nitrogen (N) and phosphorus (P) facilitate increased dominance of woody shrubs (Shaver et al. 2014). These experiments provide a helpful backdrop for investigating the effects of increased productivity and shrub dominance. In
theory, soil nutrient addition should increase plant production and relax the severe resource limitations for arthropod consumers.

In Chapters 2 and 3 of my dissertation, I evaluate the effects of long-term nutrient addition experiments on tundra arthropod community composition. The results of these two chapters were somewhat contradictory. In tussock tundra fertilized with a gradient of nutrient levels for 10 years, the arthropod community generally responded as expected: herbivores, predators, parasitoids and detritivores increased in abundance (Chapter 3). In contrast, in similar tundra fertilized for 24 years, herbivores did not increase in abundance despite an increase in plant biomass and production. Herbivores were no more abundant in fertilized plots than in controls, but an increase in the abundance of flies (detritivores) did shift community composition (Chapter 2). I argue that the difference in response is due to a buildup of non-edible woody tissues over time, which limited the ability of consumers to respond positively to increased plant biomass. These findings point to the primacy of plant growth form and palatability for consumer responses to ecological change.

*Food Web Structure and Trophic Interactions*

Food webs are a powerful tool: by tracking fluxes of resources through networks of predator-prey interactions, they can predict biotic responses to climate change otherwise missed by a single-species approach (Walther 2010). The very first energy flux food web was made for an arctic system at Bear Island, Norway, where food webs were thought to be relatively simple (Summerhayes and Elton 1923). A more recent survey of the Bear Island food web (Hodkinson and Coulson 2004) found much greater complexity in the food web than originally thought, in line with the modern consensus of food web ecologists (Polis 1991, Polis and Strong 1996, Hodkinson and Coulson 2004). Enormous
progress has been made to describe the complexity of arctic food webs, especially in the last five years.

The year I entered graduate school, Legagneux et al. (2012) made a fairly comprehensive attempt to model flows of energy in the tundra food web at Bylot Island, Canada. Although representative of a monumental amount of work, the Legagneux food web was somewhat disappointing for a terrestrial arthropod ecologist. The terrestrial arthropod community was treated (literally) as a “black box,” a placeholder that unfortunately reflected decades of thinking that arctic insects were largely inconsequential for major ecosystem processes (Ryan 1977). Soon after, however, new molecular methods allowed for a greater resolution of parasitoid and insect food webs than had ever been possible (Wirta et al. 2015) and detailed pollinator networks for Greenlandic flowers were developed (Tiusanen et al. 2016, Urbanowicz et al. 2017). These studies found a high degree of generality among arctic consumers, which in turn caused food webs to be immensely complex and densely connected. Although they offered unprecedented insight into the structure of arctic food webs, these studies still did not offer direct measures of the ecological processes performed by insects apart from pollination and predation.

Motivated by the potential of a food web approach to describe the ecological function of arthropod communities, I joined an initiative at the Arctic Long Term Ecological Research (LTER) Group with the aim of implementing a standardized food web modeling approach to describe, compare, and connect food webs across traditional aquatic-terrestrial, aboveground-belowground divides. As part of that initiative, I helped develop a comprehensive aboveground-belowground food web model of arctic tundra invertebrates (Koltz et al. in press 2017). This approach allowed us to evaluate the relative effects of microbes, insects and other invertebrates for overall food web function.
In Chapter 3, I use the same modeling framework to characterize the food web processes within the aboveground, plant “canopy”-dwelling insect community. The food web approach allowed me to estimate the rates of herbivory in the system and to evaluate the effects of increased production on food web processes like nutrient cycling and predation. I found that processes performed by the insect food web – nutrient cycling, herbivory and detritivory – all responded positively to nutrient addition, suggesting that nutrient limitation controls the rate of ecological processes in arctic tundra. I also found that herbivores consumed a miniscule fraction of aboveground plant biomass, even at large doses of soil nutrients. This study also provides an important baseline measure of tundra insect herbivory, which is likely to become more intense with a warming climate (Bale et al. 2002).

In addition to these explorations of the wider food web, in Chapter 4, I explore the importance of one trophic interaction, cannibalism. In arctic tundra, the vast majority of ground-dwelling arthropod biomass is contributed by wolf spiders and ground beetles, not herbivores (Asmus et al. unpubl. data, Gelfgren 2010a, Ernst and Buddle 2013b). The diet of these (presumably generalist) predators is largely unknown, but has been the focus of some new molecular studies (e.g., Roslin et al. 2016). Inverted biomass pyramids have been observed elsewhere, and are particularly ubiquitous in marine and aquatic systems (Wang et al. 2009). Accounting for the different rates of turnover between primary producers and consumers (i.e., short-lived plankton, zooplankton) and predators (i.e., long-lived fish) can transform inverted pyramids of biomass into upright pyramids of energy (Wang et al. 2009); however, our model suggests that even after correcting for differential turnover, cannibalism could comprise up to 25% of arthropod predator diet in the tundra (Koltz et al. 2017). In Chapter 4, I show that arctic wolf spiders have a strong propensity towards cannibalism, but likely rarely take the option –either
because opportunities to cannibalize are rare, or because alternative prey are sufficiently dense to support their populations.

**Phenology and Physiology**

A wealth of evidence indicates that warming will significantly affect arctic phenology and provoke physiological responses in terrestrial animals. Perhaps the strongest evidence for this effect comes from decades of monitoring at the Zackenberg field station in northwest Greenland. There, global warming has advanced arctic arthropod phenology (Høye et al. 2007) and triggered phenological mismatches between insect pollinators and flowers (Høye et al. 2013). These findings indicate that rapid climate change in the Arctic will destabilize arthropod-mediated ecosystem functions like pollination, decomposition and plant production.

In Chapter 5, I take a correlative approach to examine the effects of weather on arthropod activity and phenology, as a proxy for understanding how warming might affect the functional role of these consumers in food webs. Other studies have shown that capture rates of arthropods in pitfall and window traps are positively correlated with temperature in the Arctic, indicating that arthropod activity budgets are more constrained by cold temperatures than they are hampered by heat (Høye and Forchhammer 2008a, Tulp and Schekkerman 2008, Bolduc et al. 2013). Meanwhile, probably because the structure of open tundra vegetation is relatively simple, little attention has been given to the effects of microclimate on modulating arctic arthropod responses to warming (but see Coulson et al. 1993 and Hodkinson et al. 1996 for discussion of these effects on soil invertebrates). In Chapter 5, I show that weather does affect arthropod phenology and activity, but the effects are variable across groups.
Authorship Information

All of the article-based chapters in my dissertation represent collaborative work, for which I was the primary author and performed the statistical analyses, but for which all authors edited the manuscript and provided other input. In Chapter 2, I designed the arthropod sampling scheme and collected the data with Amanda Koltz and Laura Gough; Jennie McLaren provided plant and litter data and Gus Shaver designed the original nutrient addition experiment. Chapter 2 is currently in review at Oikos. In Chapter 3, I designed the arthropod sampling scheme and collected the data; John Moore provided the food web model code; I modified the food web model code with Amanda Koltz and John Moore; and Laura Gough and Gus Shaver designed the original nutrient addition experiment. Chapter 4 was developed with coauthors Taryn Flink and Laura Gough. I designed and executed the experiments in this chapter with Taryn Flink, and Laura Gough edited the manuscript. Chapter 4 is currently in review at Arctic, Antarctic and Alpine Research. In Chapter 5, I collected the arthropod data; Toke Høye contributed key advice for the statistical analysis; Laura Gough, Natalie Boelman and John Wingfield conceived the original sampling design; and Shannan Sweet, Jonathan Pérez and Jesse Krause collected the meteorological data.
Chapter 2

Long-term nutrient addition alters consumer community composition but does not increase total biomass or abundance

Ashley Asmus, Amanda Koltz, Jennie McLaren, Gus Shaver and Laura Gough
Abstract

A simple bottom-up hypothesis predicts that plant responses to nutrient addition should determine the response of consumers: more productive and less diverse plant communities, the usual result of long-term nutrient addition, should support greater consumer abundances and biomass and less consumer diversity. We tested this hypothesis for the response of an aboveground arthropod community to an uncommonly long-term (24-year) nutrient addition experiment in moist acidic tundra in arctic Alaska. This experiment altered plant community composition, decreased plant diversity and increased plant production and biomass as a deciduous shrub (*Betula nana*) replaced graminoids, cryptogams and dwarf evergreen shrubs. Consistent with strong effects on the plant community, nutrient addition altered arthropod community composition, primarily through changes to herbivore taxa in the canopy-dwelling arthropod assemblage and detritivore taxa in the ground assemblage. Surprisingly, however, the loss of more than half of plant species was accompanied by negligible changes to diversity (rarefied richness) of arthropod taxa. Similarly, although long-term nutrient addition in this system roughly doubles plant production and biomass, arthropod abundance was either unchanged or decreased by nutrient addition, and total arthropod biomass was unaffected. Our findings differ markedly from the handful of terrestrial studies that have found bottom-up diversity cascades and productivity responses by consumers to nutrient addition. This is probably because unlike grasslands and salt marshes (where such studies have historically been conducted), this arctic tundra community becomes less palatable, rather than more so, after many years of nutrient addition due to increased dominance of *B. nana*. Additionally, by displacing insulating mosses and increasing the cover of shrubs that cool and shade the canopy microenvironment, fertilization may displace arthropods keenly attuned to microclimate. These results indicate that terrestrial
arthropod assemblages may be more constrained by producer traits (i.e., palatability, structure) than they are by total primary production or producer diversity.

Introduction

Nutrient availability is a major determinant of many ecosystem properties, including primary and secondary production and community structure (Chapin et al. 1986, Gruner et al. 2008). An array of nutrient addition experiments has not only confirmed that most natural systems are nutrient-limited (Downing et al. 1999, Elser et al. 2007, Gruner et al. 2008, Fay et al. 2015), but has also shown that there can be complex feedbacks among nutrient availability, primary production, and producer community structure, especially after many years of manipulation (Leibold et al. 1997, Worm and Duffy 2003, Elser et al. 2007). Those few terrestrial nutrient addition studies that have incorporated consumers have generally explored top-down effects of consumers on producers, rather than the other way around (Gruner et al. 2008). They also tend to focus on the roles of mammalian herbivores (e.g., Borer et al. 2014), while ignoring other potentially important consumers (e.g., insects).

Theory suggests that as primary productivity increases with nutrient addition, more consumer biomass can be supported (White 1978, Oksanen et al. 1981). Likewise, the secondary effects of nutrient addition on producer community composition and diversity should affect consumer community composition and diversity (Hutchinson 1959, Hunter and Price 1992). A handful of studies—most from grasslands and salt marshes—have demonstrated such bottom-up effects on arthropod communities, which respond at spatial and temporal scales compatible with many nutrient addition experiments. Short-term (<3 years) experiments show that increased nutrient availability increases plant biomass and arthropod abundance (Hurd and Wolf 1974, Kirchner 1977, Siemann 1998,
Gruner and Taylor 2006, Wimp et al. 2010). Long-term studies in grasslands (5-14 years) have shown that when nutrient addition homogenizes the plant community, total arthropod abundance is increased (Siemann 1998, Haddad et al. 2000) even if arthropod diversity declines in tandem with plants (Haddad et al. 2000).

Evidence from aquatic systems suggests that outcomes for consumer communities are not always predicted by producer community responses to nutrient addition. For example, in temperate lakes, long-term nutrient loading tends to favor well-defended or toxic algal species, and in such cases consumers do not show a bottom-up productivity response (Leibold 1989, Leibold et al. 1997). Changes to producer community physical structure can also negate bottom-up nutrient addition effects on some consumers (Gough et al. 2016). For instance, nutrient addition in benthic marine habitats shifts the producer community from eelgrass to dense microalgae; the enhanced structural complexity impedes fish foraging and reduces overall consumer abundance (Deegan et al. 2002). Such findings suggest that producer traits control whether the direct effects of nutrient availability on primary production and diversity are passed along to consumers.

As in most aquatic and terrestrial communities, long-term nutrient addition in moist acidic tussock tundra increases primary production and homogenizes the producer community (Gough et al. 2000, Shaver et al. 2014). This occurs because a deciduous shrub, Betula nana ssp. exilis, becomes dominant while displacing lower-stature and slower-growing species including sedges, mosses, dwarf evergreen shrubs and lichens (Shaver et al. 2014). Betula's woody stem tissue, which is low in N relative to the graminoids and evergreens it replaces, accounts for the majority of producer biomass after six or more years of fertilization. Betula nana ssp. exilis is known to be unpalatable to vertebrate herbivores (Christie et al. 2015) and is not the preferred forage of local
insect larvae (MacLean and Jensen 1985). Aerial branching and litter deposition by *Betula* in fertilized plots creates a canopy and ground microenvironment cooler than that of unfertilized tussock tundra (Myers-Smith et al. 2011). Altogether, long-term nutrient addition in moist acidic tundra alters not only primary production, but also plant community traits relevant to consumers (Gough et al. 2012, Gough et al. 2016).

In this study, we examined the response of aboveground arthropod communities to 24 years of experimental nutrient addition in moist acidic tussock tundra. Based on general bottom-up theory from terrestrial communities and our knowledge of the plant community response to this treatment (Shaver et al. 2014), we hypothesized that: 1) fertilized tundra communities would support greater abundance and biomass of consumers, consistent with observed increases in primary production and plant biomass, 2) decreased plant diversity in nutrient addition plots would decrease arthropod diversity, and 3) altered plant community composition in nutrient addition plots would yield a distinct arthropod community.

**Materials and Methods**

*Study system*

This study was performed near Toolik Lake, in arctic Alaska (68°38’N, 149°43’W, el. 719m). Moist acidic tundra is characterized by mosses, lichens, a tussock-forming graminoid (*Eriophorum vaginatum*), dwarf evergreen shrubs, and low-growing deciduous shrubs including dwarf birch (*Betula nana*) and dwarf willows (*Salix* spp.) (Shaver et al. 2014). Annual production is limited not only by nutrient-poor soils, but also by extremely short growing seasons (about 70 days at our study site) (Shaver et al. 2014).
**Nutrient addition**

Fertilization experiments were established in moist acidic tundra in 1989 by the Arctic Long-Term Ecological Research (LTER) group (Shaver et al. 2014). The LTER maintains four experimental blocks in this plant community, established in an area of homogenous vegetation. Each block was comprised of ten 5 x 20 m plots separated from adjacent plots by 2 m walkways. Within each block, one plot was designated a control (no nutrient addition) and one was designated +NP (nitrogen and phosphorus addition) (other plots were dedicated to other experimental treatments). The LTER applies N (10g·m$^{-2}$·yr$^{-1}$ of ammonium nitrate) and P (5g·m$^{-2}$·yr$^{-1}$ of orthophosphate) to the ground via broadcast fertilization of pellets in early June each year, immediately after snowmelt.

**Arthropod sampling and processing**

Arthropod sampling was conducted three times during the 2013 growing season: June 13-15, July 11-13, and August 8-10. We sampled ground-dwelling arthropods with four pitfall traps placed in a 1x1 m grid in each plot. Traps consisted of a clear plastic sample cup (approximately 9 cm in diameter, 15 cm deep), placed level with the ground surface and filled 4 cm deep with 75% ethanol. Traps were left out for 48 hours, at which point the contents were brought to the laboratory for processing.

We also sampled canopy-dwelling arthropods during each pitfall sampling window (13 June, 12 July and 8 August 2013) with a modified leaf vacuum (Wilson et al. 1993). We standardized sampling of canopy-dwelling arthropods in each plot by sampling an area of 1m$^2$ over the ground and a volume of 0.5 m$^3$ of the canopy (encompassing the tallest shrubs). Total vacuum sampling time in each plot was 90 seconds; the pattern and rate of sampling through each habitat type was done by the same person and in a standardized way.
Arthropods were identified using published keys (Triplehorn and Johnson 2005, Marshall 2006) to the family level with three exceptions: parasitic Hymenoptera from the vacuum samples were identified to superfamily, while those from pitfall traps were identified only as Parasitica; Collembola were identified to order; and mites were identified as subclass Acari. We estimated the total biomass of each taxon in each sample separately by applying published taxon-specific allometric equations to the average body length of the first five individuals encountered, multiplied by its abundance (detailed methods available in Pérez et al. 2016). Body length was measured to the nearest 0.01mm using a digital microscope camera. Additionally, a trophic group was assigned to each taxonomic group following conventions used in other studies of tundra arthropods (Gelfgren 2010a) (see Table S1).

**Plant community response measures**

To document the plant community response to long-term fertilization, we estimated plant cover near the peak of the growing season after 24 years of fertilization, in early July 2013, in eight 1x1 m quadrats within each plot. We estimated plant cover for each vascular plant species, with additional categories for all mosses and all lichens, which were not identified to species. In each quadrat, we also estimated the mean and maximum height of evergreen and deciduous shrub species to the nearest cm.

**Statistical Analysis**

All statistical analyses were performed in R version 3.2.4 (R Core Team 2015). In all analyses of arthropod data, canopy- and ground-dwelling arthropod assemblages were analyzed separately, owing to the different temporal and spatial scales of the two sampling methods.
Arthropod abundance and biomass. To determine whether arthropod abundance or biomass varied according to treatment, we first summed the biomass and abundance of taxa within each sampling location (pitfall cup, vacuum plot) across the three sampling dates, and then evaluated biomass and abundance responses using linear mixed effects models (Zuur et al. 2009) in R package lme4 (Bates et al. 2014) and lmerTest (Kuznetsova et al. 2014). All models included treatment as a fixed factor and experimental block as a random effect. Models were created first for total assemblage abundance and biomass, and then separately for each functional group. Models of arthropod abundance biomass were fit with a Gaussian distribution where responses were first ln transformed (except ground-dwelling herbivore abundance and biomass, which were ln+1 transformed) (Zuur et al. 2009).

Arthropod diversity. Because arthropod taxonomic richness differences could be attributed to differences in abundance (Hurlbert 1971), we calculated individual-based rarefied richness values and rarefaction curves using the rarefy function in R package vegan (Oksanen et al. 2013). We calculated rarefied richness from arthropod abundances summed across all samples. Rarefied richness values for control and fertilized assemblages were considered significantly different when standard errors of rarefaction iterations did not overlap at the lowest number of individuals caught for the two treatments. To determine the extent to which additional sampling might have more fully characterized the community, we calculated abundance-based extrapolated richness values using the bias-corrected Chao index (Chiu et al. 2014) with the vegan function estimateR (Oksanen et al. 2013).

Arthropod community composition. To determine whether treatment affected arthropod community composition, we fit multivariate generalized linear models to the canopy- and ground-dwelling abundance data using R package mvabund (functions
We used this model-based method to analyze arthropod community composition because, unlike distance-based methods (e.g., PRIMER), multivariate generalized linear models can account for the confounding mean-variance relationships that often exist in ecological count data (Warton et al. 2012). Our models assumed a negative binomial distribution for arthropod abundances and included treatment as the independent variable. Model terms were tested for significance with a likelihood ratio test and a Monte Carlo resampling scheme with 999 iterations; we simultaneously performed tests for univariate (single-taxon) responses to treatment, adjusting these univariate $P$-values to correct for multiple testing (Wang et al. 2012). To account for repeated measures, we constrained resampling to experimental blocks. For each taxon, we calculated its percentage share of total treatment deviance as a measure of its contribution to community dissimilarity in control and fertilized plots. We used non-metric multidimensional scaling (NMDS) analysis in R package vegan to visualize differences in arthropod community composition for each assemblage (Oksanen et al. 2013).

**Arthropod size structure.** Just as our analyses of arthropod community composition helped determine which taxa were driving changes to total arthropod abundance, we performed an analysis of arthropod size structure to determine which groups were driving changes to total arthropod biomass independently of changes to arthropod abundance. We used a variance decomposition approach modified from Lepš et al. (2011) to differentiate between nutrient addition’s effects on arthropod community size structure resulting from community turnover (abundance of small vs. large taxa) versus within-taxon size variation (sizes of individuals within taxa). First, using measures of individual arthropods (a subset of the total), we calculated three community parameters for each assemblage and trophic group: (1) a specific community-weighted
mean (CWM) body size calculated from the average size of each taxon in each treatment, (2) a fixed CWM calculated from the body size of each taxon averaged across treatments, and (3) within-taxon variability, the difference between specific and fixed CWMs (Lepš et al. 2011). Both CWMs were weighted by the total abundance of each taxon in each sampling location, summed across sampling dates. We then analyzed linear mixed-effects models for each community parameter. Finally, we extracted treatment sums-of-squares (SS) from each model using lmerTest and calculated the contributions of each aspect of size structure to treatment effects on (specific) CWM body size as:

Contribution of turnover = 100 * \((SS_{\text{fixed CWM}} / SS_{\text{specific CWM}})\)

Contribution of within-taxon size variation = 100 * \((SS_{\text{within-taxon}} / SS_{\text{specific CWM}})\)

Covariation = 100 * \([ SS_{\text{specific CWM}} – SS_{\text{fixed CWM}} – SS_{\text{within-taxon}} ] / [ SS_{\text{specific CWM}} ]\)

Plant community response measures. We evaluated differences in plant species cover with a permutational MANOVA, constraining permutations to blocks (function adonis in R package vegan, Oksanen et al. 2013). We used linear mixed effects models to evaluate treatment effects on species density (plant species per m²), diversity (Shannon’s H’), and canopy height.

Results

Plant community

The plant community in control plots—a mixture of dwarf deciduous and evergreen shrubs, sedges, mosses, and lichens—differed from that of fertilized plots, which were dominated by Betula nana and a forb (cloudberry, Rubus chamaemorus) (Fig. 1; \(F_{1,63} = 111.2, P = 0.001\)). Species density in fertilized plots was 5±0 species/m², a lower density than that of controls (13±0 species/m², \(F_{1,59} = 1199.3, P <0.001\)). Diversity
in fertilized plots ($H' = 1.0\pm0.1$) was also lower than that of controls ($H' = 2.1\pm0.1$, $F_{1,59} = 613.1$, $P < 0.001$). In addition, maximum plant canopy height in fertilized plots was $55.8\pm5.5$ cm, more than double the maximum canopy height in controls ($23.9\pm0.5$ cm, $F_{1,59} = 106.0$, $P < 0.001$). Increased canopy height corresponded to greater maximum height of *Betula* in fertilized plots relative to controls ($F_{1,62} = 157.5$, $P < 0.001$).

**Arthropod abundance and biomass**

*Canopy assemblage.* In the canopy, treatment affected neither total abundance nor the abundance of any trophic group ($P > 0.05$, Table 1, Fig. 2). In addition, treatment had no effect on total canopy-dwelling biomass, nor predator, parasitoid, herbivore nor biting fly biomass (Fig. 2; Table 1; $P > 0.05$). The one group for which there was a significant treatment effect was canopy-dwelling detritivores (an assortment of flies that rely upon detrital resources as larvae, see Table S1). The total biomass of canopy detritivores was 5 times greater in fertilized plots relative to controls (Fig. 2; $F_{1,6} = 10.1$, $P = 0.02$).

Greater canopy-dwelling detritivore biomass in fertilized canopies was caused not by greater detritivore abundance, but rather by larger canopy detritivore body size in fertilized plots relative to controls (Fig. 3; $F_{1,6} = 19.7$, $P = 0.004$). Greater canopy detritivore body size resulted from a shift towards larger detritivore taxa in fertilized canopies relative to controls (Table 2).

Alongside this effect on canopy detritivore body size, canopy arthropods were on average larger in fertilized canopies relative to controls (Fig. 3; Table S2; $F_{1,3} = 16.8$, $P = 0.03$). This resulted from larger body size of detritivores, canopy herbivores ($F_{1,6} = 36.4$, $P = 0.001$), and canopy predators (Fig. 3; Table S2; $F_{1,5} = 4.0$, $P = 0.09$). Larger canopy herbivore body size resulted from a shift in community composition towards greater
relative abundance of large-bodied taxa taxa (e.g., Miridae; Table S1) relative to small-bodied taxa (e.g., Homopterans; Table S1).

Ground assemblage. Unlike in the canopy, total ground-dwelling arthropod abundance was lower in fertilized plots relative to controls (Fig. 2; Table 1; $F_{1,27} = 5.3, P = 0.030$), a result of reduced detritivore abundance (Fig. 2; Table 1; $F_{1,27} = 6.5, P = 0.017$). In contrast with this effect on detritivores, total ground-dwelling predator abundance was greater in fertilized plots relative to controls (Fig. 2; Table 1; $F_{1,27} = 12.5, P = 0.001$). The opposing treatment effects on predator and detritivore abundances decreased the predator:prey abundance ratio (“prey” = detritivores plus herbivores) from 1:9 in control plots to 1:3 in fertilized plots (Fig. 2; $F_{1,30} = 4.2, P = 0.049$).

Despite these treatment effects on ground-dwelling predator, detritivore and total arthropod abundances, treatment had no effect on the biomass of the total assemblage nor the biomass of any trophic group (Table 1; $P > 0.05$). Lower detritivore abundances were cancelled out by greater relative abundances of large-bodied detritivore taxa in fertilized plots relative to controls (e.g., Diptera: Tipulidae; Table S1), as evidenced by a treatment effect on the fixed community-weighted mean body size (Fig. 3; Table S2; $F_{1,30} = 12.2, P = 0.002$). Meanwhile, greater predator abundances were cancelled out by smaller predator body sizes in fertilized plots relative to controls (Fig. 3; Table S2; $F_{1,30} = 60.5, P <0.001$). Smaller ground-dwelling predator body size resulted primarily from within-taxon size differences (Table 2), especially for the dominant ground-dwelling predator taxon, wolf spiders (Araneae: Lycosidae; Table S1). Wolf spiders were more abundant ($F_{1,27} = 12.5, P = 0.001$, Table S1), but were also smaller in fertilized plots relative to controls ($F_{1,27} = 5.9, P = 0.022$; data not shown), resulting in equivalent total wolf spider biomass in fertilized and control plots ($P > 0.05$; data not shown). Despite reduced predator body size, ground-dwelling arthropods in fertilized plots were on
average larger in fertilized plots relative to controls (Fig. 3, $F_{1,27} = 4.7$, $P = 0.039$, Table S2), primarily due to differences in community composition (Table 2).

**Arthropod diversity**

After rarefaction to the lowest arthropod abundance in control and fertilized treatments, fertilized canopies had 3±1 fewer taxa relative to control canopies (Fig. 4). Canopy parasitoid and predator diversity were lower in fertilized plots relative to controls, while canopy herbivore richness was greater in fertilized canopies relative to controls, and canopy detritivore richness did not differ by treatment (Fig. 4).

In contrast, rarefied richness was greater in fertilized ground assemblages relative to controls (5±1 additional taxa, Fig. 4). This was primarily driven by greater rarefied richness of ground-dwelling herbivores and detritivores in fertilized plots. Ground-dwelling predator diversity did not differ according to treatment (Fig. 4).

Visual inspection and extrapolation of the rarefaction curves suggested that, at this level of identification, the ground and canopy assemblages as a whole were well-sampled, although many individual trophic groups would have benefited from additional sampling (Table S3).

**Arthropod community composition**

In the canopy, 74% of taxa were common to both treatments, while on the ground 65% of taxa were common to both treatments. The majority of taxa unique to one treatment or another were rare (<2 individuals; Table S1). Nevertheless, community composition differed in response to fertilization in both the canopy (Dev = 97.7, $P = 0.039$) and the ground assemblage (Dev = 162.5, $P = 0.001$) (Fig. 5 A-D).
In the canopy, herbivore taxa had the greatest effect on community dissimilarity in control and fertilized plots, contributing 40% of total treatment deviance (Fig. 5E). The remainder of canopy treatment deviance was spread somewhat evenly among parasitoid, predator and detritivore taxa, which contributed 10, 20 and 30% of treatment deviance, respectively (Fig. 5E). Herbivores from family Delphacidae contributed the most to community dissimilarity and were by themselves affected by treatment (Fig. 5; Dev = 14.5, \( P_{\text{adj}} = 0.017 \)). Delphacids comprised on average 10% of the abundance in control canopies, but were completely absent from fertilized canopies (Table S1). In arctic tundra habitats, this family is known to specialize on graminoids such as Carex and Eriophorum (Wilson 1997); cover of these plant species has drastically declined in fertilized plots (Fig. 1). Two additional herbivore taxa and two detritivore taxa contributed substantially (>5% deviance) to community dissimilarity, although without univariate treatment effects (Fig. 5; \( P > 0.05 \)). All four of these taxa were more abundant in fertilized plots relative to controls (Table S1).

In the ground assemblage, detritivore taxa contributed the most to community dissimilarity (63% of deviance), with predator and herbivore taxa contributing the remainder (23% and 13%, respectively; parasitoids contributed <1%; Fig. 5F). In addition to altering ground assemblage composition, treatment affected the abundance of three individual taxa: springtails from order Symphypleona, mites (Acari), and predaceous beetles from family Staphylinidae (\( P_{\text{adj}} < 0.05 \)). These three taxa also dominated the overall community response to fertilization (Fig. 5). Relative abundance of Symphypleona was 93% lower in fertilized plots relative to controls (Table S1), while mites and Staphylinid beetles were respectively 6 and 5 times more abundant in fertilized plots relative to controls (Table S1).
Discussion

**Fertilization did not increase total arthropod abundance or biomass**

Contrary to our first hypothesis, total canopy assemblage biomass and abundance were unaffected by fertilization. Further, fertilization reduced total arthropod abundance in the ground assemblage and did not affect total biomass of ground-dwelling arthropods. These findings were surprising in comparison with similar studies conducted in grasslands and coastal salt marshes. In those ecosystems, both short- and long-term soil nutrient addition increases total arthropod abundance (Hurd and Wolf 1974, Kirchner 1977, Siemann 1998, Haddad et al. 2000, Gruner and Taylor 2006, Wimp et al. 2010).

Changes to top-down (predator) control may have mitigated some bottom-up effects of nutrient addition on consumers. For example, in the ground assemblage of fertilized plots, a deeper litter layer may provide wolf spiders with some protection from intra-guild predation (Rickers and Scheu 2005). Lower intraguild predation would increase the survivorship of smaller wolf spiders, aligning with our observations of decreased mean wolf spider body size, increased wolf spider abundance and lower detritivore abundance in fertilized plots relative to controls.

Another explanation for the surprising negative and neutral responses of arthropod abundance and biomass is that long-term nutrient addition in moist acidic tundra reduces plant palatability, cancelling out the positive effects of increased plant biomass on consumers. The shift towards relatively unpalatable woody stem tissue and plant species in moist acidic tundra, via the dominance of *Betula*, may be a unique response among nutrient addition experiments in herbaceous plant communities (Clark et al. 2007). In contrast to tundra, after many years of nutrient addition temperate grasslands become dominated by relatively palatable C₃ grasses and forbs (Ilsbell et al.
2013), and salt marshes’ near-monoculture of *Spartina* grasses increase in N content (Murphy et al. 2012).

In another contrast to nutrient addition in salt marshes, where an accumulation of dead thatch benefits many arthropods (Finke and Denno 2002, Murphy et al. 2012), long-term nutrient addition in moist acidic tundra may create an unfavorable canopy and surface microenvironment for arctic arthropods. In the Arctic, shrubs create a shadier, colder canopy microenvironment (Myers-Smith et al. 2011, Shaver et al. 2014), which could have negative effects on the growth and movement patterns of the resident arthropods. In particular, the cooling effect of shrubs could be responsible for the observed increase in ground-dwelling detritivore body size (Atkinson and Sibly 1997), while also decreasing the movement (and therefore capture) rates of surface-active predators like wolf spiders. In addition to these temperature effects, nutrient addition leads to the loss of the moss cover that insulates the soil and regulates soil moisture (Blok et al. 2011). These changes likely drove out some arthropod taxa, given the sensitivity of many arctic species to decreased solar radiation and fluctuations in soil moisture (Strathdee and Bale 1998, Danks 2004, Høye and Forchhammer 2008a).

*Fertilization decreases plant diversity, but not arthropod richness*

Contrary to our second hypothesis, fertilization did not decrease arthropod diversity (rarefied richness). Instead, we found that fertilization’s effect on arthropod diversity was dependent upon microhabitat, with decreased diversity in fertilized canopies (as expected), but increased diversity in the fertilized ground assemblage. We interpret these results cautiously, because although the differences between control and fertilized richness were significant, they were small (3-5 taxa), and furthermore, the taxa identified in this study are likely each represented by multiple species. Even so, the changes to
arthropod diversity were unexpected in comparison with similar studies (Siemann 1998, Haddad et al. 2000, Wimp et al. 2010) and small relative to the loss of >50% of plant species from fertilized plots. This suggests that tundra arthropod diversity is somewhat robust to plant species loss.

On the other hand, some taxa were dramatically affected; fertilization seems to have nearly driven out a moss-associated detritivore (Collembola: Symphypleona) and a graminoid-associated herbivore (Hemiptera: Delphacidae). In the canopy, decreased abundance of these Delphacids may have propagated through the food web, contributing to the absence of taxa known to predate on this family (Hemiptera: Anthocoridae, Nabidae; Diptera: Pipunculidae) relative to control plots (Table S1).

Fertilization alters both plant and arthropod community composition

Supporting our third hypothesis, arthropod community composition differed in control and fertilized plots. As part of a whole-community response to fertilization, we expected to (and did) see changes to the community composition of first-order consumers most directly tied to the plant community—detritivores and herbivores (Hunter and Price 1992). These compositional changes suggest a functional response from the arthropod community, even though total abundance, total biomass and total diversity were mostly unaffected by nutrient addition.

Treatment effects on community composition also contributed to changes in arthropod body size structure (Table 2), with fertilized plots supporting larger taxa (the exception being ground-dwelling predatory arthropods, which were smaller in fertilized plots relative to controls). Relative to taxa with small body size, large taxa have greater per capita nutrient demands (Brown et al. 2004). The larger herbivores and detritivores in fertilized plots may have capitalized on increased N concentrations in non-woody plant
tissues even as total N constrained their total abundance and/or biomass. These changes to arthropod community composition and body size, together with the losses of certain arthropod taxa (described above), point to changes in food web and ecosystem processes (e.g., herbivory, predation) resulting from nutrient addition.

**Conclusion**

Overall, our results were surprising and in contrast with similar studies of bottom-up effects on arthropod community structure. We found that nutrient addition altered arthropod community composition, but did not affect total arthropod diversity, abundance or biomass as predicted. Despite the dramatic increase in plant productivity and substantial reduction of plant species diversity, nutrient addition did not increase arthropod abundance and biomass or reduce arthropod diversity. As predicted, plant community changes were associated with shifts in arthropod community composition, and in some cases losses of arthropod taxa, suggesting bottom-up effects from plants to arthropod consumers. In this community, the availability of palatable (non-woody) plant tissues, and not total plant production, likely set the upper limit on arthropod biomass and abundance in fertilized plots. Our findings recall how eutrophication of aquatic systems can increase primary production while detrimentally affecting consumers, and provides a striking contrast to the handful of terrestrial studies that have found parallel plant and arthropod responses to nutrient addition. Our results indicate that in some cases, producer traits exert stronger bottom-up control on consumer communities than the amount of primary production.
Table 2-1. Arthropod Biomass and Abundance Results

Results from linear mixed effects models of arthropod abundance and biomass. Biting flies were not present in ground assemblage samples.

| Assemblage | Group        | Sum   | Mean  | NumDF | DenDF | F.value | Pr(>|F|) |
|------------|--------------|-------|-------|-------|-------|---------|---------|
| Abundance  | Canopy       | All   | 0.09  | 0.09  | 1     | 3       | 0.9     | 0.403   |
|            | Parasitoids  | 0.45  | 0.45  | 1     | 3     | 2.5     | 0.215   |
|            | Predators    | 0.04  | 0.04  | 1     | 6     | 0.1     | 0.719   |
|            | Herbivores   | 0.02  | 0.02  | 1     | 6     | 0.1     | 0.764   |
|            | Detritivores | 0.53  | 0.53  | 1     | 3     | 2.4     | 0.221   |
|            | Biting Flies | 0.07  | 0.07  | 1     | 3     | 0.1     | 0.791   |
| Ground     | All          | 0.69  | 0.69  | 1     | 27    | 5.3     | 0.030   |
|            | Parasitoids  | 0.02  | 0.02  | 1     | 27    | 0.1     | 0.777   |
|            | **Predators**| 0.93  | 0.93  | 1     | 27    | 12.5    | 0.001   |
|            | Herbivores   | 0.38  | 0.38  | 1     | 30    | 1.5     | 0.236   |
|            | **Detritivores** | 1.91 | 1.91  | 1     | 27    | 6.5     | 0.017   |
| Biomass    | Canopy       | All   | 0.57  | 0.57  | 1     | 3       | 2.4     | 0.220   |
|            | Parasitoids  | 1.14  | 1.14  | 1     | 6     | 0.4     | 0.548   |
|            | Predators    | 1.20  | 1.20  | 1     | 6     | 1.3     | 0.301   |
|            | Herbivores   | 0.13  | 0.13  | 1     | 3     | 0.6     | 0.480   |
|            | **Detritivores** | 4.67 | 4.67  | 1     | 6     | 10.1    | 0.019   |
|            | Biting Flies | 0.23  | 0.23  | 1     | 3     | 0.2     | 0.684   |
| Ground     | All          | 0.03  | 0.03  | 1     | 27    | 0.2     | 0.681   |
|            | Parasitoids  | 0.39  | 0.39  | 1     | 27    | 1.3     | 0.274   |
|            | Predators    | 0.04  | 0.04  | 1     | 27    | 0.3     | 0.615   |
|            | Herbivores   | 2.36  | 2.36  | 1     | 27    | 4.1     | 0.053   |
|            | Detritivores | 7.00  | 7.00  | 1     | 27    | 4.1     | 0.053   |
Table 2-2. Community-Weighted Mean Body Size Results

Percentage contribution of community turnover, within-taxon body size variation and their covariation to treatment variance in community-weighted mean (CWM) body size, by assemblage and trophic group. Positive covariation means that a treatment with typically large taxa had larger-than-average individuals within those taxa (and vice versa); negative covariation means that a treatment with typically large taxa had smaller-than-average individuals within those taxa (and vice versa). Percentages greater than 100 occur wherever treatment differences for fixed CWM body size and/or intra-taxon size variation were greater than treatment differences for the treatment-specific CWM.

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Figure 2-1. Plant Community Composition in Control and Fertilized Plots

Visually estimated ground cover after 24 years of fertilization. Non-living includes loose litter, bare ground, frost boils (cryoturbation), vole activity (e.g. nests and haying), and standing dead shrubs (Salix spp.).
Figure 2-2. Arthropod Abundance and Biomass in Control and Fertilized Plots

Arthropod abundance (left panels) and biomass (right panels) means in control and fertilized plots in the canopy assemblage (top panels) and on the ground (bottom panels). Asterisks above bars indicate significant treatment differences in total abundance or biomass; asterisks within bars indicate significant treatment differences for the trophic group indicated (P<0.05). Error bars are 1SE for total biomass or abundance (n = 4 blocks).
Community-weighted mean (CWM) arthropod body size for each assemblage and trophic group. Gray lines represent “fixed” CWMs calculated from the average body size of each taxon averaged across treatments (treatment differences result only from turnover, i.e., relative abundances of large vs. small taxa); black lines represent a treatment-“specific” CWM calculated from the average body size of each taxon within each treatment (thus, treatment differences result both from turnover and differences in body size within taxa).

Significance of treatment differences for CWMs are marked for each type of mean (*, P<0.05; ·, P< 0.10). Error bars are 1SE (n = 4 blocks).
Figure 2-4. Rarefied Richness Curves in Control and Fertilized Plots

Taxon rarefaction curves of the canopy- and ground-dwelling arthropod assemblages, by trophic group and in total. Rarefied richness values are indicated by horizontal dashed lines; shaded areas represent standard errors of iterations of the assemblage abundance data.
Figure 2-5. Arthropod Community Composition in Control and Fertilized Plots

Non-metric multidimensional scaling (NMDS) solutions for canopy (A,C) and ground dwelling (B,D) arthropod community composition. Black text and dashed ellipses indicate centroids and 95% CI for each treatment. A, B: NMDS coordinates for vacuum and pitfall samples are shown as filled (fertilized) and open (control) circles. C, D: Coordinates for each taxon are labeled with abbreviations and colored by functional group (see Supp. Table 1 for corresponding taxon names). E, F: percent share of total treatment deviance by taxon from multivariate generalized linear models of canopy (E) and ground (F) assemblage taxonomic composition. Taxa contributing >5% of total deviance are labeled with their abbreviation. Asterisks (*) indicate taxa for which there was a significant univariate effect of treatment (Padj <0.05) and dots (.) indicate marginally significant treatment effects (Padj <0.1). Labeled arcs indicate the subtotal of deviance for each trophic group; biting flies (canopy and ground) and parasitoids (ground only) contributed <1% to deviance.
Chapter 3

Linear responses of food web function to a gradient of nutrient enrichment

Ashley Asmus, John Moore, Amanda Koltz, Gus Shaver and Laura Gough
Abstract

We used a food-web approach to examine the response of plants and insects to a gradient of experimental soil nutrient addition (N and P) in moist acidic tundra. By applying an energetic food web model to direct measurements of insect and plant biomass, we estimated the rate of various food web processes (production, herbivory, predation, and N cycling) and evaluated the effects of nutrient addition on interactions between individual functional groups and for aggregated trophic levels. Our model predicted that consumer food web processes responded positively to nutrient addition and in a strikingly linear fashion ($R^2>0.95$ for most measures); for every gram of N added, herbivory increased by 31% over controls. Surprisingly, plant production and biomass did not respond with the same degree of linearity. Instead, a linear decrease in plant C:N across the nutrient gradient drove consumer responses, suggesting that plant palatability, not plant biomass, is the main constraint on this food web. Our study found neither a saturating level nor a threshold at which nutrient addition began to have an effect on herbivory and predation rates, suggesting that this system is sensitive to even small changes in soil nutrient availability.

Introduction

Many longstanding theories in trophic ecology contain implicit predictions about the (non-) linearity of ecosystem dynamics across gradients of productivity (Power 1992). In some cases, such predictions are formally enshrined (Oksanen et al. 1981, Arditi and Ginzburg 1989, Leibold 1996). These theories generally suggest that as productivity increases, more consumer biomass, longer food chains and greater consumer diversity can be supported (White 1978, Mattson Jr 1980, Hunter and Price 1992); additionally,

A host of studies from natural productivity gradients has revealed that the relative strength of top-down versus bottom-up forces in real ecosystems rarely behaves as a simple linear function of productivity, but rather is contingent on a multitude of factors, including producer and consumer vulnerability to predation, food chain length and food web structure (van de Koppel et al. 1996, Fraser and Grime 1997, Jeppesen et al. 2000, Chase 2003, Aunapuu et al. 2007, Tewfik et al. 2007, Ward et al. 2015). Likewise, a handful of experiments has found that changes to plant community composition can produce surprising non-linear responses of key ecosystem functions (e.g., ecosystem respiration, decomposition and net carbon storage) to gradients of soil nutrient enrichment (Wedin and Tilman 1996, Arens et al. 2008, Bai et al. 2010). Foremost among these gradient experiments is a decades-old soil nutrient addition experiment at the Cedar Creek Long-Term Ecological Research site (LTER) (Tilman et al. 2006). This experiment has revealed that plant diversity plays a lynchpin role in mediating the effects of nutrient addition on consumers, producers, and the ecological interactions within each trophic level (Haddad et al. 2000, Clark and Tilman 2008, Tilman et al. 2012, Isbell et al. 2013).

Meanwhile, the vast majority of experimental tests of bottom-up and top-down theories have been performed in factorially-designed nutrient addition experiments (Gruner et al. 2008, LeBauer and Treseder 2008, Fay et al. 2015). Perhaps because such experiments are easy to implement, most employ treatments that consist of either ambient or supplemented nutrients, mainly supplied in the form of Nitrogen (N) and/or Phosphorus (P) (Gruner et al. 2008, LeBauer and Treseder 2008, Fay et al. 2015). In many cases, the amount of nutrients added probably surpasses biologically realistic
levels and greatly exceeds estimates of anthropogenic N-deposition (Bobbink et al. 2010, Pardo et al. 2011). When consumers are considered in these experiments, they are usually manipulated—like nutrients—as components to add or subtract from systems, primarily with mammalian exclosures in terrestrial systems, and predator removals in aquatic systems (Borer et al. 2006, Gruner et al. 2008, Lind et al. 2013, Borer et al. 2014). On the whole, this factorial approach—especially when experiments are only maintained for a few years (Gough et al. 2000, Isbell et al. 2013)—limits our ability to draw inference about the shape of ecosystem responses to gradual shifts in resource availability, let alone the sensitivity of real, complex food webs to eutrophication (Clark and Tilman 2008, Bobbink et al. 2010, Pardo et al. 2011) and other chronic, low-level stressors (Smith et al. 2009).

Similar factorial nutrient addition and herbivore exclosure experiments have been performed in moist acidic tundra, a common and relatively well-studied upland plant community in the Arctic (Shaver et al. 2014). As in other herbaceous systems, long-term (>5 yr) high-dose nutrient addition changes tundra plant community composition and usually increases aboveground net primary production (ANPP) (Shaver et al. 2014). Further, results from mammalian exclosures suggest herbivores play an important role in this system, increasing ANPP via selective herbivory and faster nutrient cycling (Gough et al. 2012). Many of the responses to nutrient addition in this plant community arise because a deciduous shrub, *Betula nana*, becomes dominant in fertilized plots at the expense of mosses, forbs, graminoids and dwarf evergreens, resulting in a loss of species diversity (Shaver et al. 2014). In the long term, dominance of *Betula* can have negative consequences for consumers: in experiments maintained for 24 years, insect herbivores and predators are no more abundant in fertilized plots than in controls, likely a result of a buildup of unpalatable woody tissues by *Betula nana* (Asmus et al. in review).
Alongside these factorial experiments, the Arctic LTER established an experiment in 2006 with several levels soil nutrient addition. Published studies from this experiment are few, but have shown that shifts in plant leaf traits occurred in the early years of the experiment (Heskel et al. 2012), while more substantial changes to plant diversity, total leaf area and gross primary production occurred across the experimental gradient after more than five years of nutrient addition (Prager et al. 2017). These results suggest consumers might respond positively to nutrient addition, and in a parallel manner to gross primary production. On the other hand, it was unclear at the time of this study whether changes to plant community composition had already resulted in a shift towards inedible *Betula* wood, or if decreased C:N (a common response of plant communities to nutrient addition, Shaver *et al.* 2014) had resulted in a more palatable plant community overall.

Here we take a holistic food-web approach to examine the response of producers and arthropod consumers to this gradient of experimental soil nutrient addition. To evaluate the food web response, we estimated the rate of various food web processes (production, herbivory, predation, and N cycling) with an energetic food web model applied to direct measurements of plant and insect biomass. The experimental design allowed us to evaluate the shape of the food web response, while the model allowed us to evaluate effects on individual interactions between plant and consumer functional groups in the context of the canopy food web, strengthening our ability to ascribe specific mechanisms to aggregate trophic-level (linear food chain) responses. Using a pair of alternative hypotheses, we first took a simple bottom-up view, hypothesizing that food web processes at all trophic levels would respond to nutrient addition in a linear manner along the gradient, and in proportion to the amount of nutrients added. Alternatively, we hypothesized nutrient addition would amplify top-down processes (herbivory or
predation), leading to non-linear plant and/or herbivore responses. Although these hypotheses frame our study as a test of the effects of productivity on bottom-up versus top-down forces in real food webs, we expected that the actual outcome would result from a mixture of both consumer-driven and resource-driven processes, and recognized the potential for secondary effects of nutrient addition (changes to community composition, diversity and plant palatability) to modify simple linear effects of resources and consumers.

Methods

Study system and nutrient addition

Our study was conducted in moist acidic tundra near Toolik Field Station (68°38’N, 149°43’W, el. 719m) the site of the Arctic Long-Term Ecological Research (LTER) project (Shaver et al. 2014). Moist acidic tundra is characterized by a mixture of mosses (mostly Sphagnum), graminoids (esp. Carex bigelowii, Eriophorum vaginatum), dwarf deciduous shrubs (esp. Salix pulchra, Betula nana) dwarf evergreens, and forbs (Shaver et al. 2014). The LTER maintains 4 experimental blocks in this plant community, established in an area of homogenous vegetation; for this study, blocks 1-3 were used. Each block was comprised of 8, 5 x 20 m plots separated from adjacent plots by 2 m walkways. Within each block, one plot is designated a control (“CT”, no nutrient addition). In the other plots, granular ammonium nitrate and superphosphate are broadcast by hand in early June each year, immediately after snowmelt. The treatments studied here are named after the amount of N supplied, with “F1” treatments receiving 1 g N + 0.5 g P m⁻²·yr⁻¹; and other plots receiving 2 g N + 1 g P m⁻²·yr⁻¹ (“F2”); 5 g N + 2.5 g P m⁻²·yr⁻¹ (“F5”); or 10 g N + 5 g N m⁻²·yr⁻¹ (“F10”).
Arthropod community responses: community composition and biomass

We sampled the canopy-dwelling arthropod community in 2015 (after 10 years of treatment) at approximately weekly intervals during the growing season (June 18 – July 23) in CT, F1, F2, F5 and F10 plots. In each 5 x 20 m plot, we established five, 0.25 m² areas spaced 2 m apart for sampling. Using a modified leaf vacuum set on reverse (Asmus et al. in review), we suctioned the air and plant “canopy” between 50 cm and 2 cm above the ground surface in a standardized pattern at each sampling location for 30 seconds. Arthropods were collected by a muslin bag set in the leaf vacuum intake nozzle. In the lab, arthropods were sorted from plant debris and stored in vials of ethanol. We identified all specimens except parasitic wasps (Hymnoptera: Parasitica) to family using published keys. Using a digital microscope camera, we measured the body length of all individuals, then used published taxon-specific length-mass regression equations to estimate biomass (see Pérez et al. 2016 for complete methods).

Because we were only interested in the aboveground food web, we eliminated a handful of ground- and soil-dwelling predator taxa from our analyses (wolf spiders, running crab spiders, centipedes, beetle larvae and fly larvae) but retained the primarily soil-dwelling Collembola (springtails) because these can be active far above the surface, and are often found in the webs of canopy- and near-surface dwelling predators (e.g., Araneae: Linyphiidae; A. Asmus pers. obsv.). In addition, we eliminated two very large taxa: the only horse fly we collected (Diptera: Tabanidae), which was >10SD larger than the average collected arthropod, and was unlikely to be routinely sampled by the vacuum, and a single fly from family Diptera; Empididae whose body size was >15 SD larger than that of mean predator body size.
Plant community responses: biomass, ANPP, C:N and community composition

In late July 2012 (after 7 years of treatment) we conducted a harvest of plant tissues in CT, F2, F5 and F10 plots to assess the responses of plant biomass, aboveground net primary production (ANPP), and plant tissue chemistry (%C, %N, and stable isotope ratios) to nutrient addition. In each plot, five randomly located 10 x 40 cm quadrats were harvested. For each quadrat, aboveground plant tissues and rhizomes were separated to species and tissue type, including current and previous years’ growth (Shaver and Chapin 1991). The samples were then dried and weighed for biomass. We calculated ANPP as the sum of all new aboveground plant tissue biomass, including leaves, stems and inflorescences, plus new secondary growth of woody stems, using regression equations determined for each woody species (Bret-Harte et al. 2002).

Dried samples of each plant species and tissue type were processed via mass spectrometry for %C and %N (Hobbie 2017). To achieve adequate sample weight, samples of each species and tissue were pooled for each block and treatment. To evaluate tissue chemistry responses to nutrient addition, we calculated community-weighted (biomass-weighted) C:N values for each growth form, and for the community as a whole. To arrive at these measures, we first calculated the average biomass of each plant species and tissue type for each block, and matched these average biomass values to their %C and %N values. Occasionally, %C and %N values were missing due to insufficient sample weight or machine error. In these cases, we substituted %C and %N values from other experimental blocks from the same treatment. Next, we calculated the biomass of N and C for each plant species and tissue type. Within each block and treatment, we summed the biomass of C and N for each plant species (across tissue types), each growth form (across species and tissue types), or the whole community, and
from these calculated the each plant species’ C:N and the two community-weighted C:N values (by growth form and for the whole community).

Food web model

To evaluate the functional responses of the arthropod food web to the nutrient addition gradient, we used an energetic food web modeling approach previously used to describe soil food webs (de Ruiter et al. 1994; Hunt et al. 1987; Moore and deRuiter 2012). The model assumes the system is at steady-state, i.e., that production of any given functional group (i.e., arthropod taxon or plant species) is equal to losses via predation and natural death. This method estimates C and N fluxes between each pair of consumers and resources based on the total biomass (mg C m²), feeding preferences, assimilation efficiencies, production efficiencies and C:N ratios of the various functional groups.

We created a food web for each treatment in which we sampled arthropods (CT, F1, F2, F5 and F10). Because we were interested in the effect of nutrient addition (rather than seasonality) on arthropod food web function, we first summed the biomass of each arthropod taxon for each sampling location across the 7 sampling dates. We then averaged across the five sampling locations within each plot, and finally calculated an average and standard deviation of biomass for the three replicate blocks of each treatment. To derive estimates of plant biomass available to insects, we first calculated the average total biomass for each growth form in the five quadrats of each block from the 2012 harvest data, then took an average and standard deviations for the three replicate blocks of each treatment from the result. Assuming woody tissue would be inedible for the insects owing to a lack of wood specialists in this community (Asmus et al. in review), we eliminated old stems of deciduous plants and evergreens from the
calculations. Because a harvest was not performed in the F1 treatment, we assumed that plant biomass and C:N was the same as controls based on the similarity of plant community composition in these plots in 2015. For other basal resources that we did not measure – detritus, aquatic diatoms, mammal blood and nectar – we assigned large theoretical values of biomass so that resources were not limited, and estimated C:N ratios from the literature wherever possible (Koltz et al. in press). We excluded parasitic Hymenoptera from the food web model owing to overly coarse taxonomic assignment and uncertain feeding relationships.

We assumed that 50% of the estimated dry weight biomass of each arthropod group was C (Doles 2000; Hunt et al. 1987), and relied on the literature to assign C:N, assimilation efficiency and production efficiency values of consumers. We used published accounts and personal observations to assign feeding relationships among arthropods and producers. We assumed all flying arthropods consumed nectar, and that all flies with an aquatic larval stage (e.g., Diptera: Chironomidae) relied on detritus and/or aquatic resources. For generalist predators (i.e., spiders), we assigned a feeding relationship wherever the average body size of the potential prey taxon was smaller than the average body size of the predator. For all consumers, we assumed no dietary preferences (i.e., the feeding preference was either a 0 or 1), allowing predation rates to be solely determined by prey availability.

To account for the variation in the contributions of various groups to intraspecific interactions and overall food web function, we re-simulated the food web model 1000 times. For input, every simulation had the same feeding preferences, but different random samples of the gamma distribution (a non-negative skewed distribution in the exponential family) of the biomass of each functional group. The shape and scale of each functional group’s gamma distribution were derived from the means and standard
deviations of the biomass from our field samples (mean and SD of 3 blocks). Because we
assumed predation rates were proportional to biomass availability for generalist
consumers, this also allowed us to account for uncertainty in consumer feeding
preferences.

Statistical analysis

To evaluate whether plant or arthropod biomass, plant C:N, or plant ANPP responded to the nutrient addition, we used a series of linear mixed-effects models with grams of N added (a continuous variable) as a fixed effect and experimental block as a random effect. To evaluate food web functional responses (production, consumption, N cycling) to nutrient addition we used simple linear regressions using the mean values of the output from the 1000 iterations of the model (because food webs were created for each treatment, not at the level of individual blocks). To evaluate how nutrient addition altered plant and arthropod community composition, we used multivariate linear models (mayglm) in R package mvabund with an offset equal to total sample abundance to test for compositional effects (Wang et al. 2012). We performed all statistical analyses in R, and created graphics with packages ggplot2 (Wickham 2016) and cowplot (Wilke 2016). We visualized the food webs with R package Network Dynamic (Butts et al. 2016).

Results

Plant community responses: biomass, C:N, ANPP and community composition

The effects of nutrient addition on total plant biomass were somewhat non-linear (Figure 1): when examining only CT, F2 and F5 treatments, total plant biomass significantly increased along the gradient (Est=73.2±24.9, P=0.005), but a slight decline in total plant biomass from F5 to F10 made the relationship non-significant when
examining all treatments (P>0.05). This was partly a result of declines in moss (Est=-6.8±1.3, P<0.001) and lichen (Est=-6.9±1.6, P<0.001) with increasing fertilization. Deciduous shrubs were the only plant growth form that had a significant, positive biomass response to nutrient addition across the entire gradient (Est=15.6±5.1, P=0.003).

Despite a lack of a linear plant biomass response, total plant N significantly increased along the nutrient gradient (Est=0.07±0.02, P=0.003), and C:N decreased (Figure 2). Plant C:N of all plant growth forms, species and tissues decreased linearly across the nutrient addition gradient (Figure 2; all P<0.05); as a result, biomass-weighted C:N for the whole plant community also decreased (Est=-2.3±0.4, P<0.001).

ANPP significantly increased across the nutrient addition gradient (Est=11.2±4.4, P=0.015), although visual inspection of the relationship between ANPP and nutrient addition suggests that, like plant biomass, ANPP responded less strongly to nutrient addition in F10 than in F5 (Figure 1). Both deciduous shrubs (Est=8.9±2.2, P<0.001) and, to a lesser extent, forbs (Est=0.4±0.2, P=0.045) increased ANPP in response to nutrient addition. Graminoid and evergreen ANPP were not affected by nutrient addition (P>0.05).

**Arthropod community responses: biomass and community composition**

Total arthropod biomass increased along the nutrient addition gradient (Est=0.09±0.01, P<0.001); likewise, the total biomass of parasitoids (Est=0.011±0.002, P<0.001), predators (Est=0.008±0.003, P=0.012), herbivores (Est=0.09±0.01, P<0.001) and detritivores (Est=0.059±0.006, P<0.001) increased (Figure 3). Nutrient addition had no effect on the total biomass of hematophages (mosquitoes and blackflies; P>0.05).

Along with these responses at the aggregated level of trophic groups, nutrient addition provoked a change in arthropod community composition: both the relative
abundance of taxa (Dev=321.8, P=0.001) and the distribution of biomass among taxa (F=411.1, P=0.002) were altered by nutrient addition. These community-level changes were accompanied by significant increases in the biomass of a handful of individual taxa (manyglm univariate tests; adj. P<0.05). These included two herbivore families (Hemiptera: Cicadellidae and Psyllidae); several families of aquatic and saprophagous flies (Diptera: Cecidomyiidae, Chironomidae, Chloropidae, Drosophilidae, Sciaridae); and the detritivore family, bark lice (Psocoptera: Psocidae), which were only present in F5 and F10.

Food web model results

Total consumer production (Est=6.8±0.8, P=0.003, R2=0.95) as well as production by herbivores (Est=5.1±0.7, P=0.005, R2=0.93), detritivores (Est=1.6±0.2, P=0.006, R2=0.94) and predators (Est=0.1±0.0, P=0.035, R2=0.76) estimated from the food web model significantly increased across the nutrient gradient (Figure 5). At the highest level of nutrient addition, the mean estimate of total consumer production (herbivores, detritivores, and predators combined) was 2.3 times greater than that of controls. The magnitude of the herbivore response to N addition was greater than that of predators or detritivores: for every gram of N added, herbivore production increased by 31% over controls, compared to 16% for detritivores and 17% for predators.

Herbivory (total consumption of mosses and vascular plants as estimated from the food web model) also increased across the nutrient gradient (Figure 5, 6; Est=83.9±11.2, P=0.005, R2=0.93). Comparing our estimates of herbivory to those of plant biomass and ANPP from the plant harvest, we found that nutrient addition increased the percentage of plant biomass (Est=0.01±0.00%, P<0.001, R2=0.99) and ANPP (Est=0.04±0.00%, P=0.003, R2=0.68) consumed by herbivores. Our estimates of
insect herbivory were small: in control plots, our model estimated that herbivores consumed 0.6 g m\(^{-2}\) yr\(^{-1}\) plant biomass, equivalent to 0.4% of ANPP (149 g m\(^{-2}\) yr\(^{-1}\)) and 0.06% of plant biomass (1086 g m\(^{-2}\)). In F10 plots, model estimates of herbivory were 2.3 g m\(^{-2}\) yr\(^{-1}\) plant biomass, equivalent to 0.9 % of ANPP (248 g m\(^{-2}\) yr\(^{-1}\)) and 0.17% of plant biomass (1320 g m\(^{-2}\)).

The model estimated that most of the plant biomass consumed was graminoid tissue, except in F1, where consumption of deciduous plants was 9% greater than consumption of graminoids (Figure 6). In addition to total herbivory, consumption of deciduous shrubs (Est=42.9±4.3, P=0.002, R\(^2\)=0.96), evergreens (Est=22.6±2.7, P=0.004, R\(^2\)=0.94) and graminoids (Est=118.6±26.4, P=0.021, R\(^2\)=0.83) increased across the nutrient addition gradient. Nutrient addition also increased the percentage of evergreen biomass (Est=0.006±0.001%, P=0.013, R\(^2\)=0.96) and evergreen ANPP (Est=0.03±0.0%, P=0.032, R\(^2\)=0.90) consumed by herbivores, but had no effect on the percentage of graminoid, forb or deciduous shrub biomass or ANPP consumed (P>0.05). These results suggested that the increased percentage of total ANPP and total plant biomass consumed by herbivores resulted from greater consumption of evergreens, and from some non-significant increases in the proportion of other plant growth forms consumed (Figure 6). Averaged across the five treatments, sap-feeding herbivores (Homoptera, Thysanoptera) were responsible for >99% of herbivory, while chewing herbivores (Lepidoptera and Sawfly larvae) were responsible for <1% (Figure 4); this estimate is certainly biased towards sap-feeders, because many caterpillars are too large to be picked up by the vacuum.

As predator production increased across the nutrient gradient, predation on herbivores, predators and detritivores increased in turn (P>0.05); however, the percentage of consumer production (all groups), herbivore production, detritivore
production and predator production lost to predation did not vary across the nutrient addition gradient (P>0.05), suggesting that nutrient addition did not intensify top-down control by predators on lower trophic levels. Across the nutrient addition gradient, 6-13% of herbivore production was lost to predation, compared to 2-6% of detritivore production, and 1-18% of predator production.

In control plots, consumers returned 17 mg of N to the system in the form of egestion, natural death, and N mineralization. For every gram of N added, consumers returned an additional 6.5±0.3 mg of N to the system (P<0.001, R2=0.99). In control plots, herbivore and detritivores contributed approximately equal amounts of N to the system (Figure 4). The proportion of N returned by herbivores marginally increased across the nutrient gradient (Est=2.8±0.8%, P=0.052, R2=0.68) while the relative contribution made by detritivores marginally declined (Est=-2.7±0.08%, P=0.053, R2=0.68).

Discussion

_Strikingly linear responses of insect food web, but not plants, to nutrient addition_

Supporting our first hypothesis, we found that the rate of many consumer food web processes increased across the nutrient gradient, and did so in a strikingly linear manner (R2>0.90 for many functional responses; Figure 5). The magnitude of response was greater for herbivores than for predators: for every gram of N added to the system, herbivore production increased by 31%, and predator production increased by 17%. Parasitoid biomass increased as well, likely in response to an abundance of insect hosts (Wirta et al. 2015). These findings indicate that this food web is sensitive to small increases in soil nutrient availability, and that at least for these levels of nutrient addition
there was neither a minimum threshold at which effects began to manifest, nor a saturating level of nutrient addition at which effects were attenuated.

Given these responses of the insect food web, it was somewhat surprising that plants did not respond to nutrient addition with the same degree of linearity. Both ANPP and biomass at the highest level of nutrient addition (10 g N m\(^{-2}\) yr\(^{-1}\)) were slightly less than at a lower level of nutrient addition (5 g N m\(^{-2}\) yr\(^{-1}\)). This was partly a result of a decline in moss and lichen biomass, consistent with results from previous long-term nutrient addition experiments in moist acidic tundra (Shaver et al. 2014). It is probable we captured a transitional state in this plant community response to nutrient addition: the slow-growing, perennial plant species that will respond the strongest to nutrient addition (\textit{Betula}) may take some time to respond in the expected manner via, e.g., addition of woody structures. In comparison, to tundra plants, the insects in this tundra plant canopy community have a mostly annual life cycle and disperse easily.

We expected that should insects not respond to nutrient addition in a linear fashion, changes to plant community composition or edibility would be to blame. Instead, we found that shifts to plant community composition and tissue chemistry benefitted insect consumers, such that insects responded positively and linearly to nutrient addition even when the response of plants was less straightforward. C:N of all plant species, growth forms and tissues decreased as a result of nutrient addition. Perhaps most important was the decrease in graminoid C:N. Graminoids, more than any other plant growth form, supported this insect food web. Increased consumption of graminoids drove increases in total insect herbivory for part of the nutrient addition gradient (controls – 5 grams N added), but increased consumption of dwarf shrubs was responsible for gains in total insect herbivory for the remainder. This was in keeping with a shift towards woody
deciduous shrubs in the most heavily fertilized plots, suggesting that insect herbivore community composition kept pace with changes to plant community composition.

**Weak herbivore effects on plant biomass intensified by nutrient addition**

We hypothesized that, absent significant top-down predator control on herbivores, nutrient addition would not only increase the amount of herbivory, but also intensify the top-down effects of herbivores on plants (i.e., herbivores would consume a greater amount and proportion of plant production). Supporting that hypothesis, we found minimal effects of predators on herbivores, and observed a linear increase in the percentage of plant production and plant biomass removed by herbivores along the nutrient addition gradient.

Perhaps unsurprisingly given the severe constraints imposed by the Arctic environment, we estimated that insect herbivores consumed a very small amount of ANPP (0.4 – 0.8%), a miniscule value relative to temperate or tropical systems, where defoliating herbivores can remove 1-30% of leaf production (Koltz et al. 2017 and references therein) and sap-feeding insects reduce woody plant biomass by an average of 30% across systems (Zvereva et al. 2010). Admittedly, ours is an underestimate, because the sampling method used here (an insect vacuum) likely under-sampled large-bodied insects, namely caterpillars and sawfly larvae. These and other defoliating (chewing) insects consume about 0.5% of woody plant foliage in tundra habitats (Kozlov et al. 2015), and approximately 1% of *Betula nana* leaf area in moist acidic tundra habitats near our site (Barrio et al. 2017). Assuming *Betula* leaf area is roughly proportional to leaf biomass, this value translates to 0.06% of ANPP in control plots in this experiment. Thus, by our measure, sap-feeding insects, not defoliators, perform the
majority of insect herbivory in moist acidic tundra – and the total amount of insect herbivory is very small.

**Conclusion**

In conclusion, tundra insect food web processes responded in a strikingly linear manner to this gradient of nutrient enrichment. Our food web approach revealed that graminoids, more than any other plant growth form, supported processes in this food web, and that top-down controls of predators on herbivores were minimal. Despite inconsistent changes to graminoid and total plant production, herbivores responded strongly and linearly to the nutrient addition gradient, suggesting that instead changes to plant tissue palatability (reduced C:N) are more important to consumers than the absolute abundance of food. Future changes to this plant community may change the nature of these effects for consumers, because we expect to see a shift away from relatively palatable graminoids and a buildup of woody tissues over the course of the experiment.
Figure 3-1. Plant Biomass and Production Across Nutrient Addition Gradient

Plant aboveground net primary production (ANPP), biomass, and N biomass by growth form in each treatment. Values represent means and standard errors of each treatment (N=3 blocks).
Figure 3-2. Plant C:N Across Nutrient Addition Gradient

Plant C:N ratios for each treatment by growth form (all tissues combined). Points represent the average value for each treatment (N=3 blocks). Lines represent treatment effects estimated from mixed-effects models.
Figure 3-3. Arthropod Biomass Across Nutrient Addition Gradient

Arthropod biomass per m² by trophic group for each treatment. Values and error bars represent the average and SE biomass for each treatment (N=3 blocks).
Figure 3-4. Food Webs in Control and Fertilized Plots

Arthropod food webs in control ("CT") plots and plots fertilized with 10 grams each N and P m-2 yr-1. Circles represent consumer functional groups (usually arthropod families), for which the average biomass of C per m2. Squares represent basal resources (blood, aquatic diatoms, plants). See Supplemental Table 3-1 for abbreviations.
Figure 3-5. Food Web Responses to Nutrient Addition

Arthropod food web functional measures across a gradient of nutrient addition for each consumer trophic group. Boxplots represent distributions of the 1000 iterations of the food web model.
Figure 3-6. Herbivory Across Nutrient Addition Gradient

The amount of plant biomass consumed by insect herbivores derived from the food web model (A) and percentage of ANPP, as measured by the plant harvest (See Figure 1), consumed by insect herbivores (B) for each plant growth form.
Supplemental Table 3-1

Abbreviations used in Figure 3-4

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Chapter 4
Cannibalism in arctic wolf spiders: a potential rarely realized

Ashley Asmus, Taryn Flink and Laura Gough
Abstract

In tundra habitats, wolf spiders (Araneae: Lycosidae) are far more abundant on the ground than herbivorous arthropods and other prey. This has prompted speculation that external sources (e.g., aquatic or detrital prey) maintain wolf spider populations. We used a set of experiments to investigate whether a more proximal prey source, cannibalism, supports populations of *Pardosa lapponica*, the dominant wolf spider species in Alaskan moist tussock tundra. In arena trials, *P. lapponica* cannibalized more quickly when hungry and more frequently at disparate predator:victim size ratios. Comparing our results with published arena trial studies of temperate-latitude *Pardosa* species, we found qualitative similarities but much greater cannibalistic propensity in *P. lapponica*. Despite this tendency towards cannibalism, stable isotope results suggested that *P. lapponica* diet is primarily comprised not of conspecifics, but rather an intermediate predator from the detrital food chain. This could be because most active, pitfall-captured individuals of *P. lapponica* are similarly-sized adults, and thus encounters where cannibalism is more likely (i.e., between smaller juveniles and adults) are infrequent. Like diet generalism – a common trait among arctic consumers—a propensity towards cannibalism may help wolf spiders survive in the Arctic, where unpredictable conditions can often make resources scarce.

Introduction

Cannibalism is widespread in the animal kingdom and plays an important role in the ecology of many species (Fox 1975, Polis 1981). Among some predators, cannibalism is an important dietary resource (Fox 1975) and can sustain animal populations during periods of resource scarcity (Fox 1975, Polis 1981). Even when the absolute rate of cannibalism is low, it can stabilize predator population cycles (Van den
Bosch et al. 1988, Cushing 1991). Moreover, because smaller individuals are more likely to be victims than larger individuals, cannibalism can reshape age and size structures (Fox 1975, Cushing 1991, Cushing 1992, Van Den Bosch and Gabriel 1997, Claessen et al. 2000).

Cannibalism has been well-documented in many arthropod species. Among them, wolf spiders (Araneae: Lycosidae) are probably the best-studied group (Wise 2006). Some natural history accounts suggest cannibalism comprises 16-20% of wolf spider diet (Fox 1975). In mesocosm studies, cannibalism can measurably reduce wolf spider densities (Buddle et al. 2003), depress juvenile recruitment (Wagner and Wise 1996) and dampen the strength of trophic cascades (Snyder and Wise 2001). A tendency towards cannibalism among wolf spiders is a consequence of their natural history (Wise 2006). As active hunters, they are likely to encounter conspecifics; as generalist predators (Symondson et al. 2002), they may identify conspecifics as potential prey; and, a high degree of food limitation among wolf spider populations (Wise 2006 and references therein) should induce some to cannibalize.

Conditions in the Arctic foothills of the Brooks Range, Northern Alaska, USA, suggest wolf spider cannibalism may be common in arctic tundra. Wolf spiders are extremely abundant, with densities known to exceed 1·m$^{-2}$ in tundra habitats (A. M. Koltz unpubl. data). Encounters among conspecific wolf spiders are especially likely because a single species, *Pardosa lapponica* Thorell, dominates the spider assemblage (Wyant et al. 2011). These encounters may often be between individuals that differ in size and age, because wolf spiders in northern ecosystems are thought to have a biennial life cycle, i.e., they take two years to reach maturity (Buddle 2000, Pickavance 2001). Age and size variation should increase opportunities for larger, older individuals to cannibalize smaller, younger conspecifics (Wise 2006).
In addition to evidence that *P. lapponica* spiders have ample opportunity to cannibalize, studies indicate that non-conspecific prey may be scarce in tundra. Relative to predators, herbivores and detritivores contribute little to consumer biomass or production in tundra arthropod assemblages (Gelfgren 2010, Asmus et al. in review, Koltz et al. in review). Some have noted that this uneven distribution of biomass among trophic groups approximates an inverted trophic pyramid (Gelfgren 2010a, Ernst and Buddle 2013a). Inverted trophic pyramids of biomass are sometimes maintained by external sources of production (Polis et al. 1997). In the case of tundra food webs, that external source is thought to be either aquatic, e.g., midges and other flying insects (Ernst and Buddle 2013), or detrital (e.g., from the soil food web) (Aunapuu 2004, Gelfgren 2010a). However, a third possibility exists: to some degree, predaceous tundra arthropods may sustain themselves by consuming other predators and conspecifics. A recent bioenergetic food web model of arthropods in our study region found that, if wolf spiders are complete generalists, other wolf spiders would comprise approximately 25% of their diet (Koltz et al. in review).

Our objective in this study was to determine whether cannibalism was a substantial resource sustaining the abundant *P. lapponica* populations in Alaskan arctic tundra. Our study was divided in three parts. First, we used pitfall traps to test the hypothesis that (H1) conditions at our study site were favorable for cannibalism, with *P. lapponica* both abundant relative to other wolf spider species or alternative prey, and variable in size. Second, we conducted a laboratory arena experiment to determine the likelihood that wolf spiders would cannibalize if given the opportunity. Informed by similar experiments on temperate-latitude wolf spider species (Samu et al. 1999, Buddle et al. 2003, Rypstra and Samu 2005, Mayntz and Toft 2006, Vanden Borre et al. 2006), we hypothesized that (H2) *P. lapponica’s* cannibalistic tendency would be heightened at
lower risk:reward ratios (i.e., when the cannibal was hungry and/or the conspecific prey was relatively small). Finally, given the expectations outlined above, we hypothesized that (H3) conspecifics, more than detrital or aquatic food subsidies, would comprise a substantial, detectable component of *P. lapponica* diet. We tested this last hypothesis by comparing the stable isotope signatures of spiders caught in the field with those of spiders reared on diets comprised of one of three prey types: conspecifics, collembola (primary consumers of the detrital food web) or midges (primary consumers from the aquatic food web).

**Methods**

**Study area**

We performed this study at Toolik Field Station, in Alaska’s North Slope region (68° 38’ N, 149° 36’ W). We collected specimens from a 1000m² hillslope site (68° 38’ 35” N, 149° 34’ 19” W) associated with a five-year multi-trophic monitoring study of plants, insects and birds ("TLFS" site in Boelman et al. 2011, Rich et al. 2013, Boelman et al. 2015). The vegetation community is moist acidic tundra characterized by a relatively even mix of low-stature (<20 cm) plants including mosses, lichens, graminoids, forbs, dwarf evergreens and dwarf deciduous shrubs, and is interspersed with upland areas of dry heath tundra.

**Characterization of arthropod and wolf spider assemblage and *P. lapponica* population structure**

The ground-dwelling arthropod community at our study site has been previously described by Rich et al. (2013); for this study, we employed the same monitoring scheme during the 2013 growing season. Briefly, we collected surface-active arthropods with 20
pitfall cups filled 2cm deep with 50/50 water/ethanol mixture. Traps were “active” (filled with ethanol) for two-day sampling events spaced about one week apart (9 sampling events between 12 June and 7 August).

To characterize the distribution of abundance and biomass among trophic groups in arctic tundra, we first identified all arthropods in every sample to family using published keys (Triplehorn and Johnson 2005). Within each sample, we measured the total body length of the first five individuals of each family we encountered, then used published allometric length-mass regression equations to estimate each sample’s total biomass per family from the average of these lengths (details in Pérez et al. 2016, Asmus et al. in review). We sorted arthropod families to rough trophic groups (e.g., herbivore, predator) based on their natural history (e.g., Marshall 2006) and similar studies of tundra arthropods (Gelfgren 2010a). We then summed the biomass of every family and trophic group at each pitfall trap location (N = 20 traps) across the growing season (9 sampling dates). The soil microarthropods Collembola and Acari were not counted in these samples; in addition, the biomass of bumblebees (Hymenoptera:Apidae) was ignored in our calculations of prey biomass, as they are likely too large to be eaten by wolf spiders.

We used spiders from these traps to characterize the wolf spider assemblage and P. lapponica population structure. We counted, sexed and identified wolf spiders to species using published keys (Dondale and Redner 1990) where possible, and measured the carapace length (CL) and width (CW) of every wolf spider specimen to the nearest 0.01 mm using a digital microscope camera. We used these measures to determine the likelihood that a spider would encounter a smaller conspecific. In R, we randomly sampled the carapace lengths of pairs of wolf spiders from each sampling date 1000 times, divided the size of the larger individuals by the smaller individuals, and calculated an average size ratio from the result.
Collection of spiders and prey for experiments

We collected wolf spiders and their prey on several sunny and warm days throughout the 2015 growing season (June 20 – July 30). We collected wolf spiders indiscriminately using a combination of hand-collecting and short-term (<24 hr.) dry pitfall trapping. We measured each spider’s carapace length and width to the nearest 0.01 mm using a digital microscope camera (AmScope MU035; www.amscope.com). Using carapace shape characteristics, we keyed all specimens to one of three genera known to be in the area (Wyant et al. 2011, Sikes et al. 2013): Pardosa, Alopecosa and Arctosa, and identified individuals to species using published keys (Dondale and Redner 1990). Spiders were immediately assigned to one of our three experiments: a cannibalism arena trial, a long-term feeding experiment, or stable isotope analysis (hand-collected spiders only). We determined a spider’s experimental assignment in a random manner stratified by species, sex and body size.

Along with wolf spiders, we collected two prey items: midges and collembola. During the same period, midges were collected from areas where they were swarming or basking in large numbers near the field station using a sweep-net and aspirator. Collembola were collected from the study area using a leaf vacuum fitted with a muslin bag (Asmus et al. in review). In the laboratory, we sorted living collembola from the bag contents with an aspirator. A portion of midges and collembola were allocated for stable isotope analysis, while the remainder were fed to spiders in the long-term feeding experiment and cannibalism trial.
Cannibalism arena experiment

We performed a series of arena trials to determine whether body size disparity or starvation level affected the propensity of spiders to cannibalize. We tested a total of 42 *P. lapponica* "predator" spiders up to four times each. Some predator spiders (15, 36%) died or escaped during the four-week experiment, resulting in a total of 140 trials. All "victim" spiders were juveniles from genus *Pardosa*: species-level determination of prey spiders was not possible, but it is likely that most were *P. lapponica*, the dominant species in the area (Figure 3).

We assigned predator spiders to one of four predator:victim size ratio groups (1:1, 2:1, 3:1 and 4:1) and one of four starvation treatments (0 hours, 16 hours, 36 hours, and 60 hours starved). We randomly assigned spiders to their treatments at the beginning of each trial irrespective of their previous assignment. We paired predators and victims as closely to their assigned size ratio as possible, using carapace length as our measure of size. We fed each subject 20 midges at their assigned cutoff time plus every time before that to ensure satiation at the time assigned. For example, if a subject was assigned to the 0 hours starved, we fed it at 60, 36, 16 and 0 hours before the trial, but specimens starved 60 hours were fed 60 hours before and no more.

The arenas used for the trials were clear plastic containers approximately 9.0 cm in diameter with filter paper glued to the bottom for easier traction. We added the predator and victim to the arena simultaneously, observed continuously for an hour and then checked every 20 minutes following. We ran trials for 6 hours, at which point predators and victims (if remaining) were separated, assigned to their next trial group, and provided midges and water. The next set of trails began 60 hours later to accommodate the longest starvation treatment.
We analyzed the cannibalism arena trial results with linear mixed effects models (Zuur et al. 2009) in R package lme4 (Bates et al. 2014) and lmerTest (Kuznetsova et al. 2014). We evaluated the effect of sex (male, female or juvenile), predator:victim size ratio, and starvation period on two response variables in separate models. The first model evaluated the probability of predation within a six-hour trial with a binomial logit-link response. The second model evaluated the time to predation in the subset of trials where predation occurred. Time to predation was first log+1 transformed before analysis to help meet the assumption of residual normality. In both models, we controlled for repeated measures with a random effect for spider ID, and accounted for possible changes in predator satiation or behavior across the experimental trials with a random effect for trial number.

**Long-term feeding experiment**

We raised 34 spiders, collected as described above, on controlled diets to evaluate the effect of diet type on spider growth and tissue chemistry. Spiders were raised in a laboratory at room temperature (approximately 20°C) and ambient lighting (provided by a window) for 42 days. All spiders were from genus *Pardosa*; 20 were adult female *P. lapponica*, 5 were adult male *P. lapponica*, and 9 were juveniles for which the species was undetermined. Spiders were assigned to one of three diets: cannibals (n = 10), midges (n = 14) and collembola (n = 10). *Cannibals* were fed 1 victim spider smaller than itself (maximum carapace length 2.50 mm) at each feeding time, unless the previous victim had not been consumed. Midge-fed spiders were fed 10-20 midges at every feeding, and collembola-fed spiders were fed 10-20 collembola at every feeding. Study spiders were all fed on the same days, although feeding frequency varied between two and five days depending on weather conditions for prey collection; this resulted in a mean
of 4 days between feedings across all treatments. After observing substantial initial
mortality among the treatments, we also created a “starvation” treatment (5 newly
collected spiders deprived of food for up to 15 days) to compare the survival, tissue
chemistry and growth rates of spiders in the three diet treatments to those deprived of
food, following the same methods described above.

So that prey items were as field-fresh as possible, we collected midges and
collembola immediately before feeding and captured victim spiders within approximately
3 days of feeding (these were housed in small containers with moist paper towels until
feeding). All predator spiders in the long-term feeding trail were kept individually in the
same type of containers as the cannibalism arena trial (clear plastic deli containers 90 cm
in diameter). We lined each container with a paper towel, crumpled an additional paper
towel in which the spiders could hide, and provided access to water from a test tube of
water stoppered with cotton.

We assessed the effect of diet type on spiders’ survival (number of days) and
change in body size (product of carapace width and length) during the experiment with
linear mixed effects models. For the analysis of body size, we used the daily rate of
change in carapace width (Δ mm day⁻¹) as our response variable so that we could
evaluate growth among spiders that differed in the length of time they survived in the
experiment. We controlled for differences among sexes (male, female or juvenile) by
including sex as a random effect in both models, and included starting size as a covariate
to control for the effect of age on growth rate.

*Stable isotope and C:N analysis*

We compared the tissue chemistry of spiders from the long-term feeding
experiments to that of spiders and prey items collected from the field. We analyzed four
replicate samples each of collembola and midges, where each sample was comprised of 15-20 individuals. Spiders (but not collembola or midges) were starved for two days to empty their gut. Due to human error, only 30 of the 34 long-term feeding experiment spiders were analyzed. All specimens were frozen at -20°C and dried at 50°C for 48 hours. Homogenized tissues (spider and midges) or whole individuals (collembola) were then packaged into tin capsules for stable isotope analysis.

Isotope ratios were determined by a Costech Elemental Combustion System coupled to a Thermo Scientific Delta V advance stable isotope mass spectrometer at the Texas A&M Stable Isotopes for Biospheric Sciences (SIBS) Laboratory. We used the δ notation to express stable isotope abundance for Nitrogen (N) and Carbon (C), calculated as:

$$\delta X (\%) = \frac{(R_{sample} - R_{standard})}{R_{standard}} \times 1000$$

Where X represents either $^{15}$N or $^{13}$C, and R represents either $^{15}$N/$^{14}$N or $^{13}$C/$^{12}$C. We used air as our standard for $^{15}$N, and Vienna Peedee Belemnite as the $^{13}$C standard.

To test for differences in the stable isotope composition of the spiders caught in the field and from long-term treatments, we first fit a multivariate linear model (MANCOVA) in R which contained $\delta^{15}$N and $\delta^{13}$C as dependent variables and diet type as a fixed effect. Finding no effect of sample date on isotope composition, we retained only carapace length of the spider as a covariate to control for the effects of age and body size on isotopic composition. We followed up this MANCOVA with univariate models (ANCOVAs) for $\delta^{15}$N and $\delta^{13}$C separately. We also used an ANCOVA to evaluate differences in the C:N, %N and %C among experimental groups. We evaluated univariate model treatment contrasts with R package multcomp (Hothorn et al. 2016).
Results

Arthropod and wolf spider assemblage and P. lapponica population structure

Predators comprised 63±1% of total pitfall-captured abundance and 89±1% of total biomass (Figure 1). Wolf spiders were the most abundant predator, accounting for 36±2% of total abundance and 30±4% of total biomass. Ground beetles (Coleoptera: Carabidae) were also abundant, comprising 15±2% of total abundance and 55±4% of total biomass. Herbivores (incl. Hemiptera: Cicadellidae, Delphacidae, Aphidae) comprised only 7±1% of abundance and 3±1% of biomass. Midges and gnats were more abundant than herbivores, contributing 12±1% of abundance but only 0.3±1% of total biomass.

We identified a total of 417 wolf spiders in 2013 (Figure 2). Most of the wolf spiders captured in our pitfall traps were adults: 44% were male, 29% were female, and 24% were juveniles. Of the adults, 85% were Pardosa lapponica, while 6% were Arctosa insignita. The remainder of adults were Pardosa podhorskii (6%), Pardosa sodalis (3%) and Alopecosa pictilis (1%).

Wolf spiders, particularly adult males, were most abundant in late June—presumably when they were seeking mates—and least abundant in mid-July (Figure 3). Adults and juveniles were present throughout the 2013 growing season, resulting in a wide range of wolf spider body sizes regardless of the date (Figure 3). However, the mean size ratio determined from 1000 random pairs of body sizes hovered just above 1:1 for the duration of the growing season. Across the nine sampling dates, only 1.4% of random samples of the body sizes had a size ratio greater than 2:1, suggesting that most encounters occur between similarly-sized spiders.
**Cannibalism arena experiment**

Of the 140 predator-victim pairs, 55 (40%) resulted in predation within six hours. Of the 42 predator spiders in the experiment, 30 (70%) consumed a victim in at least one trial. The smaller spider never consumed the larger. Two trials where the carapace length of the spiders were exactly equal resulted in cannibalism, but in both cases, the cannibal spider had a slightly larger carapace width than the victim (data not shown). Spiders were more likely to consume the conspecific spider at more disproportionate size ratios (Est = 1.27 ± 0.30, P <0.001; Table 1). The model-predicted predation likelihood increased from 10% at a 1:1 size ratio to 83% at a 4:1 size ratio (Table 1, Figure 4). Neither starvation nor sex affected the probability of predation during the 6-hour experiment (P>0.05; Table 1).

Spiders tended to consume their prey early in the experimental trials: 11% of predation events occurred within 1 minute, 31% within the first ten minutes, and 60% within the first hour. Starvation level significantly decreased time to predation when it occurred (Est = -0.02 ± 0.00, P < 0.001; Table 1). In trials where predation occurred, spiders fed immediately before the experiment took 141 ± 32 minutes to consume the conspecific, compared to 38 ± 22 minutes for spiders starved for 60 hours (Figure 4). Neither size ratio nor sex affected time to predation (P > 0.05; Table 1).

**Long-term feeding experiment**

Less than half (42%, 14 of 34) of *Pardosa* spiders in our long-term feeding experiment survived the entire six weeks (Figure 5), possibly partly a result of maturation: 59% of spiders that died before the end of the experiment were adults. Diet type had a significant effect on *Pardosa* survival with those fed other spiders having the lowest survival ($F_{2, 31} = 5.8, P = 0.007$). Spider-fed *Pardosa* survived an average of 13±5 fewer...
days than midge-fed *Pardosa* (Tukey HSD $P = 0.02$), and $13 \pm 5$ fewer days than collembola-fed *Pardosa* (Tukey HSD $P = 0.04$). Only 10% of *Pardosa* fed other spiders remained at the end of the experiment, compared to 50% of collembola-fed and 57% of midge-fed *Pardosa* (Figure 5). In the group of spider-fed *Pardosa*, most of the mortality (5 of 9 deaths) occurred within the first 2 weeks of the experiment, whereas mortality among midge- and collembola-fed *Pardosa* was more gradual (Figure 5).

Diet type had a significant effect on *Pardosa*’s change in body size as well over the course of the long-term feeding experiment ($F_{2,30.7} = 4.7$, $P = 0.016$). *Pardosa* fed other spiders became slightly smaller over the course of the experiment ($Est = -0.04 \pm 0.02 \text{ mm}^2 \text{ day}^{-1}$, $p = 0.090$) while those fed midges or collembola did not significantly change in size. (Figure 6, $p > 0.05$).

**Stable isotope composition and C:N of spiders and prey**

Prey items differed in their C:N ratios (Figure 7; ANOVA, $F_{2,12} = 43.6$, $P < 0.001$), a result of differences in N content (ANOVA, $F_{2,12} = 14.5$, $P < 0.001$), but not C ($P > 0.05$). Midge had a greater C:N than either collembola or field-caught *Pardosa* (Tukey HSD $p < 0.05$). Prey items were also isotopically distinct (Figure 7; MANOVA; $F_{2,11} = 58.3$, $P < 0.001$). Midges were more depleted in $\delta^{13}\text{C}$ than either collembola or juvenile *Pardosa*, and more enriched in $\delta^{15}\text{N}$ than collembola; and, small juvenile *Pardosa* were more enriched in $\delta^{15}\text{N}$ than collembola (Figure 7, Tukey HSD $P < 0.05$).

Compared to large field-caught *Pardosa*, and in keeping with prey C:N, midge-fed *Pardosa* had a higher C:N, but starved, collembola-fed and spider-fed *Pardosa* had an equivalent C:N (Figure 7). Diet type also significantly affected spiders’ isotopic composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ together; Figure 7; Table 2; MANCOVA; $F_{8,52} = 12.2$, $P < 0.001$). Differences among diet types were significant for $\delta^{13}\text{C}$ alone (ANCOVA $F = 19.1$, $P$...
p<0.001) and $\delta^{15}$N alone (F = 42.2, p<0.001). Midge-fed spiders were more depleted in $\delta^{13}$C than any other treatment group including field-caught spiders, and were more enriched in $\delta^{13}$N compared to field-caught, collembola-fed and starved spiders (Figure 7, Tukey HSD P < 0.05). Spider-fed spiders were marginally more enriched in $\delta^{13}$C compared to collembola-fed spiders (Figure 7, Tukey HSD P = 0.07). Neither collembola-fed nor spider-fed spiders were isotopically distinct from field-caught spiders (Figure 7, Tukey HSD P > 0.05). Starved spiders were less enriched in $\delta^{15}$N than any other treatment group (Tukey HSD p < 0.05). Body size had no effect on the abundance of individual isotopes nor isotopic composition (Table 2).

Discussion

*Cannibalism is a viable feeding mode for arctic wolf spiders*

The abundance of an animal in a pitfall trap is a reflection not only of its density (number per m$^2$) but also its activity level (movement rate) (Southwood and Henderson 2009). Thus, we can infer that the individuals collected by traps were active in the same habitat space (the ground surface) and are therefore representative of the types of individuals that encounter each other in the field. Supporting our first hypothesis, *Pardosa lapponica* was by far the most abundant (and active) wolf spider species in our study area, suggesting that encounters between conspecifics frequently occur. Also, consistent with our expectations of a biennial life cycle, juveniles and adults of *Pardosa* were present across the growing season at a wide range of body sizes. On the other hand, our data suggest that encounters between two spiders that differ in size (a condition that increases the likelihood of cannibalism; Wise 2006) rarely happen, because most collected individuals are similarly-sized adults.
We also found that herbivores and other primary consumers (e.g., saprophages) contributed little to total tundra arthropod biomass or abundance in the pitfall traps, while large-bodied predators (ground beetles, wolf spiders) contributed the most. Ground beetles are probably not a viable prey option for wolf spiders: ground beetles at our site are 2 times larger than wolf spiders (total body length; data not shown), and anecdotal observation suggests ground beetles and wolf spiders avoid each other (A. Asmus pers. obsv).

*Necessity and opportunity determine whether cannibalism occurs*

Supporting our second hypothesis, our results suggest that opportunity (size) determines whether cannibalism is possible, but necessity (hunger) determines whether the spider chooses the option. In our arena experiment, only two same-sized individuals consumed each other. More disparate predator:victim size ratios increased the likelihood *P. lapponica* would cannibalize, and increasing starvation levels decreased the time it took for cannibalism to occur. These findings are consistent with experiments on other wolf spider species from temperate systems, where wolf spiders seek to minimize risk by avoiding larger conspecifics (Buddle et al. 2003, Rypstra and Samu 2005) and cannibalize more frequently when starved and deprived of alternative prey (Wagner and Wise 1996, Samu et al. 1999, Rickers and Scheu 2005, Petersen et al. 2010).

Our observed 40% cannibalism rate across all trials with *P. lapponica* is higher than that of most arena experiments with other *Pardosa* species (Supplementary Table 1). For example, Mayntz and Toft (2006) observed a 10-45% cannibalism rate among pairs of *P. prativaga* with a 2:1 size ratio after 3-10 days without food; under similar conditions, our logistic regression model predicts a 30-70% cannibalism rate for *P. lapponica* (Table 1). Similarly, recently-fed *P. agrestis* cannibalized 15% of the time at a
2.8:1 size ratio in Samu et al. (1999); in contrast, our model would predict a 37% cannibalism rate for *P. lapponica* (Table 1). Petersen et al. (2010) observed cannibalism rates between 0 and 30% for pairs of similar sized *P. pratvaga* (ratios between 1:1 and 1.4:1) deprived of food for 5-12 days; we would expect cannibalism rates between 16 and 63% under the same conditions. The only study we found where cannibalism rates were consistently higher than ours was that of Borre et al. (2006), which used field-fresh spiders (spiders were not fed prior to testing). These comparisons would suggest that *P. lapponica* may be more cannibalistic than their temperate-latitude relatives, perhaps as an adaptation to frequent encounters among conspecifics and/or resource scarcity in arctic tundra.

Thus, for small-bodied juvenile wolf spiders, encounters with adult wolf spiders are risky, especially when resources are scarce. Given the fact that prey seems to be scarce and both juveniles and adults are present throughout the growing season (Figure 2), juveniles may need to avoid predation risk when adults are most active (i.e., when adult males are seeking mates). This may be difficult in arctic tundra, where the shallow surficial litter layer and short-stature plant community affords limited refuge, and could explain why so few juveniles are active during the growing season. Such ontogenetic shifts in movement rates and hunting strategies have been described in other spider species, particularly when spider densities are high (Kreiter and Wise 1996, Kreiter and Wise 2001).

*Tissue chemistry analysis suggests that cannibalism is rare*

The midges’ isotopic signature closely matched that of midges from nearby lakes (Hershey et al. 2006), and had a $\delta^{13}$C content (-31±0.5%) very similar to published values for algae in nearby Toolik Lake ($\delta^{13}$C = -32%) (Kling et al. 1992). Collembola, meanwhile,
had a $\delta^{13}$C close to that of near-surface tundra soils (Hicks Pries et al. 2013). Because $\delta^{13}$C is thought to be a strong indicator of food chain basal resources (Post 2002), we can conclude that midges and collembola are, respectively, representativers of detrital and aquatic food webs.

Despite the fact that most of the spiders in our long-term feeding experiments were adults, and therefore had limited tissue turnover (relative to juveniles) during the experiment, our 6-week feeding experiment successfully yielded differences in the isotopic composition and C:N of spiders. This finding is generally consistent with shorter (3-week) feeding experiments that resulted in changes to early-stage juvenile wolf spider stable isotope composition (Oelbermann and Scheu 2002). Starved spiders finished their two-week experiment less enriched in $\delta^{15}$N than other treatment groups, consistent with other starvation studies of spiders (Rickers et al. 2006) and chitinous arthropods (Bunn et al. 1995) suggesting that the other treatment groups were not starved during the experiment. Wolf spiders fed midges—which had a high C:N, were enriched in $\delta^{15}$N, and were depleted in $\delta^{13}$C compared to other prey items—finished the experiment with a higher C:N, greater $\delta^{15}$N content and lower $\delta^{13}$C content relative to spiders fed collembola or other spiders. Presumably corresponding to a slight difference in trophic position, spiders raised on collembola were significantly less enriched in $\delta^{13}$C (and marginally less enriched in $\delta^{15}$N, Figure 4) relative to spiders fed conspecifics.

Our findings somewhat limited our ability to support or reject the hypothesis that cannibalism would comprise a substantial, detectable component of wolf spider diet. Importantly, conspecific-fed spiders were only slightly more enriched in $\delta^{13}$C and $\delta^{15}$N relative to their field-caught counterparts, indicating that even a moderate- to long-term diet of conspecifics fails to significantly shift the stable isotope composition of wolf spiders. Given that our starvation experiment suggests these spiders were sufficiently
satiated, an alternative explanation is in order. A lack of significant shift in isotope composition could be a consequence of reduced assimilation efficiency resulting from stress (Hawlena and Schmitz 2010)—e.g., the stress of the cannibalistic event itself, or the long-term stress of being confined with another predator. Consistent with that view, and with studies of other wolf spider species (Toft 1999, Toft and Wise 1999, Mayntz and Toft 2006), spiders in our long-term feeding experiment performed poorly on cannibalistic diets: they slightly decreased in body size and had low survival rates. Meanwhile spiders raised on midges and collembola stayed the same size, and survived for similar lengths of time as *Pardosa* in other laboratory studies (Toft and Wise 1999). These results corroborate our findings from the arena experiment: spiders may only choose the option to cannibalize when resources are scarce because the potential costs (stress, injury, or death) often outweigh the nutritional benefits of cannibalism. Thus, even though cannibalism is one possible source of energy for wolf spiders, it is probably too costly to be a substantial resource—particularly if the only conspecific encounters are among similarly-sized spiders.

Instead of isotopically resembling spiders fed a diet of conspecifics, field-caught spiders were most isotopically similar to spiders raised on collembola (Figure 4). Yet, a closer investigation of the relative δ^{15}N content of collembola and wolf spiders discounts the possibility of an entirely collembola-based diet. On average, δ^{15}N is expected to become enriched by 2-4% for each trophic level (Minagawa and Wada 1984), or just over 2% for juvenile *Pardosa* (Oelbermann and Scheu 2002). In our study, field-caught spiders were 4.6% more enriched in δ^{15}N relative to collembola (Figure 4), double the difference expected in a direct feeding relationship. This implies that at least part of wolf spiders’ diet may come from intraguild predation (predation of other predators) or cannibalism. Though not predominant in our pitfall traps, predaceous mites (Acari) and Linyphiid
spiders (Araneae: Linyphiidae) are abundant in near-surface soils (Koltz et al. in review). These predators should be the focus of future efforts to resolve feeding relationships between wolf spiders and their prey. Studies that measure the cross-habitat movement of tundra soil arthropods and aerial arthropods like flies may help resolve whether belowground or aerial prey are sufficiently abundant to comprise a substantial part of wolf spider diet.

Conclusion

Our characterization of the arctic tundra arthropod community and wolf spider assemblage suggests that in addition to providing opportunities for cannibalism by way of an abundance of conspecifics, tundra arthropod assemblages may create a need for cannibalism given the lack of alternative prey. Our arena trials confirmed that, like other wolf spider species, *P. lapponica* cannibalize given opportunity (size disparity) and when provoked by necessity (starvation). On the other hand, results from our feeding experiments suggest that conspecifics are a poor diet, and that actual cannibalism rates among wolf spiders are probably low. Our data suggest that spiders likely derive a significant amount of energy from intermediate predators in the detrital food chain. The arctic is a notoriously unpredictable environment characterized by severe resource limitation; as a result, diet generalism is a common strategy among arctic consumers (Wirta et al. 2015). Like diet generalism, cannibalism may be an important strategy that enables wolf spiders’ survival when alternative prey are scarce.

Table 4-1. Cannibalism Trial Results

Mixed-effects model results for probability of cannibalism within 6 hours and for the time to cannibalism for those trials that resulted in predation.

<table>
<thead>
<tr>
<th>Pr(Cannibalism)</th>
<th>Time to cannibalism (min)</th>
</tr>
</thead>
</table>

79
|                          | est +/- SE | z    | Pr(>|z|) | est +/- SE | df  | t    | Pr(>|t|) |
|--------------------------|------------|------|---------|------------|------|------|---------|
| Intercept                | -4.11 ± 0.98 | -4.2 | <0.001  | 1.74 ± 0.47 | 19.9 | 3.7  | <0.001  |
| Size Ratio               | **1.27 ± 0.30** | **4.3** | **<0.001** | 0.12 ± 0.13 | 45.6 | 0.9  | 0.384   |
| Starvation (hours)       | 0.01 ± 0.01  | 1.1  | 0.252   | **-0.02 ± 0.00** | **37.9** | **-4.3** | **<0.001** |
| Sex (M)                  | 0.61 ± 0.57  | 1.1  | 0.282   | -0.19 ± 0.26 | 22.7 | -0.7 | 0.473   |
Table 4-2. Stable Isotope Results

MANCOVA and ANCOVA results for the effect of diet type, body size, and sex on the stable isotope composition ($\delta^{13}$C, $\delta^{15}$N) of spiders that were field-caught, starved for up to 15 days, or fed a controlled diet of either collembola, midges, or other spiders for up to 42 days.

<table>
<thead>
<tr>
<th></th>
<th>$\delta^{13}$C and $\delta^{15}$N</th>
<th>$\delta^{15}$N</th>
<th>$\delta^{13}$C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1 0.983 1512.4 2 52 &lt; 0.001 30.9 1 42.2 &lt; 0.001 901.0 1 2605.0 &lt; 0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diet Type</td>
<td>3 0.960 12.2 8 106 &lt; 0.001 25.7 4 8.8 &lt; 0.001 26.4 4 19.1 &lt; 0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body Size</td>
<td>1 0.062 1.7 2 52 0.191 1.3 1 1.8 0.183 0.9 1 2.6 0.111</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residuals</td>
<td>38.8 53</td>
<td>18.3 53</td>
<td></td>
</tr>
</tbody>
</table>
Figure 4-1. Arthropod Biomass and Abundance by Trophic Group

Distribution of biomass among trophic groups at the study site in 2013. Values represent average total biomass captured by a pitfall trap across the nine sampling dates. Error bars are ± SE for 20 traps.
Figure 4-2. Wolf Spider Community Composition

Total abundance of wolf spiders by species at the study site. Spiders were surveyed with 20 pitfall traps active for 9, two-day trapping intervals (a total of 200 trap-days) during the 2013 growing season.
Body size (carapace length) of *Pardosa* sp. wolf spiders at the Toolik Lake Field Station study site throughout the 2013 growing season. Points and boxplots represent individual observations and distributions (quantiles) of spider carapace lengths, respectively. Italicized text displays the average large:small carapace length ratio for 1000 random pairs of spiders from each date (e.g., on June 12, the average size ratio between two spiders was 1:3 to 1).
Figure 4-4. Cannibalism Arena Trial Results

Results from a cannibalism arena experiment with wolf spiders. In (A), Mixed-model predicted probability of a wolf spider consuming another wolf spider within 6 hours of introduction in an arena experiment; dots indicate actual experimental outcomes (0 = not consumed, 1 = consumed). In (B), boxplots and observed times (points) to consumption by length of time starved prior to experiment (for the trials where cannibalism occurred).
Proportion of wolf spiders (*Pardosa* sp.) surviving a feeding experiment where prey consisted of either collembola, midges or other spiders.

Figure 4-5. Wolf Spider Survival in Feeding Experiment
Figure 4-6. Change in Spider Body Size in Feeding Experiment

Change in body size (product of carapace length and width) per day of wolf spiders

(*Pardosa* sp.) fed collembola, midges, or other spiders. Letters denote significant least-squares means contrasts (adj. *p*<.05).
Figure 4-7. Spider Tissue Chemistry

C:N (A) and stable isotope ratios (B) of spiders and prey in a long-term feeding experiment. Error bars are ±SE. Letters in (A) denote significant differences among spiders (Tukey HSD p < 0.05); symbols denote significant differences among prey items.
Supplemental Table 4-1. Published Cannibalism Rates

Cannibalism rates from published arena trial studies of temperate-latitude *Pardosa* species and predicted rates for *P. lapponica* under the same conditions.

<table>
<thead>
<tr>
<th>Source</th>
<th>Pardosa species</th>
<th>Trial duration (hours)</th>
<th>Arena size (cm²)</th>
<th>Days predator starved</th>
<th>Predator: Victim Size</th>
<th>Observed Cannibalism Rate</th>
<th>Predicted Cannibalism Rate (1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buddle et al. 2003</td>
<td><em>P. milvinia</em></td>
<td>24</td>
<td>594 (2)</td>
<td>1</td>
<td>~ 2:1</td>
<td>11%</td>
<td>21%</td>
</tr>
<tr>
<td>Samu et al. 1999</td>
<td><em>P. agrestis</em></td>
<td>24</td>
<td>154</td>
<td>0</td>
<td>2.8:1 (3)</td>
<td>15% (4)</td>
<td>37%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>14</td>
<td>2.8:1 (3)</td>
<td>70% (4)</td>
<td></td>
</tr>
<tr>
<td>Mayantz &amp; Toft 2006</td>
<td><em>P. prativaga</em></td>
<td>3</td>
<td>9.6</td>
<td>3</td>
<td>2:1</td>
<td>10%</td>
<td>30%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10</td>
<td>2:1</td>
<td>45%</td>
<td>70%</td>
</tr>
<tr>
<td>Rypstra &amp; Samu 1999</td>
<td><em>P. milvinia</em></td>
<td>24</td>
<td>1.4</td>
<td>7</td>
<td>N/A (5)</td>
<td>40%</td>
<td>52% (6)</td>
</tr>
<tr>
<td>Rickers &amp; Scheu 2004</td>
<td><em>P. palustris</em></td>
<td>72</td>
<td>57 (7)</td>
<td>30</td>
<td>56:1 (8)</td>
<td>90%</td>
<td>100%</td>
</tr>
<tr>
<td>Petersen et al. 2010</td>
<td><em>P. prativaga</em></td>
<td>120</td>
<td>64</td>
<td>12 (9)</td>
<td>1.4 :1</td>
<td>5% (4)</td>
<td>63%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12</td>
<td>1.25 :1</td>
<td>0% (4)</td>
<td>58%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12</td>
<td>1.11 :1</td>
<td>15% (4)</td>
<td>55%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12</td>
<td>1:1</td>
<td>20% (4)</td>
<td>50%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5 (9)</td>
<td>1.4 :1</td>
<td>30% (4)</td>
<td>24%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>1.25 :1</td>
<td>10% (4)</td>
<td>21%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>1.11 :1</td>
<td>5% (4)</td>
<td>18%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>1:1</td>
<td>5% (4)</td>
<td>16%</td>
</tr>
<tr>
<td>Borre et al. 2006</td>
<td><em>P. monticola</em></td>
<td>11-17</td>
<td>60</td>
<td>N/A (10)</td>
<td>1:1</td>
<td>0% (4)</td>
<td>5% (11)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>N/A (10)</td>
<td>1.25:1</td>
<td>15% (4)</td>
<td>7% (11)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>N/A (10)</td>
<td>1.5:1</td>
<td>32% (4)</td>
<td>10% (11)</td>
</tr>
</tbody>
</table>
(1) Based on a six-hour trial in a 64 cm$^2$ arena with a simple substrate; see model parameters and estimates in Tab.1
(2) arenas filled with 2 cm pine bark mulch
(3) Average across trials
(4) approximated value from figure digitized at http://arohatgi.info/WebPlotDigitizer/
(5) Not reported in study
(6) assumes a 2:1 size ratio
(7) arenas included a moss substrate
(8) adult females (mean 18.17 mg) fed 2nd instar juveniles (mean 0.333 mg)
(9) Spiders were starved for 7 days prior to a 5-day trial where no food but conspecifics was provided.
(10) predators and victims were field-fresh
(11) assumes predator spider is satiated

Supplemental Table 4-1—Continued
Chapter 5

Shrub cover alters arthropod responses to weather in arctic tundra

Ashley L. Asmus, Helen E. Chmura, Toke T. Høye, Jesse Krause, Shannan Sweet,

Natalie T. Boelman, John C. Wingfield and Laura Gough
Abstract

Rapid warming has facilitated an increase in deciduous shrub cover in arctic tundra. Because shrubs create a cooler microclimate during the growing season, shrub cover could modulate the effects of global warming on the phenology and activity of arthropods, which, as small-bodied ectotherms, are acutely sensitive to their thermal microclimate. We explored this possibility using a correlative approach for the dominant arthropod groups in Alaskan tundra (flies, ground beetles and wolf spiders). We monitored arthropods with pitfall traps over five summers at four sites that varied in shrub abundance, and used generalized additive models (GAMs) to separate the two underlying relationships of pitfall trap abundance: the effects of seasonality (i.e. phenology) on arthropod density, and of short-term weather variation (air temperature, wind speed, rain fall, solar radiation) on arthropod activity. We found that shrub cover significantly altered the seasonal trend in the density of flies and beetles, in both cases reducing early-season abundance. This observation was in line with observed later snowmelt in shrub-dominated plots at these sites. Additionally, shrub cover modulated the effects of many weather variables on arthropod activity: shrub cover shifted the air temperature-activity response curves for wolf spiders and flies, and dampened the positive effect of solar radiation on the activity of arthropods in total. Additionally, shrub cover reversed the negative effects of windspeed, and positive effects of rainfall, on the abundance of flies. Thus, our results indicate that shrub encroachment will likely be accompanied by altered arthropod responses to warming and other key weather variables, because shrubs buffer the stressful effects of high temperatures and negate the dampening effects of wind speed on arthropod activity. Because the rate of ecological processes—herbivory, decomposition, predation – are controlled by arthropod activity at the organismal level, these effects will have long-term ecosystem-level consequences.
Introduction

Arctic surface temperatures have increased by 2°C in the last 50 years, more than double the global average rate of warming (IPCC 2014). In tundra plant communities, one consequence of rapid warming has been an increase in deciduous shrub cover (Myers-Smith et al. 2011). Relative to tundra—which typically supports a mix of low-stature plants including mosses, graminoids and dwarf shrubs—shrub tundra experiences less solar radiation, cooler temperatures, and reduced air circulation near the soil surface during the growing season (Myers-Smith et al. 2011). By modifying their microenvironment, shrubs could moderate the effects of global warming on temperature-dependent ecological processes like decomposition, a possible negative feedback effect that has generated significant interest in recent years (Sturm et al. 2001, Sturm et al. 2005, Myers-Smith et al. 2011).

By the same reasoning, it seems likely that shrub encroachment could modulate the effects of warming on arctic animals, especially arthropods (insects, spiders and relatives) (Kearney et al. 2009). As ectotherms, arthropods regulate their body temperature by choosing suitable thermal environments; and, as small-bodied animals, they interact with their thermal environment at the level of microhabitats, where the abiotic consequences of shrub cover are most acute (Kearney et al. 2009). Arthropods represent a significant component of tundra biodiversity and play important ecological functions as pollinators, herbivores, and decomposers (CAFF 2013). They also serve as food for migratory birds that breed in the tundra (Tulp and Schekkerman 2008). Surprisingly, arthropods – and animals in general – have rarely been considered in the context of arctic shrub encroachment, but an understanding of how they will respond to a
changing climate and plant community would help quantify the ecosystem level effects of changing vegetation.

Unlike ectotherms at lower latitudes, arctic arthropods are generally expected to respond positively to global warming, not with symptoms of physiological stress, but rather with enhanced fitness (Deutsch et al. 2008). This prediction derives from the skewed shape of ectotherm thermal performance curves, wherein ectotherm performance gradually increases from a critical minimum, peaks at a thermal optimum and declines sharply at a critical maximum temperature (Huey and Kingsolver 1989). For most ectotherms regardless of latitude or species, the thermal optimum hovers around 30-35°C, and the critical maximum internal temperature is even more constrained around 40°C (Kearney et al. 2009). In contrast, critical minimum temperatures vary widely across latitude and species owing to an arsenal of cold-tolerance strategies employed by temperate and arctic species (Danks 2004, Deutsch et al. 2008). As a result, arctic arthropods generally tolerate a wider range of temperatures than their lower-latitude counterparts; and, because arctic summers are relatively mild, they probably experience air temperatures that are lower than their thermal optimum and well below their critical maximum temperatures (Deutsch et al. 2008).

A few pieces of empirical evidence support the general prediction that warming will significantly affect arctic arthropods. First, capture rates of arthropods in pitfall and window traps are positively correlated with temperature in the Arctic, indicating that arthropod activity budgets are more constrained by cold temperatures than they are hampered by heat (Høye and Forchhammer 2008a, Tulp and Scheekerman 2008, Bolduc et al. 2013). Second, experimental warming in tundra ecosystems on the order of 2-4°C increases per-capita insect herbivory rates (Barrio et al. 2016), accelerates mosquito development (Culler et al. 2015), and amplifies arthropod-mediated decomposition (Sistla
et al. 2013). Third, decades of global warming at one high arctic site has advanced arctic arthropod phenology (Høye et al. 2007), triggering phenological mismatches between insect pollinators and flowers (Høye et al. 2013). Meanwhile, probably because the structure of open tundra vegetation is so simple, little attention has been given to the effects of microclimate on modulating arctic arthropod responses to warming (but see Coulson et al. 1993 and Hodkinson et al. 1996 for discussion of these effects on soil invertebrates).

In this study, we explored how global warming will affect the activity and seasonal patterns in density of arctic arthropods, both via the direct effects of temperature and the indirect effects of habitat change caused by warming. We took a correlative strategy, evaluating arthropod responses to seasonal development (the progression of the growing season) and short-term variations in temperature across habitats that varied in shrub abundance. We applied this approach to several groups known to be both numerous and ecologically important to arctic Alaskan ecosystems (Huryn and Hobbie 2012, CAFF 2013): flies (Diptera), ground beetles (Coleoptera: Carabidae) and wolf spiders (Araneae: Lycosidae).

To measure arthropod activity and density, we monitored arthropods over five growing seasons with pitfall traps in shrub- and open-tundra habitats located at four sites in arctic Alaska. Pitfall traps rely on the movement of arthropods for capture, and thus the number of animals in a given trap (trap abundance) reflects not only the number of animals per unit area (density) and but also arthropod movement (activity), which determines the likelihood any given animal will fall in a trap (Southwood and Henderson 2009). Our analysis of pitfall trap abundance was based on two simplifying assumptions (Figure 1): first, that arthropod density should be determined mainly by seasonal development at landscape scales (i.e., phenology -- emergence, senescence); and
second, that *activity* should be mainly determined by short-term variation in weather conditions at microhabitat scales (Taylor 1963, Southwood and Henderson 2009). Following the general approach of Høye and Forchhammer (2008a), we applied a statistical technique, Generalized Additive Modeling (GAM), to disentangle and investigate these two relationships.

Our hypotheses were that shrub shading would modulate the effects of warmer temperatures on arthropod phenology (Hypothesis 1) and activity (Hypothesis 2), and that the nature of these effects would vary according to differences in the natural history of each group. To help guide our analyses, we also made some specific predictions (Figure 1) informed by similar efforts to model arthropod trapping rates in the Arctic (Høye and Forchhammer 2008a, Tulp and Schekkerman 2008, Bolduc et al. 2013). First, we explored the explanatory power of common indices of seasonal development, and predicted that thawing degree-days (TDD)—an integrated measure of temperature during the snow-free period—would be a superior seasonal predictor of arthropod density relative to day of the year (DOY) or snow-free days. Second, we predicted that—after accounting for seasonal trends in density—temperature would have an approximately unimodal positive relationship with arthropod activity, solar radiation would positively affect arthropod activity, and wind speed and rain fall would negatively affect arthropod activity. From our hypotheses, we predicted that shrub shading would delay the seasonal peak in arthropod density, change the shape of arthropods’ temperature-activity response curves and dampen the strength of the other weather effects on arthropod activity.
Methods

Sampling design

Our study region encompassed an area near Toolik Lake Field Station (68 38’ N, 148 34’ W), the site of the Arctic Long-term Ecological Research project (ARC LTER) in the North Slope region of arctic Alaska (Figure 2). Within this study region, four sites were chosen based on the presence of neighboring shrub-tundra and tussock-tundra habitats; access to the Dalton Highway and Toolik Lake Field Station; and the presence of passerine nesting habitat, a focus of related studies, e.g. Boelman et al. (2015). Our sites were named for nearby landmarks: Roche Mountonee, Toolik Lake Field Station, Imnavait Creek and the Sagavanirktok River Department of Transportation (DOT) camp. Our four sites each contained two 10,000 m² plots: one in open tussock tundra and the other in shrub tundra. The plant community in these sites is described in detail in related studies (Rich et al. 2013, Sweet et al. 2015).

In each plot, two 100 m transects were established for arthropod sampling. We sampled arthropods with 10 pitfall traps spaced 10 m apart along each designated transect (N = 10 traps per transect, 20 traps per plot, 40 traps per site, 160 traps in total). Traps were clear plastic cups (~7.5 cm in diameter and 10 cm deep) filled 2 cm deep with a clear, 1:1 water:ethanol mixture. Traps were left in the field for 48 hours, at which point the contents were transferred to the laboratory, sieved of any excess plant material, and placed in vials of 70% ethanol for storage. Arthropods were counted and identified to coarse taxonomic groups (usually family, see Rich et al. 2013) using published keys (Triplehorn and Johnson 2005). The soil microarthropods Collembola and Acari were not counted. We sampled at approximate weekly intervals during the 2010-2014 growing seasons for a total of 181 sampling events spread across the four sites (see Figure 3 for
start and end dates in each year). Snow cover, ice, small mammal disturbance and human error reduced the number of pitfall samples to 7072 out of a possible 7240.

**Measures of plant canopy shading**

We assessed canopy shading on a clear, sunny day near noon (between 11 AM and 3PM) with a SunScan SS1 (Delta-T Devices Ltd, U.K). This instrument detects incoming photosynthetically active radiation (PAR) at 64 diodes equally spaced along a narrow 1-meter long surface. Centering the wand over each pitfall trap, we measured incoming PAR twice at the ground surface in a perpendicular fashion to capture a cross-section of the habitat surrounding the trap. We then immediately measured incoming PAR once above the plant canopy. For each measure, we averaged the PAR detected by the 64 diodes, then calculated the amount of shading at each trap as:

\[
\frac{\text{PAR}_{\text{above}} - \text{mean}(\text{PAR}_{\text{below}})}{\text{PAR}_{\text{above}}}
\]

**Meteorological data collection and processing**

We monitored meteorological conditions at each of the four sites with sensors placed 3 m above ground level except at the Toolik Field Station site, where sensors were placed 5 m above ground level. Environmental data for Toolik were downloaded from the Toolik Field Station Environmental Data Center (Environmental Data Center Team 2016). Data for Imnavait were downloaded from the Imnavait Arctic Observatory Network (AON) Tussock Site (Euskirchen et al. 2012). Air temperature was monitored with a capacitive ceramic THERMOCAP® sensor (Campbell Scientific, UT, USA) at Roche Mountonee and the Sagavanirktok River DOT, a HP45C-L temperature probe (Cambell Scientific, UT, USA) at Imnavaiat, and a HUMICAP® relative humidity and temperature probe (Vaisala, Helsinki, Finland) at Toolik. Wind speed was monitored with
an RM Young potentiometer at Toolik, a 3-cup anemometer at Imnavait (Campbell Scientific, UT, USA), and a WINDCAP® sensor (Vaisala, Helsinki, Finland) at Roche Mountonee and the Sagavanirktok River DOT. Precipitation was monitored with a Pluvio N Rain Gauge (OTT) at Toolik, a TE525 rain gauge (Campbell Scientific, UT, USA) at Imnavait, and a RAINCAP® sensor (Vaisala, Helsinki, Finland) at Roche Mountonee and the Sagavanirktok River DOT.

Incoming short-wave (solar) radiation was monitored at Toolik using a CNR-4 pyranometer (Kipp & Zonen, Delft, The Netherlands. Solar radiation at the other three sites was monitored less consistently than at Toolik (Supplementary Figure 2). Using available data, we checked that solar radiation at the temporal scale used in this study (48-hour averages) was similar across sites, and found strong correlation among sites’ measures ($R^2 > 0.95$, Supplementary Figure 2). Thus, for simplicity and best coverage, we used the Toolik solar radiation values for all sites in this study.

We trimmed the meteorological dataset to span the earliest and latest pitfall trap collection dates: Julian day 135 (14-15 May) to Julian day 225 (12-13 August). Due to occasional sensor malfunction, 16% (6913 observations) of all hourly observations in the meteorological dataset were missing one or more measures. Within pitfall sampling windows, 2% (833) of hourly observations were missing. To maximize our dataset for modeling data and generating predictions, we filled these gaps with a two-step process. First, for gaps of 12 hours or less (200 missing observations), we interpolated values in a linear fashion with function `na.approx` in R package `zoo` (Zeileis et al. 2017). For the remaining gaps of more than 12 hours, we filled in each site’s missing values with those of other sites in order of their geographic proximity.

To match our meteorological variables to arthropod data, we calculated total rainfall, average temperature and average wind speed for the 48-hour window during
which the traps were active. We also calculated cumulative thawing degree days (TDD): the cumulative sum of the daily mean temperatures above zero for all dates after snow melt up to the collection date. Snow melt was defined as the first day of the year when the landscape was 50% snow free as assessed by image analysis of landscape photographs (Krause et al. 2016a). In 2010, our cameras were not installed at Roche Mountonee or the Sagavanirktok River DOT; in these cases, we set the 50% snow free date to the mean value of the other years for that site (2011-2014). In another special case, cameras were installed at the Sagavanirktok River DOT too late to detect snowmelt in 2014. In this case, we set the snow free date to May 5, 7 days prior to camera installment date (the average number of days between 50% and 100% snow free at the Sagavanirktok River DOT in 2011-2013).

Statistical analysis

To evaluate the respective effects of weather on arthropod activity and seasonality on arthropod density, we used generalized additive models (GAMs) (Wood 2006). GAMs are extensions of generalized linear models that allow for one or more nonlinear “smooth” parameters (penalized regression splines) for which the shape of the response is unknown. In this way, a GAM smooth term is ideal for modeling the seasonal (density, phenology) component of arthropod abundance when that seasonal trend must be estimated from the data (Høye and Forchhammer 2008a).

We relied on the gamm function in R package mgcv (Wood 2016) to build our models. Our dependent variable was the raw abundance in each pitfall trap; these models assumed a negative binomial distribution with a log-link function, which is appropriate for low-mean count data (O’Hara and Kotze 2010). To account for the hierarchical structure of the data, models included a nested random effect term (traps
nested within transects, plots, sites, and years). We estimated \( \theta \), the dispersion parameter for the negative binomial distribution, from identical GAMs fit without random effects.

First, we evaluated the relative explanatory power of different indices of seasonal development with a set of six candidate GAMs for each arthropod group (flies, ground beetles and wolf spiders) and for arthropod abundance in total. The first three GAMs for each group modeled the density component of pitfall trap abundance as a smooth function of one of three candidate indices of seasonality: cumulative TDD (TDD), days since 50% snow-free (SNO), and day of the year (DOY). All three indices were measured at the site-level, where we expected phenological processes (arthropod emergence, senescence) that determine density would occur. To facilitate comparison across models, we ensured that each model was allowed the same amount of “wiggliness” \(^{sensu} \text{Wood 2006}\) by setting the smoothing parameter for TDD and SNO models to that of the DOY model, and setting the basis dimension \((k)\) to 10 (the maximum number of weeks for arthropod sampling).

For the next three GAMs, we evaluated the effects of shrub cover on arthropod phenology (seasonal trends in density). We re-fit the same three candidate models as described above, this time allowing the smooth term to vary according to plot type (shrub or open). To determine which seasonal index provided the best fit, and whether the addition of plot type significantly improved model fit, we compared the AIC values for each of the six candidate GAMs (TDD, SNO, DOY, TDD x Plot, SNO x Plot, and DOY x Plot).

Finally, using the best (lowest AIC) smooth term from the six candidate models described above, we evaluated the combined effects of weather and seasonality on arthropod abundance. The weather variables we included were air temperature, solar
radiation, rainfall and wind speed. We fit models with a seasonal smooth term, parametric effects of weather, and the interaction between weather and canopy shading at each trap. All four weather variables as well as canopy shading were zero-mean centered and scaled prior to analysis. To approximate the expected nonlinear relationship between temperature and arthropod activity (Huey and Kingsolver 1989), we modeled temperature as a second-order polynomial.

Results

Descriptive results

We captured a grand total of 53,025 arthropods from the four sites over the five years of pitfall trap sampling. An average of 7 individuals were in each sample. One-third (33%, 17,415 individuals) of the individuals caught were flies, while 29% (15,131 individuals) were wolf spiders. Ground beetles comprised 7% of total abundance (3,652 individuals).

Weather conditions and pitfall trap abundances varied across sites and years (Figure 3). Peak temperature occurred between 11 June and 10 July, depending on the site and year (DOY 162-191; mean DOY 178±2 days). Peak solar radiation occurred earlier than that of temperature, between 20 May and 14 June, depending on the year (DOY 140-165; mean DOY 159±6 days). Within 48-hour sampling events, mean temperatures were between -1 and 22°C (mean: 10±0.3°C), and 48-hour solar radiation means were between 106 – 361 W·m⁻² (mean: 222±11 W·m⁻²), indicating that we sampled during a wide range of weather conditions.

In addition, we sampled across a wide range of canopy shading values (Figure 4). Canopy shading in shrub plots fell between a minimum of 3% and a maximum of 98%,
with a mean of 48%. Open plots had a lower mean value of canopy shading (19%) and a narrower range of values (0 – 57%) compared to shrub plots.

**Seasonal arthropod density trends in shrub and open habitats**

The best seasonal predictor of arthropod abundance varied across taxa. For arthropods in total, snow-free days (SNO) was the best predictor, with the lowest AIC. This model predicted two peaks in abundance, the first at 30 days after snowmelt, and the second 69 days after snowmelt (Figure 5). For wolf spiders, day of the year (DOY) was the best predictor; this model predicted a single peak in abundance at day 163, or June 11-12. Modeling the seasonal trend in total arthropod abundance and wolf spider abundance separately for each plot type did not improve model fit (lower the AIC) in either case.

Meanwhile, the best models for ground beetle and fly abundance incorporated separate smooth terms for each plot type, suggesting that habitat type (shrub or open) affected the seasonal trends in density for these two groups. For ground beetles, the best model incorporated separate smooth terms for SNO in shrub and open habitats, while for flies, separate smooths for DOY provided the best fit. For both taxa, the models predicted that abundance would be greater in open plots compared to shrub plots early in the season (Figure 5). In addition, the model predicted that the single, early-season peak in ground beetle abundance would occur 5 days later in shrub plots (17 days after snowmelt) than in open plots (12 days after snowmelt; Figure 5).

**Weather effects on arthropod activity across levels of shrub shading**

The addition of weather variables improved the ability of the model to capture the substantial within-season variability in arthropod catches (Figure 6).
Temperature\(^2\) was always a significant predictor of arthropod abundance, either alone or via an interaction with canopy shading (Table 2, Figure 5). Across all taxa and for arthropods in total, model estimates for temperature\(^2\) were negative and estimates for temperature\(^1\) were positive (Table 2), indicating concave-downward responses (Figure 5). For example, in the case of total arthropod abundance, the model estimated positive effects of temperature on abundance along the range of temperatures we observed (-1.4°C to 20.9°C, Figure 5), and predicted negative effects of temperature on abundance only past 28°C, beyond the temperatures measured here (Table 2, Figure 5).

Models of fly abundance had a significant, positive interaction between canopy shading and temperature\(^1\) (Table 2), indicating that the effects of temperature on arthropod abundance were stronger in shaded canopies than open canopies (Figure 5). Because temperature\(^2\) was also significant in this model, the interaction shifted the “optima” of the temperature-abundance relationship – i.e., the temperature at which peak fly abundance was predicted to occur was warmer in shaded canopies than it was in open canopies (Figure 5). The predicted optimum temperature in completely shaded canopies (12°C) was 3.5°C greater than the optimum temperature in completely open canopies (15.5°C) (Figure 5).

For models of wolf spiders, the interaction between canopy shading and temperature\(^2\) was significant (Table 2). This interaction caused the shape of the temperature-abundance relationship to differ according to the level of canopy shading (Figure 5). In open canopies (52% shaded or less), the temperature-wolf spider abundance response was concave-down, with predicted optima between 19°C in completely unshaded canopies, and 23°C in partially shaded (25% shaded) canopies. In shaded canopies, the temperature-abundance response was concave-up (Figure 5).
Solar radiation had a positive effect on the abundance of wolf spiders, ground beetles, and flies, and interacted with canopy shading to affect total arthropod abundance. Solar radiation had a positive effect on total arthropod abundance in open canopies, but a slight negative effect on total abundance in shaded canopies (Table 2, Figure 5).

Wind speed had a positive effect on wolf spider abundance, and interacted with canopy shading to affect total arthropod abundance, ground beetles and flies (Table 2, Figure 5). For flies and for arthropods in total, wind speed had a negative effect on abundance in open canopies, but a positive effect on abundance in shaded canopies (Figure 5). The interaction was opposite for ground beetles, which responded more negatively to wind in shrub habitats than in open habitats.

Rainfall had a negative effect on total arthropod abundance, and interacted with canopy shading to affect abundance of flies and ground beetles, but had no effect on the abundance of wolf spiders (Table 2). For flies, the negative effect of rainfall on arthropod abundance diminished with increasing canopy openness; for ground beetles, the opposite was true, and a positive effect of rain on arthropod abundance diminished with increasing canopy openness (Figure 5).

Discussion

Shrub cover reduces early-season abundance of flies and beetles

We found partial support for our hypothesis that shrub cover would delay seasonal trends in arthropod abundance relative to open tundra: our models predicted that fly and beetle densities were lower in shrub habitats compared to open habitats early in the season, and that the peak in beetle density would occur 5 days later in shrub habitats compared to open habitats. These results are consistent with observed later
snowmelt, delayed plant green-up and slower soil thaw in the shrub plots at these study sites (Sweet et al. 2014). However, we found no such effects on wolf spiders or on arthropods in total, suggesting that the effects of shrub cover on arthropod seasonality vary significantly among arthropod taxa.

As part of our exploration of arthropod seasonality, we predicted that cumulative TDD would be a superior predictor of arthropod abundance relative to the number of snow-free days or the day of the year. We found instead that snow-free days (for total abundance and ground beetles) and day of the year (for wolf spiders and flies) were the most parsimonious explanatory variables. This was somewhat surprising, given that it is generally expected that in warmer conditions, arthropods develop faster, emerge earlier and complete their life cycle sooner. These results suggest that the life history of these groups may be somewhat constrained by the short duration of the Arctic growing season, and may use strategies like behavioral thermoregulation to compensate for colder growing season temperatures in order to complete their development on time.

These results echo previous studies showing that number of snow-free days is a significant predictor of arthropod seasonality in the Arctic (Høye and Forchhammer 2008b), but contrast with those of a similar study that found significant relationships between TDD and arthropod trapping rates (Bolduc et al. 2013). Unlike previous studies, which modeled the effect of temperature on phenology and abundance in a linear fashion, our GAM smooth term is equipped to model arthropod phenology at coarse taxonomic levels like the ones used here, where synchronous emergence is unlikely and multiple “peaks” in abundance are expected. Our selection of smooth terms by parsimony (AIC) rather than strict significance could also be a factor that resulted in different outcomes in our study compared to others.
One implication of the relationship between arthropod abundance and snowmelt is that arthropod phenology should advance lock-step with earlier snowmelt in the Arctic. The inter-annual variability in snowmelt timing we observed provides a starting point for understanding such effects (Krause et al. 2016b). For example, 50% snowmelt was reached 16 days earlier in 2012 compared to 2014 (Figure 2). Correspondingly, the median date of emergence (Høye and Forchhammer 2008b) for total arthropods was 14 days later in 2013 compared to 2012 (data not shown). In tundra habitats, ground beetles comprise up to 50% of total surface-dwelling arthropod biomass (Asmus et al. in review) and comprise a significant share of passerine nestling diet ( Pérez et al. 2016). Thus, changes to arctic seasonality could drastically affect the provisioning of insect biomass for breeding birds.

Shrub shading and weather interact to affect arthropod activity

Our second hypothesis, that shrub shading would modulate the effects of warming on arthropod activity, was largely supported by our findings. Although there were exceptions, at unshaded traps and in open plots, temperature and solar radiation usually increased arthropod activity, while wind and rainfall often had a negative effect.

In some cases, shrub cover altered the shape and/or strength of weather effects. Our findings from the model were generally consistent with what we might expect. For example, our findings from models of fly and total arthropod abundance suggest that solar radiation increases arthropod activity more in open canopies than in shrub canopies. This is consistent with the fact that completely shaded canopies in our study intercepted up to 98% of incoming PAR. Also, presumably because shrub canopies act as a windbreak, flies and arthropods in total were more active in shaded canopies than in open canopies at high windspeeds.
The effects of shrub shading on temperature-activity relationships in the models were more complicated than those of windspeed or solar radiation owing to the quadratic form of temperature effects. For example, our model predicted greater wolf spider activity in open habitats relative to shaded habitats only at low to moderate air temperatures; at high temperatures, the opposite was true. This shading*temperature interaction likely results from the effects of shading and shrub structure on the microenvironment. In arctic tundra, shrubs lessen the compounding effects of solar radiation on near-surface temperatures. This cooling effect could restrict wolf spider activity at low temperatures, and release wolf spiders from the risks of desiccation and heat stress at high temperatures. A reduced risk of heat stress can also explain why the predicted thermal optima for the activity of flies and arthropods in total were warmer under shaded canopies than in open habitats.

*Thermal optima of arthropod activity exceed typical temperatures in arctic tundra*

Ectotherm performance (activity, efficiency, metabolism) has an approximately unimodal relationship with temperature (Huey and Kingsolver 1989). Our analysis found significant effects of the polynomial term temperature² on arthropod trapping rates, confirming that such temperature-activity relationships underlie arthropod movement in natural environments. Using our model, we estimated "optimal" temperatures at which arthropod trapping rates reached their predicted maxima. In the case of wolf spiders, ground beetles and arthropods in total, the thermal optima were near or greater than the maximum air temperature observed in this study, suggesting that these arthropods may be able to tolerate a substantial amount of warming. Flies, on the other hand, had a temperature optimum around 14°C, suggesting that the effects of warming are more likely to be negative for this group. Flies are the most important insect pollinators in the Arctic
(Høye et al. 2013, Tiusanen et al. 2016). Empirical evidence already points to the disruptive effects of warming for the phenological matches between pollinating flies and plants; our results suggest that these effects on seasonality will be compounded by short-term effects of heat stress on activity.

**Conclusion**

In sum, our findings show that shrub cover will affect both arthropod activity and seasonality, but that the exact nature of these effects will depend on the natural history of the various arthropod groups and species therein. Previous studies have documented differences in arctic arthropod community structure across gradients of shrub abundance, suggesting that climate change-induced shrub expansion will alter arthropod communities (Rich et al. 2013, Hansen et al. 2016). This study builds upon such findings by showing that changes to arthropod community structure will likely be accompanied by altered arthropod activity rates, because shrubs buffer the stressful effects of high temperatures and negate the dampening effects of wind speed on arthropod activity. Because the rate of ecological processes—herbivory, decomposition, predation— are controlled by arthropod activity at the organismal level, these effects will have long-term ecosystem-level consequences.

Table 5.1. Fit of Seasonal Models of Arthropod Abundance

AIC values from GAMMs of arthropod abundance fit with random effects and a smooth term (“s()”) for one of three indices of seasonal development: cumulative degree-days (TDD), number of snow-free days (SNO) or day of the year (DOY).

<table>
<thead>
<tr>
<th>DOY</th>
<th>Total</th>
<th>Wolf Spiders</th>
<th>Ground Beetles</th>
<th>Flies</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>17558</td>
<td><strong>22201</strong></td>
<td>27472</td>
<td>22748</td>
</tr>
<tr>
<td></td>
<td>17201</td>
<td>22472</td>
<td>27218</td>
<td>22822</td>
</tr>
<tr>
<td>----------</td>
<td>-------</td>
<td>-------</td>
<td>-------</td>
<td>-------</td>
</tr>
<tr>
<td>SNO</td>
<td>17424</td>
<td>22225</td>
<td>27372</td>
<td>22955</td>
</tr>
<tr>
<td>TDD</td>
<td>17689</td>
<td>22264</td>
<td>27491</td>
<td>22269</td>
</tr>
<tr>
<td>DOY x Plot</td>
<td>17270</td>
<td>22401</td>
<td>27204</td>
<td>22601</td>
</tr>
<tr>
<td>SNO x Plot</td>
<td>17522</td>
<td>22302</td>
<td>27396</td>
<td>22465</td>
</tr>
<tr>
<td>TDD x Plot</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5-2. Summaries of Models of Arthropod Abundance

Summaries of GAMMs of arthropod abundance fit with a smooth term for seasonality (SNO: days after snowmelt, DOY: day of the year) and all linear effects for weather.

<table>
<thead>
<tr>
<th>Linear Terms</th>
<th>Total</th>
<th>Wolf Spiders</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Est.</td>
<td>SE</td>
</tr>
<tr>
<td>(Intercept)</td>
<td>1.91</td>
<td>0.06</td>
</tr>
<tr>
<td>Temp</td>
<td>0.32</td>
<td>0.01</td>
</tr>
<tr>
<td>Temp(^2)</td>
<td>-0.05</td>
<td>0.01</td>
</tr>
<tr>
<td>Shade</td>
<td>0.04</td>
<td>0.02</td>
</tr>
<tr>
<td>Solar</td>
<td>0.15</td>
<td>0.01</td>
</tr>
<tr>
<td>Wind</td>
<td>-0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>Rain</td>
<td>-0.05</td>
<td>0.01</td>
</tr>
<tr>
<td>Temp*Shade</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>Temp(^2)*Shade</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Solar*Shade</td>
<td>-0.07</td>
<td>0.01</td>
</tr>
<tr>
<td>Wind*Shade</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td>Rain*Shade</td>
<td>-0.02</td>
<td>0.01</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Smooth Terms</th>
<th>EDF</th>
<th>RefDF</th>
<th>F</th>
<th>P</th>
<th>Smooth Terms</th>
<th>EDF</th>
<th>RefDF</th>
<th>F</th>
<th>P</th>
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<tbody>
<tr>
<td>s(SNO)</td>
<td>7.8</td>
<td>7.8</td>
<td>20.9</td>
<td>&lt;0.001</td>
<td>s(DOY)</td>
<td>7.326</td>
<td>7.326</td>
<td>141.7</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

| Ground Beetles | Linear Terms    | Est.  | SE  | z   | Pr(>|z|) | Linear Terms    | Est.  | SE  | z   | Pr(>|z|) |
|----------------|-----------------|-------|-----|-----|--------|-----------------|-------|-----|-----|--------|
| (Intercept)    | -0.82           | 0.16  | -5.18 | <0.001 | (Intercept) | 0.78  | 0.11 | 7.25 | <0.001 |
| Temp           | 0.58            | 0.03  | 22.42 | <0.001 | Temp       | 0.13  | 0.02 | 6.16 | <0.001 |
| Temp\(^2\)     | -0.05           | 0.02  | -3.48 | 0.001 | Temp\(^2\) | -0.10 | 0.01 | -8.10 | <0.001 |
| Shade          | -0.01           | 0.05  | -0.23 | 0.820 | Shade      | 0.14  | 0.03 | 5.26 | <0.001 |
| Solar          | 0.12            | 0.03  | 4.03  | <0.001 | Solar      | 0.05  | 0.02 | 2.17 | 0.030 |
| Wind           | -0.08           | 0.03  | -3.31 | 0.001 | Wind       | 0.01  | 0.02 | 0.32 | 0.747 |
| Rain           | 0.05            | 0.03  | 2.08  | 0.037 | Rain       | 0.00  | 0.02 | -0.08 | 0.935 |
| Temp*Shade     | -0.01           | 0.03  | -0.46 | 0.645 | Temp*Shade | 0.04  | 0.02 | 2.10 | 0.036 |

Table 5-2—Continued
<table>
<thead>
<tr>
<th>Term</th>
<th>EDF</th>
<th>RefDF</th>
<th>F</th>
<th>P</th>
<th>Term</th>
<th>EDF</th>
<th>RefDF</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp$^2$*Shade</td>
<td>0.03</td>
<td>0.02</td>
<td>1.79</td>
<td>0.074</td>
<td>Temp$^2$*Shade</td>
<td>0.00</td>
<td>0.01</td>
<td>-0.13</td>
<td>0.899</td>
</tr>
<tr>
<td>Solar*Shade</td>
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<td>0.03</td>
<td>1.03</td>
<td>0.304</td>
<td>Solar*Shade</td>
<td>-0.01</td>
<td>0.02</td>
<td>-0.39</td>
<td>0.699</td>
</tr>
<tr>
<td>Wind*Shade</td>
<td>-0.05</td>
<td>0.03</td>
<td>-2.04</td>
<td>0.041</td>
<td>Wind*Shade</td>
<td>0.07</td>
<td>0.02</td>
<td>4.46</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Rain*Shade</td>
<td>0.11</td>
<td>0.03</td>
<td>3.81</td>
<td>&lt;0.001</td>
<td>Rain*Shade</td>
<td>-0.04</td>
<td>0.02</td>
<td>-2.07</td>
<td>0.038</td>
</tr>
<tr>
<td>Smooth Terms</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Smooth Terms</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(SNO): open</td>
<td>6.2</td>
<td>6.2</td>
<td>51.7</td>
<td>&lt;0.001</td>
<td>s(DOY): open</td>
<td>7.5</td>
<td>7.5</td>
<td>31.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>s(SNO): shrub</td>
<td>7.0</td>
<td>7.0</td>
<td>31.6</td>
<td>&lt;0.001</td>
<td>s(DOY): shrub</td>
<td>7.0</td>
<td>7.0</td>
<td>96.4</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Figure 5-1. Hypotheses

Hypothesized relationships between weather and activity, and seasonality and density, that underlie a theoretical pattern in pitfall trap abundance (top panel). Dashed lines represent predictions for increased shrub cover.
Figure 5-2. Map of Study Sites

Locations of the four field sites used in this study: ROMO (Roche Mountonee), TLFS (Toolik Lake Field Station), IMVT (Imnavait Creek) and SDOT (Sagavanirktok River–Department of Transportation camp).
Figure 5-3. Weather and Arthropod Abundance

Average daily weather conditions and average total pitfall trap abundance in each site and year. Points represent observations. For temperature and wind speed, lines represent loess smoothers (span = 1).
Figure 5-4. Canopy Shading

Boxplot of canopy shading values by site and plot. Observed raw values are represented as points.
GAMM-predicted responses of arthropod trap abundance for each model term. Dashed lines (seasonality only) represent predictions for shrub habitats; dotted lines (temperature) represent predicted values beyond the range of temperatures observed in the study (max. 21°C). Where statistical interactions between canopy shading and weather were significant, predictions for temperature and wind speed were made over a range of values of canopy shading shown by different line colors; otherwise, predictions were made with covariates set at their means.
Example of model-predicted arthropod abundances by day of year (DOY) from SDOT in 2013. Observed average abundances for each site and plot (mean of 20 traps) are presented as points. GAM-predicted values of arthropod trap abundance for seasonality-only models are presented as dotted lines. GAM-predicted values from full models with all weather variables included are shown as solid lines.
Supplementary Figure 5-1. Solar Radiation

Correlation plots for sites' two-day average solar radiation values. These data were trimmed to dates encompassing the range of arthropod sampling (Julian dates 135 – 225). $R^2$ values are Pearson's correlation coefficients. Dotted lines represent 1:1 relationships. Solid lines represent the linear fits of the data, made with a 0-intercept.

Data for ROMO were made available by C. Williams (unpubl. data).
Chapter 6
Conclusions & Future Directions

In my dissertation, I explored the underpinnings of arthropod food web and community structure in moist acidic tundra near Toolik Lake, Alaska. I found that tundra plant community composition not only determines what kind of arthropods can be supported by a given ecosystem but also how arthropods interact with their abiotic environment. Changing tundra plant communities via experimental nutrient addition revealed that plant community composition, particularly the abundance of woody tissue, is an important control on insect herbivores. These findings suggest that the arthropod community response to tundra shrub encroachment may change over time. As warming triggers an increase in soil nutrient availability, plants may at first become more palatable to insect herbivores, and provoke responses at higher trophic levels within the arthropod food web. As the trend continues and woody tissues become prominent, insect herbivores could face declines.

For the most part, my research has used arthropod food webs and communities as a kind of multivariate barometer of ecosystem responses to global change in the Arctic. In pursuing this research, I have been keenly aware of what such an approach lacks: a more mechanistic framework for understanding why community- and food web-level effects arise. Future efforts to manipulate the structure of the arthropod food web directly, especially those that use a cross-site or distributed experiment approach, would be ideal. Given the current implementation of NEON and the success of recent distributed experiments (e.g., Roslin et al. 2017) and protocols (e.g., Barrio et al. 2017) in the Arctic, the infrastructure and interest exist for such studies to flourish.
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Biographical Information

Ashley Asmus is a community and food web ecologist interested in how global change processes will affect trophic interactions. She has an undying passion for herbivorous insects, a mild tolerance for birds and a strong preference for treeless ecosystems. Ashley briefly attended Middlebury College in Vermont, but was motivated to pursue national service in Americorps in the years after Hurricane Katrina. After two years of building houses in Louisiana and patrolling national parks in Texas, Ashley re-enrolled at the University of Texas at Austin, where she discovered her passion for field ecology. She completed her bachelor’s degree in 2011, then drove 200 miles north to earn her Ph.D. at the University of Texas at Arlington. During graduate school, Ashley became active in a wide variety of research networks, especially the Long-Term Ecological Research (LTER) network, which supported many of her endeavors. Ashley has accepted a Post-Doctoral position at the University of Minnesota, where she will coordinate the Nutrient Network, a global distributed experiment investigating the role of nutrient availability and diversity in grassland ecosystems.