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DIRECT EFFECTS OF WARMING INCREASE WOODY PLANT ABUNDANCE IN

A SUBARCTIC WETLAND

by

Lindsay G. Carlson

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

MASTER OF SCIENCE

in

ECOLOGY

Approved:

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Karen H. Beard, Ph.D.  
Major Professor

---

Peter Adler, Ph.D.  
Committee Member

---

Andrew Kulmatiski, Ph.D.  
Committee Member

---

Mark R. McLellan, Ph.D.  
Vice President for Research and  
Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY  
Logan, Utah

2017

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## ABSTRACT

Direct Effects of Warming Increase Woody Plant Abundance in a Subarctic Wetland

by

Lindsay G. Carlson, Master of Science

Utah State University, 2017

Major Professor: Dr. Karen H. Beard  
Department: Wildland Resources

Both the direct effects of warming on species' vital rates and indirect effects of warming caused by interactions with neighbouring species can influence plant populations. Furthermore, herbivory mediates the effects of warming on plant community composition in many systems. Thus, determining the importance of direct and indirect effects of warming, while considering the role of herbivory, can help predict long-term plant community dynamics. We conducted a field experiment in the coastal wetlands of western Alaska to investigate how warming and herbivory influence the interactions and abundances of two common plant species, a sedge, *Carex ramenskii*, and a dwarf shrub, *Salix ovalifolia*. We used results from the experiment to model the equilibrium abundances of the species under different warming and grazing scenarios and to determine the contribution of direct and indirect effects to predicted population changes. Consistent with the current composition on the landscape, model predictions suggest that *Carex* is more abundant than *Salix* under ambient temperatures with grazing (53% and

27% cover, respectively). However, with warming and grazing *Salix* becomes more abundant than *Carex* (57% and 41% cover, respectively), reflecting both a negative response of *Carex* and positive response of *Salix* to warming. While grazing reduced the cover of both species, herbivory did not prevent a shift in dominance from sedges to the dwarf shrub.

Direct effects of climate change explained about 97% of the total predicted change in species cover, whereas indirect effects explained only 3% of the predicted change. Thus, indirect effects, mediated by interactions between *Carex* and *Salix*, were negligible, likely due to use of different niches and weak interspecific interactions. Results suggest that a 2 °C increase could cause a shift in dominance from sedges to woody plants on the coast of western Alaska over decadal time scales, and this shift was largely a result of the direct effects of warming. Models predict this shift with or without goose herbivory. Our results are consistent with other studies showing an increase in woody plant abundance in the Arctic, and suggests that shifts in plant-plant interactions are not driving this change.

## PUBLIC ABSTRACT

## Direct Effects of Warming Increase Woody Plant Abundance in a Subarctic Wetland

Lindsay G. Carlson

Climate change is expected to continue to cause large increases in temperature in Arctic and sub-Arctic ecosystems which has already resulted in changes to plant communities; for example, increased shrub biomass and range. It is important to understand how warmer temperatures could affect the plant community in a wetland system because this region provides crucial high-quality forage for migratory herbivores during the breeding season. One mechanism by which warming could cause change is directly, where warming influences the vital rates of a species; these effects may be either positive or negative. Warmer temperatures may also affect a species indirectly, by impacting neighboring plants which compete with, or facilitate that species. Altering interspecific interactions may affect the abundances of the surrounding species. Recent research shows these ‘indirect’ effects which are mediated by biotic interactions may be important enough to reverse ‘direct’ effects of climate change in some plant communities. Furthermore, herbivores have been shown to mediate the effects of warming, in some systems, even preventing shrub expansion. However, the abundance of herbivores may change because of climate change so it is important to understand the role of herbivores in mitigating climate change effects to inform management strategy. Therefore, we aimed to determine the importance of direct and indirect effects of warming on this plant community while considering changing herbivore pressures.

We conducted a two-year field experiment in the coastal wetlands of western Alaska to investigate how warming and herbivory will impact the abundances of two common species, a sedge and a dwarf shrub. We used the results from the experiment to predict the equilibrium abundances of the two species under different climate and herbivory scenarios and determine the contribution of direct and indirect effects to predicted community change.

The sedge, *Carex ramenskii*, remained dominant in under ambient conditions, but the dwarf shrub, *Salix ovalifolia*, became dominant in warmed treatments. Herbivory mediated some of the effects of warming; where grazing was present community composition did not change as much as where it was not grazed. Results suggest that in the absence of goose herbivory, a 2°C increase could cause a shift from sedge to woody plant dominance on the coast of western Alaska. However, if grazing pressure by geese continues at the present rate, it may help retain the current community composition, though herbivory pressure was not sufficient to entirely reverse the effect of warming. Finally, we found that direct effects were more important than indirect effects in causing changes to this plant community.

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Lindsay G. Carlson



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## CHAPTER 1

### INTRODUCTION

#### LITERATURE REVIEW

##### *Effects of warming in the subarctic*

Mean global temperature is predicted to increase 1.8 - 4.0 °C by 2099, following an increase of 0.4 °C over the last century (1906-2005) (IPCC 2014). At the northern latitudes, the intensity and effects of a warming climate are amplified; warming in the Arctic has been as much as two to three times greater than the global mean (IPCC 2014). Warmer temperatures have been well documented to affect species distribution, as well as productivity and phenology (Walther *et al.* 2002; Parmesan & Yohe 2003; Hinzman *et al.* 2005; Doiron, Gauthier & Lévesque 2014). As a result, a warming climate may have long term and large scale implications for plant community dynamics (Chapin *et al.* 2000; Post *et al.* 2009).

One well documented effect of climate warming is the increase in woody plant biomass in areas such as the Arctic and alpine (Chapin *et al.* 1996; Tape, Sturm & Racine 2006; Myers-Smith *et al.* 2011, 2014; Elmendorf *et al.* 2012). An increase in shrub productivity as well as range advancement to a higher latitude and altitude has been consistently documented (Sturm *et al.* 2001; Hallinger, Manthey & Wilmking 2010). Additionally, wetter regions (such as our study site) are more inclined to experience an increase in shrub abundance than are dry sites (Myers-Smith *et al.* 2014). An alteration of vegetation communities due to warming may result in loss of native species, habitat shifts

for herbivores, modified hydrology, and a change in the local carbon cycle (Post *et al.* 2009; Leffler & Welker 2013; Doiron *et al.* 2014; Doiron, Gauthier & Levésque 2015). Therefore, it is important to understand how vegetation communities will change with warming. While there is a good deal of literature describing shrubification on tundra or alpine systems (Chapin & Shaver 1985; Rixen & Mulder 2009; Hallinger *et al.* 2010; Myers-Smith *et al.* 2011; 2014), fewer have examined shrub increase in coastal systems (Zinnert *et al.* 2011; Fraser *et al.* 2014).

#### *Importance of plant-plant interactions*

The distribution and abundance of plant species and their associated communities are influenced both by environmental conditions such as latitude, altitude, temperature, precipitation, and nutrient availability; as well as by interactions with neighboring species (Callaway *et al.* 2002). Plant-plant interactions may be intraspecific (affecting homospecific species) or interspecific (affecting heterospecific species). Interactions may be competitive, neutral, or facilitative. In general, plants compete with one another for light, water, and nutrient resources. These competitive effects limit the growth of: the individual itself, neighbors of its own species, as well as heterospecific neighbors (Chesson 2000). However, in some stressful environments, such as Arctic and alpine systems, positive or facilitative interactions have been well documented to be more important than competitive interactions (Callaway *et al.* 2002; Cavieres & Sierra-Almeida 2012; Cavieres *et al.* 2014; Schöb *et al.* 2014). Plants in such environments can be exposed to extreme weather events, such as cold and wind, short growing seasons, water limitation, high salinity concentrations, strong herbivory pressures, or nutrient

limitation (Bret-Harte *et al.* 2004). Plants may utilize individual niches in severe environments, allowing them to coexist despite limitations (McKane *et al.* 2002). In harsh environments, plants may also have positive effects on their neighbors by ameliorating disturbances, providing shade or shelter, and protecting from herbivory (Brooker & Callaghan 1998; Callaway *et al.* 2002).

The stress-gradient hypothesis suggests that interspecific interactions may shift steadily from negative to positive effects, correlated with increasing environmental severity (Bertness & Callaway 1994; Brooker & Callaghan 1998). Our study system may be considered severe due to high salinity, short growing seasons, and nutrient limitation (Jorgenson 2000). However, a warming climate may extend the growing season or increase the rate of decomposition to increase nutrient availability (Hobbie 1996; Tye *et al.* 2005; Post *et al.* 2009), making the system less severe and potentially shifting interspecific interactions toward a more competitive state. Because plant interactions exert strong influence on the distribution and abundance of vegetation communities, understanding climatic effects on them is crucial to predicting how a community may shift across latitudinal, elevational, and climatic conditions (Michalet *et al.* 2014).

#### *Direct and indirect effects of climate change*

Plant community responses to warming result from one of two mechanisms. Warmer conditions can alter the abundance of a species directly, through changes in the vital rates of that species (Adler, Dalgleish & Ellner 2012). Warmer temperatures may also affect a species indirectly by altering interspecific interactions with neighbors (Adler *et al.* 2012; Kleinhesselink & Adler 2015). Indirect effects occur when climate change

alters the abundance of neighboring species (by direct effects on the vital rates of neighbors) or the per capita strength of interactions between a plant and its neighbors (Adler, Leiker & Levine 2009; Adler *et al.* 2012). For example, one species may gain an advantage due to competitive release from its neighbor under warmer conditions.

Alternatively, one species may become a stronger competitor under the new conditions, so that the neighboring species is more limited by it. Adler, Leiker & Levine 2009 describes the pathways by which climate change may exert indirect effects through interspecific interactions using a simple equation:

$$r = r_0 - \alpha C$$

where  $r$  is the population growth rate of a species (e.g., species  $i$ ),  $r_0$  is the change in the growth rate under altered climatic conditions,  $\alpha$  is a competition coefficient describing the per capita effect of competitors on the focal species, and  $C$  is the abundances of heterospecific competitors. Climate change affects species  $i$  directly by altering the growth rate ( $r_0$ ). Climate change can also affect species  $i$  indirectly through changes to  $\alpha$ , which usually occur when climate change alters the resources both species use. Indirect effects may also occur via changes to  $C$ , which can be altered due to changes in the abundances of neighboring species, extinction of a neighbor, or immigration of a new species (Adler & Levine 2007; Adler *et al.* 2009).

Recent literature suggests that indirect effects may be more important than direct effects, in some cases even reversing direct effects (Brooker 2006; Suttle, Thomsen & Power 2007; Tylianakis *et al.* 2008; Gilman *et al.* 2010). It is important to understand how plant interactions will change and how those interactions might contribute to driving

community change or range shifts to better predict the effects of warming on ecosystems (Bret-Harte *et al.* 2004; Brooker 2006; Saccone *et al.* 2009; Adler *et al.* 2012; Michalet *et al.* 2014).

One experiment explored the effect of manipulated precipitation regime on indirect effects in a prairie grassland in Kansas (Adler *et al.* 2009). The study found that altered precipitation had both direct and indirect effects. Direct effects of decreased rainfall decreased the growth ( $r_0$ ). For indirect effects, decreased rainfall did not change interspecific interactions enough to affect per capita competitive effects, but did have a gradual effect on long-term persistence of some species and thereby, community composition (Adler *et al.* 2009).

Using a population dynamic modeling approach, one group analyzed experimental data from an alpine tundra meadow in Colorado where they manipulated winter precipitation, nitrogen deposition, and temperature for seven years (Farrer *et al.* 2014). Overall, climate change had negative effects on population growth, though the eight present alpine species responded differently to the environmental alterations; some increased while others declined. For three of the species, direct effects were most important, but for four of the species, indirect effects were more important than direct effects (Farrer *et al.* 2014).

A precipitation manipulation experiment in a grassland in California found that forbs experienced negative indirect effects of increased rainfall because neighboring grass species increased in abundance due to a favorable direct effects (Suttle *et al.* 2007). These negative indirect effects, which opposed the direct effects on forbs, had a more



important impact on the plant community (Suttle *et al.* 2007). One possible reason for the strength of indirect effects in this system is that these grass species utilize the same niche as the forbs and therefore have strong indirect effects due to strong interspecific interactions.

In a theoretical study, Kleinhesselink & Adler (2015) demonstrated that importance of indirect effects of environmental change increases as niche-overlap increases. They used a mechanistic resource competition model and showed how competitor response is linked to sensitivity of that species to change in resource supply. This study highlighted the possibility of using niche overlap as a predictor of the strength of indirect effects in various ecosystems (Kleinhesselink & Adler 2015).

A recent study by Chu *et al.* (2016) tested this theory. In this study, the authors evaluated data from five communities in the western United States, including Sonoran desert in Arizona, sagebrush steppe in Idaho, southern mixed prairie in Kansas, northern mixed prairie in Montana and Chihuahuan desert in New Mexico. They found that in four of five communities, species that utilized different niches (strong negative frequency dependence) were less affected by indirect effects of climate change (Chu *et al.* 2016). In these systems, the direct effects of climate perturbations were more important than indirect effects.

#### *Neighbor removal experiments and response surface experimental designs*

We addressed our study question using a response surface design, neighbor removal experiment. Neighbor removal experiments have commonly been utilized to study the effects of plant competition (Olofsson 2004; Veblen 2008; Rixen & Mulder

2009; Cavieres & Sierra-Almeida 2012; Compagnoni & Adler 2014). Greenhouse experiments allow perfectly manipulated density combinations, but cannot accurately reproduce environmental conditions or soil qualities that affect natural plant neighbor interactions (Bret-Harte *et al.* 2004). While field experiments introduce natural variation and error, the neighbor removal methodology is useful for studying plant interactions *in situ*. Neighbor removal experiments require the removal (or termination) of above and belowground biomass of specific species to create the desired experimental density.

The majority of neighbor removal experiments utilize additive designs or replacement series methods (substitutive) (Inouye 2001). Additive designs hold the density of one species constant while the density of the competitor is varied. An additive design falls short in that intra-specific effects may not be estimated and frequency dependent effects are confounded with inter-specific competition (Law & Watkinson 1987; Inouye 2001). Replacement series experiments hold the total density of individuals constant while varying the proportion of each. A replacement series design confounds the effects of variation in intra-/inter-specific density of each species and is limited in its inference by the arbitrary endpoints chosen (Inouye 2001). These approaches may qualitatively determine the presence or absence of competition, but not quantify the direction or intensity of plant-plant interactions (Inouye 2001).

Response surface designs vary the density of both species independently, using factorial (not necessarily fully factorial) combinations of the two species at two or more densities. A response surface design allows description of intra- and inter-specific effects without limiting inference to particular densities; a consideration that is necessary to

model population dynamics and coexistence properly (Inouye 2001; Hart & Marshall 2013).

Response surface experimental designs and analyses have been previously underutilized; however, these designs are useful because satisfactory parameter estimates and associated confidence intervals may be estimated using a relatively low number of replicates or with limited density combinations (Inouye 2001). In addition, response surface experiments may be used to link theoretical and empirical approaches to complex long term community dynamic or short term competition questions, and have been utilized appropriately for studies of both plants and animals (Law & Watkinson 1987; Inouye 2001; Hart & Marshall 2013).

### *Herbivore effects*

Herbivores rely on vegetation for a food source, simultaneously modifying their environment by grazing it (Cargill & Jefferies 1984; Person, Babcock & Ruess 1998). Because Arctic and subarctic herbivores consume a large proportion of high latitude vegetation, their impact on primary productivity and biogeochemical cycling is well documented (Olofsson 2004; Van Der Wal & Brooker 2004; Gornall *et al.* 2009; Post 2013). In our system, geese are thought to modify up to 90% of the terrestrial landscape <2 km from the coast (Sedinger, unpubl. data). Goose herbivores act on the community by removing biomass, adding nutrients to the system via fecal material, and trampling which increases litter decomposition rates (Ruess *et al.* 1997; Gillespie *et al.* 2013).

Herbivory may have interactive effects with warming in the north. Some studies have found that herbivory may counteract the increase in vegetation productivity and

biomass, resulting in no net change (Ripple & Beschta 2004; Post & Pedersen 2008). Other studies imply that warming and herbivory may result in a net increase in C sequestration (Olofsson 2004; Van Der Wal & Brooker 2004; Knapp *et al.* 2008; Kelsey *et al.* 2016; Peng *et al.* 2017). Some studies have found that communities respond differentially to warming when herbivores are present versus absent; when grazed, the current community persists while when ungrazed, shrubs increased substantially (Post & Pedersen 2008; Olofsson *et al.* 2009; Kaarlejärvi, Hoset & Olofsson 2015). Despite this important finding, few studies have examined whether herbivores can maintain present species composition or prevent range expansions in the rapidly warming Arctic and subarctic and none so far have investigated the transformative ability of avian herbivores in this context (Christie *et al.* 2015).

#### *Herbivore ecology in the Yukon Delta National Wildlife Refuge*

The coastal region of the Yukon Kuskokwim (Y-K) Delta, in subarctic western Alaska, is an important nesting and brood rearing area for waterfowl (Baldassarre 2014). During the breeding season, it supports ~70% of the world's Pacific black brant (*Branta bernicla nigricans*), the entire population of emperor geese (*Chen canagica*), all cackling geese (*B. canadensis minima*), and many greater white fronted geese (*Anser albifrons frontalis*), as well as an abundance of other waterfowl such as eiders, scaup, scoters, longtail and pintail ducks, shovelers, and loons (Ruess *et al.* 1997; Baldassarre 2014). Many seabirds and shorebirds also nest in the Y-K Delta, and even more utilize it as a staging area (Gill & Handel 1990).

Migratory herbivores, such as geese, rely on high nutrient vegetation for survival, but also as a part of successful reproduction (Sedinger & Raveling 1984; Mulder & Ruess 1998; Doiron *et al.* 2014). Adult geese must replace fat stores and complete molt; goslings require sufficient nutrition to grow large enough to migrate successfully in the fall (Sedinger & Raveling 1984). Gosling overwinter survival is related directly to mass at fledging, and availability of high quality forage is the best predictor of gosling mass (Sedinger & Chelgren 2007). Therefore, accessing high quality forage during the summer is crucial for goose herbivores (Sedinger *et al.* 2016).

Proteins are the most limiting nutrient for herbivores (Sedinger & Raveling 1984). Nitrogen concentrations, a proxy for protein content, are highest in new growth, but decline throughout the short growing season as more biomass is added and senescence begins (Lepage, Gauthier & Reed 1998; Person *et al.* 2003). The preferred forage of Pacific black brant (*Branta bernicla nigricans*) is the nitrogen-rich *Carex subspathacea* grazing lawn (Person *et al.* 1998). Monotypic grazing lawn habitat is often found on the coast (>15km) or in tidally influenced zones, not far from dense colonial nesting areas (Sedinger & Raveling 1984; Babcock & Ely 1994).

The *C. subspathacea* grazing lawns in the subarctic are largely maintained by goose herbivores; by applying heavy grazing pressure, geese maintain the low-lying, nitrogen-rich growth form (Sedinger, Flint & Lindberg 1995; Ruess *et al.* 1997; Person *et al.* 1998). With an extreme reduction, delay, or exclusion of goose herbivory, these *C. subspathacea* grazing lawns are eventually replaced by *Carex ramenskii* meadows (Person *et al.* 2003; Sedinger *et al.* 2016). Though classified as separate species (Hultén

1968), recent experiments suggests that these sedges are effectively the same species or some hybrid of the two, with the *C. subspathacea* morphology maintained by grazing (Person *et al.* 2003). Because *C. ramenskii* has a taller growth form and higher carbon to nitrogen ratio (C:N), (Person *et al.* 2003) it is a much less desirable grazing choice, particularly for goslings, which have inefficient gastrointestinal tracts and a high demand for energy to support growth (Sedinger & Raveling 1984; Sedinger *et al.* 1995). However, strong herbivory pressure can convert monotypic *C. ramenskii* meadows into valuable grazing lawn (Sedinger *et al.* 2016). While *C. ramenskii* is considered a low-quality forage for herbivores, it has the possibility of conversion into beneficial grazing habitat in the future and is therefore an important plant community for herbivores in this system. On the contrary, non-berry producing prostrate dwarf shrubs such as *Salix ovalifolia* are of little to no value to brood rearing geese as their woody biomass is difficult to digest, high in carbon, and low in nitrogen (Sedinger & Raveling 1984; Gillespie *et al.* 2013).

The nesting habitats, brood rearing areas, and preferred forage of Pacific black brant are specific and limited. A rapidly changing climate could further impact an already declining population of brant geese (Sedinger *et al.* 2016). However, the ability of herbivores to self-modify their habitat and potentially mediate the effects of warming could prevent or delay changes to it. Understanding the interaction between warming and herbivory in coastal Alaskan ecosystems could be crucial to future management strategy (Post & Pedersen 2008).

*Vegetation communities in the Yukon Delta National Wildlife Refuge*

The vegetation communities that dominate the central coastal portion and greater Kashunuk region of the Y-K Delta have been well described (Kincheloe & Stehn 1991; Babcock & Ely 1994; Jorgenson 2000). Slight elevational changes (less than 1 m elevation gain over 7.5 km), represent a gradient from active (lowest elevation) to abandoned (highest elevation) coastal terraces, each associated with a unique vegetation community (Jorgenson & Ely 2001). Generally, these regions can be described as mudflat, meadow, and upland tundra (Jorgenson 2000). Each region is dominated by unique vegetation communities, which are controlled by micro-elevational changes as well as hydrologic properties, salinity concentrations, and soil types (Kincheloe & Stehn 1991; Jorgenson 2000).

The upland region (highest elevation) supports the southernmost extent of tundra. Upland tundra is often underlain by shallow permafrost is commonly associated with larger fresh-water or very slightly brackish ponds (Jorgenson 2000). The vegetation is predominantly salt intolerant plants, especially mosses, lichens, shrubs (Kincheloe & Stehn 1991). Coastal regions are more tidally affected and therefore subject to more frequent inundation due to their slightly lower elevation. Salt tolerant species are more prolific in coastal meadow communities. These communities are often dominated by sedges or grasses (Kincheloe & Stehn 1991). Plant communities on the active floodplain are interlaced by brackish ponds and small tidal sloughs, keeping them well saturated though not affected by daily tidal action (Jorgenson 2000). Mudflat regions are bordered by mudflat on at least one side, and usually a wet meadow on the other. The vegetation

often occurs in monospecific stands and is highly subject to monthly if not daily inundation. Commonly dominant on the lowest lying areas, and making up ‘grazing lawns’, are *C. subspathacea* and *Puccinellia phryganodes*. Slightly higher, but also commonly occurring directly adjacent to downriver mudflats are *C. ramenskii* and *P. egedii* (Kincheloe & Stehn 1991).



## PURPOSE OF STUDY

Climate warming in northern latitudes has resulted in an increase in the range and productivity of shrubs and other woody biomass in grassland, tundra, and alpine systems. The mechanism of shrub expansion is not well understood; it is unclear whether the direct effects of warming or indirect effects of interspecific interactions with neighboring species (i.e. competitive release or facilitation) are causing this trend. Additionally, herbivory may slow, reduce, or prevent shrub expansion and maintain current plant community composition, even under warmed conditions. In this way, herbivores may be an important force in mitigating climate change effects. In western coastal Alaska, the primary herbivores are geese, which rely on the high-quality forage in this region for breeding and brood-rearing habitat. The purpose of our study is to explore how a coastal plant community may change with climate warming and determine whether the presence of herbivory can mediate change. Additionally, we aim to determine whether direct or indirect effects of warming are more important in this system. A better understanding of the importance of direct and indirect effects in Arctic and subarctic systems will improve large-scale modeling of climate change effects. Chapter 2 is written as a manuscript, prepared for submission to *Journal of Ecology* and co-authored with Dr. Karen Beard and Dr. Peter Adler.

## CHAPTER 2

# DIRECT EFFECTS OF WARMING INCREASE WOODY PLANT ABUNDANCE IN A SUBARCTIC WETLAND

## INTRODUCTION

Climate change can influence plant communities through both direct and indirect effects. Direct effects occur when warming alters plant populations through changes in a focal species' own vital rates (Adler *et al.* 2009). Indirect effects occur when warming alters the vital rates and abundances of neighbouring species, which in turn affects the fitness of the focal species (Adler *et al.* 2009; Gilman *et al.* 2010). While the relative importance of these two mechanisms is still being explored, theory and some empirical evidence show that direct effects will dominate in communities where plant species have little niche overlap (Kleinhesselink & Adler 2015; Chu *et al.* 2016). In contrast, where plants occupy the same niche, indirect effects appear more important and can even override direct effects (Klanderud 2005; Suttle *et al.* 2007; Tylianakis *et al.* 2008; Gilman *et al.* 2010). In communities with strong indirect effects, climate change projections that do not account for these interactions will not adequately predict future abundances of important species (Suttle *et al.* 2007; Levine, Adler & HilleRisLambers 2008; Tylianakis *et al.* 2008; Mod *et al.* 2015).

Over the past 150 years, northern latitudes have experienced dramatic increases in temperature, two to three times greater than the global mean surface temperature rise of 0.4 °C (IPCC 2014). We might expect direct effects of climate to be more important than

indirect effects in northern systems because of the lack of strong competitive interactions between species in severe environments, such as northern or alpine ecosystems (Callaway *et al.* 2002; Cavieres *et al.* 2014). However, the importance of indirect effects of climate change has not been well studied in Arctic systems, and interspecific interactions could become increasingly important with warming (Klanderud, Vandvik & Goldberg 2015). Warmer temperatures have been linked to the range expansion and increasing abundance of shrubs and woody plants in arctic tundra and alpine ecosystems (Sturm *et al.* 2001; Tape *et al.* 2006; Myers-Smith *et al.* 2011; Elmendorf *et al.* 2012), but it is unclear whether direct or indirect effects are driving this change.

While warming has been shown to influence community composition in northern latitudes, herbivory has been found to counteract the effects of warming in some systems by maintaining plant species composition and preventing shrub expansion (Post & Pedersen 2008; Olofsson *et al.* 2009; Christie *et al.* 2015; Kaarlejärvi *et al.* 2015). Unlike mammalian herbivores, migratory geese rely on nutrient-rich vegetation, such as sedges, in their Arctic and subarctic breeding areas (Sedinger & Raveling 1984; Post *et al.* 2009; Doiron *et al.* 2015). Because migratory geese are abundant during the short growing season, they have the potential to transform vegetation at the landscape scale and increase the nutrient content of grazed plants (Cargill & Jefferies 1984; Person *et al.* 1998; Sedinger *et al.* 2016). However, if climate change favors woody plants over preferred nutrient-rich species such as sedges in their breeding ground, it could reduce the amount of forage available for these herbivores. Thus, it is important to consider whether current

levels of grazing pressure could maintain the present vegetation community and prevent shrub expansion in light of warming.

The goal of our research was to disentangle the effects of climate warming, herbivory, and plant-plant interactions on a subarctic coastal wetland community. We had three main objectives. First, we conducted an experiment, using a response surface design, to determine how the abundances of two dominant species, *Carex ramenskii* (sedge) and *Salix ovalifolia* (dwarf shrub), change under warmed and grazed conditions. Second, we used our experimental data to parameterize competition models to predict the equilibrium abundances of these species under warmed and grazed conditions, and to determine whether herbivory mediates the effects of warming in the long term. Finally, we determined the relative importance of direct versus indirect effects of warming, with or without grazing, on plant species abundance.

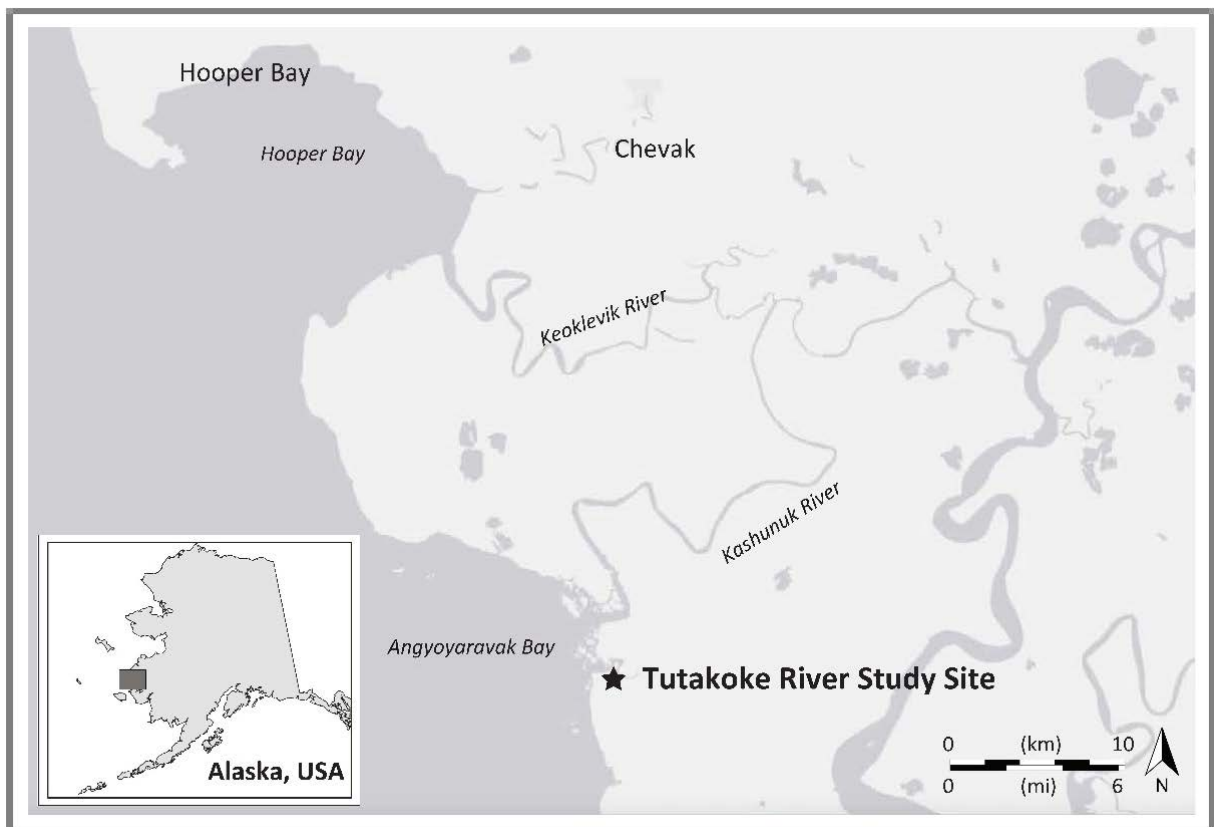
## METHODS

Our research was conducted on the Tutakoke River in the central portion of the coastal Yukon-Kuskokwim (Y-K) Delta in western Alaska (61°15'N, 165°30'W; elevation 3 m). The Y-K Delta is 75,000 km<sup>2</sup> of subarctic wetland and tundra between the Yukon and Kuskokwim Rivers, and along the coast of the Bering Sea (Fig. 1). Climate in the region is maritime, with mean monthly temperature ranging from -14.1 °C in midwinter to 13.3 °C in midsummer with a growing season from late May through late August (Terenzi, Jorgenson & Ely 2014). Mean annual rainfall is 41.1 cm and snowfall is 157 cm (Terenzi *et al.* 2014).

The Y-K Delta is an important breeding area for migratory birds (Baldassarre 2014). Our site provides primary nesting and brood rearing habitat mainly for a colony of Pacific black brant (*Branta bernicla nigricans*), but emperor geese (*Chen canagica*), cackling geese (*B. canadensis minima*), and greater white-fronted geese (*Anser albifrons*) also utilize the area (Ruess *et al.* 1997). While mammalian herbivores are mostly absent from the coastal Y-K Delta, Alaskan moose (*Alces alces gigas*) are occasional visitors.

Our experiment was conducted in a brackish wet sedge meadow on the active floodplain. The meadow is 10-20 cm higher than adjacent tidal channels, the soil is silty loam underlain with deposits of silts and sands, and has neutral soil pH (Jorgenson 2000). *Carex ramenskii*, a salt-tolerant sedge, is the dominant species within 3 km of the coast (Kincheloe & Stehn 1991; Jorgenson 2000). *C. ramenskii* has a shorter, more nutritious growth form (often referred as *C. subspathacea* or grazing lawn), which is the preferred forage for geese and goslings (Sedinger & Raveling 1984).

At our study site, *C. ramenskii* is intermixed with the dwarf shrub, *Salix ovalifolia* (hereafter *Carex* and *Salix*) in a slightly brackish wet sedge meadow (Fig. 2). While *Salix* is not the preferred forage of geese, some geese may consume minimal amounts and moose may prefer it. At peak growing season in control plots in 2015, *Carex* cover was  $55\% \pm 16$  SD, *Salix* cover was  $37\% \pm 12$  SD, all other species made up  $<3\%$  cover, and remaining cover was dead biomass or bare ground.



**Fig. 1.** Our study site was located near the coast on the Tutakoke River. This region is part of the Yukon Delta National Wildlife Refuge and one of the major black brant breeding colonies.



**Fig. 2.** The experiment was located on a slightly brackish wet sedge meadow. Cones are open top passive solar radiation warming chambers. Fences are herbivore exclosures.

### *Experimental methods*

To accomplish our first objective, to conduct an experiment using a response surface design to determine how the abundances of *Carex* and *Salix* change under warmed and grazed conditions, we conducted a two-season field experiment during the spring and summer of 2015 and 2016. In May 2015, we established 80, 0.85-m diameter circular plots. Within each plot, we established four circular (20-cm diameter) subplots or “neighbourhoods”. The four neighbourhoods were randomly placed in non-overlapping areas in the interior 0.8-m diameter of the plot (to limit edge effects). The center of each neighbourhood was marked so that the exact subplot could be re-measured. The data

analyzed in this study is the percent cover of both species in each neighbourhood subplot at the beginning and end of the experiment using the point-intercept method. Initial cover was measured shortly after the removal treatments were completed in 2015 (see below). Final cover was measured at the end of the growing season (mid-August) in 2016.

To create the warming and grazing treatments, we had a factorial combination of two factors, warming (+/-) and grazing (+/-). Treatments were: ambient temperature, grazed (hereafter, ambient, grazed); ambient temperature, ungrazed (hereafter, ambient, ungrazed); warmed, grazed; and warmed, ungrazed. We created warming treatments using fiberglass open-top warming chambers (OTCs) following International Tundra Experiment specifications (as in Molau & Mølgaard 1996). Thermochron iButtons in our plots showed that OTCs raised air temperature at the soil surface by on average 1.75 °C over the growing season. We used OTCs because, unlike greenhouses, they minimally alter precipitation and gas exchange (Molau & Mølgaard 1996; Marion *et al.* 1997). Because OTCs exclude herbivores, warming and natural grazing could not be simultaneous. Therefore, we excluded all treatments from natural herbivory by using OTCs on warmed plots and 1-m tall, 2.54-cm hexagonal mesh fencing on ambient temperature plots. We simulated grazing treatments by manually clipping vegetation grazed plots on four occasions throughout the season. We based grazing treatments on black brant seasonal biomass offtake at the study site (Person *et al.* 1998). Both species received the same intensity of grazing with respect to its proportion of total cover. We normally distributed the amount of vegetation clipped across four dates around peak black brant hatch, when herbivory is greatest (Sedinger & Flint 1991). To simulate fecal



deposition, we added goose feces four times per season to each plot receiving grazing based on nearby fecal deposition monitoring plots.

Nested within these four treatments, we also conducted vegetation removals to create a response surface design. There were four removal targets to create plots where where 1) *Carex* was low but *Salix* was high (high = natural density), 2) *Salix* was low but *Carex* was high, 3) both were reduced, or 4) both were at natural density. We achieved this using the following removal targets: 95% removal of *Carex* and 0% removal of *Salix*, 95% removal of *Salix* and 0% removal of *Carex*, 50% removal of both *Carex* and *Salix*, and 0% removal neither *Carex* nor *Salix* (Fig. S1). To be clear, our analysis ignores the categorical removal targets and instead uses the continuous variation in initial (post-removal) cover. We implemented the removals by hand-pulling plants each year in May. We assigned removal targets based on the initial percent cover of each species in the plot as quantified by the point-intercept method. We repeated point intercept counts after removals to record post-removal percent cover (Veblen 2008). It was possible to have percent cover greater than 100% because our sampling method allowed for multiple hits per point-intercept. Throughout the experiment, we continuously removed any non-*Carex* or *Salix* species. To limit belowground interactions, we trenched around each circular plot then inserted 0.8 mm root barrier to 25 cm below the soil surface. The plastic barrier remained in place throughout the experiment.

### *Statistical Methods*

To accomplish our second objective, to predict how the equilibrium abundances of *Carex* and *Salix* change under warmed and grazed conditions, we first determined how

warming and grazing affected the strength and direction of intra- and interspecific interactions between *Carex* and *Salix*. To do so, we fit data from our response surface removal experiment to seven candidate competition models (Table S1) (Law & Watkinson 1987; Inouye 2001; Levine & HilleRisLambers 2009; Hart & Marshall 2013). We used nonlinear least squares to fit the experimental data (neighbourhood cover) to the model and estimate parameter values. We fit models using the `nls()` function and the port algorithm in base R v. 3.3.2 (R Development Core Team 2014). We opted to fit models using `nls()` and exclude the random effect of neighbourhood because when tested in exploratory models, random effects were small (orders of magnitude smaller than the residual).

We included treatment as a four-level categorical grouping factor that allows parameters to vary by treatment, so that we could simultaneously fit all of our experimental data for each species using a single model (Ritz & Streibig 2008). Each model had three parameters for each species:  $\lambda$ , the density-independent growth rate,  $\alpha_{ii}$ , the per capita (or per unit cover) effect of intraspecific neighbours, and  $\alpha_{ij}$ , the per capita effect of interspecific neighbours. By allowing these parameters to vary among each of the four treatments, the resulting models had 12 total parameters. For our first step in model selection, we used Akaike Information Criterion (AIC) to determine which candidate model best described our system (Table 1). The model that best described our data is a modified Ricker model (Ricker 1954):

$$N_{c,t+1} = N_{c,t}(\lambda_{[tx]} \exp(-\alpha_{cc[tx]} \log(N_{c,t}) - \alpha_{cs[tx]} \log(N_{s,t})))$$

where  $N_{c,t}$  and  $N_{s,t}$  are the initial (post-removal) percent covers of *Carex* and *Salix*, respectively, and  $N_{c,t+1}$  is the final percent cover of *Carex* at the end of the second growing season. The subscript [tx] denotes where we allowed coefficients to vary between the four treatments. We repeated model fitting for *Salix* with the same notation:

$$N_{s,t+1} = N_{s,t}(\lambda_{[tx]} \exp(-\alpha_{ss[tx]} \log(N_{s,t}) - \alpha_{sc[tx]} \log(N_{c,t}))).$$

**Table 1.** Results of Akaike Information Criterion (AIC) model selection, number of estimated parameters (k), difference in AIC<sub>c</sub> between best model and model  $i$  ( $\Delta\text{AIC}_c$ ), Akaike's weight which indicates weight of evidence in favor of model  $i$  ( $w_i$ ), negative log likelihood (-2lnl). Candidate models excluded from this table were not able to be fit for both species due to convergence failure. The response variable for all models is  $N_{i,t+1}$  and model structure is  $N_{i,t+1} = N_{i,t}f(X_t, Y_t)$ .

Candidate models $f(X_t, Y_t)$	k	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	$w_i$	-2lnl
<i>Carex</i>					
$\lambda e^{-\alpha_{cc} \ln(N_{c,t}) - \alpha_{cs} \ln(N_{s,t})}$	13	-162.15	0.00	1	-187.15
$\lambda e^{-\alpha_{cc} N_{c,t} - \alpha_{cs} N_{s,t}}$	13	-82.58	79.57	0	-108.58
$1 + \lambda(1 - \alpha_{cc} N_{c,t} - \alpha_{cs} N_{s,t})$	13	-42.08	120.06	0	-68.08
<i>Salix</i>					
$\lambda e^{-\alpha_{ss} \ln(N_{s,t}) - \alpha_{sc} \ln(N_{c,t})}$	13	-286.65	0.00	1	-312.65
$\lambda e^{-\alpha_{ss} N_{s,t} - \alpha_{sc} N_{c,t}}$	13	-259.79	26.87	0	-285.79
$1 + \lambda(1 - \alpha_{ss} N_{s,t} - \alpha_{sc} N_{c,t})$	13	-237.04	49.62	0	-263.04

For the second step of our model selection procedure, we simplified the best model using likelihood ratio tests (LRT) to remove parameters that did not improve goodness of fit at confidence level of 0.10 (Ritz & Streibig 2008; Hart & Marshall 2013). We first determined whether a model that allows all parameters to vary by treatment is more favorable than a model that holds a particular parameter constant across treatments while allowing the other parameters to vary by treatment. We repeated this process across all three parameters for both species models. We also conducted a LRT where we

completely removed each parameter from the model individually. In all cases, the full model, that allowed all parameters to vary, was better than simpler models (Table 2).

Code for model selection and simplification is available in Supporting Information 1.

**Table 2.** Result of likelihood ratio tests (LRT) for simplified models including p-values and degrees of freedom (df). P-values < 0.10 mean more complex model explain significantly more variation than the simplified models. P-values > 0.10 mean the simplified model represents the data as well or better than more complex model and should be used.

	<i>Carex</i>		<i>Salix</i>	
	p	df	p	df
$\lambda$ held constant	1.01e <sup>-6</sup>	10	0.02	10
$\lambda$ removed	1.81e <sup>-9</sup>	9	4.76e <sup>-6</sup>	9
$\alpha_{ii}$ held constant	2.86e <sup>-6</sup>	10	0.04	10
$\alpha_{ii}$ removed	0	9	0	9
$\alpha_{ij}$ held constant	0.026	10	0.03	10
$\alpha_{ij}$ removed	3.15e <sup>-6</sup>	9	0.04	9

To visualize response surfaces, we used package ‘rgl’ in R (R Development Core Team 2014). The surface was created by using the model to predict the response variable (final cover) for all combinations of the explanatory variables (initial cover of both species). Response surfaces represent modeling predictions, but experimental data are represented in the plots to model error.

Next, we calculated equilibrium abundances using an analytical solution to the Ricker model (Supporting Information 2). We inserted treatment-specific parameters and solved for the equilibrium cover of each species for each treatment using the following formulas:

$$\ln N_{c,t} = \frac{a_{ss} \ln \lambda_c}{a_{cc} a_{ss} - a_{cs} a_{sc}}$$

$$\ln N_{s,t} = \frac{a_{cc} \ln \lambda_s}{a_{ss} a_{cc} - a_{sc} a_{cs}}$$

We simulated our original models over a range of starting cover values to confirm the accuracy of our analytical solution and ensure equilibrium was reached within an ecologically relevant time period, regardless of initial conditions (Fig. S2). Equilibrium was reached in all scenarios within 5-10 time steps. We did not consider parameter uncertainty in our model projections.

To address our third objective, we determined the contribution of direct and indirect effects to the overall treatment effect on *Carex* and *Salix* cover. Changes in predicted cover projected by our treatment-specific models with respect to the current baseline represent the full effect of our experimental warming; it includes both the direct effect of the treatment on each species plus the altered plant-plant interactions that are the indirect effects (Fig. 3).

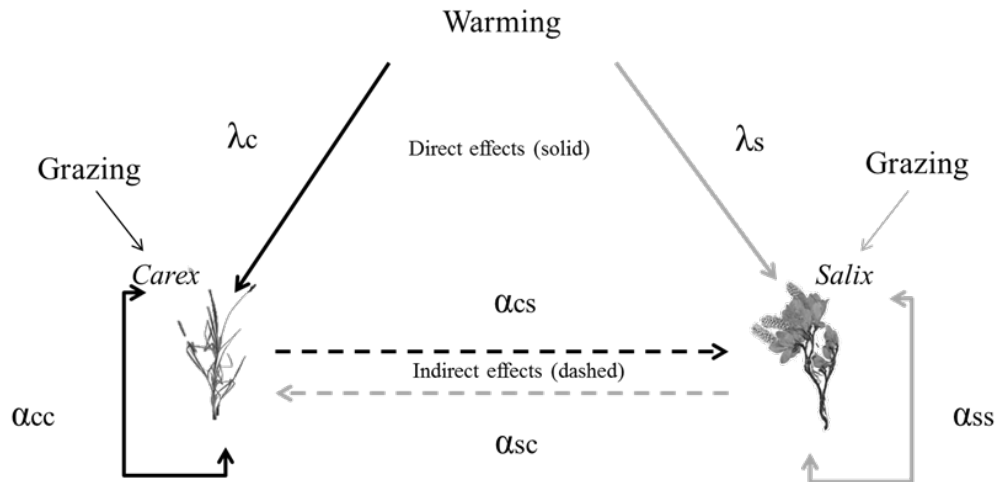
$$\textit{Full effect} = \textit{Direct effect} + \textit{Indirect effect}$$

To calculate the direct effect, we returned to our model but held the interspecific parameter constant such that the effect of the neighbour species on the focal species was unchanged by treatment conditions. Parameters for the neighbour species were not allowed to vary by treatment; they were kept at the parameter associated with the ambient, grazed treatment. We used the ambient, grazed treatment as the baseline condition for the model parameters of the competitor species because it represents the scenario that occurs naturally on the landscape. Parameters for the focal species were allowed to vary for the other three treatments as denoted by the subscript [treatment]. In the first equation below, *Carex* is treated as the focal species so the parameters for *Salix*

(the neighbour) are held constant. In the second equation, *Salix* is treated as the focal species, so the parameters for *Carex* (the neighbour) are held constant.

$$\ln N_{c,t[treatment]} = \frac{a_{ss[ambient,grazed]} \ln \lambda_c[treatment]}{a_{cc[treatment]} a_{ss[ambient,grazed]} - a_{cs[ambient,grazed]} a_{sc[treatment]}}$$

$$\ln N_{s,t[treatment]} = \frac{a_{cc[ambient,grazed]} \ln \lambda_s[treatment]}{a_{ss[treatment]} a_{cc[ambient,grazed]} - a_{sc[ambient,grazed]} a_{cs[treatment]}}$$



**Fig. 3.** Warming affects each plant directly, by altering the density independent growth rate and intraspecific coefficient. Warming can also influence plants indirectly, or through alterations to the strength or direction of the interspecific interaction with its neighbour.

The difference between equilibrium cover for this set of parameters, and equilibrium cover projected using baseline parameters is the change in cover resulting from direct effects only, as we removed the possibility of altered indirect effects with a changing climate by holding interspecific effects constant.

## RESULTS

In these modeling predictions, *Carex* was largely unaffected by interspecific effects and density of *Salix* under ambient temperatures in both grazed and ungrazed treatments (Fig. 4a, b), and under the warmed, grazed treatment (Fig. 4c). Only under warmed, ungrazed treatments did *Carex* respond (negatively) to the initial percent cover of *Salix* (Fig. 4d).

Under ambient conditions in both grazed and ungrazed treatments, *Salix* final percent cover was lower under high *Carex* percent cover due to negative interspecific effects (Fig. 5a,b, and Table 3). In the warmed, grazed treatment, *Salix* was unaffected by *Carex* (Fig. 5c). In contrast, in the warmed, ungrazed treatment, a slight facilitative effect was apparent in that *Salix* final cover was higher where *Carex* cover was highest (Fig. 5d).

Warming affected some model coefficients. Warming decreased the density independent growth rate of *Carex*, but increased the density independent growth rate of *Salix* (Table 3). In warmed conditions, *Carex* experienced greater intraspecific competition and *Salix* experienced less intraspecific competition. *Salix* had a slightly stronger competitive effect on *Carex* when warmed. Notably, *Carex* had a competitive effect on *Salix* in ambient temperatures that shifted to a slight facilitative effect on *Salix* with warming.

Grazing also affected model coefficients. Both *Carex* and *Salix* had higher density-independent growth rates when ungrazed; however, the increase in growth rate when ungrazed was greater for *Carex* than *Salix*. *Carex* experienced greater intraspecific

competition when it was grazed, and *Salix* intraspecific interactions were not affected.

There were no consistent directional trends of grazing on interspecific interactions.

### *Model projections*

Our analysis of the outcome of species interactions showed coexistence and stable equilibrium (in <10 time steps) in all treatments, though community composition differed across treatments (Fig. 6). For the ambient, grazed treatments, our model predicted *Carex* cover would reach equilibrium at 53%, which is similar to the mean cover of *Carex* in control plots ( $55\% \pm 16$  SD). In the ambient, grazed treatment, equilibrium cover of *Salix* was 26%, which is similar to natural abundances measured on the in control plots ( $37\% \pm 12$  SD). In both grazed and ungrazed ambient treatments, *Carex* was the dominant species. In the ambient, ungrazed treatment, equilibrium for *Carex* was 129% and 43% for *Salix*. However, in warmed treatments, *Salix* abundance increased and became the dominant species. In the warmed, grazed treatment, *Carex* equilibrium percent cover was 41% while *Salix* reached 57%. In the warmed, ungrazed treatment, *Carex* equilibrium percent cover was 73% and *Salix* equilibrium percent cover was 89%.

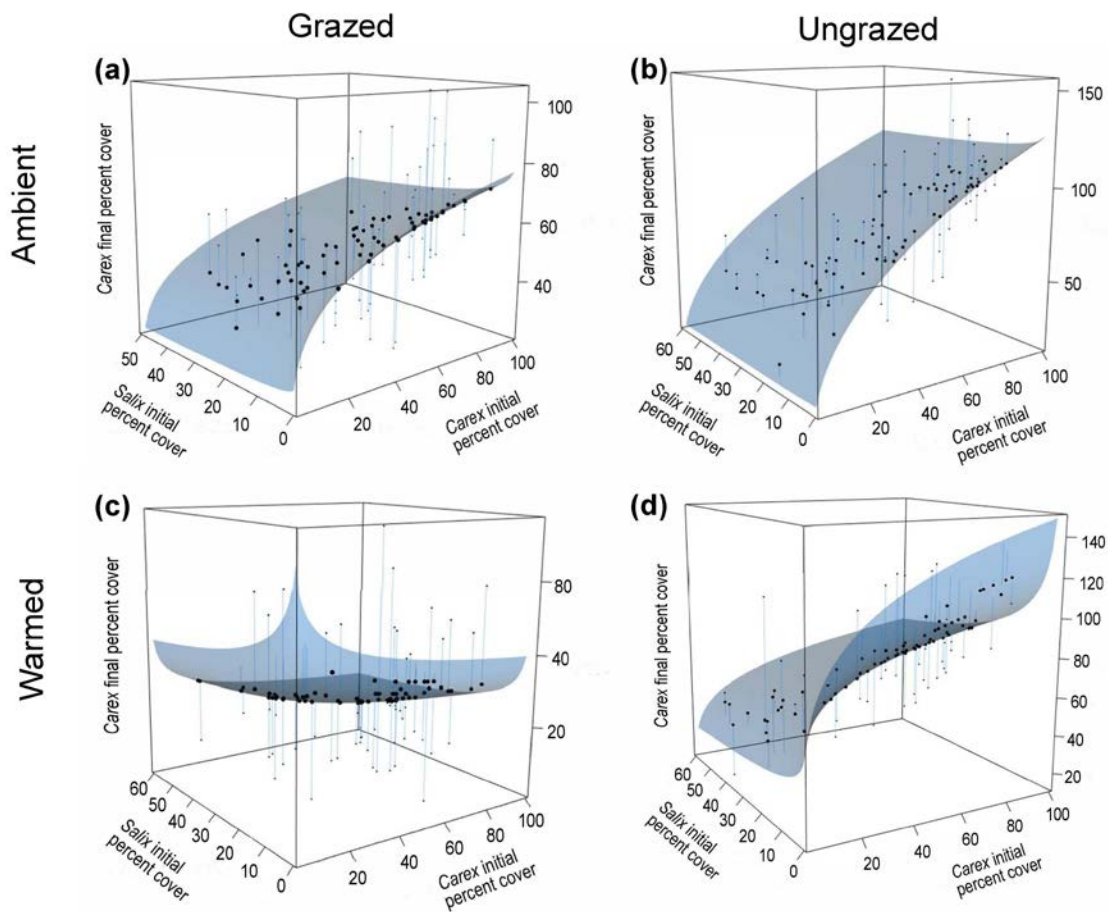
### *Direct and indirect effects*

We found that direct effects of warming and grazing on plant growth were greater than indirect effects in all treatments for both species (Fig. 7). Direct effects accounted for 90-100% of the total predicted changes in equilibrium cover between the ambient, grazed condition and the other conditions. Indirect effects accounted for only 0-10% of the predicted changes in cover.

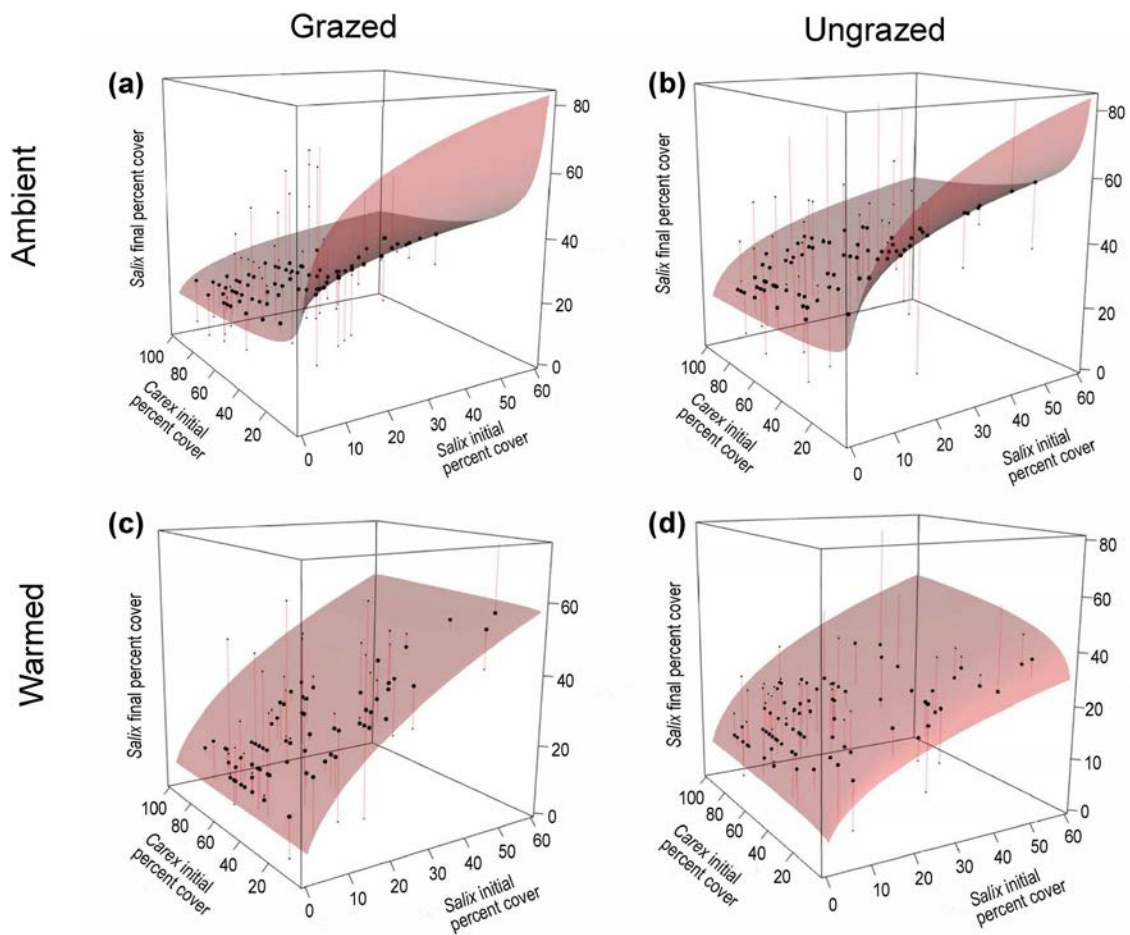


**Table 3.** Calculated parameter estimates, 95% confidence limits (CL), residual standard error (RSE), and degrees of freedom (df) of best fit competition models for each species. \* indicates parameters where confidence intervals do not overlap zero

Model	Parameter	Estimate	Lower CL	Upper CL	RSE/df
<i>Carex ramenskii</i>	$\lambda_{ambient,grazed}$	0.625 *	0.449	0.864	0.183/345
	$\lambda_{ambient,ungrazed}$	1.144 *	0.931	1.399	
	$\lambda_{warm,grazed}$	0.381 *	0.263	0.544	
	$\lambda_{warm,ungrazed}$	0.704 *	0.560	0.878	
	$\alpha_{cc\,ambient,grazed}$	0.763 *	0.587	0.923	
	$\alpha_{cc\,ambient,ungrazed}$	0.534 *	0.413	0.648	
	$\alpha_{cc\,warm,grazed}$	1.087 *	0.918	1.247	
	$\alpha_{cc\,warm,ungrazed}$	0.776 *	0.672	0.873	
	$\alpha_{cs\,ambient,grazed}$	0.045	-0.058	0.147	
	$\alpha_{cs\,ambient,ungrazed}$	0.023	-0.043	0.087	
	$\alpha_{cs\,warm,grazed}$	0.097	-0.088	0.202	
	$\alpha_{cs\,warm,ungrazed}$	0.162 *	0.093	0.232	
<i>Salix ovalifolia</i>	$\lambda_{ambient,grazed}$	0.355 *	0.210	0.589	0.151/345
	$\lambda_{ambient,ungrazed}$	0.534 *	0.380	0.750	
	$\lambda_{warm,grazed}$	0.772 *	0.437	1.341	
	$\lambda_{warm,ungrazed}$	0.934 *	0.628	1.378	
	$\alpha_{ss\,ambient,grazed}$	0.791 *	0.597	0.972	
	$\alpha_{ss\,ambient,ungrazed}$	0.740 *	0.601	0.870	
	$\alpha_{ss\,warm,grazed}$	0.464 *	0.248	0.665	
	$\alpha_{ss\,warm,ungrazed}$	0.578 *	0.414	0.731	
	$\alpha_{sc\,ambient,grazed}$	0.207 *	0.011	0.390	
	$\alpha_{sc\,ambient,ungrazed}$	0.126	-0.001	0.243	
	$\alpha_{sc\,warm,grazed}$	-0.005	-0.248	0.227	
	$\alpha_{sc\,warm,ungrazed}$	-0.089	-0.217	0.034	



**Fig. 4.** Response surface for modeling predictions of *Carex* cover response to all treatments. (a) corresponds to ambient,grazed, (b) to ambient,ungrazed, (c) to warmed,grazed, (d) to warmed,ungrazed. Note that the scale of the vertical axes varies among panels. Also, final cover of *Carex* may exceed 100%. Surface and bold points are modeling predictions, small points are experimental data, vertical lines are residuals.



**Fig. 5.** Response surface for modeling predictions of *Salix* cover response to all treatments. (a) corresponds to ambient,grazed, (b) to ambient,ungrazed, (c) to warmed,grazed, (d) to warmed,ungrazed. Note that the scale of the vertical axes varies among panels. Surface and bold points are modeling predictions, small points are experimental data, vertical lines are residuals.

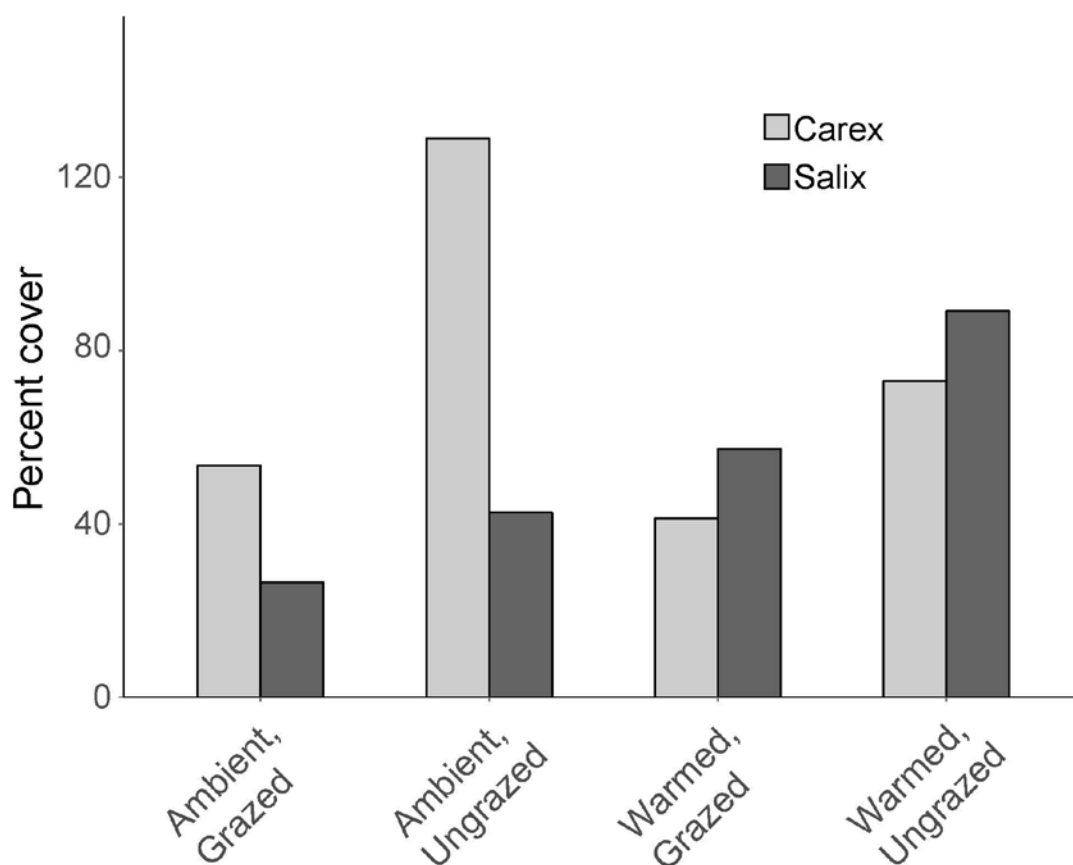
## DISCUSSION

Our study sought to determine how the abundances of *Carex* and *Salix* might change under warmed conditions, with and without herbivory. Similar to other studies investigating the interaction between sedges and woody plants (Elliott & Henry 2011), we found that *Carex* was the dominant species under ambient conditions. Using experimental data to parameterize competition models, we found that models predicted that *Salix* will overtake *Carex* as the dominant species in the system under warmed conditions whether the system is grazed or ungrazed. While this result is surprising because *Salix* currently occupies a smaller percent of the landscape, it is consistent with other studies from across the Arctic showing that warming causes a community shift (i.e., a decline in sedges and increase in deciduous shrubs) (Chapin *et al.* 1995; Sturm *et al.* 2001). We found that direct effects of climate change on individual plant species vital rates were substantially more important than the indirect effects, mediated through species interactions.

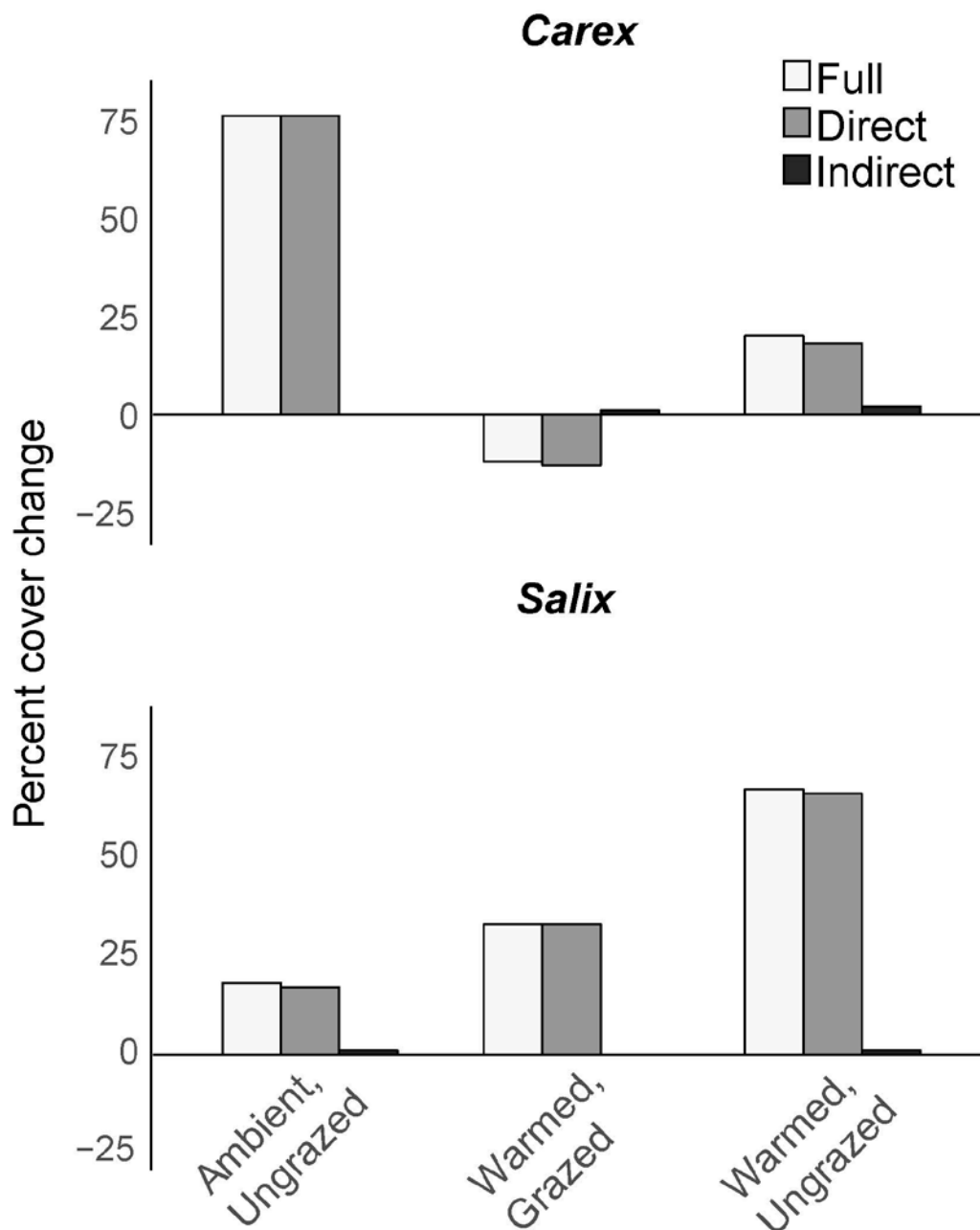
### *Effect of warming*

Species with different functional types or growth strategies may respond differently to warmed conditions (Post & Pedersen 2008; Post 2013; Burt *et al.* 2014). We found that warming increased the growth rate of *Salix* but decreased the growth rate of *Carex*. Our models are consistent with previous studies that have found that warming increases the abundance of *Salix* and other deciduous shrubs across the Arctic (Sturm *et al.* 2001; Tape *et al.* 2006; Myers-Smith *et al.* 2011; Elmendorf *et al.* 2012), while

warming decreases the abundance of *Carex* and other graminoids (Chapin & Shaver 1985; Chapin *et al.* 1995; Chapin *et al.* 1996). Although our study did not identify a physiological mechanism for this shift, results from our models suggest that an increase in deciduous shrubs and decrease in graminoids across the Arctic may be a direct response of these species to warming rather than an indirect response, such as competitive release of *Salix* or suppression of *Carex*.



**Fig. 6.** Predicted equilibrium percent cover for each species as calculated using the analytical solution to the model and treatment specific parameters.



**Fig. 7.** Contribution of full effect, direct, and indirect effects to change in cover between the natural condition (ambient, grazed) and the other three temperature, grazing combination treatments. Negative values indicate a decrease in cover from the natural condition. The full effect is the sum of direct and indirect bars.

### *Effect of herbivory*

In other systems, grazing can mitigate climate change effects by preventing a change in community composition or limiting shrub expansion (Post & Pedersen 2008; Olofsson *et al.* 2009; Kaarlejärvi *et al.* 2015). In our study, herbivory did not prevent a community shift, but it substantially reduce the cover of both species. Herbivory in our system may not prevent a shift in species dominance with warming for two reasons. First, other studies showing that herbivores can reduce shrub growth with warming have focused on mammalian herbivores that prefer to browse shrubs (Bråthen & Oksanen 2001; Eskelinen & Oksanen 2006; Post & Pedersen 2008). In our experiment, we simulated goose grazing on plants in proportion to their cover; however, geese would likely only graze sedges, which further supports the finding that geese would not mediate a woody plant increase in our system. Second, the amount of vegetation removed by geese may not be as substantial as that removed by the mammalian herbivores (Kaarlejärvi *et al.* 2015).

### *Direct and indirect effects*

In modeling projections of our system, direct effects of warming were more important than the indirect effects of warming mediated by plant-plant interactions, as has been found in other graminoid-dominated systems (Chu *et al.* 2016). Direct effects explained an average of 97% of the total change in cover. These direct effects, which resulted in *Salix* becoming the dominant species, were driven by a reduction in the density independent growth rate of *Carex*, and an increase in the density independent

growth rate of *Salix* in warmed conditions. They were also driven by a reduction in intraspecific competition for *Salix*, but an increase in intraspecific competition for *Carex*.

More specifically, warming and grazing together had negative effects on *Carex* by reducing the growth rate and increasing the per capita effect of intraspecific competition. Therefore, *Carex* increased substantially in the ambient, ungrazed condition and declined in the warmed, grazed. In contrast, warming positively affected *Salix*, and grazing did not affect it as strongly. Because warming increased the growth rate and reduced intraspecific competition, our models project that *Salix* will eventually become the dominant species in warmed conditions.

Indirect effects only explained 8-10% of the total change in *Carex* cover and 0-2% of *Salix*. Weak interspecific interactions are common in stressful alpine and Arctic systems (Callaway *et al.* 2002). Consistent with this finding, most of our estimated interspecific coefficients overlapped zero. Holding these interspecific interactions constant in the model and considering only direct effects had negligible effects on projected outcomes.

Greater niche overlap is thought to be correlated with greater importance of indirect effects (Adler *et al.* 2012; Kleinhesselink & Adler 2015). For example, Arctic plants often partition resources by utilizing different rooting depths for nutrient acquisition (Nadelhoffer *et al.* 1991; McKane *et al.* 2002). Sedges and herbaceous plant usually have shallower rooting depths than shrubs (Canadell *et al.* 1996), which may be a mechanism for niche differentiation in this system and therefore weak indirect effects.



### *Limitations*

Our model of plant responses to warming reflects changes we observed in treatments that increased temperatures by 1.75 °C during the spring and summer only. While our results show a shift in plant dominance even under this minimal increase, our predictions are limited to this small, consistent increase. Continually increasing temperatures may further alter the community beyond our predictions. Furthermore, climate change could have other effects on this system, such as increased soil salinity or sedimentation rates due to more extreme flood events and sea level rise, that we do not address and could be contrary to the effects of warming alone (Person & Ruess 2003; Terenzi *et al.* 2014).

### *Future climate and herbivore change*

Our models suggest that an instantaneous increase in temperature of 1.75 °C could result in a shift from sedge to deciduous shrub dominance in an important brood-rearing habitat for migratory geese in 5-10 time steps regardless of initial conditions, suggesting we might observe this change over decadal time scales. *C. ramenskii* is an important goose forage species in this coastal wetland ecosystem and a shift toward a dwarf-shrub dominated landscape would reduce the availability of high quality forage for the migratory geese that utilize this habitat (Sedinger & Raveling 1984). The amount of high quality forage consumed is a strong predictor of gosling survival, thus a shift toward less nutritious forage, such as *Salix*, could further reduce this already declining black brant population (Sedinger & Chelgren 2007; Sedinger *et al.* 2016). With climate change, late arrival to the breeding grounds by geese (in comparison to date of green-up),

migration to more suitable environments, or continued population decline could result in reduced herbivore pressure and compound the effects of warming on this plant community (Ward *et al.* 2005, 2016; Sedinger *et al.* 2016). Managers may wish to consider the impacts of shrub expansion on the active floodplain when assessing habitat availability for goose herbivores. Finally, the consequence of novel herbivores moving into the system, such as moose (Tape *et al.* 2016) or snow geese, is unknown and should be considered.

### *Conclusions*

Climate change can affect species vital rates and interactions, and the effects of herbivory may be important in mediating climate change effects on plant communities. The results of our study suggest that an increase of less than 2° C could cause a shift in dominance from sedges to dwarf shrubs on the coast of western Alaska. This shift will likely be a result of the direct effects of warming and not a result of changes to plant-plant interactions or competitive release. Our results provide evidence for an increase in woody plant abundance on the subarctic coast and add to literature suggesting that direct effects of warming are stronger in systems where species have different growth strategies. If direct effects are more important than indirect effects in other Arctic systems, this greatly influences our understanding of how woody plant abundance is increasing. Further, we show that goose herbivores may not be able to mitigate shrubification in a manner similar to mammalian herbivores. Future changes in the relative abundance of these plant species has implications for how many herbivores and what types of herbivores these landscapes can support.

## AUTHOR CONTRIBUTIONS

Conceived and designed the experiments: LC KB PA. Performed the experiments:  
LC. Analyzed the data: LC PA. Wrote and edited the paper: LC KB PA.

## DATA ACCESSIBILITY

Data are available through the Arctic Data Center at [doi:10.18739/A2MP11](https://doi.org/10.18739/A2MP11).

## CHAPTER 3

### CONCLUSIONS

Existing literature has emphasized the importance of considering direct and indirect effects when making predictions about plant community change under climate change scenarios (Suttle *et al.* 2007; Levine *et al.* 2008; Levine, McEachern & Cowan 2010). While some studies have found that indirect effects can be very important (Klanderud 2005; Suttle *et al.* 2007; Tylianakis *et al.* 2008; Gilman *et al.* 2010), we found that the direct effects of warming were far more important than indirect effects. Indirect effects may be unimportant in our system because our two study species had weak interspecific interactions (Mitchell, Cahill & Hik 2009). Many studies do not calculate interaction coefficients, rather quantify competition using relative neighbor effects (RNE) or relative competition intensity (RCI) (Callaway *et al.* 2002; Brooker 2006). Most studies of competition in any system do not calculate or report explicit interaction coefficients, though one study described interactions  $<0.01$  as weak (Hart & Marshall 2013). Previous work has demonstrated that indirect effects are less important where there is less niche overlap (Kleinhesselink & Adler 2015). Future work may focus on quantifying niche overlap using isotope tracer experiments to determine whether resource partitioning is the mechanism behind the weak indirect effects in our system.

Previous studies have found evidence of sedge decline and deciduous shrub increase with climate change (Chapin & Shaver 1985; Chapin *et al.* 1995). Our study system is a useful addition to this literature because *Carex ramenskii*, a sedge, is the most common plant on the active floodplain and *Salix ovalifolia* is an increasingly prevalent

dwarf shrub (Jorgenson & Ely 2001). While shrubification in the Arctic has been well documented, particularly in tundra systems (Sturm *et al.* 2001; Tape *et al.* 2006; Knapp *et al.* 2008; Myers-Smith *et al.* 2014), relatively few studies have examined shrubification in coastal systems (Zinnert *et al.* 2011). Our study indicates that shrub expansion could also be occurring in coastal wetland systems and suggests that these changes are largely due to direct effects of warming. We only considered the interactions of these two species in this experiment. Future studies might consider evaluating the importance of direct and indirect effects of climate change across the coastal terraces in this system. While indirect effects may not be important in this wet sedge meadow, plant interactions may play a more important role in upland tundra in coastal Alaska, where the community is more diverse and is already densely populated by at least two deciduous shrubs (Jorgenson 2000). This region may see the most rapid changes with a warming climate because it is slightly higher in elevation, rarely utilized by herbivores, and underlain by permafrost, which could degrade with further warming (Jorgenson 2000). Our results suggest that shrub expansion could be an important aspect of community change in this system. A shift toward a shrub-dominated landscape could alter carbon cycling, productivity, hydrology, and albedo (Post *et al.* 2009; Myers-Smith *et al.* 2011; Leffler & Welker 2013; Doiron *et al.* 2014, 2015; Kelsey *et al.* 2016). Further work could address the biogeochemical impacts of these changes.

Because we only manipulated temperature, our results are similar to existing literature which states that warming may be a main driver of shrub expansion at northern latitudes (Chapin *et al.* 1995; Sturm *et al.* 2001; Tape *et al.* 2006; Myers-Smith *et al.*

2011). However, other factors such as precipitation, soil nutrient cycling, and atmospheric carbon dioxide levels will be altered by climate change (IPCC 2014). We did not examine the impacts of these other potential climate change effects separately in our experimental design and they may play a critical role in determining how plant communities may change. In our system, summer precipitation is common and generally comes in small, frequent events (Kincheloe & Stehn 1991). Climate change can alter precipitation regimes, often making precipitation events come in larger, less frequent events (Easterling *et al.* 2000; Frich *et al.* 2002). Wetland plants may not be well adapted to an altered precipitation regime; soil drying due to infrequent rain events or a lower water table could benefit levee vegetation or shrubs more adapted to dry conditions (Chapin & Shaver 1985).

Additionally, increased temperatures may increase the rate of litter decomposition and microbial nitrogen fixation (Nadelhoffer *et al.* 1991; Hartley *et al.* 1999; Rustad *et al.* 2001; Schmidt *et al.* 2002). Atmospheric nitrogen deposition has also increased throughout the world, as well as in the Arctic (Jónsdóttir, Callaghan & Lee 1995; Vitousek *et al.* 1997; Kaiser 2001). These factors may reduce nitrogen limitation in a usually nutrient limited system, an event that could also drive community change (Bret-Harte *et al.* 2004). Previous studies found that nitrogen fertilization decreased the carbon:nitrogen (C:N) ratio in *Carex ramenskii* biomass and increased productivity (Ruess *et al.* 1997), but the effects of fertilization on competitive interactions between *Carex* and *Salix* has not been studied. Future studies could incorporate precipitation

manipulations, drought treatments, or fertilization treatments to better isolate and understand the effects of climate change, beyond warming.

Another potential effect of climate change in this region is sea level rise (IPCC 2014). Sea level rise could cause more frequent inundation of coastal areas and increased inundation would increase the salinity of the soil (Terenzi *et al.* 2014). Plants in the coastal regions already experience at least yearly inundation, so they are fairly well adapted to saline soils, but plant communities slightly further inland are rarely inundated and are not dominated by salt-tolerant species (Jorgenson & Ely 2001). The frequency of large fall storm surges has increased in recent decades (Terenzi *et al.* 2014), so it is possible that areas of the inactive floodplain could also experience more frequent inundation. Increased salinity could alter plant communities, especially those which are less tolerant and not adapted to frequent inundation (Kincheloe & Stehn 1991; Babcock & Ely 1994). Additionally, storm surges can deposit up to 10 cm of sediment in a single event (Terenzi *et al.* 2014). Areas such as our study site, which are located on the active flood plain near the coast could experience increased sedimentation rates with more frequent storm surges (Terenzi *et al.* 2014). Increased sedimentation can reduce valuable habitat for geese such as Pacific black brant (*Branta bernicla nigricans*), which nest coastally and forage on coastal vegetation (Babcock & Ely 1994; Terenzi *et al.* 2014). Previous work has indicated that *C. ramenskii* makes physiological adjustments to tolerate high salinity (Ruess *et al.* 1997). *Salix ovalifolia* is able to tolerate moderate salinity as it exists in regions which flood at least yearly (during fall months and after senescence), but it is unclear what salinity threshold the dwarf shrub can compensate for.



One study found that increased salinity caused a decline in *Salix* species (Person & Ruess 2003). Future studies could incorporate salinization and sedimentation treatments to determine how sea level rise or more frequent flooding events could affect vegetation communities.

Another possible factor that we did not consider in our experiment is the effect of sea ice extent on growth patterns. A recent study found that a decline in the extent of sea ice caused a decline in the yearly growth of dwarf shrubs in the Arctic (Forchhammer 2017). Though many experimental studies have shown that warming increases the growth of shrubs, few have simultaneously considered the effect of sea ice decline (Girardin *et al.* 2014). Warming paired with declining sea ice can amplify moisture stress, thereby causing growth declines (Forchhammer 2017). Additionally, reduced coastal sea ice can cause warmer and wetter winters which lead to more frequent icing events, and consequently, browning of dwarf shrubs (Hansen *et al.* 2014). These studies suggest that climate change may have more complex interactive effects than warming which increases productivity in the Arctic. Future studies may consider the effect of reduced sea ice extent (as well as warming) on this vegetation community.

Simulated herbivory (clipping) decreased cover of both species, by removing vegetation. Though we do not present the data here, that cover reduction is correlated with reduced aboveground biomass and reduced C:N ratios of both species (Person *et al.* 2003; Van Der Wal & Brooker 2004; Elliott & Henry 2011; Falk *et al.* 2015). We also found that herbivory treatments maintained cover of the two species in amounts more similar to that of the current community, in both ambient and warmed temperatures. We

suggest that goose herbivores have a strong impact on this system, potentially enough to mediate some of the effects of warming (Post & Pedersen 2008; Olofsson *et al.* 2009; Kaarlejärvi *et al.* 2015). However, the Tutakoke river colony of black brant has been declining for the past two decades (Sedinger *et al.* 2016). It is unclear what is causing this decline. Current literature suggests a few possibilities: increased fox predation of nests due to fox populations becoming decoupled from natural prey (because of anthropogenic subsidies and less harsh winters), more frequent nest failure due to flooding, a limitation in winter forage (eelgrass), a decline in the quality of summertime forage, a shift toward nesting in locations further north such as the North Slope, fewer adult or fewer adult geese entering the breeding population due to high fitness costs (Ward *et al.* 2005; Flint, Meixell & Mallek 2014; Sedinger *et al.* 2016). Whatever the cause, population decline could result in reduced herbivory pressure that is insufficient to mediate warming in coastal regions. This in turn could reduce forage quality and be limiting to future population increase (Sedinger *et al.* 2016). However, recent surveys suggest that the number of emperor geese (*Chen canagica*), cackling geese (*B. canadensis minima*), and greater white-fronted geese (*Anser albifrons*) nesting near the Tutakoke river colony has increased (Jim Sedinger, personal communication). Recent literature has suggested that herbivores may play an important role in mitigating climate change effects by reducing the rate of shrubification in the Arctic (Post & Pedersen 2008; Olofsson *et al.* 2009; Kaarlejärvi *et al.* 2015). The other goose species could play an important role in maintaining herbivory pressure in the region. Future studies could simulate a range of herbivory pressures (light, average, and intense) under warmed conditions to determine

what intensity of herbivory pressure is required to maintain the current plant community and prevent a decline in forage quality. Such an experiment could be informative to managers' population goals for brant and other goose species in the Pacific flyway.

Finally, while dwarf shrub increase may be detrimental for some herbivores, it may be beneficial for others. The range and population of the Alaskan moose (*Alces alces*) has increased over the past century (Tape *et al.* 2016). However, the impacts of a larger moose population utilizing coastal regions in the Y-K delta has not been studied. Greater number of moose in this area could be beneficial for native subsistence hunters. However, if mammalian predators (such as grizzly bears) follow ungulate prey into coastal regions, the effect on nesting birds could be catastrophic. Artic foxes are capable of up to 80% nest predation in a season (Sedinger *et al.* 2016). A larger predator may have even more damaging effects (Campbell 1991). While an increase in shrub abundance in coastal systems may seem of minimal consequence, the implications of landscape level change may be far reaching. It is important for managers to understand implications (such as novel species moving in to the area) and consider the ability of herbivores to mitigate change when addressing management goals (Post & Pedersen 2008; Olofsson *et al.* 2009; Kaarlejärvi *et al.* 2015).

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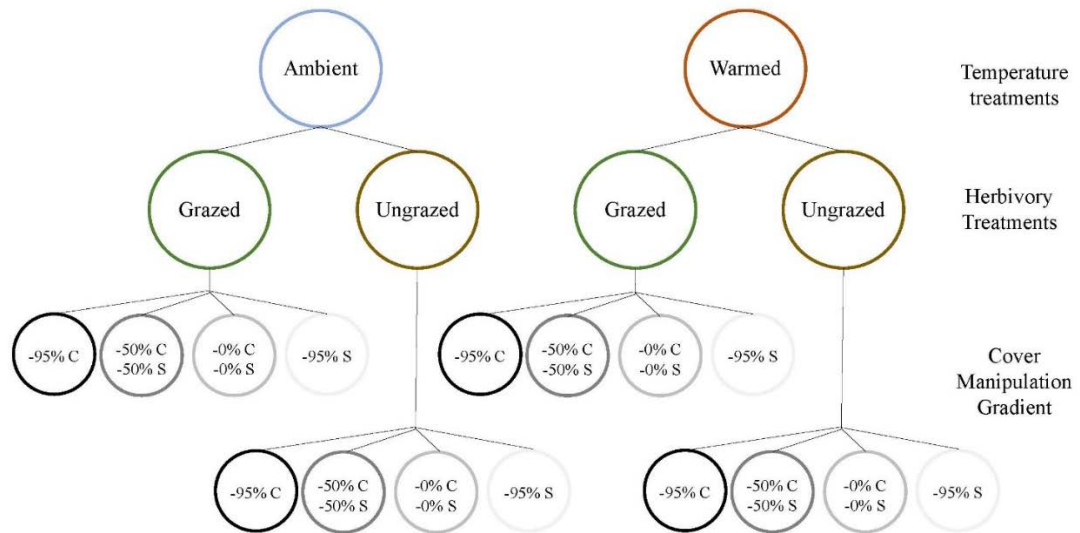
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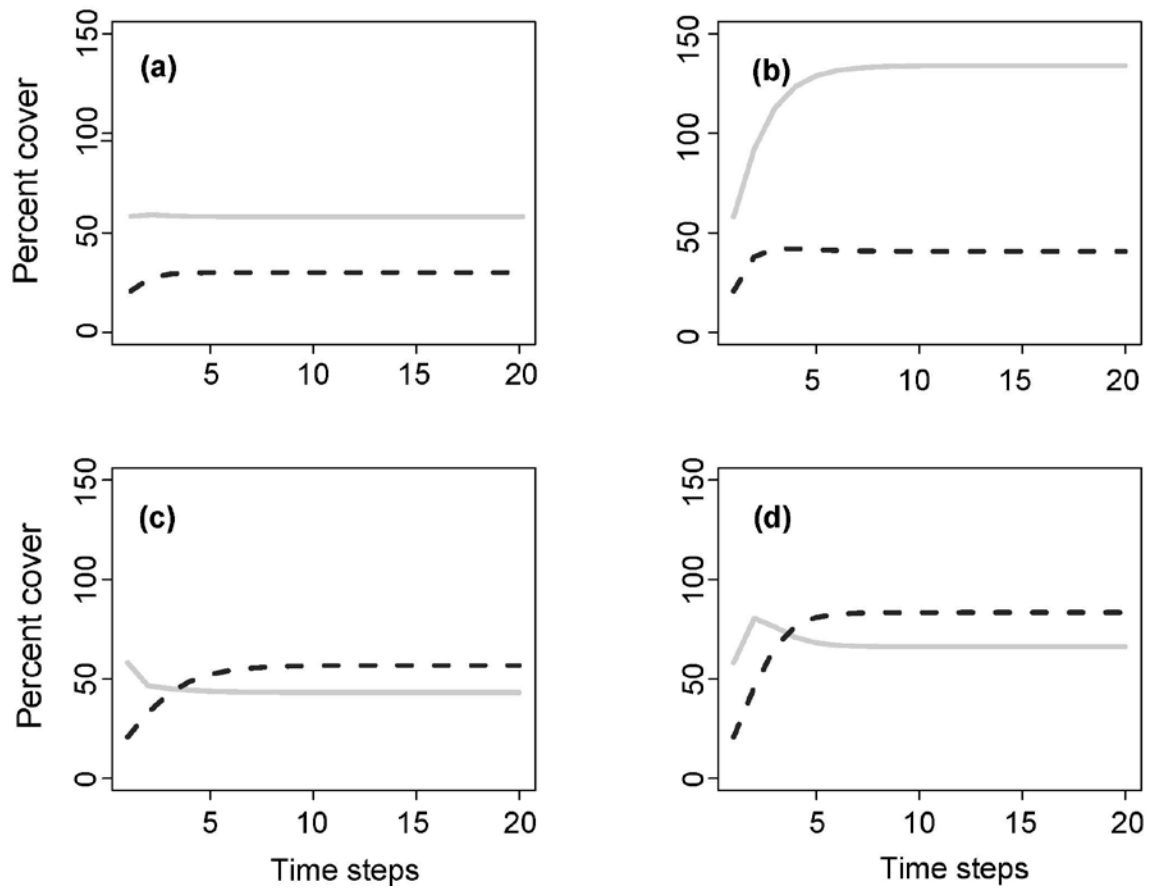
APPENDICES

**Table S1.** Relevant models from the literature suggested by Inouye 2001 and reparametrized by Hart & Marshall 2013 to include an explicit term for intraspecific competition (rather than a carrying capacity). The response variable for all models  $N_{i,t+1}$  when  $N_{i,t+1} = N_{i,t}f(X_t, Y_t)$ ,  $\lambda$  is the growth rate,  $\alpha_{ii}$  and  $\alpha_{ij}$  are intra and interspecific competition coefficients respectively,  $N_{i,t}$  and  $N_{j,t}$  are initial percent cover of the focal species and the competitor respectively, and  $b$  is a parameter that allows for a more flexible fit. Only models one, three, and four could be fit for both species. The rest failed to converge.

$f(X_t, Y_t)$
$\lambda e^{-\alpha_{ii}N_{i,t} - \alpha_{ij}N_{j,t}} *$
$\lambda / (1 + \alpha_{ii}N_{i,t} + \alpha_{ij}N_{j,t})$
$\lambda e^{-\alpha_{ii}\ln(N_{i,t}) - \alpha_{ij}\ln(N_{j,t})} *$
$1 + \lambda(1 - \alpha_{ii}N_{i,t} - \alpha_{ij}N_{j,t}) *$
$\lambda / (1 + N_{i,t}^{\alpha_{ii}} + \alpha_{ij}N_{j,t})$
$\lambda / 1 + (\alpha_{ii}N_{i,t} + \alpha_{ij}N_{j,t})^b$
$\lambda / (1 + \alpha_{ii}N_{i,t} + \alpha_{ij}N_{j,t})^b$



**Fig. S1.** Our experimental design contained of 5 replicates of 4 treatments created from the factorial combination of (+/-) warming and (+/-) grazing. Nested within each treatment were four possible cover manipulations to create a cover gradient for both species.



**Fig. S2.** We used models to predict the equilibrium cover of *Carex* (solid, light gray) and *Salix* (dashed, dark gray) for each of our treatment combinations. (a) corresponds to ambient, grazed, (b) to ambient, ungrazed, (c) to warmed, grazed, (d) to warmed, ungrazed. We tested the equilibrium outcomes of our models under a range of initial cover combinations: 1) 5% *Carex*, 95% *Salix* 2) 95% *Carex*, 5% *Salix*, 2) 50% *Carex*, 50% *Salix*, 4) and natural abundance 55% *Carex*, 37% *Salix*. Here, we only show the natural abundance as the initial condition because the same equilibrium was reached after 5-10 time steps, regardless of initial values.

## Supporting Information 1. Reproducible R code for analysis

```

#find and cite dataset at:
#Gray Carlson, L. (2017). Point-count cover of Carex ramenskii and Salix ovalifolia
under #warmed and grazed conditions. Yukon-Kuskokwim Delta, Alaska, 2015-2016
[Data set]. #Arctic Data Center. https://doi.org/10.18739/a2mp11
path.coverdata<-("C:\\Users\\grad\\Desktop") #please reset working directory for your
data source
setwd(path.coverdata)
cover<-read.csv("arctic-data.14103.1.csv",header=T) #import neighborhood
cover dataset from above citation
head(cover)
str(cover)

cover.frame<-data.frame(cover) #convert to a dataframe
c.cov<-
cover.frame[c("plot_num","warm_treatment","herb_treatment","Nct0","Nst0","Nct1")]
#create data frames with only data needed for each model
s.cov<-
cover.frame[c("plot_num","warm_treatment","herb_treatment","Nct0","Nst0","Nst1")]
Nct1<-c.cov$Nct1
Nct0<-c.cov$Nct0
Nst0<-c.cov$Nst0
c.cov$env.fac = as.factor(paste(c.cov$warm_treatment,c.cov$herb_treatment,sep = "."))
#add column containing factorial combination of warming + herbivory
Nst1<-s.cov$Nst1
s.cov$env.fac = as.factor(paste(s.cov$warm_treatment,s.cov$herb_treatment,sep = "."))
#add column containing factorial combination of warming + herbivory

#test models#
#####Model 2#####
###Carex Ricker 2###
carex.model2 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac] * exp(-
alpha.cc[env.fac]*Nct0 - alpha.cs[env.fac]*Nst0)),
data=c.cov,
start = list(lambda = c(5,5,5,5), alpha.cc = c(1,1,1,1), alpha.cs = c(0,0,0,0)),
algorithm = "port")
summary(carex.model2)

#structure is formula calling data from specified data frame
#[env.fac] term allows this param to vary by treatment ie amb/graz, amb/ungraz,
warm/graz, warm/ungraz

```

```
#start is a list of starting "guesses" for each parameter, modifying these (within reason)
does not alter parameter estimate (ie model will not converge if starting value is
10000000 but WILL be the same if you guess 10)
#algorithm, changing algorithm did not alter params or change coverage status
```

```
####Salix Ricker 2###
salix.model2 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac] * exp(-
alpha.ss[senv.fac]*Nst0 - alpha.sc[senv.fac]*Nct0)),
  data=s.cov,
  start = list(lambda = c(5,5,5,5), alpha.ss = c(1,1,1,1), alpha.sc = c(0,0,0,0)),
  algorithm = "port")
summary(salix.model2)
```

```
nls.control(maxiter = 1000) #increasing iterations to max did not allow convergence
#####Model 3#####
####Carex Ricker 3###
carex.model3 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]/(1 + alpha.cc[env.fac]*Nct0
+ alpha.cs[env.fac]*Nst0)),
  data=c.cov,
  start = list(lambda = c(11,6,9,4), alpha.cc = c(9,7,5,7), alpha.cs = c(1,0,0,0)),
  algorithm = "port")
summary(carex.model3) #convergence failure#
#changing starting value did not allow convergence
```

```
####Salix Ricker 3###
salix.model3 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]/(1 + alpha.ss[senv.fac]*Nst0
+ alpha.sc[senv.fac]*Nct0)),
  data=s.cov,
  start = list(lambda = c(5,5,5,5), alpha.ss = c(1,1,1,1), alpha.sc = c(0,0,0,0)),
  algorithm = "port")
summary(salix.model3) #convergence failure#
```

```
#####Model 4#####
####Carex Ricker 4###
carex.model4 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]*exp((-
alpha.cc[env.fac]*log(Nct0)-(alpha.cs[env.fac]*log(Nst0))))),
  data=c.cov,
  start = list(lambda = c(5,5,5,5), alpha.cc = c(1,1,1,1), alpha.cs = c(0,0,0,0)),
  algorithm = "port")
summary(carex.model4)
```

```
####Salix Ricker 4###
```



```

salix.model4 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]*exp((-
alpha.ss[senv.fac]*log(Nst0))-(alpha.sc[senv.fac]*log(Nct0))))),
  data=s.cov,
  start = list(lambda = c(5,5,5,5), alpha.ss = c(1,1,1,1), alpha.sc = c(0,0,0,0)),
  algorithm = "port")
summary(salix.model4)

#####Model 5#####
###Carex Ricker 5###
carex.model5 = nls(formula=Nct1 ~ Nct0*(1 + lambda[env.fac]*(1-
alpha.cc[env.fac]*Nct0-alpha.cs[env.fac]*Nst0)),
  data=c.cov,
  start = list(lambda = c(5,5,5,5), alpha.cc = c(1,1,1,1), alpha.cs = c(0,0,0,0)),
  algorithm = "port")
summary(carex.model5)

###Salix Ricker 5###
salix.model5 = nls(formula=Nst1 ~ Nst0*(1 + lambda[senv.fac]*(1-
(alpha.ss[senv.fac]*Nst0)-(alpha.sc[senv.fac]*Nct0))),
  data=s.cov,
  start = list(lambda = c(5,5,5,5), alpha.ss = c(1,1,1,1), alpha.sc = c(0,0,0,0)),
  algorithm = "port")
summary(salix.model5)

#####Model 6#####
###Carex Ricker 6###
carex.model6 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]/(1 +
Nct0^(alpha.cc[env.fac])+Nst0^(alpha.cs[env.fac]))),
  data=c.cov,
  start = list(lambda = c(11,6,9,4), alpha.cc = c(9,7,5,7), alpha.cs = c(1,0,0,0)),
  algorithm = "default",
  control = list(maxiter = 1000))
summary(carex.model6) #convergence failure#

salix.model6 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]/(1 +
Nst0^(alpha.ss[senv.fac])+Nct0^(alpha.sc[senv.fac]))),
  data=s.cov,
  start = list(lambda = c(11,6,9,4), alpha.ss = c(9,7,5,7), alpha.sc = c(1,0,0,0)),
  algorithm = "port",
  control = list(maxiter = 1000))
summary(salix.model6) #convergence failure#
#increased iterations or changing start valued did not allow convergence

#####Model 7#####

```

```

####Carex Ricker 7####
carex.model7 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]/1 +
(((alpha.cc[env.fac]*Nct0)+(alpha.cs[env.fac]*Nst0))^b)),
      data=c.cov,
      start = list(lambda = c(5,5,2,3), alpha.cc = c(3,3,2,3), alpha.cs = c(0,0,0,0), b
= 2),
      algorithm = "default")
summary(carex.model7)
##failed##

```

```

####Salix Ricker 7####
salix.model7 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]/1 +
(((alpha.ss[senv.fac]*Nst0)+(alpha.sc[senv.fac]*Nct0))^b)),
      data=s.cov,
      start = list(lambda = c(5,5,2,3), alpha.ss = c(3,3,2,3), alpha.sc = c(0,0,0,0), b
= 2),
      algorithm = "default")
summary(salix.model7)
##failed##
#increased iterations or changing start valued did not allow convergence, nor did
changing algorithm

```

```

#####Model 8#####
####Carex Ricker 8####
carex.model8 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]/(1 +
(alpha.cc[env.fac]*Nct0)+(alpha.cs[env.fac]*Nst0))^b[env.fac])),
      data=c.cov,
      start = list(lambda = c(5,5,2,3), alpha.cc = c(3,3,2,3), alpha.cs = c(0,0,0,0), b
= c(2,2,2,2)),
      algorithm = "default")
summary(carex.model8)
##failed##

```

```

####Salix Ricker 8####
salix.model8 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]/(1 +
(alpha.ss[senv.fac]*Nst0)+(alpha.sc[senv.fac]*Nct0))^b[senv.fac])),
      data=s.cov,
      start = list(lambda = c(5,5,2,3), alpha.ss = c(3,3,2,3), alpha.sc = c(0,0,0,0), b
= c(2,2,2,2)),
      algorithm = "default")
summary(salix.model8)
##failed##

```

```
#increased iterations or changing start valued did not allow convergence, nor did
changing algorithm
```

```
#install.packages("AICcmodavg")          #install this package if you do not already
have it, note this only works in version 3.3.3 or later
library(AICcmodavg)
```

```
###create candidate model list for getting AICc table###
```

```
Cand.c.mod  <- list()
Cand.c.mod[[1]] <- carex.model2
Cand.c.mod[[2]] <- carex.model4
Cand.c.mod[[3]] <- carex.model5
###create vector of the model names
cmod.name <- c("carex.model2","carex.model4","carex.model5")
```

```
###get AICc table for ranking predictive models-----
```

```
c.aictab<-aictab(cand.set = Cand.c.mod, modnames = cmod.name, second.ord = TRUE,
sort = TRUE)
print(c.aictab)
#write.csv(c.aictab,file = "carexmodelaic.csv",row.names = FALSE,col.names = TRUE)
```

```
###create candidate model list for getting AICc table###
```

```
Cand.s.mod  <- list()
Cand.s.mod[[1]] <- salix.model2
Cand.s.mod[[2]] <- salix.model4
Cand.s.mod[[3]] <- salix.model5
###create vector of the model names
smod.name <- c("salix.model2","salix.model4","salix.model5")
```

```
###get AICc table for ranking predictive models-----
```

```
s.aictab<-aictab(cand.set = Cand.s.mod, modnames = smod.name, second.ord = TRUE,
sort = TRUE)
print(s.aictab)
```

```
#write.csv(s.aictab,file = "salixmodelaic.csv",row.names = FALSE,col.names = TRUE)
```

```
#####
```

```
#for both C and S, model4 is the best fitting by AICc#
```

```
#####
```

```
#####LRT#####
```

```

#####likelihood ratio tests of reduced models#####

#Carex LRT#
#####Model 4#####
###Carex Ricker 4###
carex.model4 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]*exp((-
alpha.cc[env.fac]*log(Nct0))-(alpha.cs[env.fac]*log(Nst0)))),
  data=c.cov,
  start = list(lambda = c(5,5,5,5), alpha.cc = c(1,1,1,1), alpha.cs = c(0,0,0,0)),
  algorithm = "port")
summary(carex.model4)

# model which does not allow lambda to vary by treatment
carex.model4r1.1 = nls(formula=Nct1 ~ Nct0*(lambda*exp((-
alpha.cc[env.fac]*log(Nct0))-(alpha.cs[env.fac]*log(Nst0)))),
  data=c.cov,
  start = list(lambda = 1, alpha.cc = c(1,1,1,1), alpha.cs = c(0,0,0,0)),
  algorithm = "port")
summary(carex.model4r1.1)
#####tested model not varying lambda#####
anova(carex.model4,carex.model4r1.1)
Qcr1 = -2 * (logLik(carex.model4r1.1) - logLik(carex.model4))
df.Qcr1 = df.residual(carex.model4r1.1) - df.residual(carex.model4)
1 - pchisq(Qcr1, df.Qcr1)

# model which does not allow alpha.cc to vary by tx
carex.model4r2.2 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]*exp((-
alpha.cc*log(Nct0))-(alpha.cs[env.fac]*log(Nst0)))),
  data=c.cov,
  start = list(lambda = c(5,5,5,5), alpha.cc = 1, alpha.cs = c(0,0,0,0)),
  algorithm = "port")
summary(carex.model4r2.2)

#####tested model not varying alpha.cc#####
anova(carex.model4,carex.model4r2.2)
Qcr2 = -2 * (logLik(carex.model4r2.2) - logLik(carex.model4))
df.Qcr2 = df.residual(carex.model4r2.2) - df.residual(carex.model4)
1 - pchisq(Qcr2, df.Qcr2)

# model which does not allow alpha.cs to vary by treatment

```

```

carex.model4r3.3 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]*exp((-
alpha.cc[env.fac]*log(Nct0))-(alpha.cs*log(Nst0))))),
      data=c.cov,
      start = list(lambda = c(5,5,5,5), alpha.cc = c(1,1,1,1), alpha.cs = 0),
      algorithm = "port")
summary(carex.model4r3.3)
#####tested model not varying alpha.cs#####
anova(carex.model4,carex.model4r3.3)
Qcr3 = -2 * (logLik(carex.model4r3.3) - logLik(carex.model4))
df.Qcr3 = df.residual(carex.model4r3.3) - df.residual(carex.model4)
1 - pchisq(Qcr3, df.Qcr3)

```

```

#model which removed lambda
carex.model4r1 = nls(formula=Nct1 ~ Nct0*(exp((-alpha.cc[env.fac]*log(Nct0))-
(alpha.cs[env.fac]*log(Nst0))))),
      data=c.cov,
      start = list(alpha.cc = c(1,1,1,1), alpha.cs = c(0,0,0,0)),
      algorithm = "port")
summary(carex.model4r1)
#####tested model removing lambda#####
anova(carex.model4,carex.model4r1)

Qcr1 = -2 * (logLik(carex.model4r1) - logLik(carex.model4))
df.Qcr1 = df.residual(carex.model4r1) - df.residual(carex.model4)
1 - pchisq(Qcr1, df.Qcr1)

```

```

#model which removed alpha.cc
carex.model4r2 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]*exp((-
(alpha.cs[env.fac]*log(Nst0))))),
      data=c.cov,
      start = list(lambda = c(5,5,5,5), alpha.cs = c(0,0,0,0)),
      algorithm = "port")
summary(carex.model4r2)
#####tested model removing alpha.cc#####
anova(carex.model4,carex.model4r2)

Qcr2 = -2 * (logLik(carex.model4r2) - logLik(carex.model4))
df.Qcr2 = df.residual(carex.model4r2) - df.residual(carex.model4)
1 - pchisq(Qcr2, df.Qcr2)

```

```

#model which removed alpha.cs

```

```

carex.model4r3 = nls(formula=Nct1 ~ Nct0*(lambda[env.fac]*exp((-
alpha.cc[env.fac]*log(Nct0))))),
  data=c.cov,
  start = list(lambda = c(5,5,5,5), alpha.cc = c(1,1,1,1)),
  algorithm = "port")
summary(carex.model4r3)
#####tested model removing alpha.cs#####
anova(carex.model4,carex.model4r3)

```

```

Qcr3 = -2 * (logLik(carex.model4r3) - logLik(carex.model4))
df.Qcr3 = df.residual(carex.model4r3) - df.residual(carex.model4)
1 - pchisq(Qcr3, df.Qcr3)

```

#Salix LRT#

```

####Salix Ricker 4###
salix.model4 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]*exp((-
alpha.ss[senv.fac]*log(Nst0))-(alpha.sc[senv.fac]*log(Nct0))))),
  data=s.cov,
  start = list(lambda = c(5,5,5,5), alpha.ss = c(1,1,1,1), alpha.sc = c(0,0,0,0)),
  algorithm = "port")
summary(salix.model4)

```

```

#model which did not allow lambda to vary by treatment
salix.model4r1.1 = nls(formula=Nst1 ~ Nst0*(lambda*exp((-
alpha.ss[senv.fac]*log(Nst0))-(alpha.sc[senv.fac]*log(Nct0))))),
  data=s.cov,
  start = list(lambda = 1, alpha.ss = c(1,1,1,1), alpha.sc = c(0,0,0,0)),
  algorithm = "port")
summary(salix.model4r1.1)
#tested model not varying lambda
anova(salix.model4,salix.model4r1.1)
Qsr1 = -2 * (logLik(salix.model4r1.1) - logLik(salix.model4))
df.Qsr1 = df.residual(salix.model4r1.1) - df.residual(salix.model4)
1 - pchisq(Qsr1, df.Qsr1)

```

#model which did not allow alpha.ss to vary by treatment

```

salix.model4r2.2 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]*exp((-
alpha.ss*log(Nst0))-(alpha.sc[senv.fac]*log(Nct0))))),
      data=s.cov,
      start = list(lambda = c(5,5,5,5), alpha.ss = 1, alpha.sc = c(0,0,0,0)),
      algorithm = "port")
summary(salix.model4r2.2)
#####tested model not varying alpha.ss#####
anova(salix.model4,salix.model4r2.2)
Qsr2 = -2 * (logLik(salix.model4r2.2) - logLik(salix.model4))
df.Qsr2 = df.residual(salix.model4r2.2) - df.residual(salix.model4)
1 - pchisq(Qsr2, df.Qsr2)

```

```

#model which did not allow alpha.sc to vary by treatment
salix.model4r3.3 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]*exp((-
alpha.ss[senv.fac]*log(Nst0))-(alpha.sc*log(Nct0))))),
      data=s.cov,
      start = list(lambda = c(5,5,5,5), alpha.ss = c(1,1,1,1), alpha.sc = 0),
      algorithm = "port")
summary(salix.model4r3.3)
#####tested model not varying alpha.sc#####
anova(salix.model4,salix.model4r3.3)
Qsr3 = -2 * (logLik(salix.model4r3.3) - logLik(salix.model4))
df.Qsr3 = df.residual(salix.model4r3.3) - df.residual(salix.model4)
1 - pchisq(Qsr3, df.Qsr3)

```

```

#####model reduced by removing lambda#####
salix.model4r1 = nls(formula=Nst1 ~ Nst0*(exp((-alpha.ss[senv.fac]*log(Nst0))-
(alpha.sc[senv.fac]*log(Nct0))))),
      data=s.cov,
      start = list(alpha.ss = c(1,1,1,1), alpha.sc = c(0,0,0,0)),
      algorithm = "port")
summary(salix.model4r1)
#####teste model removing lambda#####
anova(salix.model4,salix.model4r1)

Qsr1 = -2 * (logLik(salix.model4r1) - logLik(salix.model4))
df.Qsr1 = df.residual(salix.model4r1) - df.residual(salix.model4)
1 - pchisq(Qsr1, df.Qsr1)

```

```

#####model reduced by removing alpha.ss#####

```

```

salix.model4r2 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]*exp(-
(alpha.sc[senv.fac]*log(Nct0))),
      data=s.cov,
      start = list(lambda = c(5,5,5,5),alpha.sc = c(0,0,0,0)),
      algorithm = "port")
summary(salix.model4r2)
#####tested model removing alpha.sc#####
anova(salix.model4,salix.model4r2)

Qsr2 = -2 * (logLik(salix.model4r2) - logLik(salix.model4))
df.Qsr2 = df.residual(salix.model4r2) - df.residual(salix.model4)
1 - pchisq(Qsr2, df.Qsr2)

#####model reduced by removing alpha.sc#####
salix.model4r3 = nls(formula=Nst1 ~ Nst0*(lambda[senv.fac]*exp((-
alpha.ss[senv.fac]*log(Nst0))),
      data=s.cov,
      start = list(lambda = c(5,5,5,5), alpha.ss = c(1,1,1,1)),
      algorithm = "port")
summary(salix.model4r3)

#####tested model removing alpha.sc#####
anova(salix.model4,salix.model4r3)

Qsr3 = -2 * (logLik(salix.model4r3) - logLik(salix.model4))
df.Qsr3 = df.residual(salix.model4r3) - df.residual(salix.model4)
1 - pchisq(Qsr3, df.Qsr3)
#If the LRT p-value is less than your alpha level (usually 0.05 or 0.10),
#you conclude that the unconstrained 2-parameter model offers significantly
#better goodness-of-fit than the 1-parameter model for your sample data.

#####END OF LRT#####

#calculate confidence intervals of parameters#
confint(carex.model4)
confint(salix.model4)

#Calculate equilibrium abundance based on model parameters#

#####FULL EFFECT#####
#####

```



#ambient,grazed#

lambda.c = 0.625

#params specific for each envt

lambda.s = 0.355

alpha.cc = 0.763

alpha.ss = 0.791

alpha.cs = 0.045

alpha.sc = 0.207

#equilibrium solution

$\ln.Ns1 = (\alpha.cc * (\log(\lambda.s))) / ((\alpha.ss * \alpha.cc) - (\alpha.sc * \alpha.cs))$

$\exp(\ln.Ns1)$

#final cover of Salix at equilibrium in ambient, grazed

$\ln.Nc1 = (\alpha.ss * (\log(\lambda.c))) / ((\alpha.cc * \alpha.ss) - (\alpha.cs * \alpha.sc))$

$\exp(\ln.Nc1)$

#final cover of Carex at equilibrium in ambient, grazed

#####

#ambient,ungrazed

lambda.c = 1.144

lambda.s = 0.534

alpha.cc = 0.534

alpha.ss = 0.740

alpha.cs = 0.023

alpha.sc = 0.126

$\ln.Ns1 = (\alpha.cc * (\log(\lambda.s))) / ((\alpha.ss * \alpha.cc) - (\alpha.sc * \alpha.cs))$

$\exp(\ln.Ns1)$

#final cover of Salix at equilibrium in ambient, ungrazed

$\ln.Nc1 = (\alpha.ss * (\log(\lambda.c))) / ((\alpha.cc * \alpha.ss) - (\alpha.cs * \alpha.sc))$

$\exp(\ln.Nc1)$

#final cover of Carex at equilibrium in ambient, ungrazed

#####

#warm,grazed

lambda.c = 0.381

lambda.s = 0.772

alpha.cc = 1.087

alpha.ss = 0.464

alpha.cs = 0.097  
alpha.sc = -0.005

$\ln.Ns1 = (\alpha.cc * (\log(\lambda.s))) / ((\alpha.ss * \alpha.cc) - (\alpha.sc * \alpha.cs))$   
exp(ln.Ns1)  
#final cover of Salix at equilibrium in warm,grazed

$\ln.Nc1 = (\alpha.ss * (\log(\lambda.c))) / ((\alpha.cc * \alpha.ss) - (\alpha.cs * \alpha.sc))$   
exp(ln.Nc1)  
#final cover of Carex at equilibrium in warm,grazed

#####

#warm,ungrazed  
lambda.c = 0.704  
lambda.s = 0.934  
alpha.cc = 1.087  
alpha.ss = 0.578  
alpha.cs = 0.162  
alpha.sc = -0.089

$\ln.Ns1 = (\alpha.cc * (\log(\lambda.s))) / ((\alpha.ss * \alpha.cc) - (\alpha.sc * \alpha.cs))$   
exp(ln.Ns1)  
#final cover of Salix at equilibrium in warm,ungrazed

$\ln.Nc1 = (\alpha.ss * (\log(\lambda.c))) / ((\alpha.cc * \alpha.ss) - (\alpha.cs * \alpha.sc))$   
exp(ln.Nc1)  
#final cover of Carex at equilibrium in warm,ungrazed

## Supporting Information 2. Algebraic equilibrium solution to best fit model

*Original Equations:*

$$\frac{N_{c,t+1}}{N_{c,t}} = \lambda_c e^{-\alpha_{cc}\ln(N_{c,t}) - \alpha_{cs}\ln(N_{s,t})a_{cc}}$$

$$\frac{N_{s,t+1}}{N_{s,t}} = \lambda_s e^{-\alpha_{ss}\ln(N_{s,t}) - \alpha_{sc}\ln(N_{c,t})a_{ss}}$$

*Rearranged:*

$$\ln \frac{1}{\lambda_c} = -a_{cc} \ln N_{c,t} - a_{cs} \ln N_{s,t} \Rightarrow \ln \lambda_c = a_{cc} \ln N_{c,t} + a_{cs} \ln N_{s,t}$$

$$\ln \frac{1}{\lambda_s} = -a_{sc} \ln N_{c,t} - a_{ss} \ln N_{s,t} \Rightarrow \ln \lambda_s = a_{sc} \ln N_{c,t} + a_{ss} \ln N_{s,t}$$

$$\ln N_{c,t} = \frac{1}{a_{cc}} (\ln \lambda_c - a_{cs} \ln N_{s,t})$$

$$\ln N_{s,t} = \frac{1}{a_{ss}} (\ln \lambda_s - a_{sc} \ln N_{c,t})$$

*Substitution:*

$$\ln N_{s,t} = \frac{1}{a_{ss}} \left( \ln \lambda_s - \frac{a_{sc}}{a_{cc}} (\ln \lambda_c - a_{cs} \ln N_{s,t}) \right)$$

$$\ln N_{s,t} \left( 1 - \frac{a_{sc} a_{cs}}{a_{ss} a_{cc}} \right) = \frac{1}{a_{ss}} \ln \lambda_s$$

$$\ln N_{s,t} = \frac{\frac{1}{a_{ss}} \ln \lambda_s}{1 - \frac{a_{sc} a_{cs}}{a_{ss} a_{cc}}}$$

*Solution:*

$$\ln N_{s,t} = \frac{a_{cc} \ln \lambda_s}{a_{ss} a_{cc} - a_{sc} a_{cs}}$$

*Therefore:*

$$\ln N_{c,t} = \frac{a_{ss} \ln \lambda_c}{a_{cc} a_{ss} - a_{cs} a_{sc}}$$

We compared our analytical solutions to simulation models and tested for sensitivity to initial conditions. In the simulations, we evaluated the outcome using our parameterized models for each treatment at a range of starting values (5-95% cover), over 20 time steps. We stopped at 20 time steps because models reached equilibrium after 5-10 time steps and equilibrium did not change beyond that, tested up to 100 time steps.