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PHENOLOGY IN A CHANGING ARCTIC: LINKING TROPHIC INTERACTIONS
ACROSS SCALES

A Dissertation in

Ecology

by

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ABSTRACT

Phenology - the study of the timing of periodic biotic events or processes - is an integrative science that links the phenotypes of individual organisms with forces of global change. In recent decades it has evolved from an obscure pursuit of naturalists into a critical tool for evaluating the ecological consequences of climate change. Beyond simply reflecting climatic variability, phenology acts as a driver of ecological dynamics and a source of insight about an organisms' evolutionary history.

The proximal drivers of phenology vary among species, sometimes resulting in asynchronous phenological responses to shared changes in climate. The match/mismatch hypothesis attributes changes in reproductive success to phenological asynchrony between trophic levels when asynchrony arises during sensitive periods of a consumer/predator life history progression. In *chapter 2* I explore the genesis of this concept, review its contemporary relevance, and suggest avenues of future research that I explore in more detail in later chapters.

No global region is warming faster than the Arctic, and widespread ecological perturbations have already been documented throughout high latitudes. Combining traditional field observations, novel phenological monitoring techniques, and data from a long-term study of tundra ecology, I examine how phenological dynamics link ecological processes across trophic levels and spatial scales in Arctic West Greenland. In *chapter 3* I test predictions about how consumer reproductive strategies and directional changes in resource phenology interact to differentially affect the reproductive performance of two Arctic ungulate species.

Sea ice loss is a broad scale abiotic driver of regional warming in the Arctic, but the indirect ecological consequences of these dynamics are poorly studied in terrestrial systems. In *chapter 4* I identify a sea ice signal in the terrestrial phenological dynamics of plant phenology and herbivore reproductive performance. These findings suggest sea ice loss may have more wide reaching impacts on terrestrial Arctic ecology than are currently appreciated.

Spatial patterns of phenological dynamics are relevant to ecological processes across multiple spatial scales, but often information on plant phenology is derived solely from localized vegetation plots or broad scale satellite derived metrics. In *chapter 5* I explore landscape scale variability in plant phenology, its drivers, and evidence for scale dependency within and between years. I do so using a novel quantitative dataset derived from a network of time-lapse cameras distributed across the focal tundra landscape. Scale dependent dynamics were identified in metrics of phenological variability and landscape drivers of this variability, results that suggest traditional data sources may be insufficient to understand landscape-scale consequences of ongoing rapid changes in Arctic plant phenology.

TABLE OF CONTENTS

List of Figures	vi
List of Tables	xv
Acknowledgments.....	xviii
CHAPTER 1 – General Overview.....	1
References.....	7
CHAPTER 2 - Climate change, phenology, and the nature of consumer-resource interactions: Advancing the Match/Mismatch Hypothesis	12
Abstract	13
Main Text.....	14
Figures	34
References.....	38
CHAPTER 3 – Capital and income breeding traits differentiate trophic match-mismatch dynamics in large herbivores	48
Abstract.....	49
Introduction.....	50
Methods.....	52
Results.....	55
Discussion.....	57
Figures and Tables	61
References.....	70
CHAPTER 4 – Advancing plant phenology and reduced herbivore production in a terrestrial system associated with sea ice decline	78
Abstract/Introduction	79
Results.....	80
Discussion.....	83
Methods.....	85
Figures and Tables	91
References.....	99
CHAPTER 5 – Spatial variability, drivers, and scale-dependency of tundra greenup phenology at a landscape extent	105
Abstract.....	106
Introduction.....	106
Methods.....	111
Results	123
Discussion.....	128
Figures and Tables	133
References.....	164

LIST OF FIGURES

Figure 2.1. The temporal mismatch hypothesis. The abundance of consumers and resources are shown as distributions in time. The relative overlap between consumer and resources varies with resource phenology and results either in a match and high consumer population recruitment (light shading), or a mismatch with low consumer population recruitment (dark shading). Modified from Durant <i>et al.</i> (2007)	34
Figure 2.2. Factors which may affect the degree of match/mismatch independent of a shift in the peak timing of resource abundance. A shift in consumer or resource abundance (a), or temporal variance (a, b) about the peak can conceptually limit or magnify the effects of temporal trophic mismatch. Reproduced from Miller-Rushing <i>et al.</i> (2010).	35
Figure 2.3. Conceptual diagram demonstrating how both the type (a) and strength (b) of species interactions may change over time as a consequence of differential shifts in the phenology of ontogeny. Shading represents the transition in type (a) or strength (b) of an interaction. For example, a hypothetical species A may switch from consumer of species B to its competitor, or even a prey item for species B as a function of the relative timing of growth between the two species (a). Similarly, a differential timing of growth between interacting species C and D can alternately ease or strengthen competition (b). Reproduced from Yang and Rudolf (2010)	36

Figure 3.1. Match-mismatch framework adjusted by reproductive strategy. The match-mismatch framework depicted above was modified to display the difference in exogenous (i.e. environmental) resource acquisition requirements of capital and income breeders during their breeding period. Endogenous (i.e. stored energetic capital) reproductive resource stores and costs are not pictured. Match and mismatch scenarios for income and capital breeders alternate by panel. Panel **a** shows a temporal match between the peak environmental resource needs of income breeders with environmental resource availability/quality. It also depicts a temporal ‘mismatch’ between the peak environmental resource needs of capital breeders and available environmental resources. These scenarios are reversed in panel **b**. Note the contrasts in energetic mismatch (non-overlapping areas) between capital breeders and environmental resources (panel a – minimal) and income breeders and environmental resources (panel b – extensive)61

Figure 3.2. Variation in herbivore calving and vegetation phenology. a.) ‘Caribou’ and ‘Vegetation’ show the range, quartiles, and median of the date of 50% caribou calf births and date of 50% plant species emergent respectively from the years 1993, 2002-2011. ‘Muskoxen’ is a depiction of the approximate calving period of muskoxen at this site. A conservative end-date of muskox calving was selected May 13 (Day of Year 133). Vertical dotted lines signify the first day of May and June (non-leap years). b.) a 1:1 graph of caribou calving phenology vs. vegetation phenology. If caribou calving phenology consistently tracked vegetation phenology these points would fall on the 1:1 line.....63

Figure 3.3. Variation in calf production for muskoxen and caribou in the Kangerlussuaq population from 2002-2011 (years with observations for both species). Boxplots depict the range, quartiles, and median of calf production in each population64

Figure 3.4. Relating trophic mismatch and population abundance to calf production. Each panel shows the relationship between herbivore production and the population specific index of trophic mismatch in immediate (a,c) or previous (b,d) years after accounting for the effect of population abundance in the immediate year. Panels showing lagged effects of trophic mismatch contain two fewer data points (no 1993, 2002) due to analytical requirements for including the lagged effect. Subsetting the non-lagged panels to the same data series resulted in nearly identical relationships to those depicted here (Supplementary Table 3.A). Lines represent significant partial regression fits. Panel **a.** and **b.** show that caribou calf production is closely related to immediate mismatch conditions, whereas panels **c.** and **d.** demonstrate that muskoxen are more sensitive to the lagged consequences of mismatch65

Figure 4.1. Monthly Arctic Sea Ice Extent Index anomalies. Anomalies calculated from 1979-2011 mean are color coded by season (winter and spring: Dec –May; summer and autumn: Jun – Nov). The rate of decline in monthly Arctic sea ice extent over this time period increased significantly in the summer and autumn months (red dashed) beginning in 2000 (95% CI: 1997-2002)91

Figure 4.2. Long term differential response between trophic levels to diminishing

Arctic sea ice. Panel a. Time series of observed (black triangles, black line) and predicted (gray lines) timing of 50% plant species emergence at the study site near Kangerlussuaq, Greenland, based on January (or February) and June multiple regression ($y = \beta_0 + \beta_1\text{Jan(or Feb)E} + \beta_2\text{JunE} + \epsilon$; where y = date of 50% plant species emergence in year t , Jan(or Feb)E = January (or February) sea ice extent [10^6 km^2] in year t , JunE = June Sea Ice Extent [km^2] in year t). 1993 (red triangle) was not included in the parameterization of the model, but is plotted in panel a to show the minimal difference between observed and predicted values for that year. The gap in the January and June modeled phenology series reflects a gap in the satellite based sea ice extent record (1988). Panel b. Observed dates of 50% caribou calves born at the study site near Kangerlussuaq, Greenland (black circles, solid black regression line) plotted over the same phenology models as panel a. These time series document a divergence in the phenologies of caribou and the plant community in recent years, but also demonstrate a sustained flip in the timing of plant growth relative to herbivore parturition since the year 2000, a change driven primarily by earlier plant phenology relative to the comparatively fixed timing of caribou calving.....92

Figure 4.3. Vegetation phenology models informed by temperature and sea ice

metrics at local and broad scales. Each panel depicts the best-fit phenology model for a temporal or spatial scale of abiotic predictor(s). Predicted values of the timing of 50% plant species emergence are plotted against observed values from the study site. Model fits are organized in rows by local temperature (top row – 2 temporal scales), sea ice

cover (center row – two spatial scales), and Arctic-wide temperature (bottom row – 2 temporal scales). The dashed line in each panel depicts the 1:1 relationship between predicted and observed values. All panels used models parameterized with data from 2002-2011 (black circles) except panel d. where no 2011 data was yet available. Red circles represent data from 1993 not used in model parameterization. Abiotic predictors identified for each best-fit model scale are as follows: panel a. May mean monthly temperature from Kangerlussuaq, Greenland; panel b. Kangerlussuaq, Greenland Summer Warmth Index (SWI) [i.e. thawing degree months] in the current year of plant emergence; panel c. January and June arctic sea ice extent; panel d. is the Davis Strait/Baffin Bay regional sea ice extent in June of the year of plant emergence; panel e. Arctic-wide SWI of the year prior to plant emergence; panel f. April Arctic-wide mean monthly temperature94

Figure 4.4. Correlations between sea ice and inland temperature. Pearson's r correlation coefficients between linearly detrended local mean monthly temperature near the study site in Kangerlussuaq, Greenland and a.) Arctic-wide sea ice extent or b.) regional Baffin Bay/Davis Strait sea ice extent. Correlations between ice extents from the months that precede each monthly mean temperature value are included for the calendar year up to and including June, the month when caribou calving and midpoint of the plant growing season occurs96

Figure 4.5. Reproductive consequences of trophic mismatch. Panels a and b. The relationships between the magnitude of trophic mismatch, i.e. the percentage of plant

species emergent at the date of 50% caribou calves born, and early calf mortality (a) or caribou calf production (b) at the study site. Filled circles were calculated using data from the 11 years of the authors' long term observational study, whereas open circles depict empirical records of caribou reproductive performance from 1979 in relation to sea-ice informed estimates of trophic mismatch in that year. The lack of satellite derived sea ice data prior to 1979 prevented the inclusion of the caribou data from 1977 and 1978 that are shown in Figure 2b. Panel c. The relationship between the observed trophic mismatch index and observed dates of 50% plant species emergence at the study site. Earlier plant emergence results in increasing mismatch with the timing of offspring production by caribou, a period of critically high resource demand ^{28,29,44}. Panel d. Relationship between the original trophic mismatch index derived from plot-based vegetation phenology and the trophic mismatch index derived from a sea-ice only model estimate of vegetation phenology. The year 2005, circled in red, was characterized by a severe caterpillar outbreak ²⁷, when plant phenology was anomalously delayed by defoliation, resulting in lower plot-derived mismatch in that year97

Figure 5.1 Distribution of camera sites and corresponding MODIS pixels. a. Site locations are overlaid on a digital elevation model enhanced with a hill shade effect to delineate the topographic variability of the study region. b.-d. show representative grain-size approximations, where the dark blue rhombus in b. represents a MODIS pixel, the light blue shaded area in c. represents a localized mixed-species community, and d. represents uniform composition graminoid (pink) and *Betula* (turquoise) patches.....134

Figure 5.2 Density plots of the timing of snowmelt and peak rate of greenup across all sites for all vegetation indices overlaid with the seasonal progression of thawing degree days (TDD)136

Figure 5.3 Across site variation in the timing of leaf onset within and between years for the a.) PlantCam *sGcc*, and b.) MODIS NDVI datasets137

Figure 5.4 Landscape greenup profiles and model-parameter covariation with landscape factors at different grains and in years with contrasting abiotic conditions. The left column contains models containing data from 2012 and the right from 2013. The population-level mean logistic fit is color-coded by dataset (green - PlantCam *sGcc*; orange - MODIS *sNDVI*) and the site-specific fits are plotted in gray over the VI data points in black. Second-level model fits of logistic parameters to landscape covariates are plotted, when present in the best-fit model, as subpanels adjacent to their corresponding lower-level model. Second-level fits to the leaf onset (b_i) are plotted with squares and a red hierarchical regression line, and fits to the growing season rate parameter (a_i) are plotted with triangles and a blue hierarchical regression line. Squares and triangles are posterior means and vertical bars are 90% CIs, shaded areas around hierarchical regression fitted lines are 90% credible regions. Panel a. characterizes the timing, duration, and heterogeneity of the greenup season measured at the community-grain (individual PlantCam FOVs) across the extent of the study area. The upper left subpanel a. depicts the positive relationship between later timing of leaf onset and increasingly north-facing landscape aspects. The lower right subpanel a. depicts the

positive relationship between the later timing of leaf onset and increasingly east-facing landscape aspects. Panels b-d. follow this basic layout. The second-level model in the upper left of panel b. depicts the positive relationship between longer greenup season and increasing TWI, whereas the second-level model plot in the lower-right of panel b. indicates shorter length of the greenup season with more northerly facing site aspect. The second-level model fit in the lower-right of panel d. indicates a longer greenup season with increasing site. For site parameters for all models, see Supp Tables 5.2-5.11138

Figure 5.5 Heterogeneity of cross scale 1:1 plots of greenup profiles (5% to 95% of logistic fits). The left column represents comparisons from 2012, and the right from 2013. Panels a and b depict the cross-grain bias between community level models (PlantCam FOVs) and local landscape level models (MODIS Vis). Panels c and d depict seasonal bias between functional-group patches and the local community grain, whereas panels e-h relate greenup patterns from uniform functional group vegetation patches to local landscape greenup curves.....140

Figure 5.6. Landscape greenup profiles and model-parameter covariation with landscape factors at the grain of *Betula nana* (light blue) and graminoid (yellow) patches across the study region in years with contrasting abiotic conditions. Subplot formatting is consistent with Figure 5.4. For site parameters for all models, see Supp Tables 2-11.....142

Supplementary Figure 5.S1. Relationship between timing of first snowmelt and a. elevation and b. degree of north facing aspect in 2012 and 2013.....145

Supplementary Figure 5.S2. Across site variation in the timing of leaf onset between and within years for MODIS *Gcc* dataset146

Supplementary Figure 5.S3. Landscape greenup profiles and model-parameter covariation with landscape factors for MODIS *Gcc* (orange) dataset across the study region in years with contrasting abiotic conditions. Subplot formatting is consistent with Figure 4. For site parameters for all models, see Supp Tables 5.2-5.11.....147

LIST OF TABLES

Table 3.1. A summary of the trait and other local-population characteristics identified in the literature review that informed our a priori classification of West Greenland caribou and muskoxen as income and capital breeders, respectively.....66

Table 3.S1. Trophic Mismatch and Abundance Models. CP and MP are species-specific calf ratios at time t, tmm is the species-specific index of trophic mismatch at lag t, abund is species-specific abundance at the breeding ground at lag t. The designation (sub) indicates analyses with subset of data (excluding 1993,2002) to allow for goodness of fit comparison with analyses where response years were sacrificed to explore lagged effects. * $p \leq 0.1$, ** $p \leq 0.05$ 67

Table 3.S2. Temporal Trends in Response and Predictor Variables. Temporal trends in response and predictor variables were assessed by regressing the variable in question against year using data from 2002-2011 and by examining model significance. * $p \leq 0.1$, ** $p \leq 0.05$ 68

Table 3.S3: Trophic Mismatch and Abundance Models with Detrended Data. CP and MPd (muskox detrended by year) are species-specific calf ratios at time t, tmmd is the detrended (by year) species-specific index of trophic mismatch at lag t, abund is species-specific abundance at the breeding ground at lag t. The designation (sub) indicates analyses with subset of data (excluding 1993, 2002) to allow for goodness of fit

comparison with analyses where response years were sacrificed to explore lagged effects.

* $p \leq 0.1$, ** $p \leq 0.05$ 69

Table 5.1 Mean monthly temperature (°C) from the local meteorological station.....142

Table 5.2 Mean and standard deviations of greenup season characteristics at different grains and vegetation indices across all camera sites. MODIS samples were subsetted to correspond with annual number of functional camera sites (2012 $n=41$, 2013 $n=27$).....143

Supplementary Table 5.S1. Summary of landscape predictors of greenup phenology in each year, vegetation index, and dataset subset. We report the landscape covariates from the best 2 parameter (Inflection and Rate) logistic model for each subset, including posterior means, 90% credible intervals, and the probability that the direction of the posterior mean matches its sign (positive or negative).....148

Supplementary Table 5.S2. 2012 PC Community FOV Model Output.....149

Supplementary Table 5.S3. 2013 PC Community FOV Model Output.....150

Supplementary Table 5.S4. 2012 MODIS sNDVI Model Output.....151

Supplementary Table 5.S5. 2013 MODIS sNDVI Model Output.....153

Supplementary Table 5.S6. 2012 MODIS sGcc Model Output155

Supplementary Table 5.S7. 2013 MODIS sGcc Model Output157

Supplementary Table 5.S8. 2012 PC sGcc *Betula* Model Output.....159

Supplementary Table 5.S9. 2013 PC sGcc *Betula* Model Output.....161

Supplementary Table 5.S10. 2012 PC <i>sGcc</i> Graminoid Model Output.....	162
Supplementary Table 5.S11. 2013 PC <i>sGcc</i> Graminoid Model Output.....	164

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Chapter 1 - General Overview

Phenology - the timing of periodic biotic events or processes, like reproduction, migration, or growth (Schwartz 2003, Post 2013, Richardson et al. 2013, Wolkovich et al. 2014) - is tied to forces of global change, but reflected in the phenotypes of individual organisms. Phenological traits, and their year to year variability or lack thereof, reflect the historical context in which organisms evolved, and can provide insights into how limited resources are partitioned in dynamic environments among diverse species (Williams 1966). In highly seasonal regions like the Arctic, niche axes are constrained, both directly and indirectly, by the seasonal timing of extreme abiotic conditions that limit the availability of resources required for growth, reproduction, and somatic maintenance throughout much of the year. Organisms in these regions have adapted to these seasonal challenges by timing their life-history progression to coincide with and/or respond to the brief annual pulse of increased solar radiation and its subsequent effects on temperature and resource availability (Post 2013). As a consequence, growth and reproduction are, to some extent, temporally synchronized not only within species, but also within and across trophic levels during the few weeks each year that correspond with Arctic spring and summer. This temporal pulse of productivity across all trophic levels reflects a strong bottom-up influence on the timing of growth and reproduction in Arctic species, and its subsequent influences on the structure and function of Arctic ecosystems.

Historically, phenology was considered an obscure natural history pursuit of farmers and amateur naturalists, a pastime that predated even the modern concept of science (Aono and Kazui 2008, Tooke and Battey 2010). In recent decades, however, phenology has emerged as a critical tool for evaluating and understanding the ecology of

climate change (Parmesan 2006, Richardson et al. 2013). Among all global regions, none are warming at the rate of the Arctic (Stocker et al. 2013), and with widespread ecological responses already identified and further forecast, it may well act as a ‘bellwether’ of ecological changes to come in other regions (Meltotte et al. 2008, Post et al. 2009).

In the context of climate change research, phenology has matured from a means of documenting ecological responses to warming, to that of an interdisciplinary science that considers the role of phenology as both an integrator and driver of ecological dynamics (Post 2013, Wolkovich et al. 2014). This has driven a shift away from studies that only document climate-driven shifts in phenology with respect to calendar dates, to those that place greater emphasis on understanding these shifts in the context of those experienced by other organisms within and among trophic levels and across spatial scales (Visser and Both 2005) - goals I pursue in the chapters that follow.

While nearly all species in highly seasonal environments grow and reproduce during annual periods when abiotic constraints on niche breadth are relaxed, variability in phenology at finer temporal resolutions may still markedly influence selective pressures on Arctic organisms (Hoye et al. 2013, Iler et al. 2013). Some of this variability can be attributed to the expression of life-history strategies seeking release from biotic pressures, like competition and/or predator avoidance (Visser et al. 2004, Miller-Rushing et al. 2010, Schindler et al. 2015). Over many generations, tradeoffs in the selective pressures mediated by both abiotic and biotic forces have led to the current frequencies of phenological traits observed within and among contemporary populations. Rapid, and perhaps more importantly, directional climate change will not only alter selection forces

along abiotic axes, but likely have widespread indirect consequences on horizontally and vertically structured biotic interactions like those detailed above. The resulting changes to selection environments caused by climate change may be without analogue in the evolutionary history of contemporary Arctic species (Williams and Jackson 2007), leading to knock-on effects on species interactions, population dynamics, community composition, and ecosystem function. Despite this general understanding, the extent and predictability of these outcomes remain poorly understood. For vertically structured interactions, the ecological and evolutionary consequences of phenological asynchrony coinciding with consumer reproductive efforts are frequently discussed in the context of trophic match and mismatch. In *chapter 2*, I examine the genesis of the trophic match/mismatch concept, review its relevance across diverse ecological contexts under climate change, and suggest directions for future research, some of which are pursued in later chapters of this dissertation.

While the apparent phenological synchrony of growth and reproduction across multiple species or trophic levels in the Arctic ultimately arises from extreme abiotic seasonality, the proximal mechanisms behind the specific timing of growth and reproductive traits are highly variable among species (Post et al. 2001, Visser and Both 2005, Thackeray et al. 2010, Kerby and Post 2013). The terms ‘capital’ and ‘income’ breeding have been used in life-history context to facilitate discussions on how a reliance, or lack thereof, on stored energetic capital to finance reproduction explains aspects of trait diversity observed across species (Stephens et al. 2009). In turn, these terms have served well as proximate explanations for observed behavioral and physiological diversity of organisms living in seasonal environments, but less often, have hypotheses

about the evolutionary, or ultimate, basis of these strategies been used to predict the ecological consequences of trait diversity in the context of rapid climate change (Stephens et al. 2009). In *chapter 3*, I adapt the capital-income typology to explore predictions about how large herbivore life-history strategies related to the phenology of energy storage and reproduction affect reproductive performance in an Arctic environment undergoing a climate-driven shift towards earlier resource availability.

Accounting for scale is a central challenge in ecological research (Levin 1992, Schneider 2001), particularly when the complex dynamics of individuals or populations are interpreted in the context of global abiotic change. Meta-analyses have demonstrated clear global signals of phenological response to warming in many plants and animals (Parmesan and Yohe 2003, Root et al. 2003), and literature reviews have further documented rapid and widespread signs of ecological change in the Arctic (Walther et al. 2002, Post et al. 2009, Post et al. 2013). These approaches identify a ‘fingerprint’ of global warming on ecological dynamics, but cross-scale linkages between specific instances of broad-scale abiotic change and local-scale ecological dynamics remain difficult to identify. Models that incorporate large-scale climate indices, such as the North Atlantic Oscillation (NAO) or El Niño, are perhaps the clearest exception to these challenges (Hallet et al. 2004). In some regions and seasons, these large scale weather indices outperform local weather variables as predictors of animal performance (Hallet et al. 2004) by integrating metrics of local weather simultaneously across multiple spatial and temporal scales (Stenseth and Mysterud 2005). Large-scale atmospheric modes have been linked to terrestrial ecological dynamics for decades (Post et al. 1999), but their effects are most clearly observed during winter months and their physical relationship

with climate change is sometimes difficult to interpret or project into the future (Marshall et al. 2001). Other large-scale abiotic phenomena that are more clearly related to climate change may also bridge scales to drive local dynamics, particularly with respect to the rapidly changing Arctic cryosphere. Sea ice loss, for example, is not only an indicator of climate change in the Arctic, but a significant driver of increasingly rapid regional warming through a process called Arctic Amplification (Serreze and Barry 2011, Stroeve et al. 2011). In *chapter 4*, I explore the potential indirect ecological consequences of large-scale Arctic sea ice declines, primarily those mediated through its indirect effects on plant phenology, in a terrestrial tundra community.

Changing seasonality in the Arctic is not restricted to the temporal domain, yet few studies have examined spatial dynamics of plant phenology at intermediate landscape scales. The ecological consequences of processes that are affected by this heterogeneity, like large herbivore foraging and biosphere-atmosphere interactions, are interpreted at landscape scales, but almost exclusively with phenology data derived from localized vegetation plots or coarse grain satellite imagery (Senft et al. 1987, Wang et al. 2006, Richardson et al. 2013). Scale-dependent dynamics are commonplace in ecology (Levin 1992, Schneider 2001), and they pose considerable challenges to the interpretation and understanding of spatial heterogeneity of phenological expression because these processes are dynamic through both space and time during greenup. I address this knowledge gap in *chapter 5*, where I derive a novel phenological dataset from a network of near-surface time-lapse cameras to explore heterogeneity of fine-grained phenological dynamics at the spatial extent of a caribou calving range in West Greenland. I then use

this dataset to examine landscape drivers of heterogeneity, and identify scale dependency in these patterns within and between years.

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Chapter 2 - Climate change, phenology, and the nature of consumer-resource interactions: Advancing the Match/Mismatch Hypothesis

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Abstract:

Trait-mediated effects are rife in ecological communities. However, most analyses of these effects adopt a strict top down perspective. Changes in phenology - the timing of periodic biological events like flowering or migration - caused by climate change can have a strong effect on interspecific interactions and introduce a bottom-up forcing in food web dynamics by influencing species' traits. Plasticity of life history traits, like age-structured growth and development, can be prompted by changes in phenology. For example, as the timing of biological processes shifts, organisms become exposed to novel ecological and environmental conditions and may respond to emerging trade-offs by adjusting their life-history strategies. This non-trophic influence on traits can conflate the effects of trait-responses to top-down trophic forcings, like the presence of a predator. This perspective, made relevant by the ongoing perturbation of climate change, brings new context to the understanding of traits in consumer-resource interactions.

Widespread inter- and intra-trophic variability in the magnitude of phenological shifts is a well-documented global signature of climate change. These shifts have left many consumer-resource interactions perturbed. The match/mismatch hypothesis is a simple framework that addresses the consequences of these trait changes for species interactions. It traces its conceptual origins to the marine fisheries literature in the 1970s, but it has since been generalized across many systems.

The match/mismatch hypothesis proposes that consumers are unable to consistently track variability in the timing of resource abundance in lower trophic levels during a sensitive period of consumer life history, and that this failure significantly limits

recruitment to the consumer population. Trophic mismatch linked with climate change has been reported in diverse systems, but the demographic and community-wide consequences of these mismatches remain relatively uncertain.

This chapter traces the origins of the match/mismatch hypothesis, reviews examples from a wide range of systems, and discusses recent conceptual developments with empirical studies. The concepts and implications of spatial mismatch and life-history mismatch are discussed in detail. Future studies will need to take advantage of these developments to address how phenological shifts and food-web dynamics will interact to affect consumer resource interactions in a rapidly changing world.

Introduction:

Understanding how species cope with ecological and environmental variation is a fundamental concern of ecology. Over the course of their lives, many organisms alter their phenotypes in response to biotic and abiotic pressures (Miner *et al.* 2005), responses that cascade through the food web to, in turn, affect the dynamics of species interactions. These effects, called trait-mediated effects, are pervasive in ecological communities, and their study has offered new insights into community ecology, a subject previously dominated by a density-mediated understanding of species interactions (Werner & Peacor 2003). Most analyses of trait-mediated effects take a top-down perspective where variation in consumer traits causes phenotypic responses by prey species. These phenotypic responses include behavioral, morphological, and/or physiological plasticity that have ramifying consequences for the food web by influencing how predators and prey interact (Werner & Peacor 2003). This top-down perspective on the influence of

traits in communities suggests that it is consumers that determine the nature and strength of the mediated effects.

Climate change is an ongoing global perturbation that also affects the densities and phenological traits of interacting species, although these effects are not necessarily related to food web trade-offs. Cohesive shifts in phenology - the timing of periodic biological events, such as migration, flowering, mating or parturition - reveal the global scale of climate change's influence on species' traits (Parmesan & Yohe 2003; Root *et al.* 2003). These phenological changes affect conditions that influence the relative fitness contributions of life-history traits, traits like age-structured growth, reproductive timing or developmental rates. For some species, these traits are plastic to fitness tradeoffs created by phenological shifts. In this way, climate change can affect the expression of traits that have an overwhelming influence on species interactions. Unlike the top-down influence of consumers, this non-trophic forcing can affect food webs via bottom-up processes. Phenology not only affects the nature and timing of species interactions, but also influences the very likelihood that two species will interact at all. In this manner, it can conflate or confound prey trait responses to immediate food web trade-offs, like those mediated by predators. Climate driven phenological variability provides new context for understanding the interaction between trophic and non-trophic traits and how this influences overall food web dynamics.

The consequences of phenological shifts for consumer-resource interactions have been most clearly documented when interacting species experience a differential response in time and/or space to a shared change in climate (Parmesan 2006). Phenological asynchrony related to climate change has been identified among trophic levels (Thackeray

et al. 2010), species (Visser & Both 2005) and even within species (Høye *et al.* 2007). These differential shifts reveal chronic changes in consumer-resource interactions that many communities are likely to experience (Walther *et al.* 2002; Post *et al.* 2009). Emergent inter-trophic asynchrony can trigger demographic changes that affect the entire food web by affecting interactions that structure communities, (Costello *et al.* 2006; Borcherting *et al.* 2010). For example, at high latitudes, the collapse of avian and rodent population cycles - population irruptions that provide periodic flushes of nutrients for predators and regulate successional dynamics for plants (Ims *et al.* 2007) - have in some instances, been the consequence of differential climate-driven phenological shifts between trophic levels (Ludwig *et al.* 2006).

Analyses of the ramifications of climate-driven shifts in phenological traits trace their conceptual origins to the 'match/mismatch hypothesis' - a simple framework that links climate driven trophic mismatch with population and community-level consequences.

Origins of the match/mismatch hypothesis

The match/mismatch hypothesis emerged in the 1970s from the marine fisheries literature to explain the extreme variation in population recruitment of economically important fish stocks of cod (*Gadus spp.*) and herring (*Clupea spp.*) in the North Atlantic (Cushing 1974). It proposes that in seasonal waters, fish recruitment is determined by the degree of temporal overlap between a 'critical period' of fish larval development, a period marked by high food- and predator-mediated mortality, and the timing of the peak abundance of their food resource, pelagic zooplankton. The magnitude of this overlap, conceptualized by two bell curves of species abundance resting on a temporal axis

(Figure 2.1), conceivably results in either a temporal overlap of resource demand and availability, a trophic match, and thus high fish population recruitment, or a temporal disjunction between resource demand and availability, a trophic mismatch, with low fish population recruitment.

Over the course of several decades, David Cushing, a British fisheries biologist, expanded on hypotheses proposed in the early 20th century (Hjort 1914) and developed what he named the 'match/mismatch hypothesis' (Cushing 1974; 1982; 1990). Cushing observed that the mean timing of peak fish spawning, and by extension, the phenology of the critical period for the majority of fish larvae, was relatively fixed from year to year, whereas the appearance of zooplankton populations was regulated from the bottom-up by stochastic climatic processes (Cushing 1990). Earlier hypotheses had assumed that the critical period for these fishes was brief, lasting only from the time of hatching to first feeding (Hjort 1914). Cushing broadened the application of the critical period to include all of larval development and just beyond (Cushing 1990). By relaxing this assumption, Cushing's hypothesis emphasized an outlook where the per-capita effects of life-history stage transitions were regarded as processes rather than fixed events. Cushing's match/mismatch hypothesis also emphasizes that climate variability plays a decisive, but indirect role in species interactions by affecting the expression of species' life history-traits via its influence on their reproductive phenology. When generalized, the match/mismatch hypothesis proposes that nascent consumers are unable to consistently track variability in the reproductive phenology of lower trophic levels, and that this failure has disproportionately large consequences on population recruitment relative to other instances of interspecific interaction throughout their ontogeny.

Empirical support for Cushing's match/mismatch hypothesis has been somewhat equivocal; however, this has often been the result of data limitations and the model's simplification of complex multi-trophic dynamics (Leggett & DeBlois 1994; Durant *et al.* 2007). Despite this, in the fisheries literature alone, the match/mismatch hypothesis has spawned decades of research, numerous allied hypotheses, and encouraged ongoing debate about the mechanisms of bottom-up community regulation in marine systems (reviewed in Durant *et al.* 2007).

Climate change and the match/mismatch hypothesis

Cushing's simple framework is not conceptually bound to marine systems, and has proven readily adaptable for the study of the consequences of differential phenological responses to climate change across several systems. In recent decades, the scientific community has drawn increasing attention to the ecological consequences of climate change (IPCC 2007; Fig. 2 in Forchhammer & Post 2004; Post *et al.* 2009; Walther *et al.* 2002). Phenological shifts relative to calendar dates (Fitter & Fitter 2002), and more recently phenological shifts relative to other species' phenologies (Visser & Both 2005), have emerged as foci for climate ecology research. Cushing himself perceived the relevance of his framework for addressing questions related to climate change (Cushing 1982), however, the first applications of this framework beyond the North Atlantic system focused on the mistimed reproduction in great tits (*Parus major*) in the Netherlands (Visser *et al.* 1998).

Since this advance in the late 1990s, population-level effects of trophic mismatch caused by differential phenological shifts among species have been documented in detail across diverse consumer-resource pairings, including interactions between birds and

invertebrates (Visser *et al.* 1998; Both *et al.* 2009; Hipfner 2008), birds and fish (Durant *et al.* 2005; Gremillet *et al.* 2008), vertebrate herbivores and plants (Post & Forchhammer 2008; Post *et al.* 2008a), invertebrate herbivores and plants (Visser & Holleman 2001), pollinators and plants (Memmott *et al.* 2007; Hegeland *et al.* 2009) and marine and freshwater fishes and invertebrates (Winder & Schindler 2004; Edwards & Richardson 2004). Trophic mismatch may occur at any level in a food web, or even in multiple levels simultaneously, from primary producers to apex predators (Primack *et al.* 2009; Thackeray *et al.* 2010; Both *et al.* 2009; Gremillet *et al.* 2008; Grebmeier *et al.* 2006; Montes-Hugo *et al.* 2009). Cushing's match/mismatch hypothesis is the progenitor of these studies, but several key conceptual advances, some of which are discussed below, have granted this framework broader relevance to the abovementioned and future investigations of the ecological consequences of climate change.

Accounting for abundance, temporal variance & adaptation

Resource and/or consumer abundance can influence the strength of a trophic match/mismatch by decreasing or increasing the likelihood that consumers will encounter resources at the 'tails' of their temporal distributions (Cushing 1984; Durant *et al.* 2005). While the original match/mismatch hypothesis focused on the mean timing of peak abundances, it is clear that the magnitude of either resource or consumer abundance, represented by a narrower or more highly dispersed distribution (Figure 2.2a), can influence the degree of temporal matching during the critical period by increasing the area of potential overlap between the consumer and resource curves (Durant *et al.* 2005). The relative effects of resource timing versus resource abundance can be separated from one another using time series analyses (Durant *et al.* 2005); however, the prevalence and

significance of these relationships across diverse systems remains relatively under-reported and, at times, equivocal (Hipfner 2008).

The extent to which the abundance curves of interacting species overlap is also determined by their temporal variance (Figure 2.2a,b). Warming manipulations of two arctic shrub and one forb species in Greenland demonstrate that in addition to shifts in the timing of phenological events, the duration of phenological life-history periods, or phenophases, may also be sensitive to climatic factors (Post *et al.* 2008b). Most match/mismatch studies have focused on the timing of the first or mean date of phenological processes, whereas few have explored the prevalence and consequences of shifts in phenological duration (but see Both & Visser 2001; Both & Visser 2005). Despite this, differential shifts in the duration of phenophases in response to climate change could conceivably give rise to match/mismatch conditions similar to, but independent of, those linked with the mean date of peak abundance.

To understand the consequences, both observed and expected, of phenological shifts requires, at the minimum, a coarse understanding of the evolutionary context of the development of each interacting species' phenological trait plasticity. For example, fish-zooplankton interactions in the North Atlantic, the focus of Cushing's original hypothesis, presumably coevolved in an environment that commonly experiences variable climatic conditions. In these fish populations, a mismatch between the timing of the peak in larval food requirements and the timing of peak food availability can clearly limit population recruitment. A complete mismatch between consumers and resources in these populations is, however, unlikely, because the duration of fish spawning throughout the season may occur for well over a month, albeit at low levels, before and after the 'fixed'

peak date of spawning (Cushing 1984; Cushing 1990). This wide temporal variance about the peak spawning date ensures that at least some individuals of each year class will experience high-quality resource conditions and presumably thrive in 'mismatch' years (Cushing 1984; Cushing 1990). Such a prolonged period of spawning represents a bet hedging strategy (Slatkin 1974); one that emerged from the evolutionary context of selective pressures that existed while this community was formed.

In many regions, climate is changing at rates that exceed those under which existing communities have been formed and maintained - a situation predicted to become increasingly commonplace in the coming decades (IPCC 2007). Without ecological precedent of such climatic pressures, species will not have evolved the adaptive plasticity necessary to hedge against emergent mismatches (Williams 1966). In some cases, species will have sufficiently plastic traits capable of tracking climatic and ecological shifts merely by chance, thus minimizing the potential for mismatches. Conversely, other species will be unable to respond at a sufficient rate to remain functional members of interaction webs under the selection pressures brought on by climate change (Visser 2010). This element of chance makes predicting future instances of mismatch more difficult.

Spatial Mismatch

The spatial dimension of trophic mismatch (Post *et al.* 2008a) can also influence the magnitude and type of consumer-resource interactions in ecological communities. While many factors, including species interactions, combine with environmental conditions to ultimately determine spatial patterns of consumers and resources within and

among trophic levels (Hutchinson 1957), the influence of climate change on these patterns has recently been the subject of increasing research and debate (Levinsky *et al.* 2007; Pearson & Dawson 2003). As with phenological trends, mean distributional shifts in response to climate change have been documented across numerous taxa around the globe (Parmesan & Yohe 2003; Root *et al.* 2003). Of particular significance to community ecology is how species' distributions covary in response to shared climate change. The match/mismatch hypothesis can again act as a framework for this line of study, by focusing on the consequences of trophic asynchrony using new methods to overcome the complexities associated with spatial analyses.

Until recently, temporal mismatch, that which occurs at a single point in space, was the primary focus of research related to the match/mismatch hypothesis. Unlike temporal processes that occur in one ordinal dimension, spatial changes in the same processes can occur in three; these additional factors, combined with variable interpretations of the term 'spatial mismatch', complicate studies that seek to account for spatiotemporal components of trophic match or mismatch. The term 'spatial mismatch' has been used in several, often complimentary, mechanistic explanations of trophic asynchrony that arise from spatiotemporal variability, some examples of which are discussed below.

One usage of 'spatial mismatch' refers to predicting how distributions of interaction-paired species will differentially respond to climate change by using bioclimatic-niche models (Levinsky *et al.* 2007). The methodologies of these models are diverse, but their basic aim is to project a species' realized niche onto a map and explore how this niche space will respond in a geographic sense to predicted changes in niche-

limiting variables. Comparisons between the predicted niche spaces of interacting species under various climate models often reveal niche divergence. For example, it has been suggested that climate-linked niche divergence may cause a spatial mismatch between a monophagous butterfly (*Boloria titania*) and its larval host plant (*Polygonum bistorta*) in Europe (Schweiger *et al.* 2008). Using a combination of climate, soil, and land-cover variables, the authors of that study suggest that the potential northward expansion of these butterflies may outstrip the dispersal ability of their larval host plant over the next 70 years, resulting in a reduced and increasingly fragmented consumer niche-space (Schweiger *et al.* 2008). In some areas this could lead to a complete extirpation of this interaction pairing, and therefore, all components of the interaction web that stem from it. Interaction diversity is an essential component of biodiversity (Price 2002; Thompson 1996), and the loss of interactions to mismatch, potentially independent of immediate changes in taxonomic diversity, may presage future taxonomic losses, yet this area of research continues to be relatively under-emphasized by conservation scientists.

Despite predictions of complete niche divergence, there are few empirical examples of this that can be directly linked to climate change. This paucity of empirical evidence may be the result of many factors, including difficulties in defining niche space. To some extent, this difficulty may also owe to conflation of the concepts of "niche" and "habitat", which is one of the most easily quantified and described niche components. Beyond this conceptual hurdle are the empirical challenges of measuring dynamic changes in niche-limiting factors across large geographic areas. Broad scale phenological monitoring networks, like the USA National Phenology Network (NPN) and the

European Phenology Network (EPN), may be able to ease some of the data limitations that plague coarse scale modeling approaches. Because many species traits that influence niche space are plastic with respect to both climatic and ecological influences, realistic parameterization of bioclimatic niche models is difficult. Furthermore, niche modeling studies are currently unable to incorporate the possibility of the emergence of new species interactions, which may be particularly important for so called 'specialist' species like the butterflies described above. As a resource becomes rare or disappears, it is unclear whether or not 'specialist' consumers will express latent plasticity in their ability to respond to these pressures (Miller-Rushing *et al.* 2010), and if not, this raises questions about the evolutionary advantages for specialization in what are inherently dynamic environments. Future studies will need to clarify how species interactions emerge from rapidly changing community milieus across a continuum of spatial scales (see Araujo & Luoto 2007).

The term spatial mismatch is also used to describe how the *strength* of consumer-resource interactions is affected by climate-sensitive distance relationships (Durant *et al.* 2007; Gremillet *et al.* 2008). In this case, the effects of differential shifts of species distributions in space are analogous to the effects of phenological mismatch. A conceptually simple model of this scenario might arise for central place foragers if the mean distance between the forager and its resource varies with climate or other pressures (Durant *et al.* 2007). Greater distance between resources and reproductive sites can lead to trade-offs of increased travel and/or search time, which translate to decreased efficiency in provisioning young, a situation that could have serious repercussions during an energetically demanding 'critical period' around reproduction (Durant *et al.* 2007). For

example, Cape gannets (*Morus capensis*) are central place foraging sea birds that have recently experienced this type of spatial mismatch with their primary prey - sardines and anchovies (Gremillet *et al.* 2008). These large seabirds nest along the Atlantic coastlines of South Africa and Namibia, but make long foraging flights out to marine regions of high primary productivity, regions that traditionally have been linked with abundant stocks of their preferred food (Gremillet *et al.* 2008). Spatial mismatch between the distributions of copepods and fish, potentially caused by a combination of climate factors and direct anthropogenic influences, has contributed to a strong decline in Cape gannet prey in these foraging regions, decreasing the efficiency with which Cape gannets can find and acquire resources needed to provision their chicks (Gremillet *et al.* 2008). This type of spatial mismatch, which arises from linear distance-time relationships between resources and consumers, may be widespread, although it is not widely reported outside of the context of apex marine predators (Veit *et al.* 1997; Grebmeier *et al.* 2006; Montes-Hugo *et al.* 2009).

Many species rely on environmental cues to inform them of current or future ecological conditions and they respond to this information by altering their phenotype to address perceived trade-offs (Miner *et al.* 2005). If the relationship between a cue and an associated environmental factor changes *and* if these changes occur at a rate that exceeds a species ability to adapt their decision making to these changes, species' responses to these cues may be poorly informed and lead to trophic asynchrony or even ecological traps (Visser 2010). Climate change is capable of influencing the relationship between cues and environmental conditions in several ways. For example, photoperiod and mean expected temperature may diverge with climate change because only temperature is

affected by current global climate forcings. If species were to make decisions that rely on one to inform about the other, they may experience a decoupling between the type of phenotypic trait plasticity they express and the type of phenotypic plasticity that might be best suited to actual conditions (Visser *et al.* 1998; Phillimore *et al.* 2010). A prominent spatial dimension to these decouplings can arise because climate change occurs unevenly in space (IPCC 2007). As distance increases between two ecosystems, they are increasingly unlikely to experience similar climatic change as the result of variability in regional biosphere-atmosphere interactions. The potential for trophic mismatch in migratory species is therefore heightened relative to residents. These animals experience this temporal variability across a spatial continuum, not just at a single point, and can be particularly vulnerable to mismatch if they rely upon cues in one location to inform about another. Said another way, match or mismatch may arise from differential species response at any one point in space, and/or from the influence of differential climate change at multiple locations. This forms the basis for another usage of the term 'spatial mismatch'.

In Europe, many long distance migrant bird populations are in decline relative to non-migrants (Sanderson *et al.* 2006), part of which can be explained by the above type of spatial mismatch between wintering and breeding grounds (Jones & Cresswell 2010; Both *et al.* 2010). One study of Palearctic passerines found evidence to support the 'distance hypothesis' - that long-distance migrants are more likely to experience population declines associated with mismatch than shorter-distance migrants or range residents because the probability of mismatch occurring at any one location along the migration route increases with migratory distance. However, this was only supported by

empirical evidence when distance was considered in context with the seasonality of the migrant's breeding ground, where seasonality was defined as the temporal variance about the mean peak in consumer resources (Both *et al.* 2010). Long-distance migrants that bred primarily in more seasonal forest habitats, with a narrow window of food abundance, experienced significantly sharper population declines than long-distance migrants that bred in less seasonal marshy areas (Both *et al.* 2010). Irrespective of seasonality, resident and shorter-distance migratory species that lived in both areas were comparatively less affected than long-distance migrants (Both *et al.* 2010). Another study, that did not incorporate a seasonal variance component, but included migratory birds from both hemispheres, also found evidence that suggested absolute migration distance could be a factor in bird population declines, and that overall, migratory birds were more likely to experience mismatch conditions and population declines than were residents (Jones & Cresswell 2010). In both of these studies, the great distances between wintering and breeding grounds implies an increasingly likely probability that ineffective migratory cues will result from divergent climate regimes (Jones & Cresswell 2010; Both *et al.* 2010). Studies at these broad scales require simplified assumptions about abiotic influences on trait plasticity that inevitably accompany low-resolution phenological data. However, that these studies were still able to detect effects of migratory distance and divergent climates in spite of these limitations raises important questions about how spatiotemporal components of species interactions that occur over continental scales will be affected by climate change.

The pattern of resource distribution at the landscape scale may also vary with changing climate conditions. For example, by differentially affecting the timing of plant

emergence - a phenophase with high nutrition and low digestive costs for herbivores - climate is capable of affecting spatial *patterns* of resource quality across a wide array of scales from thousands of kilometers to less than one meter (Chen *et al.* 2005; Post & Stenseth 1999; Post *et al.* 2008b; Post & Forchhammer 2008). This variation in spatial patterning can have repercussions for consumer foraging decisions and manifest itself as another type of spatial mismatch. At the landscape scale, a spatial continuum of temporal shifts in resource availability and/or quality is expressed as spatiotemporal resource heterogeneity, an important factor in population dynamics (Roughgarden 1974; Levin 1976). Consumers have evolved foraging strategies to cope with and even rely on heterogeneous distributions of high quality resources. In seasonal environments, migratory ungulates take advantage of spatiotemporal resource heterogeneity by following the early/mid phases of plant phenology through the landscape. This can effectively prolong their access to high quality resources (Senft *et al.* 1987). Because climate change alters the pattern of resource quality expressed in a landscape by affecting plant phenology, it can impact the efficiency of herbivore foraging strategies designed to maximize high quality forage intake required to offset the high costs of reproduction. For example, in highly seasonal West Greenland, reproductive success of migratory caribou (*Rangifer tarandus*) depends on their ability to arrive and give birth at their calving site around the mean temporal peak in resource abundance (Post & Forchhammer 2008), but also on their ability to track spatial phenological heterogeneity along a local forage horizon during and around the calving period (Post *et al.* 2008b). These studies are an early step towards unifying the spatial match/mismatch hypothesis with landscape ecology concepts (e.g. Turner 2005), but future investigations will need to explore a more

complete range of climatic effects on species interactions in relation to resource patterning, rather than just timing, across a hierarchy of spatial scales.

Migratory species may offer a clear insight into how differential spatiotemporal shifts in the distributional patterns of resources can be expected to influence trophic interactions. In some situations, migration itself may become an ineffective strategy as a result of what might be termed a spatial mismatch. This would be spatial mismatch in the sense that changes in the spatial patterning at one trophic level would negatively influence foraging success in higher trophic levels and result in a trophic mismatch, potentially independent of the mean timing of resource availability throughout the study area. Ungulate migration has been studied for decades and may provide a good starting point for these investigations. If migration is the result of spatial patterns of resource distribution, as is predicted by the forage maturation hypothesis (Fryxell 1991), spatial compression (i.e. homogeneity) of plant phenology along the migratory route, as has been observed at local scales in West Greenland (Post *et al.* 2008b), could conceivably alter selection coefficients between non-migratory and migratory members of populations. For instance, elk (*Cervus elaphus*) populations in the Canadian Rockies are composed of both migratory and non-migratory individuals (Hebblewhite *et al.* 2008). A three year observational study found that on average, migrant individuals of these populations were exposed to more nutritious and digestible food resources than residents, owing to their strategy of exploiting heterogeneous spatial patterns of plant phenology during migration (Hebblewhite *et al.* 2008). The advantages that migration confers on individuals could diminish in this population should spatial compression of resource phenology occur here. In seasonal environments, even slight shifts in foraging efficiency can have dramatic

impacts on reproductive success (White 1983). Large herbivores are often important interactors in ecological communities, and their removal from interaction networks has been shown to induce significant community restructuring (Post & Pedersen 2008; Pringle *et al.* 2007). While the potential for this type of spatial mismatch to influence migratory species' population dynamics is clear, future studies will be required to verify to what extent these concepts may apply to empirical situations.

Integrating match/mismatch with life-history strategies

Trophic mismatch is most widely documented in seasonal environments where food resources are limited throughout much of the year, however, even within these environments, consumer sensitivity to temporal resource limitation will vary among species as a function of, among other factors, variation in their life-history strategies. Income breeders, for example, require a continuous influx of energy to offset the high costs of reproduction, and thus are likely to have a critical period clearly related to food acquisition around the timing of their reproductive efforts. Conversely, capital breeders build up an energy surplus throughout the year that they later expend during reproduction, giving their reproductive effort relatively more independence from immediate food resource conditions (Drent *et al.* 2006). Capital breeders may thus prove less sensitive, but by no means immune, to climate-driven fluctuations in resources.

Traditionally, infant or juvenile mortality associated with what is assumed to be a fixed and intuitively described critical period of breeding phenology has been the sole effect reported by match/mismatch investigations (Durant *et al.* 2007). While this may be the most tractable metric of mismatch, it has almost certainly drawn attention away

from efforts to document other potential consequences of a mismatch. For some insect species, ecological and environmental conditions during an early critical stage of ontogeny may have a delayed influence on adult body size and fertility (Prout & McChesney 1985) - both of which are life-history linked traits that greatly contribute to fitness. These delayed effects on traits could also have ramifications for the strength and type of interactions species experience throughout their development (Yang & Rudolf 2010). Identifying a broader range of direct effects that trophic mismatch can have on populations is a pressing, but presently poorly documented component of the demographic consequences of mismatch (Miller-Rushing *et al.* 2010). This approach, however, will challenge the traditional interpretation of the 'critical period' concept.

In a general sense, a species' 'critical period' is the product of interactions from within a hierarchy of biological sensitivities, integrating individual's traits from embryology, neurobiology, and/or behavior (Browman 1989). Ecological or environmental factors can induce trait plasticity within each level of this hierarchy, and by extension, affect how biological sensitivities interact to be expressed as a critical period of the life history of an organism. In contrast to this perspective, most analyses treat the critical period of a species' life history as an intrinsic property, i.e. as though it were a fixed trait (Visser & Both 2005). This assumption may limit our understanding of trophic decoupling in some species, whereby new critical periods will emerge as a consequence of novel ecological forcings associated with phenological shifts of life-history traits.

In many communities, species interact over their respective life spans. These interactions can change in intensity or type depending on the timing of one or both

interacting species' stage specific development and/or body size (figure 2.3a,b) (Yang & Rudolf 2010; Werner & Gilliam 1984; Osenberg *et al.* 1988). For example, fish eggs of one species may initially be prey items for fish or larvae of another, but once hatched, these larvae may compete with or even prey upon their former predators before eventually becoming generalist predators that consume prey from several trophic levels. When species interactions are stage structured in this manner, as might be expected in many invertebrate and/or aquatic ecosystems, the timing, duration, and physical traits associated with life-history stages can determine the magnitude and type of interactions a species experiences (Yang & Rudolf 2010; Werner & Gilliam 1984; Osenberg *et al.* 1988). Similarly in plant-herbivore interactions, invertebrate herbivores may transition from predators to pollinators depending on the timing and duration of both species' ontogeny (Bronstein *et al.* 2009). Because shifts in the timing or duration of ontogeny may be variable in response to climate change (Post *et al.* 2008b; Yang & Rudolf 2010; Werner & Gilliam 1984), there is potential for species interactions to change, decouple, or even strengthen over the entire span of their respective life histories. Instead of limiting focus to the differential shifts in phenological events to a traditionally critical period of development (Visser & Both 2005), some match/mismatch studies will benefit by focusing on stage-specific per capita effects of species interactions throughout the entire span of their trophic coupling (Yang & Rudolf 2010). A focus on per-capita interactions throughout aggregate life history may clarify how trait plasticity and ecological sensitivity interact to affect population fitness, even via delayed responses to mismatch. This may be an effective approach to better understand a broader suite of the ecological consequences of climate change, even in less seasonal environments where

sensitivities to resource limitation may be harder to predict and are certainly less well documented.

Conclusions

As empirical evidence of climate change's perturbing effects on ecological communities mounts, phenology has emerged as an essential component of species trait-responses to these emergent forcings. Trait-mediated ecological effects are increasingly the subject of community ecology research. However, the affects of non-trophic forcings on species traits must not be overlooked. Differential phenological shifts will continue to affect trophic interactions as climate regimes change by not only influencing the timing of species interactions, but also their very nature.

The match/mismatch hypothesis has been a popular framework for analyses documenting the immediate consequences of these climatic perturbations, but future research will need to continue to further clarify spatial dimensions of these consequences. Spatial mismatch is currently a popular subject of study, but inconsistent use of terminology among studies has made a concise definition of the concept challenging. Integrating the study of trait- and density-mediated interactions with landscape ecology is a logical next step for community ecology research.

Furthermore, the spectrum of possible effects stemming from trophic mismatch is relatively unknown apart from recruitment failures. Future studies will benefit from an approach that links shifts in the life history traits of interacting species with the delayed consequences of these shifts on species' traits. This will further clarify the interaction between trophic and non-trophic traits' influence on ecological communities.

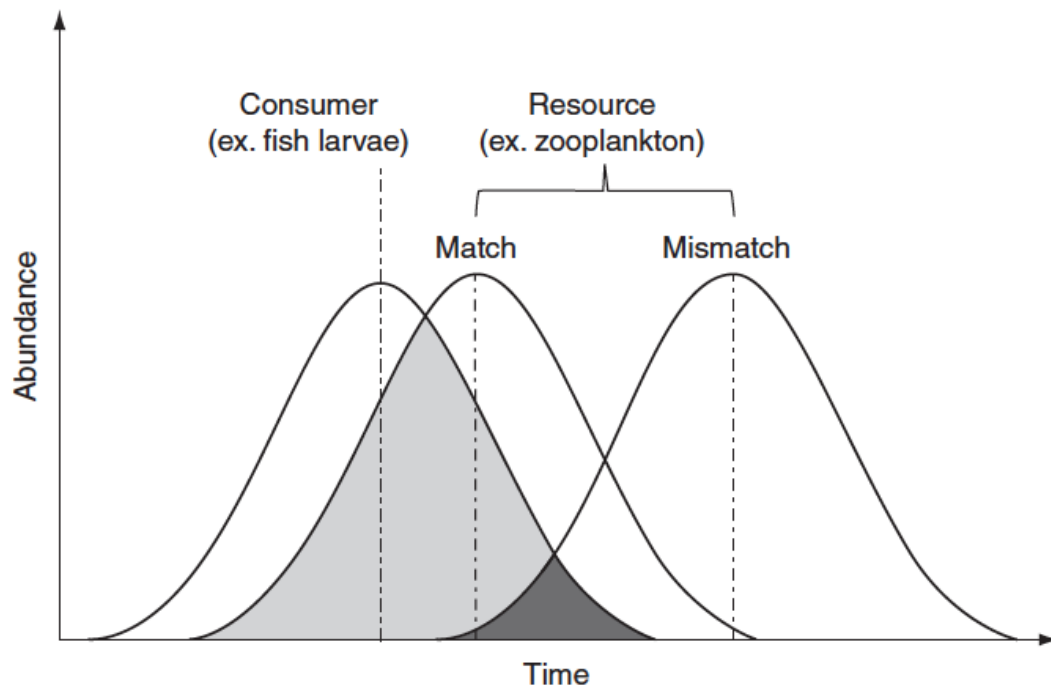


Figure 2.1. The temporal mismatch hypothesis. The abundance of consumers and resources are shown as distributions in time. The relative overlap between consumer and resources varies with resource phenology and results either in a match and high consumer population recruitment (light shading), or a mismatch with low consumer population recruitment (dark shading). Modified from Durant *et al.* (2007).

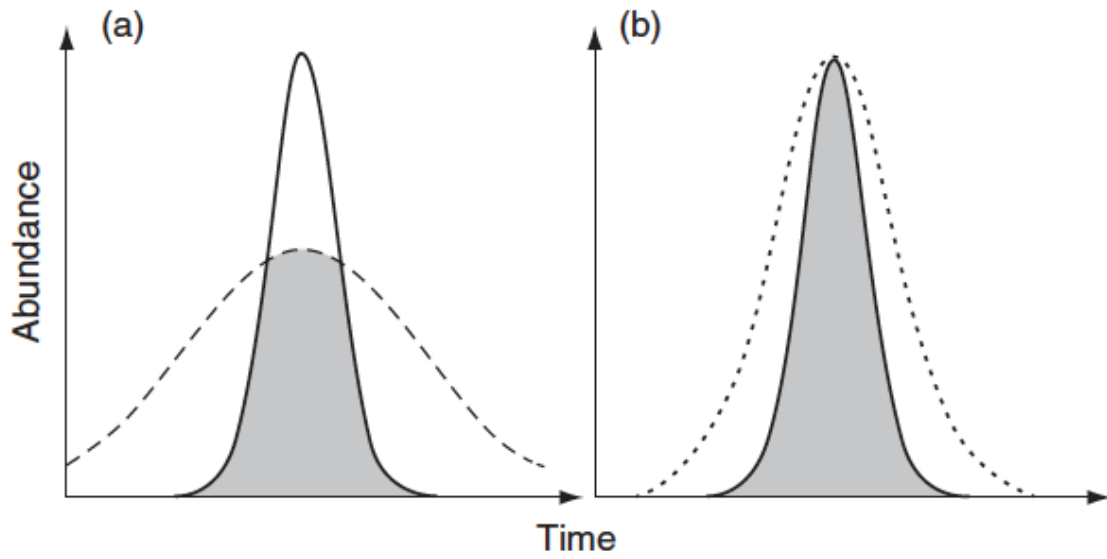


Figure 2.2. Factors which may affect the degree of match/mismatch independent of a shift in the peak timing of resource abundance. A shift in consumer or resource abundance (a), or temporal variance (a, b) about the peak can conceptually limit or magnify the effects of temporal trophic mismatch. Reproduced from Miller-Rushing et al. (2010).

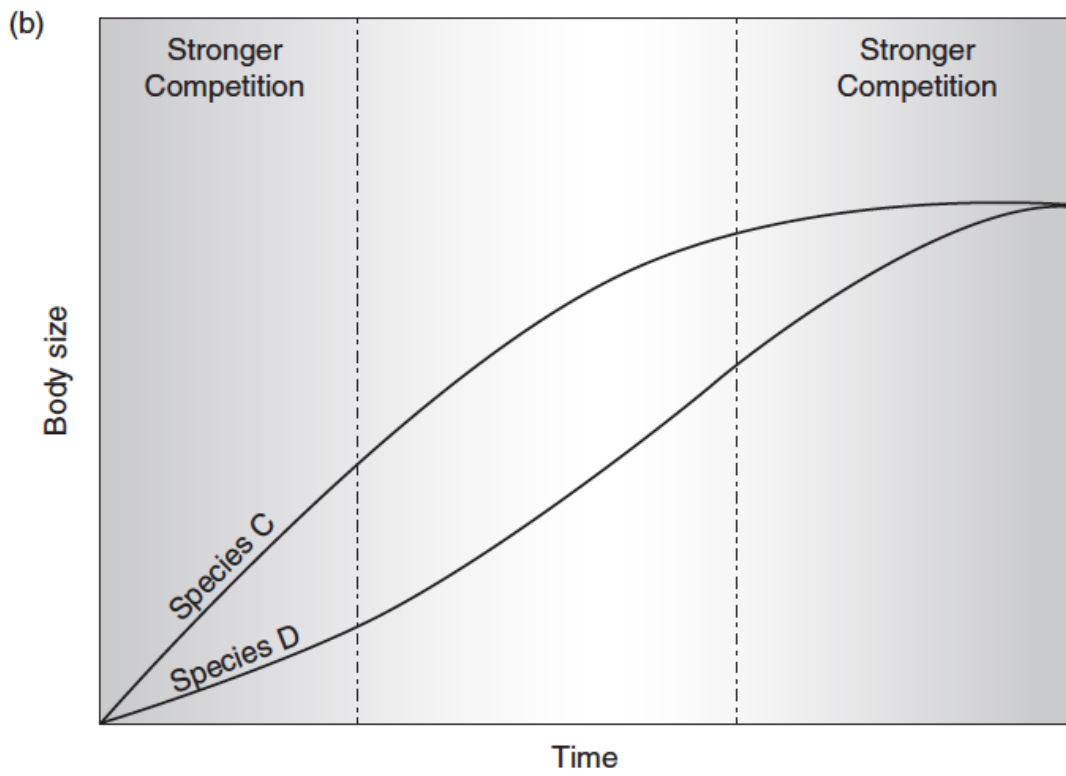
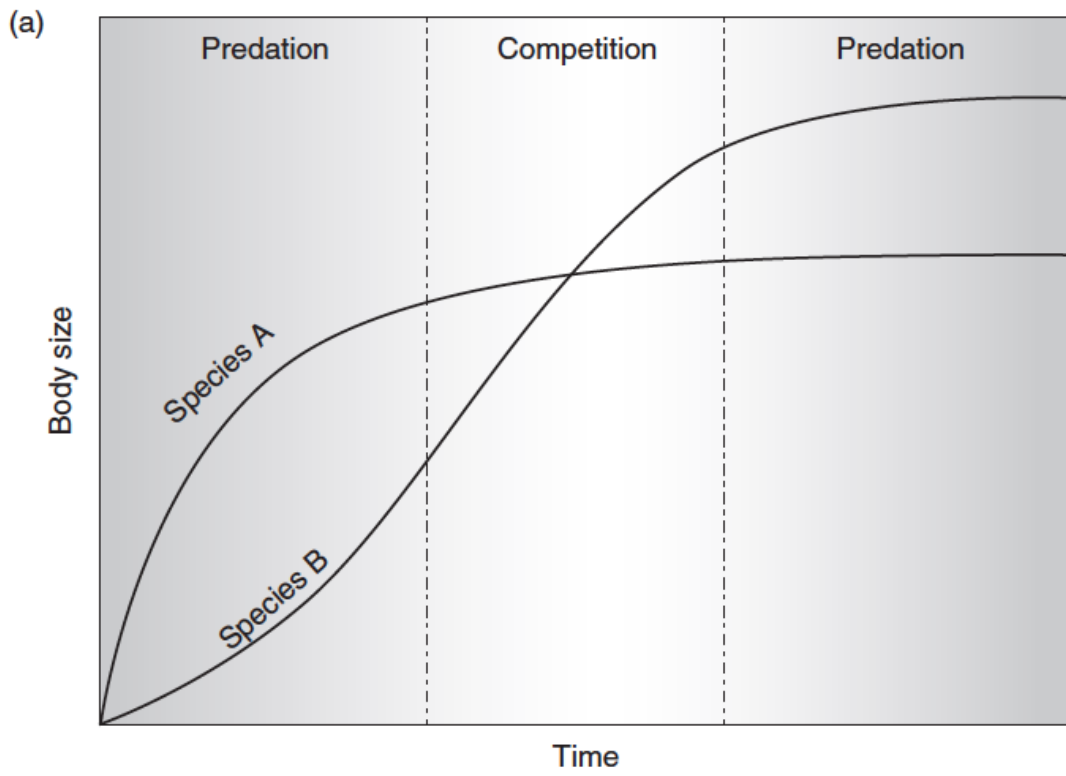


Figure 2.3. Conceptual diagram demonstrating how both the type (a) and strength (b) of species interactions may change over time as a consequence of differential shifts in the phenology of ontogeny. Shading represents the transition in type (a) or strength (b) of an interaction. For example, a hypothetical species A may switch from consumer of species B to its competitor, or even a prey item for species B as a function of the relative timing of growth between the two species (a). Similarly, a differential timing of growth between interacting species C and D can alternately ease or strengthen competition (b). Modified from Yang and Rudolf (2010).

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Chapter 3 - Capital and income breeding traits differentiate trophic match-mismatch dynamics in large herbivores

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Abstract:

For some species, climate change has altered environmental conditions away from those in which life-history strategies evolved. In such cases, if adaptation does not keep pace with these changes, existing life-history strategies may become maladaptive and lead to population declines. We utilize life-history theory, with a specific emphasis on breeding strategies, in the context of the trophic match-mismatch framework to form generalizable hypotheses about population-level consumer responses to climate-driven perturbations in resource availability. After characterizing the income and capital breeding traits of sympatric caribou and muskoxen populations in western Greenland, we then test trait-informed hypotheses about the reproductive performance of each population using data collected during a period of high environmental resource variability at that site. The immediate reproductive performance of income breeding caribou decreased with trophic mismatch. In contrast, capital breeding muskoxen were relatively unaffected by current breeding season resource variability, but their reproductive performance was sensitive to resource conditions from previous years. These responses matched our expectations about how capital and income breeding strategies should influence population susceptibility to phenological mismatch. We argue for a taxon-independent assessment of trophic mismatch vulnerability based on a life-history strategy perspective in the context of prevailing environmental conditions.

Introduction:

Rapid climate change has increased the global frequency of extreme weather (1-3), driven uneven shifts in the phenology of coexisting taxa (4-6), and altered the relationship between physical cues and ecological processes (7-9). The trophic mismatch concept (reviewed in 10-12) examines the population-level consequences of climate-driven phenological asynchrony between consumer resource requirements and the availability of these resources during the consumer's breeding period. Trophic mismatch affects diverse taxa in numerous environments (13-19), but demonstrating generality in patterns among species or populations has proven elusive (8, 12). Here, we employ a case study based on a long-term dataset to integrate concepts from life-history theory, focusing specifically on life history traits that form the basis of breeding strategies, with the trophic match-mismatch framework. We promote simplified, generalizable, and testable hypotheses about consumer population-level responses to climate driven perturbations of resource environments.

Breeding Strategies and Match-Mismatch

Reproduction is constrained by fundamental tradeoffs linked with resource acquisition and subsequent allocation to offspring production and provisioning (20). Capital- and income-breeding strategies mark endpoints of a continuum of solutions to these tradeoffs that are distinguished by the degree to which an organism relies on stored energy to finance reproductive costs (21, 22). A capital breeder primarily invests in offspring production from its own resource reserves, which are acquired prior to reproduction. In contrast, an income breeder relies on financing its reproductive costs

from resources acquired from the environment during the breeding period (21, 22). Purely capital- or income-breeding birds and mammals are uncommon (23), but interpretation of life history traits, particularly those associated with breeding, allow for *a priori* classification of individuals as more representative of one strategy than the other (21, 22).

As climate change continues to affect the predictability of seasonal resource pulses relative to consumer breeding phenology, consumer demographic responses (10, 12) may vary according to their breeding strategy (22). For example, we predict that the reproductive performance of an income breeder will exhibit an immediate positive response to an increasing trophic match, but an immediate negative response to an increasing trophic mismatch. In contrast, while capital breeder reproductive performance may respond to increasing trophic match, it should be relatively insensitive to increasing mismatch in the year of offspring production. This is because capital breeders finance a critical portion of their reproductive costs with energetic capital accrued prior to costly breeding phases, and as a result their reproductive performance during a given breeding period is comparatively less dependent on phenological synchrony with environmental resource availability (Figure 3.1). Ultimately, however, changes in resource dynamics at any point in the year may affect capital acquisition and capital storage costs that can have a cascading impact on future reproductive performance.

Case Study – Large Herbivores in the Arctic

Rapid warming has already strongly affected plant phenology in the Arctic (24-26) and, by extension, arctic herbivores (18, 19, 25, 27). Muskoxen (*Ovibos moschatus*) and caribou (*Rangifer tarandus*) are the only large herbivore species that are resident in

and breed in arctic tundra environments, yet they have markedly contrasting life history traits and reproductive strategies that place them on opposing sides of the capital-income breeder continuum (28, 29). Using a literature review, we classify west Greenland caribou as income breeders and muskoxen generally as capital breeders on the basis of differences in their life-history traits (sensu 22) drawing specific focus to differences in calving phenology, body composition and size, metabolic rate, factors that influence conception, and general patterns of productivity (Table 3.1). In this case study, we use this classification system and a long-term dataset from ongoing research in low-Arctic west Greenland (30) to explore our general predictions about capital- and income-breeder responses to environmental perturbations. Specifically, we focus on the reproductive performance of sympatric caribou and muskox populations during a period of sustained warming. As income breeders, caribou should display immediate consequences of trophic mismatch during their breeding season, whereas muskox reproductive performance should be little impacted by the timing of resource availability in the year of offspring production.

Methods:

Phenology and Herbivore Productivity Data

Near-daily records of plant community emergence and herbivore calving progression were collected between May and June for 11 years (1993, 2002-2011) at a long-term research site situated near a shared caribou and muskox calving ground in low-arctic west Greenland (67.11° N 50.34° W)(30). Calf production was recorded annually for both caribou and muskoxen several weeks after the conclusion of their respective

calving seasons and thus after the critical period of early calf mortality had passed (31). All observational and analytical methods quantifying phenological data are consistent with previous reports from this site (19) as is our method for calculating caribou calf production (18, 19, 32-34).

Annual muskox calf production, like that of caribou, is reported as the post-calving ratio of calves to total individuals observed in the roughly 20 km² calving area. The large post-calving herd(s) of caribou make a comprehensive calf census possible on a single day in late June, but because resident muskoxen are dispersed in small family groups throughout the post-calving season, we used the annual maximum single day ratio of calf to total individuals from *ad lib* censuses of the study area repeated throughout June.

Quantifying the Phenology of Trophic Interactions (match-mismatch)

The phenology of caribou calving is tightly coupled with vegetation phenology (34, 35). The annual extent of synchrony between caribou calving and vegetation emergence constitutes the trophic mismatch index (19). This index is quantified as the proportion of plant species emergent in the community, averaged across twelve 0.5 m² long-term monitoring plots that are spread across three sites separated by several hundred meters encompassing differing microclimates (19), on the date of 50 percent caribou births (32, 36). Said another way, this index quantifies the resource state at the mid-point of the annual season of caribou parturition. Annual estimates of trophic mismatch therefore vary between zero and one, with higher values indicating increasingly earlier

vegetation emergence with respect to the peak of the caribou calving season and thus increasing mismatch (19).

Unlike caribou, muskoxen calve four to eight weeks prior to the plant growing season throughout their circumarctic range (37-39). At the study site, muskox calving occurs before our initiation of fieldwork each year. To quantify trophic mismatch for muskoxen we used a conservative estimate of the end date of the focal population's calving period (40) and calculated the difference between this and the observed annual date of 50% plant species emergent for each year. This metric quantifies the duration of the window between the latest possible onset of lactation (i.e. parturition) and the midpoint of the vegetation emergence season, a date when offspring provisioning costs can first be reliably sourced from the environment rather than solely from endogenous stores. This index therefore only reflects interannual variation in vegetation emergence, with larger numbers indicating a longer delay between the estimated end of the calving period and the observed timing of environmental resource availability in a given year. There is little published information available about the patterns and drivers of interannual variation in the timing of muskox calving, so at present, we are unable to factor this potential bias into our analyses.

Relating Trophic Asynchrony to Herbivore Demographic Response

To link herbivore calf production to the degree of phenological asynchrony (mismatch) between herbivore calving and vegetation emergence, we conducted multiple- and simple-linear regression in the R statistical computing environment (41) incorporating mismatch terms in current and previous years for each herbivore

population. Previous studies have documented the critical relevance of density dependence in both *Rangifer* (42-45) and muskoxen (44, 46, 47) population dynamics, so current and one-year lagged calving season abundances were included as covariates during model construction. Seasonal herbivore abundance was calculated as the maximum number of individuals of each species seen on a single day at the study site throughout May-June. There are no apex predators in this system, and regulated hunting is restricted to the late summer and winter seasons; therefore no top-down factors were included in our models. Furthermore, we examined each time series for temporal trends and repeated our analyses with detrended data when necessary to isolate potential drivers of interannual variation in calf productivity from those primarily related to trends.

Results:

Variation in Vegetation and Herbivore Phenology

Over the 11-year study period, the date of 50% plant species emergence ranged over a 19-day window with a mean date of June 1 (day of year 151.8 +/- 6.4) (Figure 3.2a). In contrast, the midpoint of the caribou calving season showed little interannual variation around its mean of 6 June (day of year 156.8 +/- 1.9) spanning a range of just 7 days over the same period (Figure 3.2a). Among all years, the latest recorded date of 50% plant species emergence was one day earlier than the latest recorded date of 50% caribou births, but the earliest date of 50% plant emergence occurred 13.5 days before the earliest recorded date of 50% caribou births. The largest difference in a single season between the midpoint of vegetation emergence and midpoint of caribou births was 18 days. There was no correlation between the annual timing of vegetation emergence and

caribou calving (Pearson's $r = 0.23$, $p = 0.50$; Figure 3.2b). The midpoint of the local muskox calving season occurs in late-April (37, 48), prior to the onset of our field season and approximately 6 weeks before peak green-up (Figure 3.2a). We therefore provide only a depiction of the duration of the muskox calving season (Figure 3.2a) and an estimate of 13 May (day of year 133) as a conservative end-of-calving date on the basis of a literature review (37, 38, 40, 48, 49) to provide comparative trophic context to the calving phenology of each herbivore population.

Calf Production

Caribou were marginally more productive than muskoxen (Two-tailed Welch's Two Sample t-test, $t = -1.621$, $df = 14.34$, $p = 0.13$) but exhibited greater interannual variability in calf production (One tailed F-test: $F = 3.04$; $df = 9,9$; $p = 0.06$; Figure 3.3) and a higher maximum productivity (0.42 vs. 0.30 calves/total individuals) across all years that both species were monitored. Muskox calf production increased significantly over this time ($\beta_1 = 0.02 \pm 0.005$, $R^2 = 0.61$, $p = 0.007$), while caribou displayed a declining but non-significant trend in caribou calf production ($\beta_1 = -0.02 \pm 0.014$, $R^2 = 0.15$, $p = 0.28$).

Relating Magnitude of Trophic Mismatch to Herbivore Productivity

Caribou calf production was significantly negatively related to trophic mismatch in a given year ($\beta_1 = -0.55 \pm 0.15$, $R^2 = 0.60$, $p = 0.005$), but not with that of the previous year ($\beta_1 = 0.33 \pm 0.22$, $R^2 = 0.24$, $p = 0.18$). This contrasted with observed patterns of muskox calf production, which related negatively to the timing of vegetation

emergence in the previous year ($\beta_1 = -0.0064 \pm 0.0029$, $R^2 = 0.41$), but displayed no relationship with vegetation emergence in the current year ($\beta_1 = -0.0037 \pm 0.0037$, $R^2 = 0.11$, $p = 0.34$). The overall sign, magnitude and significance of these relationships persisted even after accounting for herbivore abundance (Figure 3.4), a factor that, surprisingly, did not contribute to better model fits (Supplementary Table 3.S1). Significant temporal trends existed in muskox calf production ($p = 0.007$) and trophic mismatch ($p = 0.02$), while caribou trophic mismatch displayed only a marginal trend ($p = 0.08$)(Supplementary Table 3.S2); only caribou calf production was significantly related to a de-trended mismatch index ($p = 0.003$)(Supplementary Table 3.S3).

Discussion:

As income breeders, caribou lose proportionally less forage energy to capital conversion and storage costs but experience more volatility in reproductive performance among years than muskoxen (Figure 3.3). Iteroparous income breeders may hedge the risk of energetic shortfall even in highly variable resource environments if they express plasticity in parturition phenology capable of tracking resource variability (21, 22), or if resource uncertainty varies about a long term mean. Under the latter scenario, multiple reproductive opportunities may buffer intermittent reproductive failures in some years with strong reproductive performance in others. Neither situation exists in southwest Greenland, however, where a strong trend toward advancement of the timing of peak resource availability (26) may render income breeding for caribou maladaptive if calving phenology does not adjust to the consistently earlier timing of vegetation emergence. Indeed, recent evidence suggests that *Rangifer* lack the molecular clockwork that drives

circadian rhythms in other mammals, and as a result calving phenology in this species may be constrained directly by photic cues (50). This implies that caribou lack sufficient phenotypic plasticity in their ability to track long-term directional shifts in vegetation phenology (as in Figure 3.2b), and that reducing trophic mismatch can therefore only be achieved via cross-generational selection.

For muskoxen in this population, the absence of an immediate effect of vegetation emergence on recruitment is consistent with our expectation for a capital breeder. The presence of a one-year lagged effect of resource phenology not associated with density dependent factors (Figure 3.4d) can also be interpreted in the context of capital breeding. In contrast to caribou, muskoxen store a greater proportion of their total body mass as fat and will avoid conception when fat to body mass ratios drop below ~20%, a threshold roughly 2-4 times higher than conception-inhibiting leanness in caribou (28, 51). As a result, extreme resource variability more commonly contributes to breeding pauses in muskoxen (40, 52), whereas caribou reproductive performance is more strongly influenced by calf mortality (53-55).

In contrast to their North American conspecifics, the calving period of Palearctic reindeer (also *Rangifer tarandus*) typically occurs several weeks prior to the onset of the spring resource pulse (45, 56), a life-history trait associated with capital breeding (22). Consistent with this classification, the reproductive performance of nineteen semi-domestic reindeer populations in Norway increased as the result of widespread trophic match in years with earlier vegetation emergence (45). Svalbard reindeer on the high-arctic island of Spitsbergen exhibit capital breeding traits comparable to those of muskoxen (39, 56). Like muskoxen in southwestern Greenland, Svalbard reindeer

fecundity increased during a multi-year warming period characterized by more favorable but less predictable environmental conditions outside of their breeding period (57).

Capital breeding marmot populations in the Rocky Mountains (*Marmota flaviventris*) and French Alps (*Marmota marmota*) provide further examples of life-history trait driven population response to resource variability. These phylogenetically closely-related populations are both emerging from hibernation earlier in response to shifting environmental conditions, and as a result, are experiencing longer growing seasons (58-60). Marmots in the Rocky Mountains have capitalized on this longer growing season with increased seasonal capital accrual that has resulted in larger litter sizes (59). In contrast, the positive effect of the longer growing season has been offset by higher capital storage costs associated with changing environmental conditions and a higher temperature-dependent metabolic rate in the French Alps marmot population, ultimately resulting in smaller litters there (60).

Changing trophic interactions, rather than the direct effects of weather on energy balance, are perhaps the best-documented proximate causes of climate-linked population declines and local extinctions (61). The match-mismatch framework has traditionally formed the conceptual basis for describing climate-driven changes in trophic interactions (10, 11), but few cross-species or -population comparative match-mismatch studies have been undertaken (but see 62). Rather than focusing on species-level vulnerabilities, however, we argue for a taxon-independent assessment of trophic mismatch vulnerability based on a life-history strategy perspective in the context of prevailing environmental conditions.

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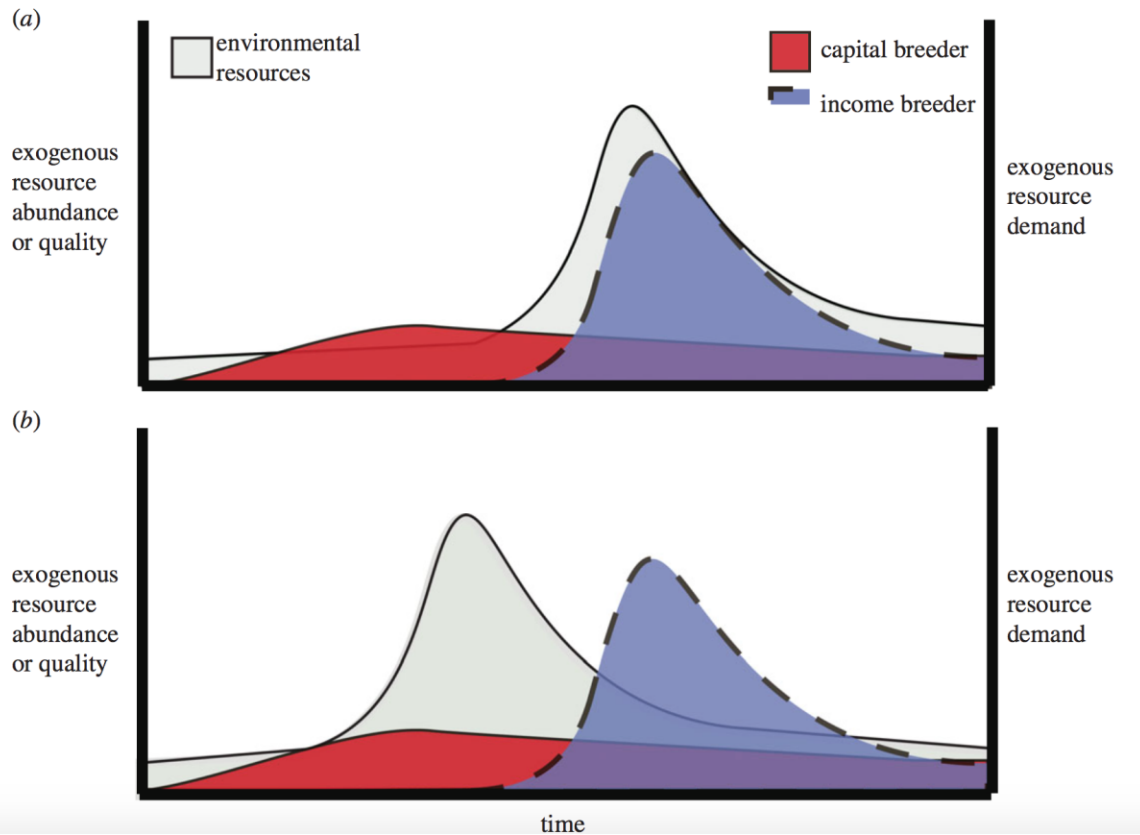


Figure 3.1. Match-mismatch framework adjusted by reproductive strategy. The match-mismatch framework depicted above was modified to display the difference in exogenous (i.e. environmental) resource acquisition requirements of capital and income breeders during their breeding period. Endogenous (i.e. stored energetic capital) reproductive resource stores and costs are not pictured. Match and mismatch scenarios for income and capital breeders alternate by panel. Panel **a** shows a temporal match between the peak environmental resource needs of income breeders with environmental resource availability/quality. It also depicts a temporal ‘mismatch’ between the peak environmental resource needs of capital breeders and available environmental resources. These scenarios are reversed in panel **b**. Note the contrasts in energetic mismatch (non-

overlapping areas) between capital breeders and environmental resources (panel a – minimal) and income breeders and environmental resources (panel b – extensive).

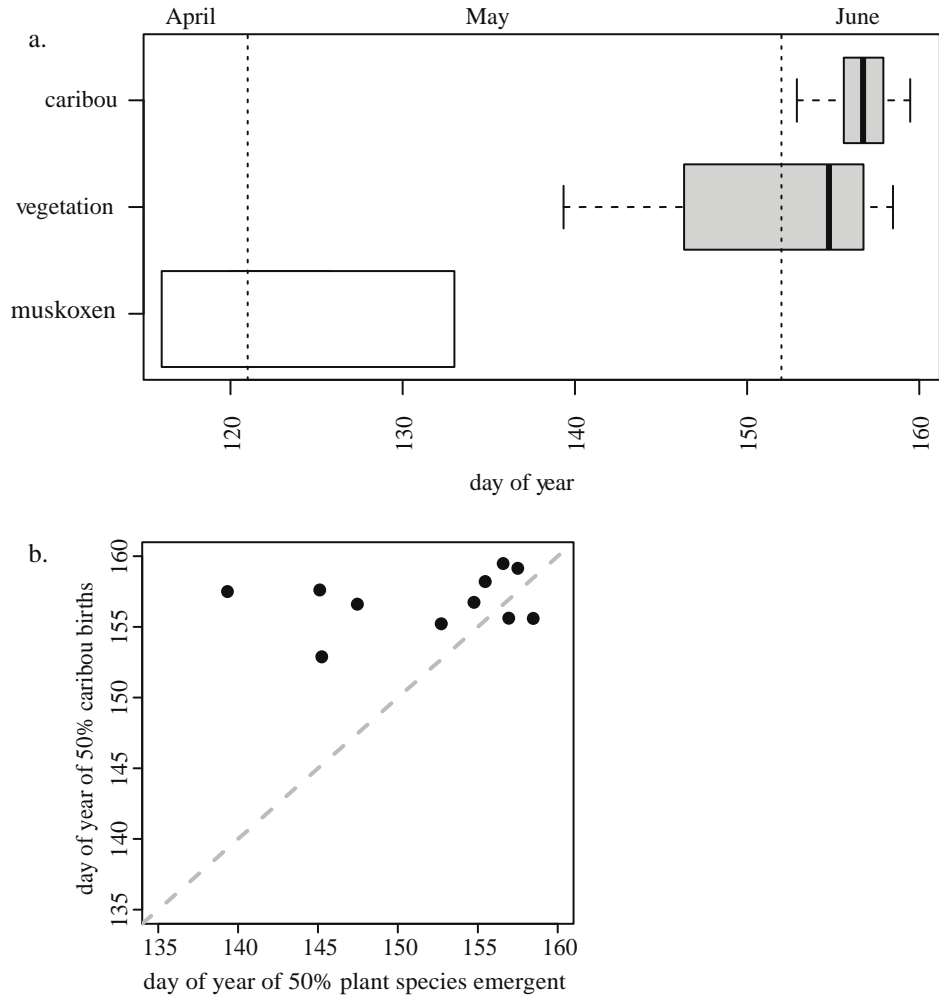


Figure 3.2. Variation in herbivore calving and vegetation phenology. a.) ‘Caribou’ and ‘Vegetation’ show the range, quartiles, and median of the date of 50% caribou calf births and date of 50% plant species emergent respectively from the years 1993, 2002-2011. ‘Muskoxen’ is a depiction of the approximate calving period of muskoxen at this site. A conservative end-date of muskox calving was selected May 13 (Day of Year 133). Vertical dotted lines signify the first day of May and June (non-leap years). b.) a 1:1 graph of caribou calving phenology vs. vegetation phenology. If caribou calving phenology consistently tracked vegetation phenology these points would fall on the 1:1 line.

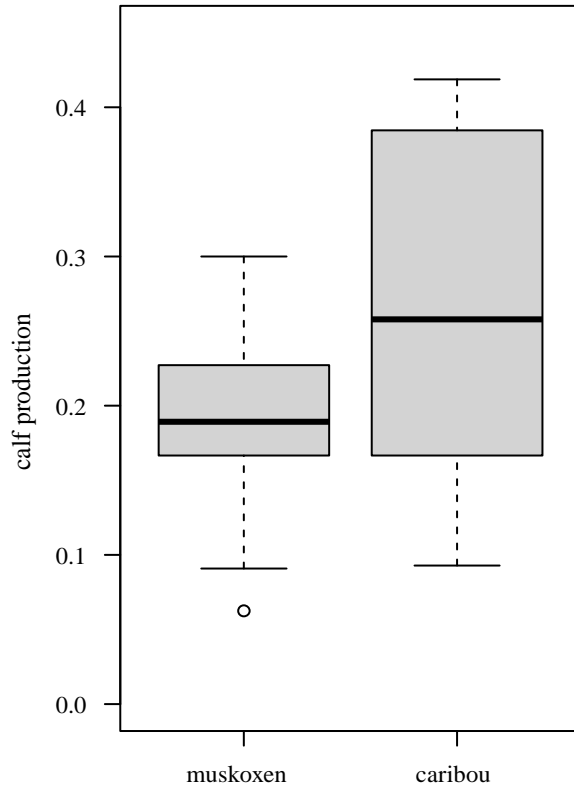


Figure 3.3. Variation in calf production for muskoxen and caribou in the Kangerlussuaq population from 2002-2011 (years with observations for both species). Boxplots depict the range, quartiles, and median of calf production in each population.

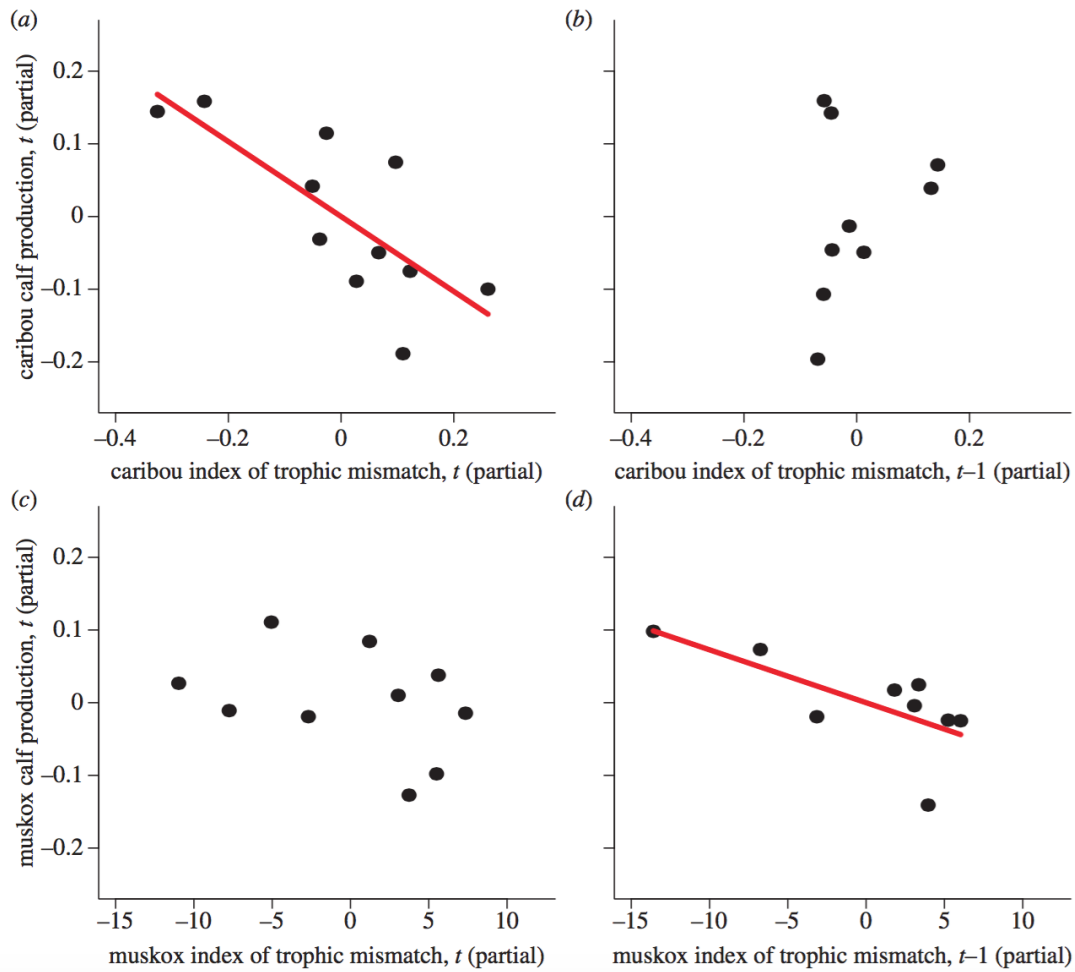


Figure 3.4. Relating trophic mismatch and population abundance to calf production. Each panel shows the relationship between herbivore production and the population specific index of trophic mismatch in immediate (a,c) or previous (b,d) years after accounting for the effect of population abundance in the immediate year. Panels showing lagged effects of trophic mismatch contain two fewer data points (no 1993, 2002) due to analytical requirements for including the lagged effect. Subsetting the non-lagged panels to the same data series resulted in nearly identical relationships to those depicted here (Supplementary Table 3.A). Lines represent significant partial regression fits. Panel **a.** and **b.** show that caribou calf production is closely related to immediate mismatch conditions, whereas panels **c.** and **d.** demonstrate that muskoxen are more sensitive to the lagged consequences of mismatch.

Table 3.1. A summary of the trait and other local-population characteristics identified in the literature review that informed our a priori classification of West Greenland caribou and muskoxen as income and capital breeders, respectively.

Trait	West Greenland caribou/muskoxen population characteristic	Reference(s)
Calving Phenology	Caribou – synchronized with resource phenology Muskoxen – several weeks prior to resource availability	(34, 37)
Infant Mortality	More variable in caribou than muskoxen	(28)
Lactation Phenology	Caribou – peak lactation 1 week post calving Muskoxen – begins 2-3 weeks before vegetation emergence	(63, 64)
Age at first reproduction	Variable, but caribou generally earlier (require less capital reserve)	(40, 65)
Body fat’s influence on conception probability	Muskoxen – more sensitive to body condition Caribou - more sensitive to recent nutrition	(28, 42, 51, 66)
Range usage	Caribou - integrate resource uncertainty through space via migration/high-mobility Muskoxen integrate uncertainty in resource quality through time by residency, prolonged browsing.	(18, 28, 67)
Metabolism and gut retention time	Muskoxen –low metabolic rate, slow but highly efficient extraction of resources from forage Caribou – faster metabolic rate, rapid but comparatively less efficient gut processing	(28, 63, 67)

Supplementary Table 3.S1: Trophic Mismatch and Abundance Models

Model	TMM Coefficient ± s.e.	Abundance Coefficient ± s.e.	n	AICc	R²
Caribou					
$CP_t = a_0 + tmm_t + \varepsilon$	-0.546 ± 0.149**	--	11	-19.77	0.60
$CP_t = a_0 + tmm_t + \varepsilon$ (sub)	-0.536 ± 0.150**	--	9	-15.39	0.65
$CP_t = a_0 + tmm_{t-1} + \varepsilon$	0.330 ± 0.221	--	9	-8.49	0.24
$CP_t = a_0 + abund_t + \varepsilon$	--	-0.0003 ± 0.0003	11	-11.24	0.12
$CP_t = a_0 + abund_t + \varepsilon$ (sub)	--	-0.0003 ± 0.0003	9	-7.79	0.18
$CP_t = a_0 + abund_{t-1} + \varepsilon$	--	0.0003 ± 0.0003	9	-7.10	0.11
$CP_t = a_0 + tmm_t + abund_t + \varepsilon$	-0.515 ± 0.157**	-0.0002 ± 0.0002	11	-17.58	0.63
$CP_t = a_0 + tmm_{t-1} + abund_t + \varepsilon$	0.392 ± 0.552	-0.0001 ± 0.0008	9	-5.08	0.24
$CP_t = a_0 + tmm_t + abund_{t-1} + \varepsilon$	-0.608 ± 0.191**	-0.0002 ± 0.0003	9	-12.58	0.67
$CP_t = a_0 + tmm_{t-1} + abund_{t-1} + \varepsilon$	0.289 ± 0.241	-0.0002 ± 0.0003	9	-5.60	0.28
Muskoxen					
$MP_t = a_0 + tmm_t + \varepsilon$	-0.00368 ± 0.00367	--	10	-19.68	0.11
$MP_t = a_0 + tmm_t + \varepsilon$ (sub)	-0.00225 ± 0.00379	--	9	-17.65	0.05
$MP_t = a_0 + tmm_{t-1} + \varepsilon$	-0.00636 ± 0.00289*	--	9	-21.93	0.41
$MP_t = a_0 + abund_t + \varepsilon$	--	-0.0001 ± 0.002	10	-18.49	0.00
$MP_t = a_0 + abund_t + \varepsilon$ (sub)	--	-0.0003 ± 0.002	9	-17.33	0.04
$MP_t = a_0 + abund_{t-1} + \varepsilon$	--	0.001 ± 0.002	9	-17.84	0.07
$MP_t = a_0 + tmm_t + abund_t + \varepsilon$	-0.004 ± 0.004	-0.0008 ± 0.002	10	-16.68	0.13
$MP_t = a_0 + tmm_{t-1} + abund_t + \varepsilon$	-0.007 ± 0.003**	-0.002 ± 0.002	9	-20.11	0.49
$MP_t = a_0 + tmm_t + abund_{t-1} + \varepsilon$	-0.001 ± 0.004	0.001 ± 0.002	9	-14.58	0.09
$MP_t = a_0 + tmm_{t-1} + abund_{t-1} + \varepsilon$	-0.006 ± 0.003	0.0001 ± 0.002	9	-18.80	0.41

CP and MP are species-specific calf ratios at time t, tmm is the species-specific index of trophic mismatch at lag t, abund is species-specific abundance at the breeding ground at lag t. The designation (sub) indicates analyses with subset of data (excluding 1993,2002) to allow for goodness of fit comparison with analyses where response years were sacrificed to explore lagged effects. * p <= 0.1, ** p <= 0.05.

Supplementary Table 3.S2: Temporal Trends in Response and Predictor Variables

Variable of Interest	Year Coefficient \pm s.e.	R²
Caribou Calf Production	-0.016 +/- 0.013	0.15
Caribou Trophic Mismatch Index	0.034 +/- 0.017*	0.33
Caribou Abundance	-14.98 +/- 14.13	0.12
Muskox Calf Production	0.019 +/- 0.005**	0.61
Muskox Trophic Mismatch Index	-1.6 +/- 0.5**	0.52
Muskox Abundance	-1.64 +/- 1.38	0.15

Temporal trends in response and predictor variables were assessed by regressing the variable in question against year using data from 2002-2011 and by examining model significance. * $p \leq 0.1$, ** $p < 0.05$.

Supplementary Table 3.S3: Trophic Mismatch and Abundance Models with Detrended Data

Model	TMM Coefficient ± s.e.	Abundance Coefficient ± s.e.	n	AICc	R²
Caribou					
$CP_t = a_0 + tmmd_t + \varepsilon$	$-0.60 \pm 0.22^{**}$	--	10	-13.73	0.47
$CP_t = a_0 + tmmd_t + \varepsilon$ (sub)	$-0.72 \pm 0.16^{**}$	--	9	-17.99	0.74
$CP_t = a_0 + tmmd_{t-1} + \varepsilon$	$0.62 \pm 0.20^{**}$	--	9	-13.65	0.57
$CP_t = a_0 + tmmd_t + abund_t + \varepsilon$	$-0.54 \pm 0.27^*$	-0.0001 ± 0.0003	10	-10.66	0.48
$CP_t = a_0 + tmmd_{t-1} + abund_t + \varepsilon$	$0.97 \pm 0.33^{**}$	0.0004 ± 0.0004	9	-12.50	0.67
$CP_t = a_0 + tmmd_t + abund_{t-1} + \varepsilon$	$-0.82 \pm 0.19^{**}$	-0.0002 ± 0.0002	9	-15.95	0.77
$CP_t = a_0 + tmmd_{t-1} + abund_{t-1} + \varepsilon$	$-0.65 \pm 0.26^{**}$	-0.00007 ± 0.0003	9	-10.30	0.58
$CP_t = a_0 + tmmd_t + tmmd_{t-1} + \varepsilon$	t: $-0.59 \pm 0.29^*$; t-1: 0.15 ± 0.28	--	9	-15.00	0.75
Muskoxen					
$MPd_t = a_0 + tmmd_t + \varepsilon$	0.005 ± 0.003	--	10	-31.57	0.30
$MPd_t = a_0 + tmmd_t + \varepsilon$ (sub)	0.005 ± 0.003	--	9	-26.77	0.05
$MPd_t = a_0 + tmmd_{t-1} + \varepsilon$	-0.002 ± 0.003	--	9	-24.04	0.05
$MPd_t = a_0 + abund_t + \varepsilon$	--	-0.002 ± 0.001	10	-31.16	0.27
$MPd_t = a_0 + abund_{t-1} + \varepsilon$	--	-0.0009 ± 0.001	9	-24.14	0.06
$MPd_t = a_0 + tmmd_t + abund_t + \varepsilon$	$0.005 \pm 0.003^*$	-0.002 ± 0.0009	9	-32.19	0.54
$MPd_t = a_0 + tmmd_{t-1} + abund_t + \varepsilon$	-0.003 ± 0.003	-0.002 ± 0.001	9	-24.15	0.35
$MPd_t = a_0 + tmmd_t + abund_{t-1} + \varepsilon$	0.005 ± 0.003	-0.0009 ± 0.001	9	-24.12	0.36
$MPd_t = a_0 + tmmd_{t-1} + abund_{t-1} + \varepsilon$	-0.002 ± 0.004	-0.0009 ± 0.001	9	-21.22	0.11

CP and MPd (muskox detrended by year) are species-specific calf ratios at time t, tmmd is the detrended (by year) species-specific index of trophic mismatch at lag t, abund is species-specific abundance at the breeding ground at lag t. The designation (sub) indicates analyses with subset of data (excluding 1993, 2002) to allow for goodness of fit comparison with analyses where response years were sacrificed to explore lagged effects. * p <= 0.1, ** p <= 0.05

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Chapter 4. Advancing plant phenology and reduced herbivore production in a terrestrial system associated with sea ice decline

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Abstract/Introduction:

The contribution of declining Arctic sea ice to warming in the region through Arctic Amplification suggests that sea ice decline has the potential to influence ecological dynamics in terrestrial Arctic systems. Empirical evidence for such effects is limited, however, particularly at the local population and community levels. Here we identify an Arctic sea ice signal in the annual timing of vegetation emergence at an inland tundra system in West Greenland. According to the time series analyses presented here, an ongoing advance in plant phenology at this site is attributable to the accelerating decline in Arctic sea ice, and contributes to declining large-herbivore reproductive performance via trophic mismatch. Arctic-wide sea ice metrics consistently outperform other regional and local abiotic variables in models characterizing these dynamics, implicating large-scale Arctic sea ice decline as a potentially important, albeit indirect, contributor to local-scale ecological dynamics on land.

Rising atmospheric CO₂ concentrations and sea ice loss have contributed to a rate of warming in the Arctic nearly double that at lower latitudes¹⁻⁵. The accelerating seasonal decline in sea ice extent^{6,7}(Fig. 4.1), concentration⁴, and thickness^{8,9} in the Arctic¹⁰ interacts with atmospheric and oceanic forcings via ice-albedo and ice-insulation feedbacks to amplify regional warming and stimulate further ice loss⁴. The main focus of ecological repercussions of projected sea ice loss has been on pagophilic species, whose dynamics have already been perturbed by diminishing sea ice cover^{3,5,11-16}. In contrast, indirect weather-mediated effects of continued ice loss on terrestrial species are less clear.

Evidence for near coastal warming associated with regional sea ice decline is widely reported¹⁷⁻²⁰, but broad-scale sea-ice and temperature feedbacks also contribute to terrestrial warming not associated with coastal advection^{17,21}. Empirical support for a role of sea ice in terrestrial ecological dynamics has thus far been limited to remotely sensed indices of vegetation productivity measured at moderate (500 m) to coarse (12 km) spatial grains along coastal regions^{18,19}. These studies, in combination with modeling and heuristic arguments^{21,22}, draw primary focus to the indirect ecosystem-level responses of terrestrial systems to sea ice loss. Less well documented so far are local-scale effects and those affecting the dynamics of ecological populations and communities, especially those far from the coast, despite long-standing acknowledgment of their importance^{23,24}.

Here, we investigate the potential for an Arctic sea ice signal in the local-scale dynamics at two trophic levels of an inland, mountainous tundra study system (67.11° N 50.34° W) near Kangerlussuaq in Low-Arctic West Greenland²⁵⁻²⁷ using data derived from an ongoing, long-term observational study of ecological responses to climate change^{28,29}. We explore the explanatory power of regional and Arctic-wide sea ice dynamics alongside other broad- and local-scale measures of climate variability in relation to the interannual variation in the timing of plant growth and the timing of parturition and reproductive performance of a migratory caribou (*Rangifer tarandus*) population. Our results suggest sea ice decline is an important driver of the timing of the plant growing season and trophic mismatch with caribou at this study site.

Results:

Recent Arctic sea ice decline

Annual sea ice extent over the Arctic has exhibited negative trends across all months from 1979 to the 2011 (Fig. 4.1). Time series of monthly Arctic sea ice extent aggregated by summer and fall months exhibited a significant change toward more rapid sea ice decline around the year 2000 (95% CI: 1997,2002) (Davies test, $k = 30$, $p < 0.001$), but no significant aggregate acceleration in sea ice loss was detectable in winter and spring (Davies test, $k = 30$, $p = 0.17$).

Drivers of plant phenology

The annual date of the mid point of the plant growing season at the study site, that of 50% species emergence, advanced from 2002 to 2011 (Fig. 4.2– triangles, solid black line) by 1.6 ± 0.53 days/year, or approximately 16 days (linear regression $R^2 = 0.53$, $n = 10$, $F(1,8) = 8.977$, $p = 0.02$). Local temperature was a poor predictor of the date of 50% emergence in all years (best fit regression models - Local monthly temperature [May]: $R^2 = 0.23$, $n = 10$, $F(1,8) = 2.421$, $p = 0.16$, Fig. 3a; Local Summer Warmth Index_{year t}: $R^2 = 0.33$, $n = 10$, $F(1,8) = 3.997$, $p = 0.08$, Fig. 3b; Local thawing degree days: $R^2 = 0.27$, $n = 9$ [2011 sub-daily temps. unavailable], $F(1,7) = 2.618$, $p = 0.15$). In contrast, monthly Arctic-wide sea ice extent [ASIE] from winter (Jan or Feb) and early summer (Jun) was a strong predictor of both interannual variation and the trend in dates of 50% plant species emergence ($R^2 = 0.80$ [Figs. 2ab, 3c] and 0.83 [Fig. 2ab], respectively; $n = 10$, $F(2,7) = 14.01$, 17.62 , $p < 0.004$). Large-scale temperature and regional sea ice cover closest to the study area (Davis Strait/Baffin Bay) were also poor predictors of the annual date of 50% emergence at the site (best fit regression models – Davis Strait/Baffin Bay Ice Cover [June]: $R^2 = 0.08$, $n = 9$, $F(1,7) = 0.621$, $p = 0.45$, Fig. 4.3d; Arctic Summer Warmth

$\text{Index}_{\text{year } t-1}$: $R^2 = 0.26$, $n = 10$, $F(1,8) = 2.785$, $p = 0.13$, Fig. 4.3e; Arctic-wide monthly surface temperature [April]: $R^2 = 0.28$, $n = 10$, $F(1,8) = 3.055$, $p = 0.12$, Fig. 4.3f), despite the expected stronger correlation between regional, rather than Arctic-wide, sea ice and local temperature in the months leading up to plant emergence (Fig. 4.4ab).

The explanatory power of the relationship between Arctic-wide sea ice extent and local-scale plant phenology at the site remained high when all time series were detrended by year ($R^2 = 0.66$ [Jan & Jun ASIE] and 0.73 [Feb & Jun ASIE], respectively; $n=10$, $F(2,7) = 6.65$ and 9.60 , $p < 0.025$). The mean error (± 1 SE) between observed and predicted dates of 50% emergence was $2.08 (\pm 0.55)$ days over the length of the observed time series, a smaller temporal range than the sampling resolution of most remote sensing and observer-based data series of plant phenology³⁰.

Hindcasting trophic mismatch

A hindcast of the timing of plant emergence at the site using the Arctic-wide monthly sea ice model [Jan or Feb & Jun ASIE] suggests a trend over the past three decades toward earlier plant phenology at the study site (Feb and June model: $\beta_{\text{Plants}} = -0.741 \pm 0.099$, $R^2 = 0.64$, $n = 33$; $F(1,31) = 55.78$, $p < 0.001$, dashed gray line Figs. 4.2ab). The observed date of 50% emergence in 1993, the earliest year plant phenology was recorded at this site²⁵, was accurately predicted by our models (Fig. 4.3a – red triangle, 1993). Notably, this date was not used to parameterize either model.

In contrast to the modeled time series of plant phenology, the observed timing of calving by caribou at the study site displayed little interannual variability (Fig. 4.2b – black circles) and only a slight rate of advance over the 33 year span of the data series

($\beta_{\text{Caribou}} = -0.114 \pm 0.036$, $R^2 = 0.45$, $n = 14$, $F(1,12) = 9.978$, $p = 0.008$, Fig. 4.2b), obtained using observations from an earlier study³¹. This pattern is consistent with earlier reports based on six and seven years of observational data on the timing of parturition by caribou in this population at the same site^{16,29}.

Increasing early mortality of caribou calves and declining production of calves in this population are related to increasing trophic mismatch driven by advancing plant phenology at this site (Fig. 4.5ab). The relationship between plant phenology and the magnitude of trophic mismatch indicates that the earlier green-up occurs the stronger is the mismatch in that year (Pearson's $r = -0.81$, $n = 11$, $p = 0.002$; Fig. 4.5c). A trophic mismatch index constructed using sea-ice modeled plant emergence data and empirical caribou calving data closely tracks our empirical index of trophic mismatch (Pearson's $r = 0.70$, $n = 11$, $p = 0.02$; Fig. 4.5d) and indicates a strong trophic match in 1979 (Fig. 4.5ab), a result that is consistent with earlier reports of caribou calf production at the study site in that year³¹.

Discussion:

That the complex interaction documented here between plant phenology and herbivore demographics is ostensibly driven by Arctic sea ice decline is suggested by several lines of evidence. First, there is a strong association between Arctic-wide sea ice extent and plant phenology at our site (Fig. 4.2). Second, prior to the acceleration of summer and autumn sea ice loss that began around the year 2000, the timing of 50% plant species emergence coincided with or followed, on average, the timing of caribou parturition at the site (Fig. 4.2b), contributing to greater trophic match (lower mismatch),

lower offspring mortality, and higher offspring production (Fig. 4.5ab). Since the acceleration of summer and autumn sea ice loss began, however, plant phenology has shifted toward increasingly earlier 50% emergence, which now, on average, precedes caribou parturition (Fig. 4.2b). This, in turn, has exacerbated the previously documented trophic mismatch^{28,29}, further reducing herbivore reproductive performance (Fig. 4.5ab). Third, and finally, our estimates of annual trophic mismatch derived from observational plant phenology data (Fig. 4.5a-c) are accurately reproduced by an index of trophic mismatch that is constructed with sea ice extent-modeled plant phenology (Fig. 4.5d).

While other large-scale and regional forcings, like Arctic surface temperature and nearby sea ice cover, are correlated with Arctic-wide sea ice extent during some periods of the year³² they are poor or inconsistent predictors of annual dates of 50% plant species emergence at this site (Fig. 4.3ab,d-f). That Arctic-wide sea ice extent outperformed even local predictors (TDD & Fig. 4.3ab,d) raises questions about the specific indirect mechanism(s) by which sea ice affects plant phenology that we cannot resolve with certainty given the current dataset. The phenomenon of large-scale integrative variables outperforming local-scale predictors in explanatory power is, however, well documented in ecological studies^{33,34}, and is particularly relevant to the relationship between plant phenology and sea ice. Arctic-wide sea ice influences many elements of climate variation at regional and local scales³⁵⁻³⁹, and plant phenology is driven by a complex interaction between many of these abiotic factors and the biotic environment integrated over a period of several months⁴⁰. Isolating the mechanistic influence of a specific time window or single abiotic factor on these dynamics will require, at a minimum, spatially

and/or temporally replicated local-scale phenology and productivity data that, at present, are rare.

As the product of correlative analyses, our results share a limitation common to other efforts to assign attribution in ecological responses to climate change^{41,42}. Recognizing this limitation is important, but not by default disqualifying⁴³. Our results strongly suggest that interannual variability and the long-term decline in Arctic sea ice cover can have important indirect consequences for highly localized ecological dynamics, and complex interactions deriving from them, in terrestrial systems. Whereas such consequences are comparatively well known, and more obviously expected, in marine systems¹³, our results highlight the need for greater focus on the indirect implications of sea ice loss for the dynamics and conservation of terrestrial species.

Methods:

Plant phenology

Plant phenology data used in these analyses were derived from near-daily observations from early-May to late-June from 2002-2011 of all species emergent on twelve (0.5 m²) permanently marked plots at three sites with differing aspects and elevations (260 – 300m)^{28,29,44}. Data from 1993 were collected using identical methods on a separate set of plots covering the same extent and elevational gradient within the study site²⁵. The annual date of 50% of plant species emergence (hereafter in methods, 50% emergence) was calculated from non-linear regression models fit to the across-plot averaged time series of the percentage of species observed on each plot on day x in year y

relative to the total number of species observed on each plot by the end of June in year y^{25,28,45}.

Herbivore phenology and demographics

Caribou abundance, demographics, and reproductive phenology were monitored at the study site and at the adjacent calving area over the same time period and at the same frequency as the vegetation phenology plots^{25,28}. Caribou calving phenology was calculated using Caughley's Indirect method A⁴⁶ modified for use in wild populations⁴⁷. Reproductive performance of the caribou population was calculated from changes in calving season demographics derived from near-daily observations of calf to population ratios excluding males. We defined calf production as the proportion of calves to the sum of calves and cows in the population in late June. Annual calf mortality was defined as the end of June proportion of calves to the sum of calves and cows divided by the peak proportion of calves to the sum of calves and cows observed during that season. These methods are consistent with those described in greater detail in previous reports from this site^{25,28,44}.

Sea ice

The monthly Arctic-wide sea ice extent (ASIE) index and monthly regional sea ice extent data for the Davis Strait/Baffin Bay area were obtained from the National Snow and Ice Data Center for January 1979 through December 2011/2010 respectively^{48,49}. These gridded (25 km x 25 km) data series quantify the extent cover (all grid cells > 0.15 percent sea ice cover multiplied by grid cell area) of sea ice as measured from a suite of satellite-based passive microwave sensors for the entire Arctic and the Davis

Strait/Baffin Bay region (region graphically defined in ref ⁵⁰) respectively.

Monthly Arctic-wide sea ice extent anomalies were calculated based on 1979-2011 monthly means. These data were separated into two groups: the months leading up to and including the onset of terrestrial primary productivity (winter through spring: December to May), and the months of peak primary productivity and senescence (summer through autumn: June through November), to examine the implications of non-uniform ice loss throughout the year using the phenology of primary productivity as a yardstick.

To identify the presence and timing of a significant acceleration in the rate of ice loss in these grouped sea ice time series we applied a Davies test ($k = 30$) using the ‘segmented’ package in R ^{51,52}. This tests for the ‘best’ value at which a significant difference in slope can be identified through the use of naive Wald statistics corrected for repeated testing across ‘ k ’ evenly spaced potential break points ⁵¹.

Temperature

Hourly (1999-2010) and mean monthly temperature (1978-2011) records for the village of Kangerlussuaq, Greenland (<25 km from study site) were obtained from the Danish Meteorological Institute (DMI) ⁵³. Thawing degree-days (TDD) were calculated from the hourly data consistent with method 2 from McMaster & Wilhelm ⁵⁴.

Accumulated TDD for each day of the year (DOY) were then calculated for 2002-2010. Local mean monthly temperature data were used to calculate the Summer Warmth Index (SWI) for the study site. The SWI is the sum of the mean monthly temperatures above zero ($^{\circ}\text{C month}^{-1}$), effectively a measure of thawing degree months.

Mean monthly Arctic-wide (65° N to 90° N) surface temperatures were acquired from NCEP Reanalysis derived data⁵⁵ provided by the NOAA/OAR/ESRL PSD, Boulder Colorado, USA (<http://www.esrl.noaa.gov/psd/>).

Relating inland temperatures to sea ice extent

To explore the possibility of immediate and lagged influence of Arctic-wide and regional sea ice extent on Kangerlussuaq temperature, correlational analyses (Pearson's r) were run on linearly detrended monthly time series of local temperature and ASIE and Davis Strait/Baffin Bay sea ice extent. Results were used to guide model selection and interpretation for models linking sea ice with temperature and sea ice with plant phenology.

Relating temperature to plant phenology

We used linear regression to explore the effect of accumulated TDD_{year t} on the DOY 50% emergence_{year t} as well as effect of accumulated TDD by June 1_{year t} on DOY of 50% emergence_{year t}. Linear regression was also used to relate local monthly mean temperatures to DOY of 50% emergence, the SWI of current and the previous summer to the DOY of 50% emergence, and mean monthly temperatures and Arctic-wide SWI to DOY of 50% emergence.

Relating inland plant phenology to sea ice extent

Sea ice extent (ASIE and regional) was related to DOY of 50% emergence using linear regression models parameterized with 2002-2011 phenology data. The best candidate models were then confronted with 1993 phenology data to assess the error

between predicted and observed values for a date outside of the continuous sampling period. To isolate the influence of trend from interannual variability, the best-fit regressions were reanalyzed with detrended (by year) phenology and sea ice data.

Relating caribou offspring production to plant phenology

The synchrony of caribou calving phenology was related to plant phenology using the index of trophic mismatch developed previously²⁸. This index is calculated, using a fitted logistic curve, as the percentage of plant species emergent on the date of 50% caribou births, and thus represents a measure of the state of forage plant resource availability mid-way through the season of herbivore parturition, a life history period with a critical influence on reproductive performance²⁸. The annual values of this index were then regressed against end of season caribou calf production and early caribou calf mortality for 1993, 2002-2011, respectively, updating previous analyses^{28,29}. Data on caribou calving from 1977 – 1979 were obtained from an earlier study that was conducted at the same study site by a different group using equivalent methods³¹.

Relating caribou offspring production to sea ice extent

Non-linear logistic models were fit to sea-ice based estimates of plant phenology (15%, 25%, 40%, 50%, 60%, 75%, 85% plant species emergent) for 1979, 1993, 2002-2011 using the same methods detailed above for estimating date of 50% species emergent. We then used these model coefficients (minimum coefficient of determination for all models was 0.68) to calculate the percent of the total number of plant species emergent on the date of observed 50% caribou births, effectively allowing for the calculation of a trophic mismatch index²⁸ solely using sea-ice extent and caribou

phenology data. This allowed for similar caribou productivity and mortality regressions against trophic mismatch as detailed above.

All statistical analyses were conducted using the base package in the R statistical computing environment unless otherwise noted⁵². Throughout, best-fit regression models were identified using an information theoretics approach, specifically Akaike's Information Criterion corrected for small sample sizes (AICc). Models were considered equivalent if $\Delta AIC < 2$.

Figures:

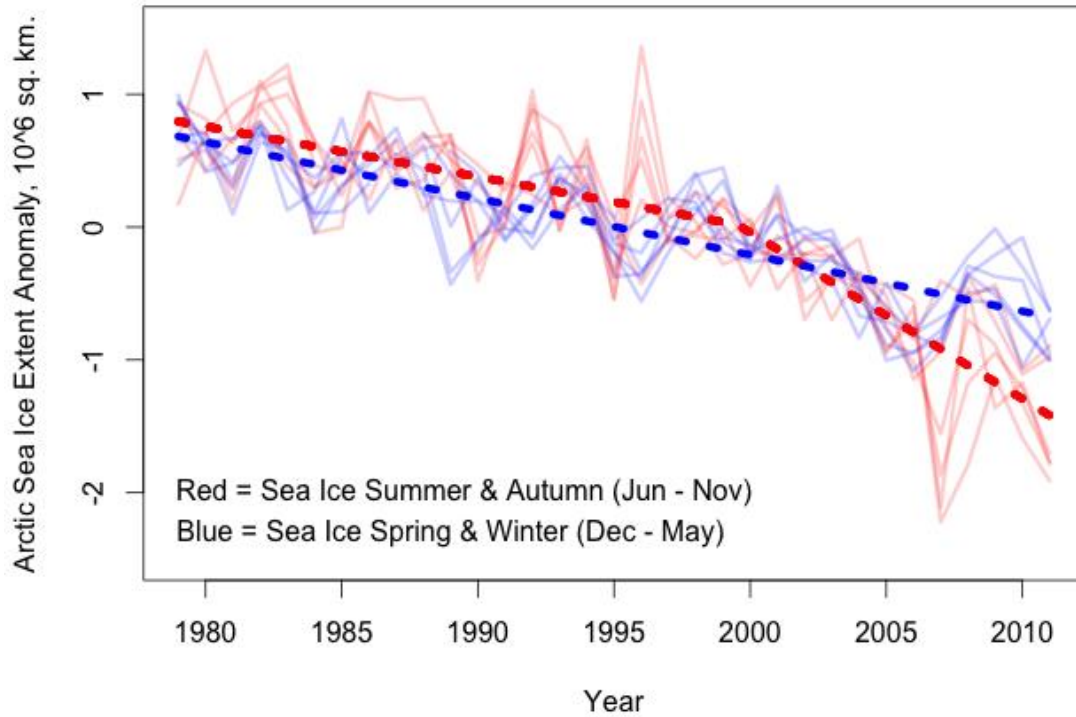


Figure 4.1. Monthly Arctic Sea Ice Extent Index anomalies. Anomalies calculated from 1979-2011 mean are color coded by season (winter and spring: Dec –May; summer and autumn: Jun – Nov). The rate of decline in monthly Arctic sea ice extent over this time period increased significantly in the summer and autumn months (red dashed) beginning in 2000 (95% CI: 1997-2002).

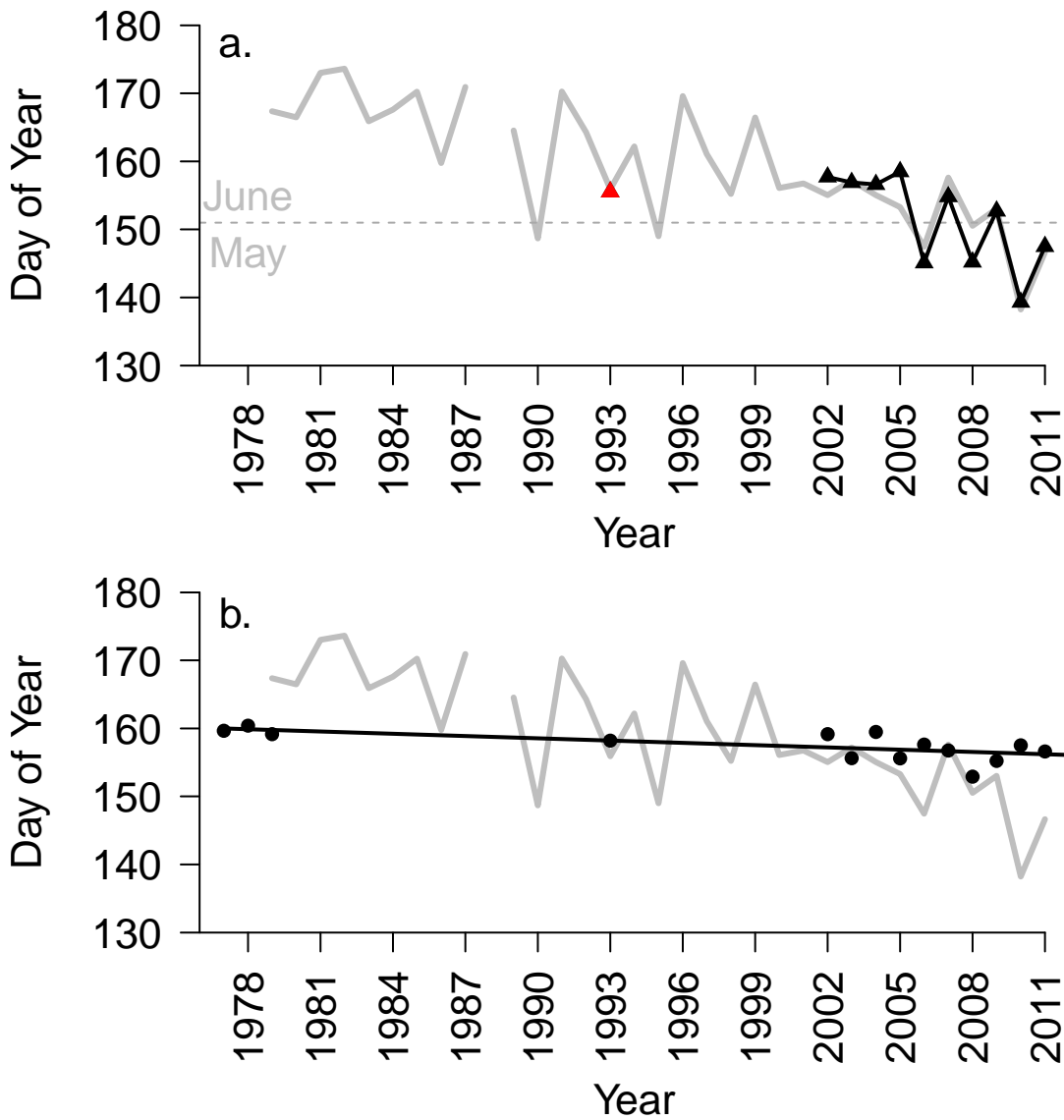


Figure 4.2. Long term differential response between trophic levels to diminishing Arctic sea ice. Panel a. Time series of observed (black triangles, black line) and predicted (gray lines) timing of 50% plant species emergence at the study site near Kangerlussuaq, Greenland, based on January (or February) and June multiple regression ($y = \beta_0 + \beta_1 \text{Jan(or Feb)E} + \beta_2 \text{JunE} + \epsilon$; where y = date of 50% plant species emergence in year t , Jan(or Feb)E = January (or February) sea ice extent [10^6 km^2] in year t , JunE =

June Sea Ice Extent [km²] in year t). 1993 (red triangle) was not included in the parameterization of the model, but is plotted in panel a to show the minimal difference between observed and predicted values for that year. The gap in the January and June modeled phenology series reflects a gap in the satellite based sea ice extent record (1988). Panel b. Observed dates of 50% caribou calves born at the study site near Kangerlussuaq, Greenland (black circles, solid black regression line) plotted over the same phenology models as panel a. These time series document a divergence in the phenologies of caribou and the plant community in recent years, but also demonstrate a sustained flip in the timing of plant growth relative to herbivore parturition since the year 2000, a change driven primarily by earlier plant phenology relative to the comparatively fixed timing of caribou calving.

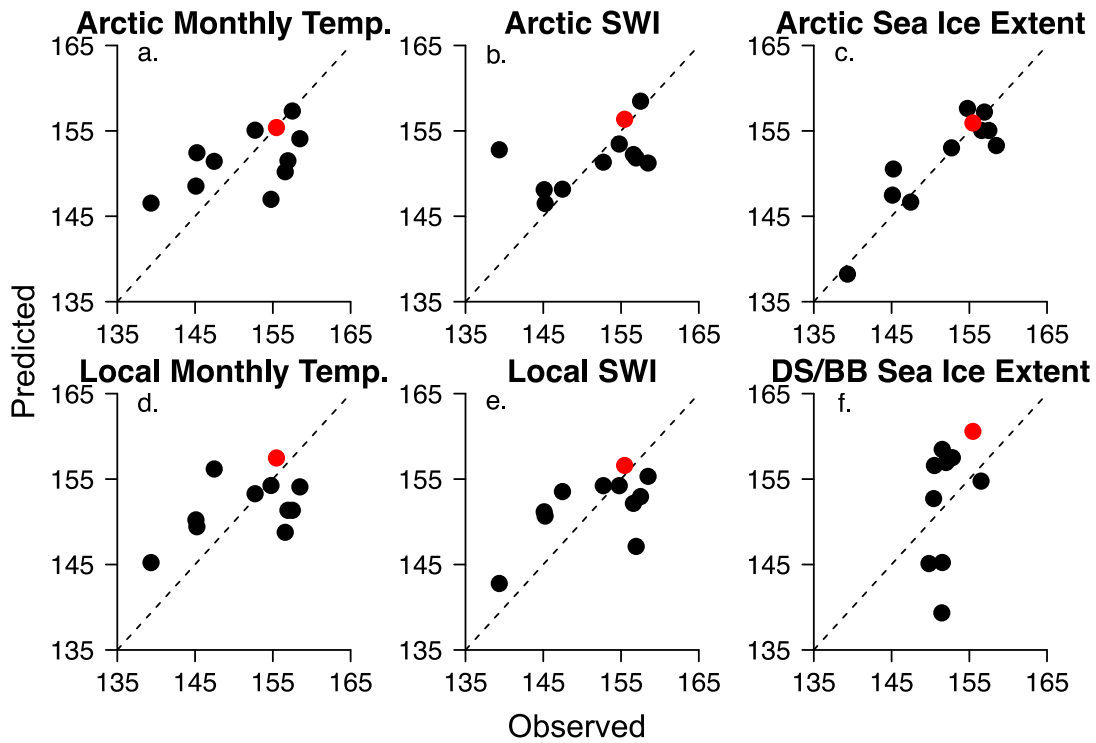


Figure 4.3. Vegetation phenology models informed by temperature and sea ice metrics at local and broad scales. Each panel depicts the best-fit phenology model for a temporal or spatial scale of abiotic predictor(s). Predicted values of the timing of 50% plant species emergence are plotted against observed values from the study site. Model fits are organized in rows by local temperature (top row – 2 temporal scales), sea ice cover (center row – two spatial scales), and Arctic-wide temperature (bottom row – 2 temporal scales). The dashed line in each panel depicts the 1:1 relationship between predicted and observed values. All panels used models parameterized with data from 2002-2011 (black circles) except panel d. where no 2011 data was yet available. Red circles represent data from 1993 not used in model parameterization. Abiotic predictors identified for each best-fit model scale are as follows: panel a. May mean monthly

temperature from Kangerlussuaq, Greenland; panel b. Kangerlussuaq, Greenland Summer Warmth Index (SWI) [i.e. thawing degree months] in the current year of plant emergence; panel c. January and June arctic sea ice extent; panel d. is the Davis Strait/Baffin Bay regional sea ice extent in June of the year of plant emergence; panel e. Arctic-wide SWI of the year prior to plant emergence; panel f. April Arctic-wide mean monthly temperature.

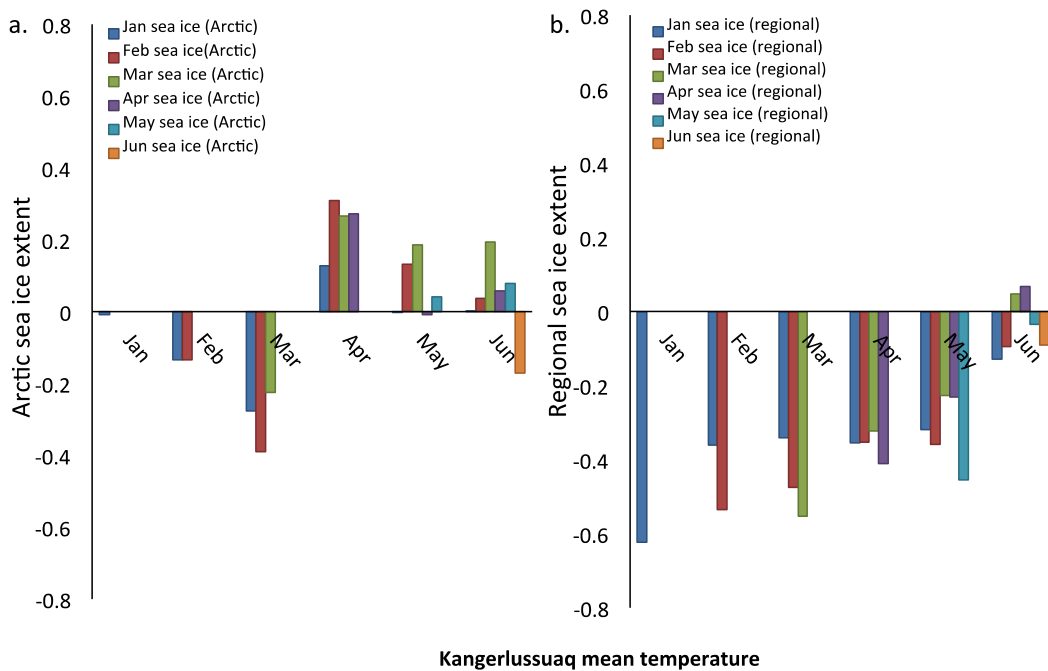


Figure 4.4. Correlations between sea ice and inland temperature. Pearson's r correlation coefficients between linearly detrended local mean monthly temperature near the study site in Kangerlussuaq, Greenland and a.) Arctic-wide sea ice extent or b.) regional Baffin Bay/Davis Strait sea ice extent. Correlations between ice extents from the months that precede each monthly mean temperature value are included for the calendar year up to and including June, the month when caribou calving and midpoint of the plant growing season occurs.

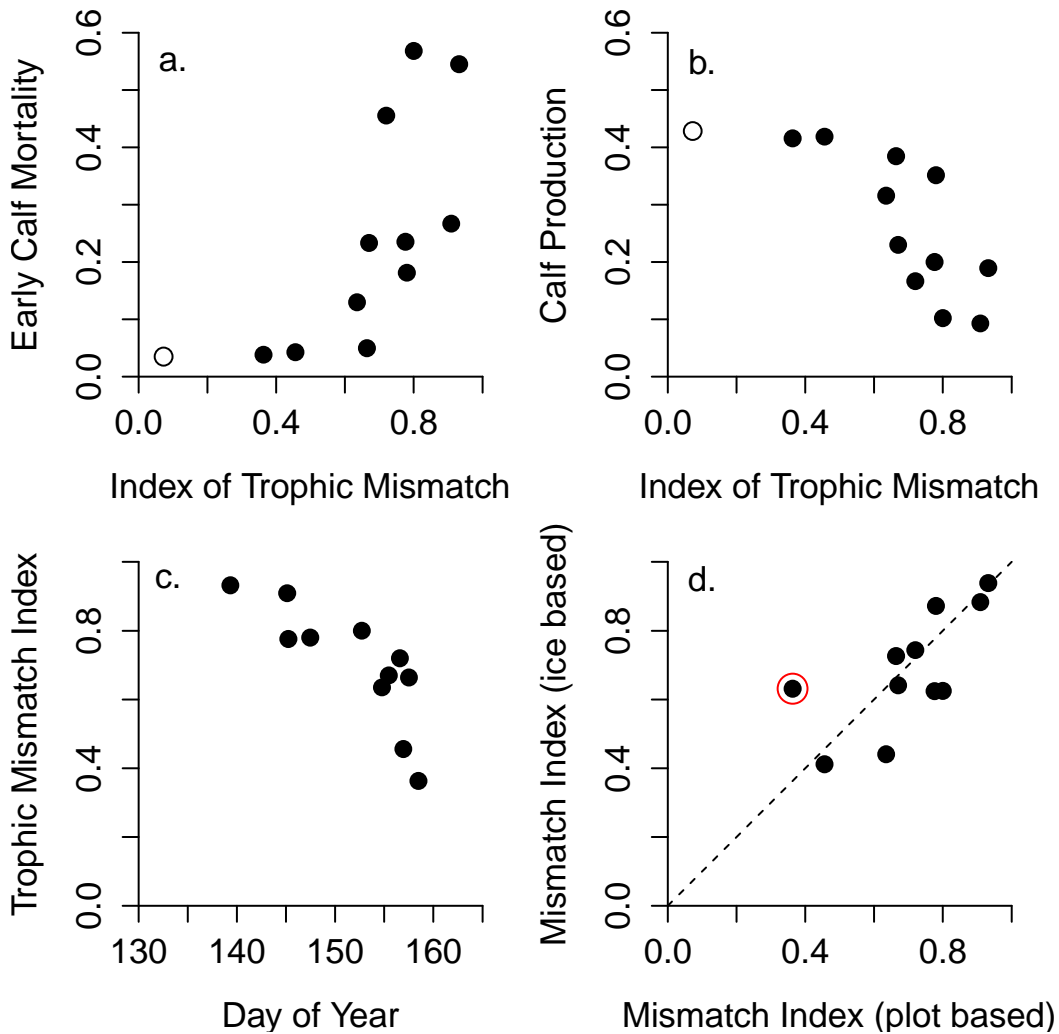


Figure 4.5. Reproductive consequences of trophic mismatch. Panels a and b. The relationships between the magnitude of trophic mismatch, i.e. the percentage of plant species emergent at the date of 50% caribou calves born, and early calf mortality (a) or caribou calf production (b) at the study site. Filled circles were calculated using data from the 11 years of the authors' long term observational study, whereas open circles depict empirical records of caribou reproductive performance from 1979 in relation to sea-ice informed estimates of trophic mismatch in that year. The lack of satellite derived sea ice data prior to 1979 prevented the inclusion of the caribou data from 1977 and 1978

that are shown in Figure 2b. Panel c. The relationship between the observed trophic mismatch index and observed dates of 50% plant species emergence at the study site. Earlier plant emergence results in increasing mismatch with the timing of offspring production by caribou, a period of critically high resource demand ^{28,29,44}. Panel d. Relationship between the original trophic mismatch index derived from plot-based vegetation phenology and the trophic mismatch index derived from a sea-ice only model estimate of vegetation phenology. The year 2005, circled in red, was characterized by a severe caterpillar outbreak ²⁷, when plant phenology was anomalously delayed by defoliation, resulting in lower plot-derived mismatch in that year.

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Chapter 5 - Spatial variability, drivers, and scale-mismatch of tundra greenup phenology at a landscape extent

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Abstract:

Spatial variability of plant phenology has widespread implications for landscape-scale processes like herbivore foraging and the carbon cycle, but has traditionally been quantified on localized plots by human observers or at broader scales using coarse satellite imagery. Heterogeneity and scale dependencies are common in ecology, but are largely unaccounted for in understanding phenological dynamics at these landscape extents, particularly in Arctic environments. We used a network of 50 near-surface time-lapse camera (PlantCam) sites to quantify spatial variability in tundra vegetation greenup across 40 km² in two years with contrasting abiotic conditions. We then explored landscape drivers of variability in mixed vegetation communities and shrub and graminoid patches. Scale-dependent dynamics were identified by comparing near-surface results with satellite-derived records across the same spatial extent. Spatial variation in leaf onset measured via the PlantCams in a given year was of a much greater magnitude than between year differences, despite contrasting seasonal climatic conditions. Satellite derived measures of vegetation greenup were much less variable between years, and were also related to different landscape drivers of heterogeneity than near-surface measures. We demonstrate that scaling relationships are non-stationary within landscapes and between years and provide evidence that landform interact with patch-level dynamics to generate spatial heterogeneity in plant phenology.

Introduction:

Variation and trends in springtime phenology are clear biological indicators of climate change documented across all levels of ecological organization, from individuals (Parmesan and Yohe 2003, Root et al. 2003) to ecosystems (Xu et al. 2013). While most

observations indicate earlier spring onset, particularly in high-latitude environments (Post et al. 2009), there is significant climate-linked variability in these patterns across regions (Zeng et al. 2011), taxa (Hoye et al. 2007), and levels of ecological organization (Steltzer and Post 2009). Despite coherent trends at the global scale, phenological responses to warming measured at different levels of ecological organization sometimes appear contradictory (Fisher et al. 2006, Steltzer and Post 2009) due to scale-dependent ecological dynamics. Identifying and exploring these phenomena, particularly in rapidly warming regions like the Arctic, will be critical to building more robust links between decades of plot- and satellite-derived phenological metrics (Fisher et al. 2006, Steltzer and Post 2009) while also continuing to expand phenological research priorities into lesser studied, but conceptually relevant intermediate scales.

Phenological variability at any scale ultimately arises from individual-level processes shaped by genetics, competitive and facilitative interactions, and (micro-) climatic conditions (Liang and Schwartz 2009, Wolkovich et al. 2014) that are then filtered through a landscape context to generate spatial pattern. In a broader ecological context, plant phenology mediated interactions with the atmosphere, pollinators, and herbivores also occur at the fine spatial grain of individual plants or patches (Steffan-Dewenter et al. 2002, Hoye et al. 2013, Richardson et al. 2013, Hinks et al. 2015), although the frequency, magnitude, and consequences of these interactions are functions of spatial heterogeneity in phenology at broader spatial extents (Levin 1992, Turner 2005, Schindler et al. 2015). Despite this context, the study of local-scale phenological dynamics at broader landscape to regional extents has been subject to remarkably little research. Logistical constraints on data collection have, instead, historically directed

phenological research towards two more established modes of monitoring: local-scale observations from plots across a limited extent, and radiometric monitoring at broad extents using coarse-grained satellite-derived vegetation indices (Morisette et al. 2009, Richardson et al. 2013).

The history, strengths, and shortcomings of these two research foci are discussed at length elsewhere [see (Fisher et al. 2006, Morisette et al. 2009, Fitchett et al. 2015)], but a few key points are summarized here: plot-based studies are critical for understanding drivers and trends in vegetation phenology, while broad-scale remote sensing studies provide a more general context and opportunity to validate empirical models derived from plot-based studies (*sensu* Fisher et al. 2006). In addition to ecological scale-dependent factors, several methodological factors make cross-scale linkages difficult between these research modes, for example, the fundamental differences in the structure and interpretation of data gathered by human observers of life-history transitions versus continuous measures of radiometric data from remote sensors (Richardson et al. 2013). To address these challenges, Fisher and Mustard (2007) proposed three basic guidelines for comparing ground- and satellite-based records of phenology: 1. The phenological metric should be observable from both the ground and satellites, 2. The phenological metric should have a similar meaning from both perspectives, and 3. Spatial phenological heterogeneity may introduce discrepancies between satellite and ground observations (Fisher and Mustard 2007). The first two criteria relate strictly to data form, whereas the third relates to the more conceptually challenging role of ecological scaling in pattern propagation (Levin 1992, Schneider 2001). Phenological variability through space, particularly variability in the intermediate

scales between plot-based and satellite-derived observations, is relevant to the aforementioned scaling challenge as a bridge between levels, but quantifying dynamics at this scale may also offer insights into processes like large herbivore foraging (Senft et al. 1987, Mueller et al. 2011) and pollinator-plant interactions (Hegland et al. 2009) that unfold at landscape extents but that are mediated by individual level phenological dynamics (see Hinks et al. 2015).

In recent years, near-surface time-lapse photography has emerged as a method for quantitative monitoring of plant phenology at temporal and spatial resolutions that fall between fine-grained plot-level and moderate- to coarse-grained satellite studies (Richardson et al. 2007, Richardson et al. 2009a), particularly in the context of the carbon cycle (Richardson et al. 2009b, Migliavacca et al. 2011). Spectral data captured in time-series of these near-surface images can be analyzed at the pixel or aggregated pixel level (Hufkens et al. 2012, Sonnentag et al. 2012, Klosterman et al. 2014), thus allowing for the same statistical models to be fit to both near-surface and satellite-derived phenology time-series data. These characteristics meet Fisher and Mustard's (2007) first two comparative criteria for comparing phenology across scales, while also closely matching the temporal frequency of moderate- to coarse-grained sensors, like the Moderate Resolution Imaging Spectroradiometer (MODIS). Using these methods, differences between ground and satellite records will more clearly reflect the effects of phenological heterogeneity on ecological scaling rather than differences caused by data structure or type.

To date, time-lapse cameras have been widely used to explore cross-scale linkages of phenological events and progressions in deciduous forest stands and local

landscapes (Hufkens et al. 2012, Klosterman et al. 2014) and phenological dynamics and heterogeneity within a diversity of vegetation canopies (Richardson et al. 2009a, Migliavacca et al. 2011, Julitta et al. 2014). Here we propose that they can also be used to effectively monitor fine-grained phenological dynamics within a broader regional-landscape extent if they are deployed at multiple locations within that focal landscape.

In this paper, we explore landscape-level variability at multiple spatial grains by analyzing phenology records derived from a network of 50 time-lapse cameras (hereafter PlantCams) distributed across 40 km² of Arctic tundra using a Bayesian hierarchical non-linear modeling framework. Our specific goals are to first characterize intra- and interannual patterns of fine-grained, community-level phenological variability across the study region, and then to identify landscape-level drivers of this variability. We predict that fine-grained variability in plant phenology and its landscape drivers will reveal scale dependent dynamics that are not captured by coarser grained metrics at the same extent. We test this prediction using moderate-grained (500m MODIS pixels) phenological data from the same landscape extent and characterized using the same modeling framework. We then explore how two common land-cover types, graminoids and *Betula nana*-dominated shrubs, contribute to within and among year patterns observed in both metrics by extending this same modeling framework to these fine-grained patch-level data. While previous studies have explored interannual biases between phenological dynamics captured by time-lapse cameras and moderate-grained satellite imagery (Hufkens et al. 2012, Klosterman et al. 2014), we focus on how these biases vary within a broader landscape, specifically one characterized by low-biodiversity and extreme abiotic seasonality. The goal of this paper is not, therefore, to strictly compare the timing of

phenology measured from time-lapse cameras with satellites, but rather to quantify and interpret interannual variability in the spatial heterogeneity of plant phenology as it is measured at multiple spatial grains at a little-studied landscape extent.

Methods:

Study site description:

The study region covers a 5 x 8 km area of low-shrub tundra in southwest Greenland (67.11° N, 50.37° W; Figure 5.1a) that forms the core of the Kangerlussuaq-Sisimuit caribou herd calving ground and summer range (Thing 1984). Dwarf shrub (*Salix glauca*, *Betula nana*, *Vaccinium uliginosum*) and graminoid (*Carex* sp., *Festuca* sp., *Kobresia* sp., *Calamagrostis* sp.) communities are the dominant vegetation cover (Thing 1984, Heindel et al. 2015). The topography is characterized by glacial valleys bounded to the north and south by melt rivers that flow from the nearby inland ice sheet, with elevations ranging between 100-600 m above sea level (Figure 5.1a).

The region has a dry, continental climate characterized by cool temperatures throughout the year (Thing 1984). Even outside of the summer months, snow cover is variable due to dry and windy conditions, exposed topography, and ice sheet-weather interactions (e.g. Foehn winds) (Thing 1984).

Temperature data were collected from a meteorological station located adjacent to the camera network at the site of a long-term study of tundra ecology (Post 2013) and from the Danish Meteorological Institute's (DMI) records from Kangerlussuaq, Greenland. Hourly air temperature records were averaged from the nearby

meteorological station to create monthly temperature values and were also used to compute Thawing Degree Days (TDD) (McMaster and Wilhelm 1997).

Study period:

Remotely-sensed data on the phenology of vegetation greenup were collected in two years (2012-2013) using near-surface digital time-lapse cameras (PlantCams) and a satellite-based spectroradiometer (MODIS - detailed below).

PlantCam setup and distribution:

Quantitative information about the timing and rate of vegetation greenup in uniform functional group patches and localized mixed-cover plant communities was extracted from time-series of digital images (Richardson et al. 2007) taken from stationary PlantCams (Wingscapes Timelapse Cam 8.0). Each weather-sealed PlantCam was affixed ~1 to 1.5m above the ground to a steel pole that was manually embedded into the tundra using an ice auger and pole driver. PlantCams were oriented with a north facing field-of-view (FOV), angled slightly downwards from the horizon (5-10°), and were programmed to take photos daily at one-hour intervals from 10am until 2pm, hours of peak sun angle, with white balance set to automatic (Migliavacca et al. 2011, Sonnentag et al. 2012). Time, date, and camera ID information were automatically appended to a bottom panel on each image. Files were stored using the Joint Photographic Experts Group (JPEG) format at 8 bits of radiometric resolution in red (R), green (G), and blue (B) channels on a removable 8-gigabyte SD memory card. Memory cards were

downloaded every 3-9 months when standard AA lithium batteries (able to function to -40° C) were replaced.

Fifty time-lapse camera sites were established in early to mid May of 2012 throughout the 40 km² study region (Figure 5.1a). Candidate sites were selected by first randomly generating multiple sets of candidate coordinates (UTM zone 22 N) to maximize distance pairings strata (tgp package, R). This process was repeated ~20 times. Each candidate set of points was imported into a geographic information system (ArcMAP 9.2) where the underlying distribution of topographic features (elevation, slope, aspect) and landcover classes (Tamstorf et al. 1996 RenVeg report) were visually compared to assess that which closest resembled population level distributions of these characteristics from across the entire study area. Slight deviations between final site selections and planned site locations were the result logistical deployment limitations (i.e. avoiding lakes, cliffs).

PlantCam image processing:

Images from the PlantCams were processed using the ‘PhenoCam GUI’ application (<http://phenocam.sr.unh.edu/webcam/tools/>) run in MATLAB (R2013a, The Mathworks, Nattick, MA). Processing consisted of spatially averaging the digital numbers within each radiometric channel (**R**ed, **G**reen, **B**lue) throughout a user defined Region of Interest (ROI) and then converting them into a green chromatic coordinate (*Gcc*) (Gillespie et al. 1987) (detailed below) for use as a continuous index of vegetation greenness that can be monitored through time. For every site-specific PlantCam FOV, we selected the following ROIs: all nearby (within ~20m) vegetated or partially-

vegetated surfaces that we define as a *community*-grain (Fig 5.1c) sample, and one or more uniform and localized ($\sim < 1\text{m}$) examples of dwarf birch (*Betula nana*) and graminoid coverages (mixed *Carex*, *Festuca*, *Kobresia spp*) that we define as being representative of a *patch*-grain (Figure 5.1d).

The green chromatic coordinate (*Gcc*) (Gillespie et al. 1987, Woebbecke et al. 1995) was calculated for each ROI within each image using the averaged digital numbers from each color channel within that ROI. The *Gcc* index was used instead of unprocessed green channel digital numbers because it reduces the effects of illumination conditions and potential effects caused by inter-camera sensor variability (Woebbecke et al. 1995, Sonnentag et al. 2012). It is calculated using the following formula:

$$Gcc = G / (R + G + B) \quad (1)$$

where R, G, B are the spatially averaged digital numbers from a given ROI from each corresponding color channel. These time series were filtered using the approach detailed in Hufkens et al. (2012) and Sonnentag et al. (2012) that involved a 3-day moving window assigning the 90th percentile to the center day with a darkness threshold that filtered out minimum digital number value (i.e. pixel brightness) set between 10% and 20% depending on scene specific factors. This process helped remove noise due to precipitation, changing illumination conditions, and other non-phenology related spikes in the time series prior to model fitting. If there was a shift in camera position during the greenup period, the time series was recalculated using images from after when the shift occurred using new ROIs that best corresponded to the true geographic location of the

original ROIs. The two time series were then merged. In instances involving multiple or substantial shifts in the FOV that could not be corrected, the time series was removed from the analysis.

Satellite phenology data acquisition and processing:

To explore variation in phenological dynamics across the extent of the study region, but at a coarser *local-landscape* grain (Figure 5.1b), we used multispectral data collected from 2012-2013 by the Moderate Resolution Imaging Spectroradiometer (MODIS) located on NASA's Terra satellite. Time series of 8-day, 500m surface reflectance product (MOD09A1, collection 5) pixels that corresponded with each camera location were downloaded from the Oak Ridge National Lab (ORNL) Distributed Active Archive Center (DAAC) server using the MODIStools package in R (Tuck et al. 2014). Separate time-series were downloaded for bands 1-4 (R, NIR, B, G, respectively [see definitions following eq. 2]) in addition to bands with quality control and day of year of acquisition records for each pixel.

At each pixel-by-PlantCam-site colocation, time series of all spectral bands were filtered to only include measurements with the highest MODIS quality score to reduce the effects of clouds, snow, and atmospheric effects on the time series. Bands were converted into vegetation indices for comparison to the PlantCam imagery, including *Gcc* (detailed above) and the more commonly used Normalized Difference Vegetation Index (NDVI) (Tucker 1979, Pettorelli et al. 2005b) calculated as follows:

$$\text{NDVI} = (\text{NIR} - \text{R}) / (\text{NIR} + \text{R}) \quad (2)$$

where NIR corresponds to the MODIS Near Infrared Band 2 (841 – 876nm), and R corresponds with the Red Band 1 (620-670 nm). As opposed to the first day of each eight-day sampling window, the specific day of year of each quality control filtered pixel was recorded for use as an independent variable in model fits. The MOD09A1 product was selected because it allowed for calculation of both NDVI and *Gcc* at each site at the local landscape grain and because we determined it to be a compromise between temporal sampling resolution and the processing and quality control constraints associated with the daily MODIS reflectance products.

Satellite snow cover data acquisition and processing:

The annual day of year of first snow free at each site was calculated from coregistered MODIS global 500m snow cover product (MOD10A1, collection 5) pixels. Data were downloaded from the National Snow and Ice Data Center (NSIDC) and the daily tiles were stacked by date. At every cam site pixel, a categorical value of: snowcover, no snowcover, or cloud/no data was extracted across all dates. All snow cover analyses were done in R using the packages: *rgdal*, *gdalUtils*, *sp*, and *Raster* (Pebesma and Bivand 2005, Bivand et al. 2013, Bivand et al. 2014). The first snow free day of the year was determined as the first day of the calendar year classified by a ‘no snowcover’ value only if the next non-cloudcover classified day record was also ‘no snowcover’. This method therefore gives a slightly conservative estimate of the first snowfree day to limit the likelihood of an early season false-positive.

Landscape characteristics for each camera site:

The landscape context of each time-lapse camera site and corresponding MODIS pixel was characterized by indices derived from a 2m resolution digital elevation model (DEM) provided by the Polar Geospatial Center at the University of Minnesota and available land cover maps (Tamstorf 1996). The landscape predictors of plant phenology are described in greater detail below:

Aspect is a potentially informative predictor of ecological and abiotic context on a landscape, but it can be difficult to interpret in a linear model because it is a circular (i.e. 360°) variable. We used trigonometric functions to transform aspect into two separate linear variables of ‘Northness’ and ‘Eastness’ that range between -1 to 1 (Roberts 1986). When the aspect is primarily northward, the northness index will express a value of 1, and when it is primarily southward, -1. The eastness index is similar, with a value near 1 indicating a primarily eastward orientation, and -1 primarily westward.

Topographic position (hilltop, sheltered valley, etc) can be correlated with abiotic and biotic processes like cold air drainage, soli erosion, and ablation at the landscape scale (Weiss 2001). A Topographic Position Index (TPI) characterizing this context at a 500m window was calculated using the Land Facet Corridor Designer extension (Jenness 2006) in ArcMap 10.1.

A steady state Topographic Wetness Index (TWI) was calculated within the 20m surrounding each camera site to describe localized topographic conditions associated with soil moisture content and nutrient load (Sørensen et al. 2006).

The remaining landscape characteristics of slope and elevation were extracted for each camera site in ArcMap v 10.1 and then standardized $[(x_i - \bar{x})/sd(x)]$ to improve model convergence.

Modeling framework:

A hierarchical non-linear Bayesian framework was selected for modeling variance in the phenology of vegetation greenup across the landscape within each dataset. Because our research questions focused on spatiotemporal characteristics of the timing of greenup rather than variation in vegetation abundance or biomass, we min/mix standardized each seasonal time series (PlantCam and MODIS). Prior to standardization, each time series was trimmed to begin and end with the min and max VI values of the annual greenup season curve to ensure we would solely be modeling greenup window characteristics and to reduce the chance of including non-informative spectral effects of snow cover, early season low-light conditions, and lens frosting on the time-lapse cameras.

Consistent with many remote sensing studies of vegetation greenup (Fisher et al. 2006, Zhang et al. 2007, Hufkens et al. 2012), we chose a two-parameter logistic curve to characterize the non-linear progression of the greenup period. Because we were specifically interested in greenup dynamics across the study region landscape, we allowed both parameters of the logistic model to vary by site (i.e., parameters were allowed to vary spatially). The general form of the model was:

$$VI_i \sim N\left(\frac{1}{1 + e^{(-a_{j(i)}(DOY_i - b_{j(i)}))}}, \sigma_{j(i)}^2\right)$$

$$\begin{pmatrix} a_j \\ b_j \end{pmatrix} \sim MVN(\boldsymbol{\mu}, \boldsymbol{\Sigma})$$

$$\boldsymbol{\mu} = (\bar{a}, \bar{b})$$

$$\log(\sigma_j) \sim N(\mu_\sigma, \omega_\sigma^2)$$

(3)

where VI_i = the standardized vegetation index from day I from one of the annually partitioned datasets: sNDVI (MODIS), sGcc (MODIS), and sGcc (entire PlantCam FOV, *Betula*, or graminoid patch), DOY_i = the day of year, a_j = the rate of increase of the logistic curve for site/ROI j , and b_j = the model inflection point, i.e. the midpoint of the greenup period that also coincides with the peak rate of leaf onset, for site j . The notation $j(i)$ indexes site j for observation i . We assumed a multivariate normal distribution (MVN) for the varying coefficients with a population average mean ($\boldsymbol{\mu}$) and a variance-covariance matrix $\boldsymbol{\Sigma}$, where $\boldsymbol{\mu}$ contains the population-average parameters (i.e., across all sites) \bar{a} and \bar{b} . To accommodate the fact that assuming a constant residual variance/covariance across sites was likely not reasonable, we allowed each site to have its own residual standard deviation (σ_j), i.e. we treated each as random variable. We assumed a normal probability distribution for \log_e -transformed σ_j , with mean μ_σ and variance ω_σ^2 .

Model parameter covariation with landscape factors:

After the non-linear model (eq. 3) was fit to each dataset, we fit models that characterized variation in the site-specific parameters (a_j and b_j) as a function of the landscape variables described above. Initially, we modeled each varying parameter with a single candidate covariate. We retained covariates for future modeling if the corresponding 90% credible interval (CI) did not overlap with zero. Models with a single covariate (cov) on the varying parameters were structured as:

$$\begin{pmatrix} a_j \\ b_j \end{pmatrix} = \begin{pmatrix} \gamma_{0a} + \gamma_{1a} * cov_j \\ \gamma_{0b} + \gamma_{1b} * cov_j \end{pmatrix} \quad (4)$$

where a_j and b_j are the site specific model parameters and γ_{0x} and γ_{1x} are the fixed slope and intercept terms describing a linear relationship between site-specific model parameters and a site-specific environmental covariate. After identifying candidate predictor covariates (based on 90% CIs that did not overlap with zero), more complex models were constructed using these covariates to explore landscape-level drivers of phenological heterogeneity within each dataset.

Model fitting and selection:

Models were fit separately by year. This allowed for later comparison of model parameter covariation with landscape factors under different observed abiotic contexts. Furthermore, models were fit to each satellite derived vegetation phenology dataset and PlantCam derived dataset separately to allow for model parameter comparisons between datasets and between years while maintaining the regional landscape extent as a constant. Each phenological greenup dataset was modeled with a single vegetation index ($sNDVI_{MODIS}$, $sGCC_{MODIS}$, $sGCC_{Camera}$, $sGCC_{Betula}$, $sGCC_{graminoid}$) as the response variable and standardized Day of Year ($[(DOY_i - \text{mean}(DOY)] / \text{sd}(DOY)$) as the predictor variable in all instances. Diffuse priors were used for all parameters. We applied uniform priors for σ and ω_σ , normal priors for \bar{a} , \bar{b} , and μ_σ , and the scaled inverse-Wishart distribution for Σ (Gelman and Hill 2007). The program JAGS (Version 3.4.0) was used in conjunction with R for all analyses (Plummer 2013; R Core Team 2015). We ran three parallel chains with different random starting values to generate 20,000 samples each, although the first 9,000 were discarded from each chain, resulting in 33,000 samples for summarizing the

posterior distributions. We examined the scale reduction factor (\hat{R}), trace plots, and plots of posterior distributions to assess convergence for all parameters.

Quantifying phenological heterogeneity at the landscape extent

To quantify spatial heterogeneity in greenup characteristics, we reported the standard deviations of the back-transformed (into day of year [DOY] units) spatially varying site-specific *date of leaf onset* (b_i) fit to each VI dataset and year. We define *date of leaf onset* as the day of year when the logistic curve reaches half of its maximum amplitude, a metric that can be interpreted as the date when most leaves are likely to emerge (White et al. 1997, Fisher and Mustard 2007). This differs from the first emerging leaves of the year (start), but was chosen to reduce error-associated fits to the tails of logistic curves and early season snowfall. We additionally report means and standard deviations of the length of the greenup season (Date of 95%-Date of 5% peak green = LOS) for each VI dataset and year. Note that LOS refers to this calculation, and is exponentially related to the site-specific rate parameter, a_i , fit to each VI dataset and year. When comparing heterogeneity in greenup between datasets (satellite vs. PlantCam) in a given year, the satellite pixels were subsetting to include only those that spatially co-registered with functional camera sites in that year.

To assess grain dependency in patterns of heterogeneity in vegetation greenup in different years, we used pairwise graphical comparisons of site-specific parameters. To explore within season variability in the relationship between community grain (PlantCam G_{cc}), greenup progression, and greenup progression at the local landscape grain (MODIS vegetation indices), we used 1:1 plots of line-segments connecting growing season profile

intervals (5, 15, 50, 85, 95% peak VI) of satellite-derived Vis vs. PlantCam-derived Gcc (Hufkens et al. 2012). As detailed in Hufkens et al. (2012), a slope exceeding that of the 1:1 line indicates a longer greenup period in the satellite derived VI compared to the PlantCam model and vice versa, whereas a shift to the right or left of the 1:1 line with no change in slope indicates a phase offset between the models (i.e. one season is consistently earlier or later but not longer or shorter). Both forms of bias can be present in the same comparison. We plotted all site-specific time series pairs (MODIS NDVI vs. PlantCam Gcc; MODIS Gcc vs. PlantCam Gcc) within each year to provide a visual representation of heterogeneity of cross-grain bias within a landscape to explore how this bias may scale differently between grains, years, and vegetation indices.

Shrubs and graminoids are the dominant vegetation landcover types in this study region and these functional groups may contribute differently to greenup profile characteristics measured by mixed landcover pixels or viewsheds at various grains. We explored heterogeneity in greenup characteristics among individual graminoid and *Betula* patch model fits across the extent of the study area, and then compared these characteristics with community- and local-landscape grained patterns of heterogeneity of greenup across the landscape.

Identifying grain specific drivers of heterogeneity

To identify grain-specific landscape drivers of spatial variability in plant phenology at the extent of the study region, we explored the model fits between the site-specific model parameters (a_j and b_j) and landscape-level factors (slope, aspect, etc) that were identified in the best-fit models for each year, grain, and VI dataset.

Results:

Site conditions

Over the two study seasons, average air temperatures in the months preceding and encompassing greenup (May-June) were greater than 4° C colder in 2013 (Table 5.1), although that year was also characterized by the earlier average date of first snow-free as well as the earlier onset in the accumulation of thawing degree days (Figure 5.2). The average greenup season temperature (May-June) in 2013 was the coldest since annual ecological monitoring began at this site in 2002 (DMI). In contrast, the greenup season of 2012 was the second warmest in that 12-year period (DMI).

Over 77,000 unique PlantCam images were collected across all sites from 2012-2013. The number of unique greenup time-series extracted from these images each year varied due to camera attrition associated with animal or human induced damage or FOV shifts, or unexplained internal camera failures. After quality screening, we included time series derived from 41 camera sites in 2012, and 27 sites in 2013.

Inter- and intrannual community-level variability of greenup phenology across the landscape

The mean timing of leaf onset and the mean duration of the greenup season measured at the community-grain (PlantCam FOV) across the landscape differed by 7.6 and 4.6 days respectively between the warmer 2012 and colder 2013 seasons (Figure 5.2; Table 5.2). Specifically, greenup was earlier in the warmer year, but of a shorter duration. Across the landscape, earlier leaf onset was not positively related to earlier

mean date of first snow free or to earlier onset of thawing degree day (TFF) accumulation (Figure 5.2).

Variation in timing of community leaf onset within the study landscape in either year was of a much greater magnitude than between year differences in the mean timing of leaf onset (Figure 5.3a), even given the contrasting climatic conditions of the two greenup periods (Figure 5.2). Using only data from camera sites that were functional in both years ($n=25$), community leaf onset ranged over a 20.8 day window and had a standard deviation of 5.8 days in the warmer spring of 2012, and ranged over 31.5 days with a standard deviation of 8.5 days around the mean in the cooler 2013.

Landscape drivers of intra-annual phenological variability at the community grain

Of the landscape-level factors tested, north-facing aspect was the only factor that explained phenological variability at the community-grain across the landscape in both years (Figure 5.4ab). It should be noted that while increasingly north-facing aspects were related to later leaf-onset (b_j) in 2012 (Figure 5.4a), these aspects were associated with longer duration (a_j), rather than later onset of the leaf out in 2013 (Figure 5.4b, Supp Table 5.S1). In 2012, locations on increasingly east facing slopes (oriented towards the nearby inland ice sheet) also experienced later leaf-onset, whereas this relationship was not apparent in 2013. A locally constant metric of soil moisture, TWI, was positively related to shorter leaf-out seasons only in 2013 (Figure 5.4b), a year with unusually early first snow melt (Figure 5.2b).

Comparing phenological variability across spatial grains

For clarity, we focus on MODIS NDVI rather than MODIS *Gcc* values in the main text (for MODIS *Gcc* results, see Figure 5.S2, 5.S3) because although both indices show generally similar patterns, NDVI is more a widely used and validated index for data collected from space-borne sensors like MODIS (but see Hufkens et al. 2012 for more on role of vegetation index selection).

Between year differences in mean leaf onset at the coarser MODIS NDVI grain were similar to those measured at the community grain (7.8 days MODIS vs. 8.0 days PlantCams), but like other studies linking time-lapse camera to MODIS phenology (Hufkens et al. 2012), were several days to weeks earlier in a given year (Figure 5.4, Table 5.2). Mean duration of the greenup season measured by MODIS showed little difference between years (<2.5 day difference), although there was more variability in greenup duration across the landscape in 2013 (Table 5.2). Spatial variability in leaf onset across the landscape captured by the PlantCams was greatly reduced at the MODIS grain (Figure 5.3ab; Table 5.2).

In contrast with the MODIS records, fine-grained patch-level records of graminoids showed similar levels of spatial variability (SD) across the landscape as the community-grained data (Figure 5.6, Table 5.2). *Betula nana* patches were also more variable than all MODIS metrics (Figure 5.6, Table 5.2). Across all grains and monitoring platforms, spatial variability in leaf onset was greater in the cooler 2013 season, although the magnitude of this variability differed considerably among grains, functional groups, and vegetation indices (Table 5.2). Notably, graminoids showed the greatest change in spatial variability in their phenology between 2012 and 2013, although

variability in *Betula* was considerably less than that observed at the mixed-species community grain (Table 5.2).

Landscape drivers of phenological variability across spatial grains

The rate of leaf-out in the MODIS NDVI data was positively related to site elevation in 2013 (Figure 5.4b). No landscape drivers of phenological variability matched those identified at the community grain, and no landscape driver of phenological variability was identified for any MODIS index from 2012 (Figure 5.4). In contrast, all patch-grained phenology records in both years were related to landscape northness in some manner. Graminoid patches experienced later leaf-out with increasing northness in both years, whereas northness was related to later leaf out for *Betula* patches only in 2012. The magnitude of this relationship varied across years and functional groups, but was strongest for graminoids in 2013 (Figure 5.6). The rate of greenup decreased with increasing northness for both graminoid and *Betula* patches in 2013 (Figure 5.6).

Cross-grain phenological bias across landscape within and between years

Comparing 1:1 plots of community-level (PlantCam FOV) versus local landscape-level (MODIS pixel) greenup periods (5% to 95% peak greenness) at paired locations across the broader study landscape reveals marked heterogeneity in scaling relationships both within and between years (Figure 5.5). The steeper slopes of the 1:1 plot from the warmer 2012 season (Figure 5.5a) relative to the cooler 2013 season (Figure 5.5b) indicate a bias of longer greenup seasons at the MODIS-grain relative to the community grain in 2012. Overall in 2013, there was greater variability in the bias

(Hufkens et al. 2012) relationship between community to landscape grain greenup timing, even though there were fewer pairwise comparative time-series in that year (Figure 5.5ab).

Graminoid patches showed less bias in greenup profiles relative to the community grain profiles than did *Betula* patch profiles in both 2012 and 2013 (Figure 5.5cd.).

Betula patch greenup happened at a faster rate than greenup at the mixed community grain in both years, although this relationship was relatively variable across the landscape (Figure 5.5cd). While the timing of the onset of *Betula* greenup across the landscape was similar to the community-grained onset of greenup across the landscape in 2012, it was markedly later than community-grained greenup profiles in 2013 (Figure 5.5cd) whereas graminoid greenup profiles exhibited much less bias in greenup rate and in phase shifts relative to community-level profiles in both years.

When comparing bias in greenup profiles from individual patches to local-landscapes (MODIS pixels), the local patches of both functional groups had delayed greenup seasons relative to the coarser grained satellite derived indices, similar to the relationship between the community-level greenup profiles and local-landscape (MODIS) indices (Fig 5.5 abefgh). *Betula* patches exhibited greater variability in how their rate of greenup scaled with MODIS Vis across the study region whereas the rate of graminoids more closely tracked these local-landscape grain greenup profiles (Figure 5.5 efgh). Variability in the magnitude of phase shifts between all PlantCam derived profiles and the coarser scale satellite indices was greater in the cooler 2013 season (Figure 5.5 abefgh).

Discussion:

These analyses demonstrate the diversity of issues that affect the monitoring and interpretation of phenological change across spatial grains and their corresponding levels of ecological resolution. As would be predicted by general scaling theory (Levin 1992, Wu 1999), larger spatial grains of phenological measurement reduced the within year variability of leaf onset across the extent of the study landscape. The magnitude of observed community- and patch-level leaf onset across the landscape varied by over three weeks in a given year, a range similar to the most extreme climate-linked decadal-scale phenological advances observed at the plot level (Post et al. in review). This magnitude of fine-grained phenological heterogeneity at a landscape extent may not be particularly exceptional, however, even over very short distances, as similar fine-scale variability has been reported previously in deciduous temperate systems (Liang and Schwartz 2009, Richardson et al. 2009a). Indeed, similar patterns were observed in the current study where, in some instances, leaf onset differed by over a week between patches of conspecifics located less than a meter apart. While some fine-grained patterns of phenological variability over small spatial extents may be attributed to micro-climatic gradients (Fisher et al. 2006), other spatial discontinuities in these patterns likely reflect the influences of genetics, spatially discontinuous herbivore-plant interactions (Wolkovich et al. 2014), or other unmeasured factors that may reduce signals of spatial autocorrelation apparent in less temporally varying landscape patterns, like vegetation patch distribution (Wu 1999, Turner 2005) or patterns of plant phenology that emerge at broader regional or biome extents, like latitudinal or alpine weather gradients (Albon and Langvatn 1992, Pettorelli et al. 2005a, Bhatt et al. 2010).

Unlike the distribution of land cover types across a landscape that may change over periods of months to years, phenological variability can vary dramatically over periods of days in Arctic environments in different years. Interannual variability in the timing of plant development is a focal point of phenological research, yet remains little studied at landscape scales. The greater than 25% increase in spatial variability (measured by the sd of the site-specific means) in the timing of community leaf onset in the cooler 2013 season reveals a landscape dynamic that is masked by the spatial and/or temporal grain of satellite-borne sensors and that can only be suggested by plot-based studies. This pattern, the observed reduction of spatial phenological variability under warmer conditions, is consistent with experimental individual-level (Post et al. 2008a) and observational community-level (Post et al. 2008b, Hoyer et al. 2013) plot-based studies that linked the effect of warming with the spatial compression (i.e. less spatial variability) of plant phenology at local to intermediate extents (hundreds of meters), but contrasts with observational reports from broad spatial extents (10^2 - 10^3 km) where warming has been associated with increased spatial variability in plant phenology (Post and Stenseth 1999, Pettoirelli et al. 2005a). While only based on two years of data, the current study reinforces the interpretation that this apparent contradiction is a scale-dependent effect mediated by gradients in the timing of snowmelt that covary with elevation or latitude. The comparatively small elevational gradients and limited winter snowpack at this site may reduce the interaction between snowmelt and temperature as a driver of phenological dynamics that have been identified elsewhere (Wipf et al. 2009, Hoyer et al. 2013, Wheeler et al. 2015). Specifically, the timing of first snowmelt occurred in relative synchrony across the regional landscape of this study in both years

(Figure 5.2), and did not spatially vary with elevation or aspect at the MODIS grain (Supplementary Figure 5.S1), thus allowing for the temperature effect on fine-grained dynamics to emerge at a broader spatial extent. Continued monitoring with this network in years with different precipitation and temperature regimes will provide the empirical data required to more thoroughly explore these scale-dependent relationships. Data at this scale are relevant to understanding warming's effects on interannual spatial patterns in a diversity of other ecological processes, like the carbon cycle (Richardson et al. 2013) and herbivore foraging ecology (Myerud et al. 2001, Post et al. 2008b), both of which are linked via fine-grained phenological dynamics at the landscape extent (Cahoon et al. 2011, Vaisanen et al. 2014).

Landscape-level controls on patterns of phenological heterogeneity have only recently been quantified at intermediate to broad spatial extents using satellite imagery (Pettorelli et al. 2005a, Fisher et al. 2006, Elmore et al. 2012), but there is a long history of descriptive links between landscape features and their average effect on phenological development (Hopkins 1918), including at this study site (Thing 1984). As expected, we found signals of landscape controls in both fine-grained (Figure 5.4ab, 5.6abcd) and coarse-grained (Fig 5.4cd) patterns of leaf onset phenology across the study region. More notable, however, is our finding that the relationship between landscape factors and leaf onset phenology differed with the grain of observation and, in some instances, varied from year to year (Figures 5.4, 5.6).

The grain dependency evident in these patterns likely reflects the scale of topographic variability in this environment, and its subsequent influence on microclimatic gradients represented in each pixel or viewshed. The north-facing

component of aspect was consistently related to either the timing and/or rate of leaf onset at community- and patch-grains (Figures 5.4, 5.6) throughout the study landscape, a finding consistent with qualitative descriptions of plant phenology in this region (Thing 1984). In Arctic environments, low sun angle and long days in the spring and summer have a much larger impact on the thermal radiation balance at soil level for south facing slopes than at lower latitudes, resulting in a substantial thermal gradient between these different aspects. This may be particularly evident at this study site due to the dominant physical geography of east-west glacial-shaped ridges. Visual assessment of the 500m MODIS pixel footprints reveals that many fall across topographical gradients that contain both north and south facing aspects, thus spatial averaging likely reduces the signal of this and other landscape factors that vary at scales smaller than the MODIS grain. Changes in elevation are more gradual, and may reflect differences in vegetation composition or abundance (Thing 1984) that then contribute to more subtle phenological patterning not captured by the viewsheds of the PlantCams. The strong effect of aspect at high latitudes, represented especially strongly at our site, may further mask the influence of elevation on microclimate and phenology, relationships that are better documented at lower latitudes (Fisher et al. 2006, Elmore et al. 2012).

While landscape topography influences microclimate and subsequently phenology (Fisher et al. 2006), numerous other factors also contribute to the timing of plant development (Wolkovich et al. 2014). The onset of greenup in *Betula* and graminoid patches was relatively synchronized in 2012, whereas *Betula* onset occurred much later than graminoid onset in 2013 (Figure 5cd). These differences are reflected by the shallower slope of the 1:1 scaling plots of *Betula* versus the local plant community in

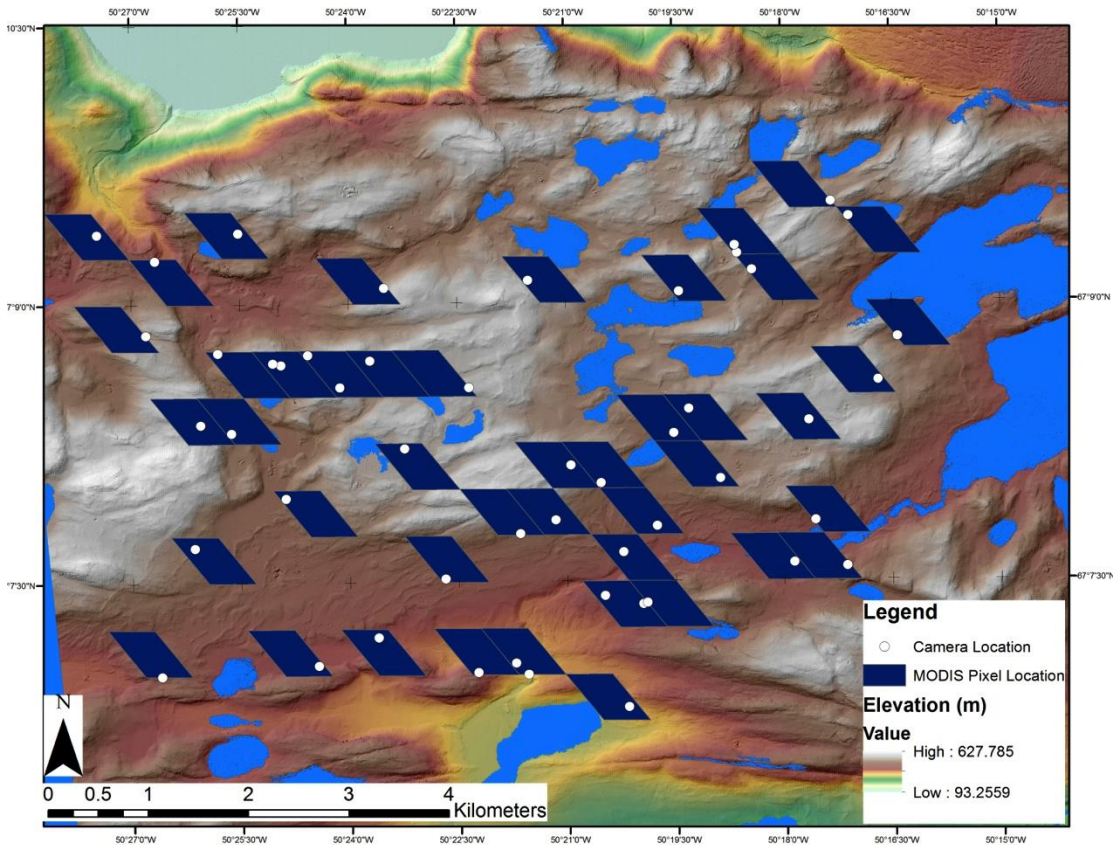
2013 relative to 2012 (Figure 5.5cd). The scaling relationship across the broader landscape between graminoids and the local-community grain (Figure 5.5cd) and local-landscape grain (Figure 5.5dh) phenology time-series varied between years, but were predominantly shifts in phase, rather than rate of emergence, whereas *Betula* varied substantially in both phase and rate in these scaling plots (Figure 5.5e-h). This may reflect a more frost-avoidant but competition-tolerant early season life-history strategy of *Betula* relative to most graminoid species at this site (Post et al. in review). Interactions between life-history traits, microclimate gradients, and general seasonal conditions like those described here are capable of generating non-linear, but potentially predictable patterns of phenological heterogeneity across years when interacting with landscape elements. This should be a continued research priority as more data is collected.

In this study we have presented phenology data at a spatial grain and extent combination that is little studied, but broadly relevant to many ecological processes, particularly in the context of rapid climate change. While these analyses demonstrate the potential for new insights into the complex processes that generate phenological heterogeneity at landscape extents, they are not without caveats. This study took advantage of contrasting abiotic patterns of temperature and snow cover over two study seasons, but a more detailed understanding of the roles of temperature and precipitation in generating phenological heterogeneity at landscape extents will require additional years of data collection. In addition, finer grained monitoring of landscape covariates, like ground temperature, soil moisture, and localized snowmelt should be prioritized. Furthermore, while time-lapse cameras allow for collection of high-resolution phenology data in both time and space, image processing and interpretation methods are rapidly

evolving (PhenoCam project)(Hufkens et al. 2012, Sonnentag et al. 2012, Klosterman et al. 2014). As with any rapidly developing technology methods will continue to be refined and standardized, facilitating greater cross-site comparability in the future.

Conclusions

Grain-dependent patterns of phenology variability and their drivers are likely widespread, yet are rarely quantified and subsequently incorporated into ecological analyses. Here we provide empirical evidence of these dynamics at a landscape extent, a scale relevant to herbivore foraging and carbon cycle processes, but one that has traditionally been difficult to monitor due to logistical factors. We show that these spatial relationships are non-stationary between years and are likely the results of phenological drivers interacting across multiple spatial scales. While these perspectives will be further refined by continued methodological advances, they can immediately inform more nuanced perspectives and hypotheses about phenology and its ecological importance in rapidly changing environments.



a. Regional Landscape (40 km²)



Figure 5.1. Distribution of camera sites and corresponding MODIS pixels. a. Site locations are overlaid on a digital elevation model enhanced with a hill shade effect to delineate the topographic variability of the study region. b.-d. show representative grain-size approximations, where the dark blue rhombus in b. represents a MODIS pixel, the light blue shaded area in c. represents a localized mixed-species community, and d. represents uniform composition graminoid (pink) and *Betula* (turquoise) patches.

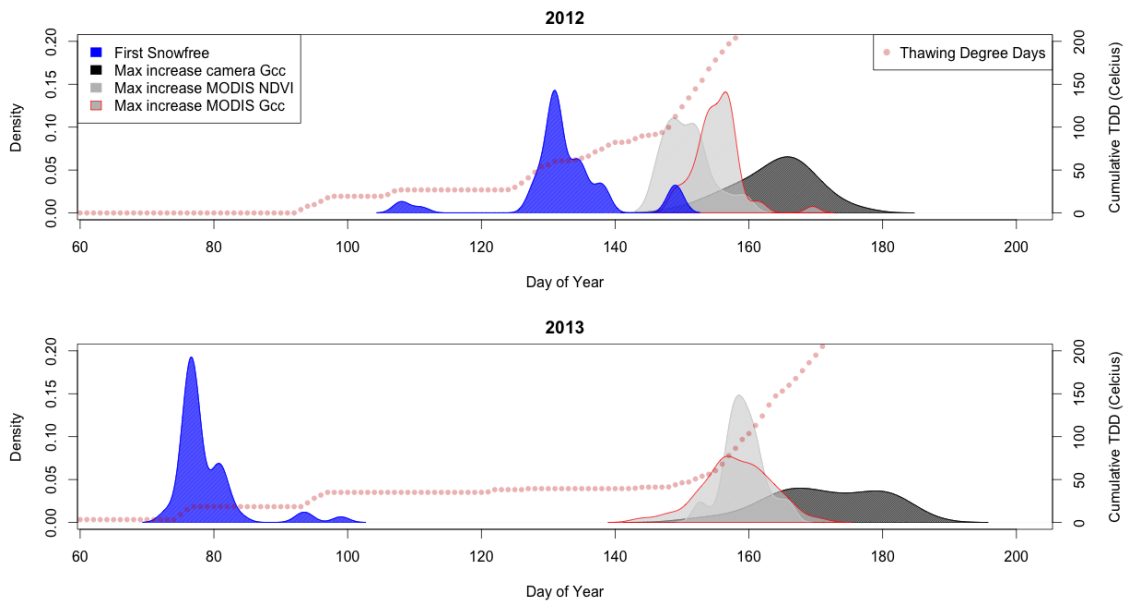
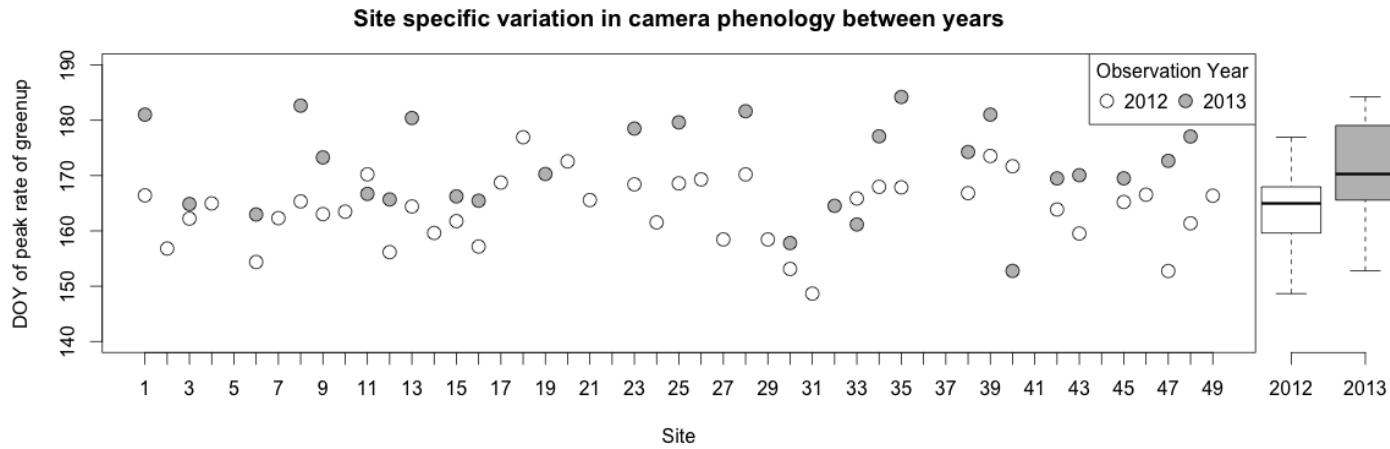


Figure 5.2. Density plots of the timing of snowmelt and peak rate of greenup across all sites for all vegetation indices overlaid with the seasonal progression of thawing degree days (TDD).

a.



b.

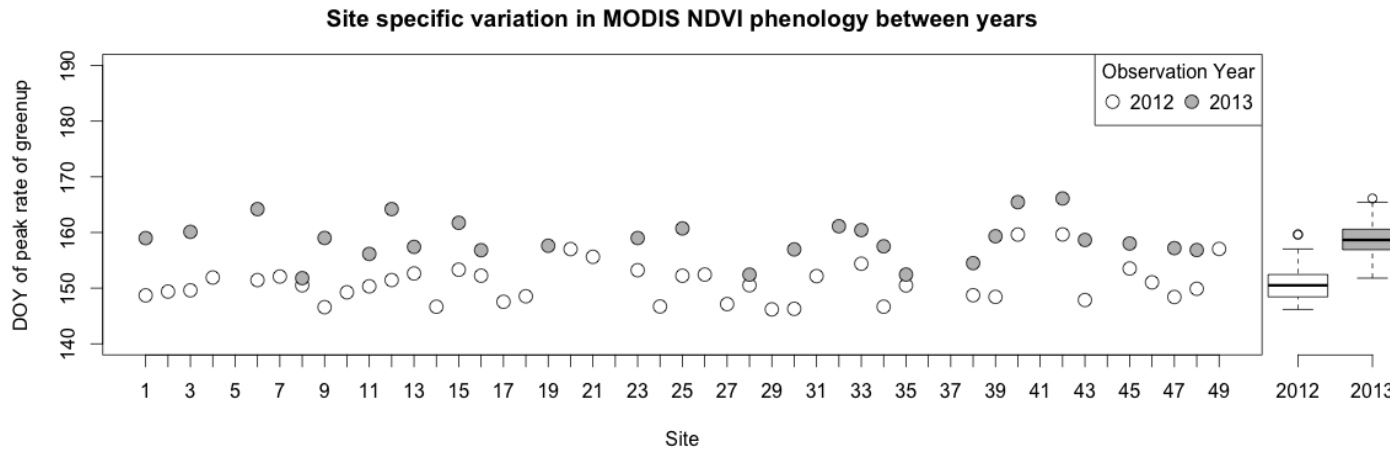


Figure 5.3. Across site variation in timing of leaf onset within and between years for the a.) PlantCam *sGcc*, and b.) MODIS NDVI datasets. Box and whisker plot adjacent to plot shows median and quantiles of all phenology data for each year.

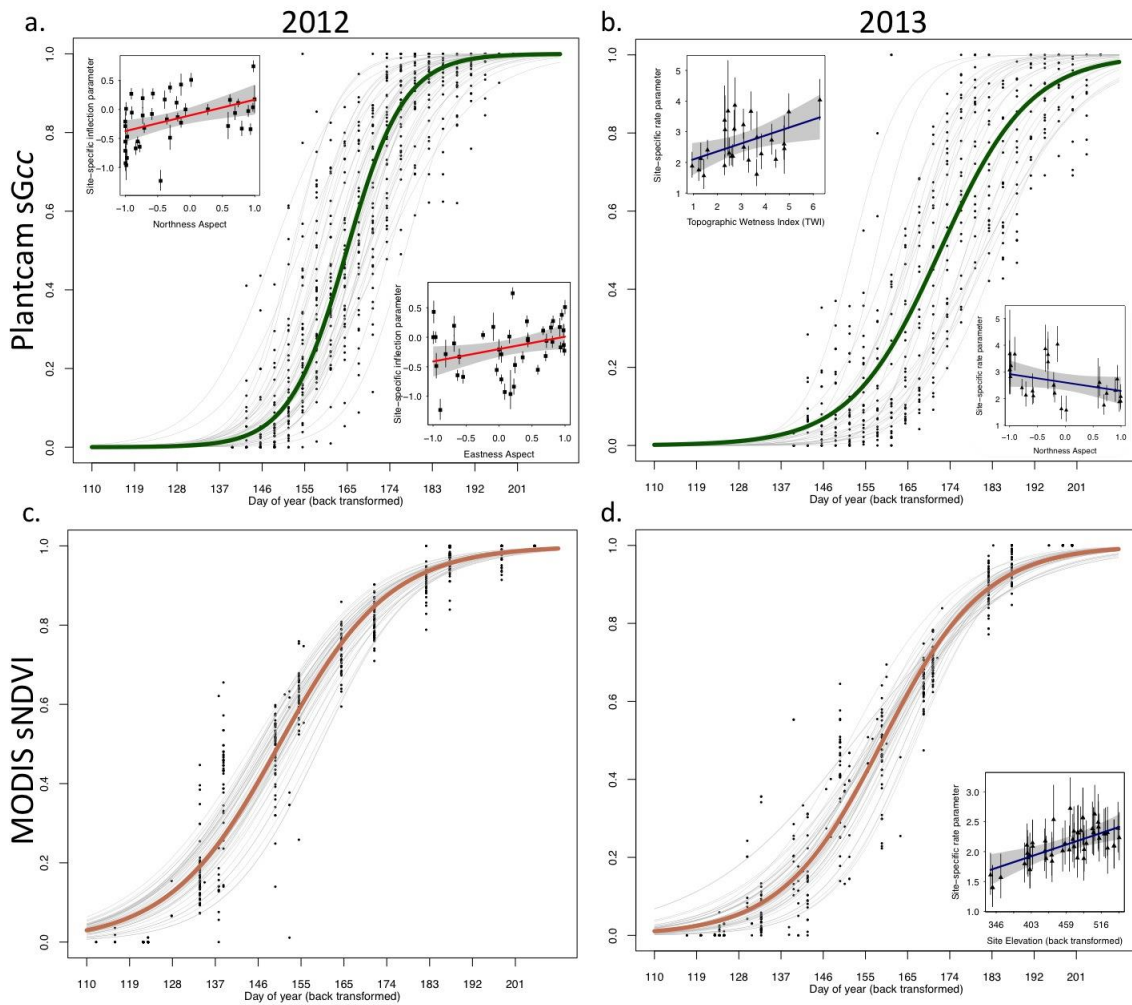


Figure 5.4. Landscape greenup profiles and model-parameter covariation with landscape factors at different grains and in years with contrasting abiotic conditions. The left column contains models containing data from 2012 and the right from 2013. The population-level mean logistic fit is color-coded by dataset (green - PlantCam *sGcc*; orange - MODIS *sNDVI*) and the site-specific fits are plotted in gray over the VI data points in black. Second-level model fits of logistic parameters to landscape covariates are plotted, when present in the best-fit model, as subpanels adjacent to their corresponding lower-level model. Second-level fits to the leaf onset (b_i) are plotted with squares and a red hierarchical regression line, and fits to the growing season

rate parameter (α_i) are plotted with triangles and a blue hierarchical regression line. Squares and triangles are posterior means and vertical bars are 90% CIs, shaded areas around hierarchical regression fitted lines are 90% credible regions. Panel a. characterizes the timing, duration, and heterogeneity of the greenup season measured at the community-grain (individual PlantCam FOVs) across the extent of the study area. The upper left subpanel a. depicts the positive relationship between later timing of leaf onset and increasingly north-facing landscape aspects. The lower right subpanel a. depicts the positive relationship between the later timing of leaf onset and increasingly east-facing landscape aspects. Panels b-d. follow this basic layout. The second-level model in the upper left of panel b. depicts the positive relationship between longer greenup season and increasing TWI, whereas the second-level model plot in the lower-right of panel b. indicates shorter length of the greenup season with more northerly facing site aspect. The second-level model fit in the lower-right of panel d. indicates a longer greenup season with increasing site. For site parameters for all models, see Supp Tables 2-11.

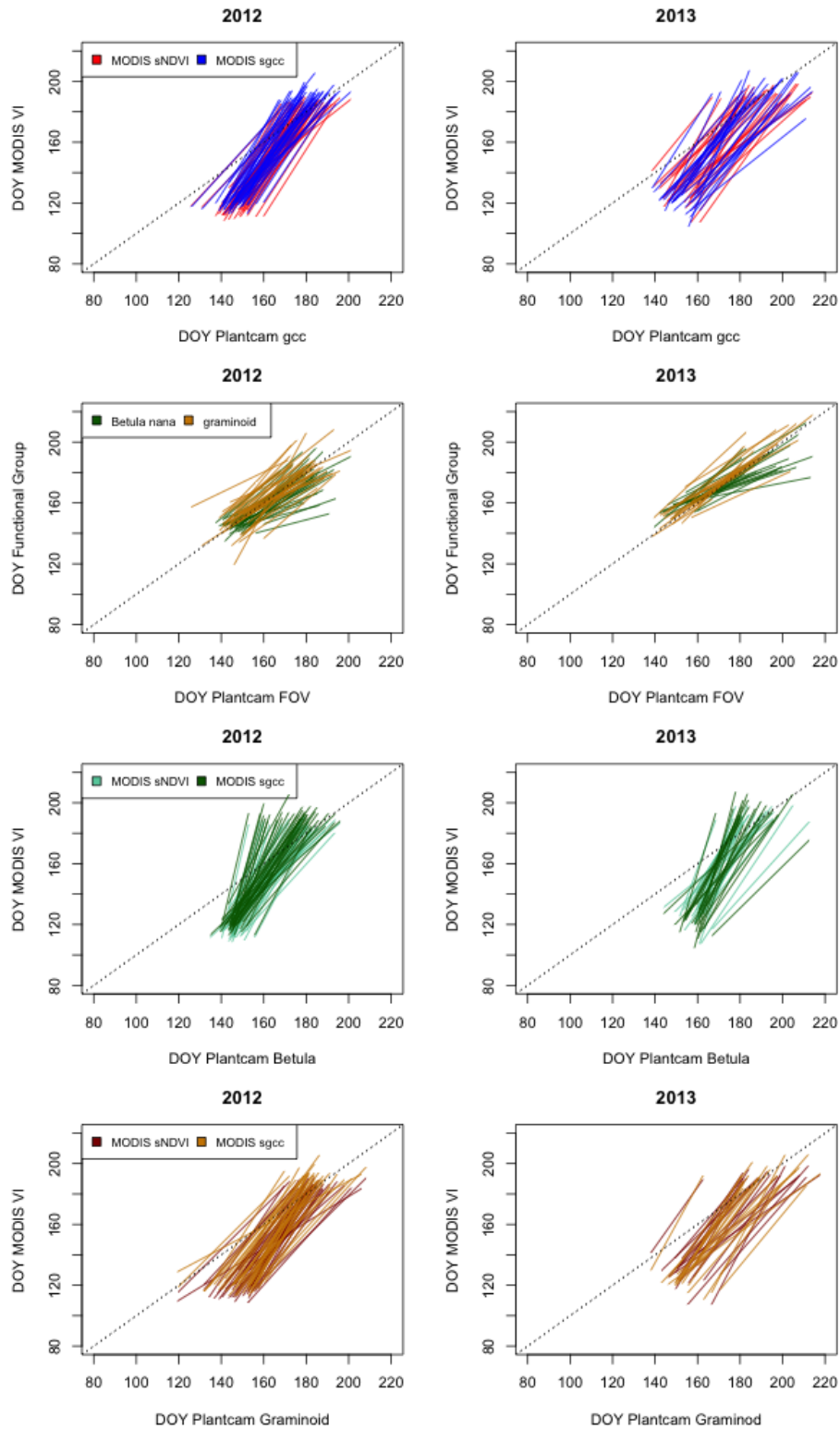


Figure 5.5. Heterogeneity of cross scale 1:1 plots of greenup profiles (5% to 95% of logistic fits). The left column represents comparisons from 2012, and the right from

2013. Panels a and b depict the cross-grain bias between community level models (PlantCam FOVs) and local landscape level models (MODIS Vis). Panels c and d depict seasonal bias between functional-group patches and the local community grain, whereas panels e-h relate greenup patterns from uniform functional group vegetation patches to local landscape greenup curves.

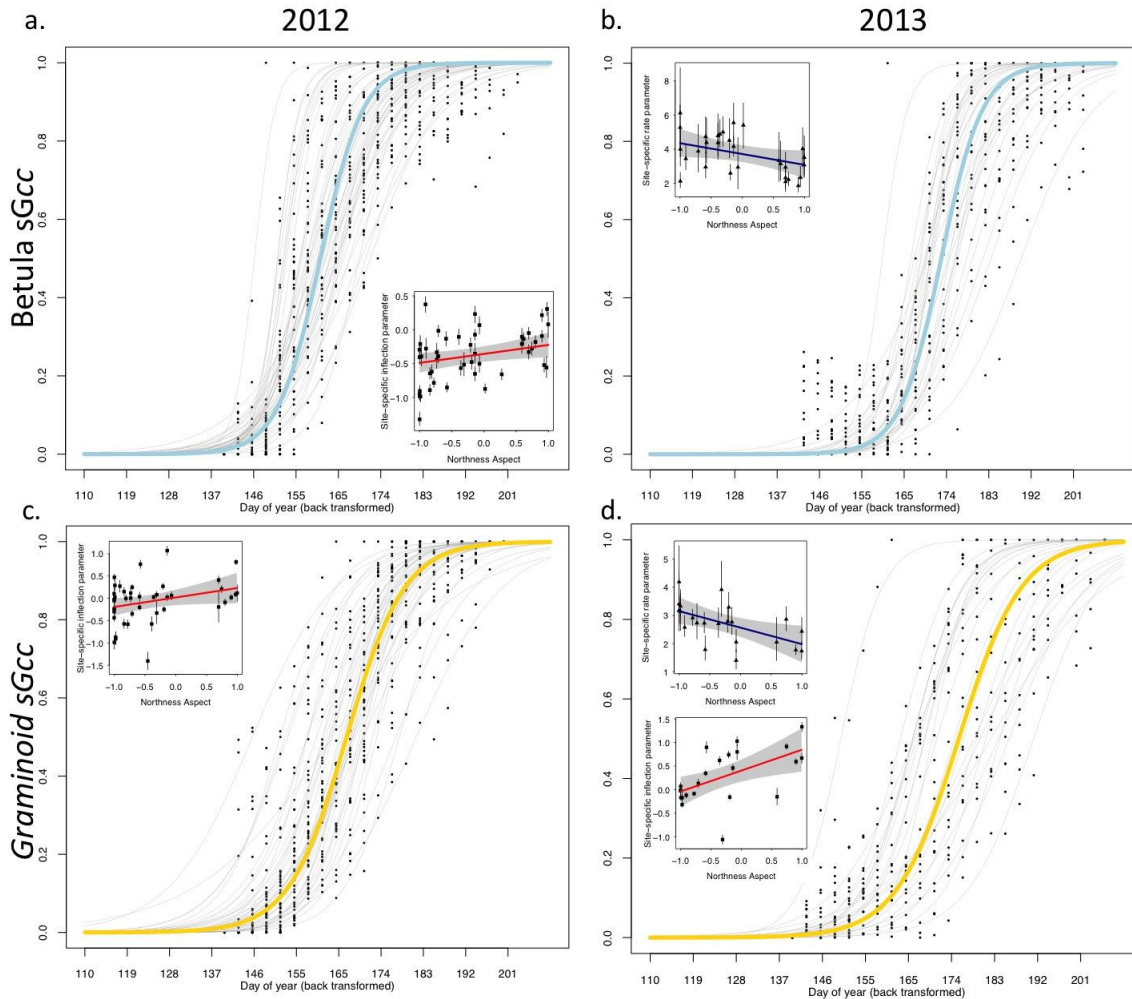


Figure 5.6. Landscape greenup profiles and model-parameter covariation with landscape factors at the grain of *Betula nana* (light blue) and graminoid (yellow) patches across the study region in years with contrasting abiotic conditions. Subplot formatting is consistent with Figure 5.4. For site parameters for all models, see Supp Tables 2-11

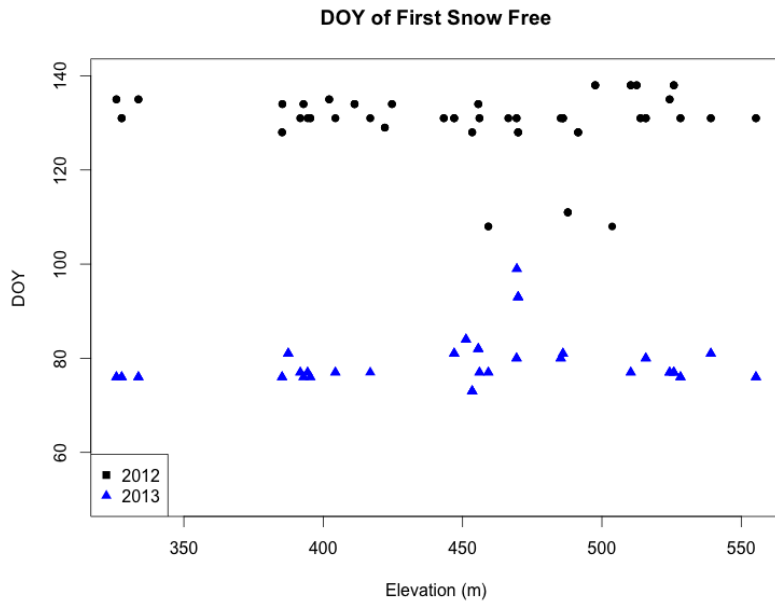
Table 5.1. Mean monthly temperature (°C) from the local meteorological station.

Year	May	June
2012	3.921	10.355
2013	-2.745	8.477

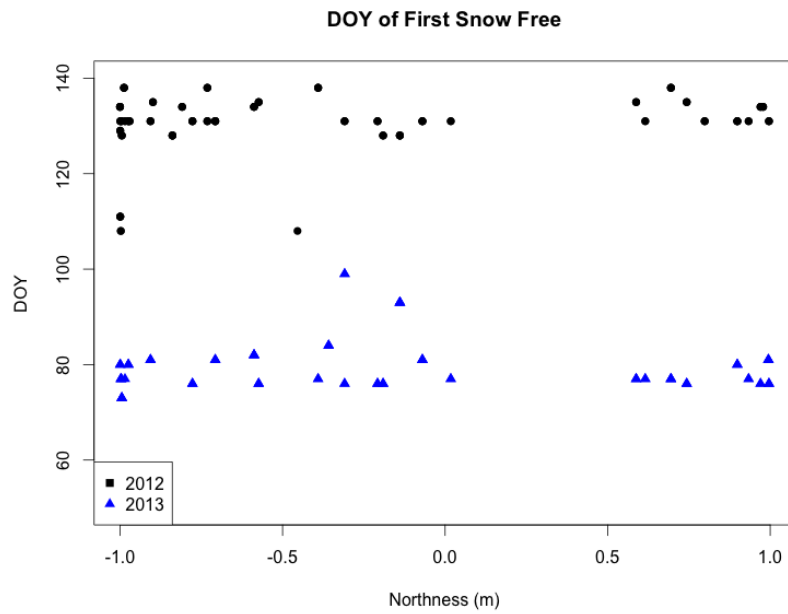
Table 5.2. Mean and standard deviations of greenup season characteristics at different grains and vegetation indices across all camera sites. MODIS samples were subsetted to correspond with annual number of functional camera sites (2012 n=41, 2013 n= 27).

Phenology Metric	Mixed Community sGcc		Graminoid Patch sGcc		Betula Patch sGcc		MODIS NDVI		MODIS sGcc	
	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013
Mean Leaf Onset	163.86	171.52	164.99	173.00	160.23	172.53	150.91	158.70	155.20	157.47
Mean Start Onset	145.25	150.60	145.74	153.32	144.69	158.13	116.39	125.28	118.84	121.78
Mean End Onset	182.47	192.43	184.25	192.65	175.89	186.92	185.44	192.11	191.56	193.16
Range Leaf Onset	28.27	31.45	35.27	40.62	24.91	29.59	13.46	14.31	21.05	22.81
sd Leaf Onset	6.09	8.28	6.70	9.46	5.52	5.82	3.47	3.68	3.90	5.31
Mean LOS	37.23	41.83	38.50	39.33	31.20	28.79	69.05	66.84	72.71	71.38
sd LOS	6.32	11.42	10.54	11.66	10.95	9.85	5.02	11.83	4.11	10.76

Supplementary Figures:

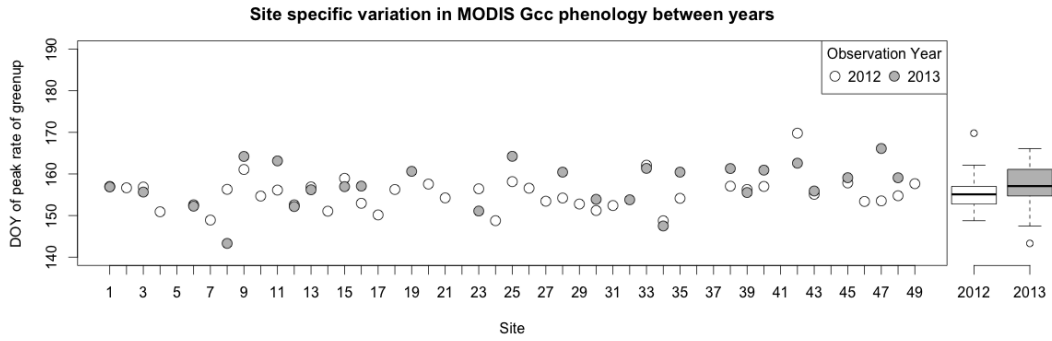


a.

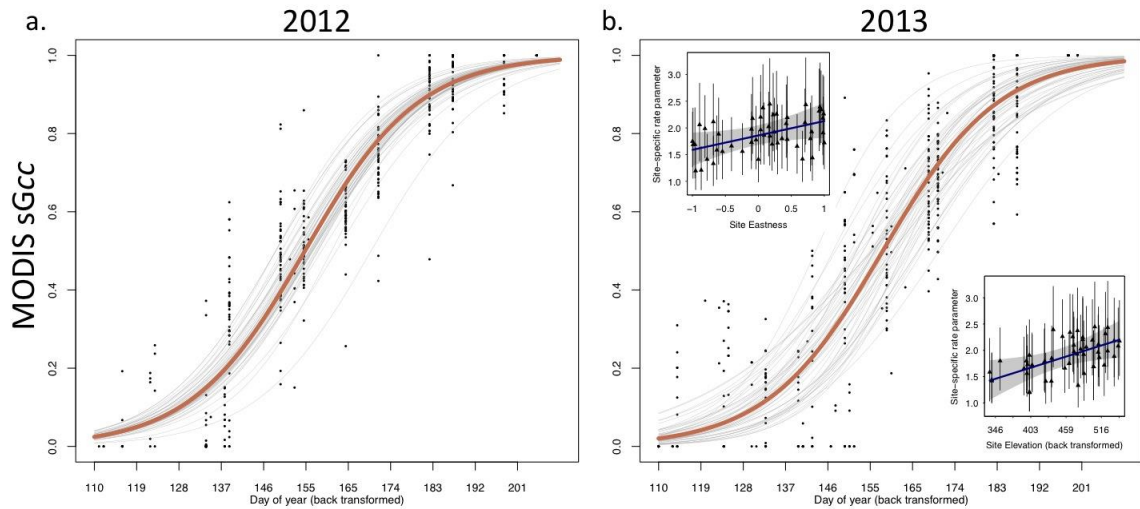


b.

Supplementary Figure 5.S1. Relationship between timing of first snowmelt and a. elevation and b. degree of north facing aspect in 2012 and 2013.



Supplementary Figure 5.S2. Across site variation in the timing of leaf onset between and within years for MODIS *Gcc* dataset.



Supplementary Figure 5.S3. Landscape greenup profiles and model-parameter covariation with landscape factors for MODIS *Gcc* (orange) dataset across the study region in years with contrasting abiotic conditions. Subplot formatting is consistent with Figure 4. For site parameters for all models, see Supp Tables 5.2-5.11.

Supplementary Tables:

Supplementary Table 5.S1. Summary of landscape predictors of greenup phenology in each year, vegetation index, and dataset subset. We report the landscape covariates from the best 2 parameter (Inflection and Rate) logistic model for each subset, including posterior means, 90% credible intervals, and the probability that the direction of the posterior mean matches its sign (positive or negative).

Dataset, index & year	Landscape predictor	Posterior mean (effect size)	90% CRI (lower, upper)	PR (direction of posterior mean)
PlantCam <i>sgcc</i> Community 2012	Northness (Inflection)	0.272	(0.123, 0.421)	0.99
	Eastness (Inflection)	0.210	(0.048, 0.368)	0.98
PlantCam <i>sgcc</i> Community 2013	Northness (Rate)	-0.318	(-0.661, 0.010)	0.94
	Topographic Wetness Index (Rate)	0.261	(0.083, 0.436)	0.99
MODIS sNDVI 2013	---	---	---	---
MODIS sNDVI 2013	Elevation (Rate)	0.194	(0.102, 0.286)	0.99
MODIS <i>sgcc</i> 2012	---	---	---	---
MODIS <i>sgcc</i> 2013	Elevation (Rate)	1.048	(0.067, 0.357)	0.99
	Eastness (Rate)	0.271	(0.048, 0.497)	0.98
PlantCam <i>sgcc</i> <i>Betula</i> 2012	Northness (Inflection)	0.133	(0.031, 0.236)	0.98
PlantCam <i>sgcc</i> <i>Betula</i> 2013	Northness (Rate)	-0.644	(-1.185, -0.110)	0.97
PlantCam <i>sgcc</i> Graminoid	Northness (Inflection)	0.215	(0.030, 0.399)	0.97
PlantCam <i>sgcc</i> Graminoid	Northness (Inflection)	0.445	(0.179, 0.713)	0.99
	Northness (Rate)	-0.584	(-0.978, -0.204)	0.99

Supplementary Table 5.S2. 2012 PC Community FOV Model Output

Site	Rate (95% CRI)			Inflection (95% CRI)			Sigma (95% CRI)		
	Mean	(lower,	upper)	Mean	(lower,	upper)	Mean	(lower,	upper)
1	2.597	2.159	3.084	0.002	-0.104	0.099	0.055	0.036	0.084
2	2.670	2.103	3.264	-0.67	-0.779	-0.558	0.079	0.055	0.118
3	2.320	1.609	3.058	-0.286	-0.507	-0.056	0.144	0.1	0.21
4	2.103	1.809	2.443	0.002	-0.085	0.092	0.057	0.04	0.081
6	2.027	1.619	2.517	-0.104	-0.249	0.036	0.088	0.063	0.124
7	1.799	1.438	2.299	-0.837	-0.965	-0.706	0.073	0.053	0.102
8	2.378	1.869	2.942	-0.288	-0.425	-0.152	0.09	0.063	0.131
9	2.240	1.803	2.761	-0.061	-0.181	0.059	0.077	0.056	0.107
10	2.487	2.115	2.889	-0.227	-0.31	-0.141	0.057	0.038	0.084
11	1.817	1.386	2.351	-0.206	-0.375	-0.036	0.091	0.064	0.131
12	2.328	1.921	2.768	0.271	0.175	0.36	0.064	0.046	0.089
13	2.499	2.140	2.909	-0.713	-0.786	-0.636	0.052	0.035	0.076
14	2.939	2.495	3.398	-0.132	-0.203	-0.061	0.053	0.035	0.081
15	2.258	1.796	2.795	-0.473	-0.608	-0.332	0.084	0.059	0.122
16	2.342	2.014	2.710	-0.318	-0.398	-0.236	0.055	0.037	0.081
17	2.513	2.082	2.987	-0.643	-0.734	-0.552	0.061	0.04	0.092
18	2.097	1.655	2.613	0.174	0.02	0.32	0.096	0.07	0.133
20	2.470	2.063	2.931	0.745	0.648	0.841	0.066	0.046	0.094
21	1.455	1.110	1.917	0.426	0.238	0.612	0.097	0.071	0.135
23	2.198	1.834	2.633	-0.054	-0.165	0.054	0.071	0.052	0.099
24	1.721	1.198	2.369	0.174	-0.056	0.411	0.126	0.09	0.18
25	2.129	1.714	2.647	-0.33	-0.453	-0.206	0.08	0.056	0.115
26	2.203	1.852	2.607	0.165	0.074	0.26	0.06	0.043	0.085
27	1.976	1.500	2.564	0.195	0.022	0.363	0.105	0.078	0.145
28	2.821	2.356	3.328	-0.551	-0.63	-0.471	0.059	0.043	0.083
29	1.890	1.640	2.191	0.274	0.186	0.364	0.054	0.039	0.076
30	2.448	2.025	2.915	-0.556	-0.655	-0.455	0.067	0.045	0.1
31	2.994	2.196	3.896	-0.928	-1.054	-0.788	0.102	0.072	0.147
33	1.875	1.416	2.516	-1.235	-1.402	-1.056	0.069	0.04	0.114
34	3.209	2.515	3.892	-0.03	-0.127	0.065	0.075	0.048	0.119
35	2.678	2.165	3.251	0.116	0.008	0.218	0.077	0.055	0.111
38	2.684	2.323	3.072	0.11	0.039	0.18	0.051	0.036	0.073
39	2.279	2.007	2.590	0.038	-0.027	0.104	0.045	0.031	0.065
40	2.430	1.941	2.975	0.509	0.397	0.618	0.077	0.056	0.107
42	1.727	1.505	1.995	0.378	0.288	0.461	0.05	0.036	0.069
43	2.076	1.800	2.405	-0.17	-0.256	-0.083	0.054	0.04	0.076
45	2.193	1.566	2.986	-0.488	-0.692	-0.277	0.126	0.092	0.177
46	2.304	1.935	2.722	-0.076	-0.176	0.021	0.063	0.043	0.094
47	2.478	2.031	2.998	0.01	-0.099	0.117	0.077	0.057	0.105
48	2.819	1.772	3.942	-0.962	-1.202	-0.585	0.169	0.106	0.275
49	2.610	2.181	3.095	-0.34	-0.429	-0.249	0.064	0.045	0.093
All	2.319	2.146	2.5	-0.132	-0.275	0.007			

Supplementary Table 5.S3. 2013 PC Community FOV Model Output

Site	Rate (95% CRI)			Inflection(95% CRI)			Sigma (95% CRI)		
	Mean	(lower, upper)		Mean	(lower, upper)		Mean	(lower, upper)	
1	1.609	1.237	2.113	0.599	0.436	0.762	0.101	0.077	0.134
3	2.446	1.621	3.567	-0.319	-0.495	-0.141	0.127	0.092	0.179
6	3.227	2.778	3.746	-0.435	-0.492	-0.379	0.049	0.032	0.074
8	1.747	1.397	2.148	0.687	0.555	0.819	0.083	0.06	0.116
9	4.045	3.412	4.758	0.155	0.105	0.206	0.049	0.035	0.069
11	3.675	3.075	4.347	-0.223	-0.281	-0.165	0.054	0.035	0.084
12	3.079	2.184	4.16	-0.28	-0.432	-0.132	0.128	0.095	0.177
13	2.208	1.886	2.592	0.562	0.471	0.652	0.066	0.05	0.089
15	2.12	1.72	2.639	-0.25	-0.357	-0.143	0.076	0.055	0.105
16	2.405	2.124	2.744	-0.294	-0.355	-0.23	0.047	0.033	0.067
19	1.894	1.608	2.244	-0.02	-0.115	0.072	0.065	0.048	0.088
23	2.075	1.681	2.547	0.453	0.334	0.576	0.082	0.06	0.112
25	2.593	2.093	3.187	0.519	0.422	0.62	0.074	0.052	0.108
28	2.098	1.82	2.416	0.637	0.558	0.713	0.055	0.04	0.076
30	3.697	2.271	5.373	-0.724	-0.912	-0.439	0.162	0.095	0.279
32	3.079	2.554	3.702	-0.347	-0.427	-0.27	0.066	0.047	0.093
33	2.308	1.893	2.816	-0.543	-0.639	-0.443	0.069	0.048	0.101
34	2.5	2.094	2.984	0.375	0.279	0.468	0.071	0.052	0.098
35	2.19	1.904	2.511	0.781	0.7	0.856	0.055	0.04	0.076
38	1.877	1.52	2.322	0.212	0.097	0.329	0.078	0.06	0.105
39	1.562	1.136	2.095	0.595	0.392	0.791	0.108	0.078	0.153
40	3.39	2.406	4.511	-1.025	-1.16	-0.888	0.107	0.07	0.168
42	3.892	2.976	4.813	-0.063	-0.131	0.005	0.064	0.04	0.101
43	3.66	3.138	4.254	-0.028	-0.076	0.021	0.046	0.033	0.063
45	2.271	1.786	2.961	-0.063	-0.18	0.058	0.084	0.063	0.114
47	2.834	2.176	3.643	0.118	-0.004	0.242	0.098	0.07	0.138
48	2.738	2.275	3.288	0.372	0.286	0.46	0.07	0.05	0.1
All	1.81	1.102	2.551	0.054	-0.144	0.25			

Supplementary Table 5.S4. 2012 MODIS sNDVI Model Output

Site	Rate (95% CRI)			Inflection (95% CRI)			Sigma (95% CRI)		
	Mean	(lower, upper)		Mean	(lower, upper)		Mean	(lower, upper)	
1	2.065	1.716	2.445	-0.481	-0.604	-0.35	0.068	0.049	0.093
2	1.914	1.557	2.304	-0.449	-0.599	-0.3	0.076	0.056	0.105
3	2.132	1.786	2.509	-0.442	-0.559	-0.326	0.061	0.043	0.084
4	2.022	1.652	2.412	-0.344	-0.491	-0.201	0.077	0.057	0.106
5	1.974	1.613	2.385	-0.496	-0.643	-0.349	0.075	0.056	0.102
6	2.088	1.768	2.441	-0.366	-0.476	-0.258	0.058	0.04	0.081
7	2.263	1.859	2.683	-0.336	-0.468	-0.203	0.077	0.057	0.107
8	2.222	1.857	2.608	-0.404	-0.521	-0.282	0.067	0.047	0.093
9	1.936	1.603	2.313	-0.564	-0.701	-0.428	0.068	0.049	0.092
10	1.932	1.589	2.307	-0.457	-0.589	-0.319	0.07	0.051	0.096
11	1.989	1.643	2.371	-0.409	-0.543	-0.279	0.067	0.048	0.092
12	2.09	1.762	2.431	-0.364	-0.475	-0.256	0.058	0.04	0.081
13	1.873	1.556	2.232	-0.317	-0.448	-0.195	0.063	0.045	0.087
14	2.122	1.717	2.557	-0.563	-0.722	-0.396	0.091	0.068	0.126
15	1.972	1.659	2.318	-0.288	-0.408	-0.176	0.058	0.039	0.081
16	2.208	1.871	2.57	-0.331	-0.436	-0.228	0.057	0.037	0.08
17	1.943	1.541	2.381	-0.525	-0.703	-0.344	0.095	0.072	0.13
18	1.919	1.546	2.342	-0.485	-0.659	-0.312	0.092	0.07	0.124
19	1.86	1.496	2.258	-0.624	-0.782	-0.464	0.078	0.058	0.107
20	2.297	1.945	2.668	-0.137	-0.243	-0.04	0.056	0.037	0.079
21	2.279	1.919	2.673	-0.195	-0.309	-0.085	0.064	0.045	0.087
22	2.001	1.651	2.383	-0.46	-0.591	-0.332	0.069	0.051	0.094
23	1.929	1.56	2.335	-0.292	-0.441	-0.147	0.076	0.056	0.104
24	2.044	1.667	2.441	-0.559	-0.704	-0.41	0.078	0.058	0.108
25	1.96	1.626	2.334	-0.334	-0.457	-0.207	0.064	0.045	0.088
26	2.235	1.881	2.613	-0.325	-0.433	-0.215	0.06	0.041	0.084
27	1.872	1.513	2.274	-0.542	-0.693	-0.389	0.076	0.057	0.104
28	2.055	1.725	2.429	-0.404	-0.526	-0.278	0.066	0.047	0.089
29	1.896	1.544	2.295	-0.579	-0.727	-0.434	0.075	0.055	0.102
30	2.142	1.738	2.557	-0.577	-0.716	-0.429	0.078	0.057	0.108
31	2.096	1.724	2.5	-0.335	-0.469	-0.204	0.073	0.054	0.099
32	1.973	1.649	2.342	-0.349	-0.473	-0.23	0.062	0.043	0.087
33	2.215	1.847	2.617	-0.245	-0.375	-0.115	0.072	0.052	0.1
34	2.042	1.658	2.442	-0.562	-0.707	-0.411	0.078	0.058	0.108
35	2.061	1.728	2.421	-0.406	-0.529	-0.287	0.066	0.047	0.09
36	2.152	1.762	2.563	-0.48	-0.615	-0.338	0.075	0.055	0.103
37	1.993	1.658	2.368	-0.217	-0.346	-0.09	0.066	0.046	0.091
38	1.954	1.594	2.344	-0.476	-0.617	-0.333	0.074	0.055	0.1
39	1.909	1.569	2.292	-0.49	-0.627	-0.347	0.072	0.053	0.098
40	2.432	2.037	2.836	-0.028	-0.143	0.082	0.064	0.044	0.089
41	2.308	1.896	2.746	-0.064	-0.194	0.057	0.072	0.052	0.098
42	2.409	1.927	2.931	-0.023	-0.206	0.135	0.1	0.073	0.141
43	1.983	1.647	2.337	-0.511	-0.643	-0.377	0.068	0.049	0.093

44	2.14	1.778	2.543	-0.332	-0.463	-0.206	0.07	0.052	0.095
45	2.178	1.855	2.529	-0.282	-0.39	-0.175	0.056	0.037	0.081
46	2.184	1.817	2.581	-0.38	-0.503	-0.253	0.069	0.05	0.094
47	1.942	1.602	2.332	-0.491	-0.625	-0.355	0.068	0.05	0.092
48	1.99	1.656	2.352	-0.427	-0.555	-0.3	0.068	0.049	0.093
49	2.303	1.954	2.694	-0.138	-0.24	-0.039	0.056	0.036	0.079
50	1.985	1.649	2.347	-0.512	-0.643	-0.381	0.067	0.048	0.092
All	2.07	1.964	2.18	-0.4	-0.45	-0.32			

Supplementary Table 5.S5. 2013 MODIS sNDVI Model Output

Site	Rate (95% CRI)			Inflection (95% CRI)			Sigma (95% CRI)		
	Mean	(lower, upper)		Mean	(lower, upper)		Mean	(lower, upper)	
1	2.028	1.681	2.42	-0.04	-0.175	0.092	0.069	0.052	0.092
2	2.03	1.654	2.426	-0.165	-0.304	-0.024	0.073	0.056	0.098
3	2.319	1.931	2.747	0.006	-0.109	0.119	0.064	0.047	0.086
4	2.404	2.019	2.83	0.118	0.014	0.217	0.058	0.039	0.078
5	2.205	1.829	2.609	-0.022	-0.143	0.1	0.067	0.05	0.09
6	2.564	2.116	3.053	0.181	0.073	0.287	0.066	0.048	0.089
7	2.489	2.044	2.949	0.012	-0.112	0.132	0.072	0.054	0.099
8	2.051	1.631	2.512	-0.341	-0.489	-0.184	0.076	0.058	0.103
9	2.018	1.674	2.397	-0.038	-0.168	0.087	0.065	0.048	0.087
10	1.888	1.559	2.257	-0.08	-0.213	0.052	0.067	0.05	0.089
11	2.386	1.987	2.824	-0.161	-0.283	-0.033	0.07	0.053	0.094
12	2.565	2.116	3.061	0.182	0.075	0.284	0.066	0.048	0.089
13	1.946	1.619	2.317	-0.1	-0.231	0.032	0.067	0.05	0.089
14	1.886	1.522	2.301	-0.156	-0.31	0	0.077	0.059	0.103
15	2.342	1.982	2.749	0.078	-0.03	0.179	0.058	0.04	0.078
16	1.607	1.29	1.969	-0.123	-0.28	0.032	0.073	0.056	0.099
17	2.299	1.911	2.748	0.089	-0.029	0.203	0.065	0.047	0.086
18	2.089	1.706	2.511	0.059	-0.078	0.195	0.074	0.056	0.099
19	1.898	1.581	2.264	-0.095	-0.225	0.034	0.065	0.047	0.086
20	2.312	1.938	2.723	0.038	-0.071	0.147	0.062	0.044	0.082
21	2.181	1.833	2.555	-0.039	-0.153	0.073	0.059	0.041	0.08
22	2.137	1.788	2.518	0.008	-0.106	0.12	0.061	0.042	0.082
23	2.231	1.862	2.657	-0.043	-0.155	0.067	0.06	0.042	0.081
24	2.096	1.721	2.523	-0.102	-0.234	0.033	0.069	0.052	0.093
25	2.106	1.772	2.47	0.033	-0.079	0.139	0.057	0.038	0.077
26	2.312	1.88	2.778	0.117	-0.014	0.244	0.073	0.056	0.099
27	1.801	1.496	2.148	0.013	-0.115	0.142	0.063	0.045	0.084
28	1.399	1.084	1.775	-0.293	-0.495	-0.088	0.088	0.067	0.12
29	2.003	1.681	2.366	0.05	-0.068	0.161	0.059	0.041	0.079
30	2.226	1.844	2.651	-0.125	-0.254	0.003	0.069	0.052	0.093
31	2.139	1.803	2.51	-0.078	-0.196	0.042	0.062	0.044	0.082
32	2.091	1.736	2.49	0.05	-0.078	0.177	0.068	0.051	0.09
33	2.379	1.977	2.841	0.022	-0.096	0.139	0.067	0.049	0.091
34	2.095	1.726	2.523	-0.103	-0.236	0.029	0.069	0.052	0.093
35	1.401	1.082	1.774	-0.295	-0.495	-0.088	0.088	0.067	0.121
36	1.946	1.61	2.311	-0.102	-0.232	0.027	0.066	0.048	0.089
37	2.318	1.914	2.764	-0.026	-0.152	0.098	0.071	0.054	0.095
38	1.976	1.628	2.347	-0.222	-0.355	-0.085	0.071	0.053	0.095
39	2.15	1.783	2.536	-0.025	-0.137	0.084	0.06	0.041	0.081
40	2.728	2.267	3.237	0.239	0.146	0.332	0.061	0.041	0.083
41	2.628	2.186	3.102	0.281	0.179	0.374	0.058	0.04	0.079
42	2.541	2.033	3.096	0.26	0.126	0.386	0.081	0.061	0.113
43	1.705	1.399	2.061	-0.049	-0.19	0.093	0.066	0.048	0.088

44	2.293	1.912	2.707	-0.077	-0.192	0.035	0.062	0.045	0.083
45	1.89	1.564	2.267	-0.079	-0.212	0.057	0.067	0.05	0.089
46	2.353	1.988	2.755	-0.048	-0.158	0.061	0.062	0.045	0.084
47	1.836	1.489	2.232	-0.112	-0.266	0.041	0.074	0.056	0.099
48	1.566	1.228	1.951	-0.12	-0.291	0.053	0.079	0.061	0.107
49	2.31	1.929	2.72	0.038	-0.073	0.143	0.062	0.044	0.082
50	1.697	1.391	2.042	-0.049	-0.189	0.089	0.066	0.048	0.088
all	2.117	2.003	2.236	-0.029	-0.089	0.031			

Supplementary Table 5.S6. 2012 MODIS sGcc Model Output

Site	Rate (95% CRI)			Inflection (95% CRI)			Sigma (95% CRI)		
	Mean	(lower, upper)		Mean	(lower, upper)		Mean	(lower, upper)	
1	1.825	1.433	2.25	-0.232	-0.43	-0.036	0.099	0.074	0.123
2	1.782	1.357	2.21	-0.243	-0.452	-0.033	0.105	0.083	0.131
3	1.646	1.273	2.072	-0.236	-0.445	-0.025	0.102	0.079	0.125
4	1.757	1.313	2.201	-0.497	-0.735	-0.256	0.116	0.095	0.152
5	1.802	1.396	2.225	-0.366	-0.57	-0.158	0.104	0.082	0.13
6	1.798	1.377	2.238	-0.422	-0.641	-0.211	0.109	0.089	0.139
7	1.995	1.539	2.488	-0.586	-0.789	-0.368	0.117	0.096	0.155
8	1.848	1.414	2.301	-0.263	-0.465	-0.058	0.105	0.083	0.132
9	2.069	1.652	2.539	-0.054	-0.233	0.117	0.096	0.068	0.119
10	1.762	1.357	2.197	-0.332	-0.549	-0.123	0.104	0.082	0.131
11	1.766	1.363	2.2	-0.267	-0.48	-0.06	0.105	0.082	0.131
12	1.801	1.387	2.26	-0.422	-0.639	-0.208	0.11	0.089	0.14
13	1.784	1.385	2.225	-0.236	-0.439	-0.038	0.102	0.079	0.126
14	1.845	1.428	2.293	-0.489	-0.696	-0.279	0.106	0.085	0.134
15	1.713	1.308	2.153	-0.15	-0.366	0.059	0.102	0.079	0.127
16	1.854	1.446	2.303	-0.403	-0.599	-0.201	0.101	0.077	0.124
17	1.988	1.525	2.49	-0.531	-0.747	-0.316	0.115	0.095	0.151
18	1.834	1.384	2.315	-0.266	-0.478	-0.047	0.105	0.083	0.133
19	1.903	1.503	2.354	-0.181	-0.378	0.007	0.102	0.081	0.127
20	1.854	1.436	2.283	-0.206	-0.414	0.003	0.105	0.083	0.132
21	1.962	1.54	2.429	-0.348	-0.536	-0.158	0.104	0.082	0.13
22	1.864	1.457	2.314	-0.373	-0.569	-0.18	0.101	0.078	0.126
23	1.597	1.22	2.029	-0.258	-0.479	-0.041	0.104	0.082	0.13
24	1.844	1.403	2.311	-0.588	-0.806	-0.361	0.112	0.091	0.144
25	1.916	1.505	2.384	-0.178	-0.377	0.015	0.103	0.079	0.128
26	1.856	1.454	2.301	-0.249	-0.443	-0.053	0.1	0.075	0.124
27	1.625	1.231	2.068	-0.386	-0.605	-0.171	0.102	0.079	0.127
28	1.866	1.457	2.299	-0.353	-0.55	-0.149	0.103	0.079	0.129
29	1.778	1.367	2.237	-0.416	-0.626	-0.206	0.103	0.08	0.129
30	1.794	1.381	2.245	-0.482	-0.7	-0.267	0.112	0.091	0.143
31	1.877	1.428	2.352	-0.431	-0.649	-0.204	0.117	0.096	0.153
32	1.809	1.401	2.236	-0.303	-0.505	-0.093	0.106	0.084	0.133
33	1.762	1.352	2.194	-0.01	-0.234	0.227	0.111	0.09	0.142
34	1.848	1.412	2.323	-0.588	-0.808	-0.37	0.112	0.091	0.144
35	1.864	1.457	2.303	-0.351	-0.545	-0.149	0.103	0.079	0.128
36	1.927	1.498	2.377	-0.344	-0.537	-0.151	0.105	0.082	0.131
37	1.849	1.434	2.295	-0.25	-0.454	-0.041	0.108	0.087	0.136
38	1.735	1.353	2.157	-0.228	-0.434	-0.029	0.099	0.074	0.123
39	1.79	1.381	2.219	-0.265	-0.463	-0.067	0.099	0.073	0.122
40	1.793	1.411	2.208	-0.233	-0.428	-0.037	0.098	0.074	0.121
41	1.81	1.379	2.266	-0.24	-0.444	-0.028	0.107	0.086	0.134
42	1.827	1.376	2.334	0.325	0.077	0.556	0.111	0.09	0.144
43	1.915	1.504	2.354	-0.314	-0.508	-0.13	0.099	0.073	0.123

44	1.825	1.415	2.262	-0.328	-0.542	-0.122	0.108	0.087	0.135
45	1.891	1.476	2.34	-0.193	-0.397	0.005	0.102	0.078	0.126
46	1.839	1.409	2.296	-0.391	-0.601	-0.179	0.109	0.088	0.138
47	1.959	1.533	2.428	-0.379	-0.565	-0.186	0.1	0.076	0.124
48	1.874	1.475	2.324	-0.331	-0.526	-0.134	0.101	0.076	0.125
49	1.854	1.442	2.303	-0.206	-0.408	-0.001	0.105	0.083	0.133
50	1.906	1.494	2.341	-0.312	-0.501	-0.115	0.099	0.073	0.123
all	1.833	1.711	1.964	-0.308	-0.381	-0.234			

Supplementary Table 5.S7. 2013 MODIS sGcc Model Output

Site	Rate (95% CRI)			Inflection (95% CRI)			Sigma (95% CRI)		
	Mean	(lower, upper)		Mean	(lower, upper)		Mean	(lower, upper)	
1	1.759	1.282	2.313	-0.207	-0.446	0.029	0.119	0.091	0.148
2	1.555	1.05	2.131	0.03	-0.245	0.296	0.125	0.1	0.159
3	1.987	1.43	2.649	-0.257	-0.475	-0.039	0.116	0.084	0.143
4	2.109	1.477	2.83	-0.24	-0.471	-0.014	0.123	0.095	0.158
5	2.271	1.586	3.072	-0.067	-0.298	0.145	0.126	0.1	0.163
6	2.248	1.576	3.042	-0.403	-0.65	-0.169	0.131	0.106	0.173
7	1.964	1.313	2.679	0.083	-0.183	0.341	0.13	0.106	0.171
8	2.452	1.699	3.344	-0.783	-1.012	-0.538	0.126	0.1	0.162
9	2.269	1.659	2.974	0.108	-0.106	0.31	0.119	0.088	0.148
10	1.417	0.993	1.951	-0.371	-0.649	-0.102	0.118	0.09	0.146
11	2.084	1.43	2.814	0.064	-0.183	0.299	0.123	0.097	0.156
12	2.213	1.543	2.995	-0.401	-0.636	-0.166	0.131	0.107	0.175
13	1.913	1.3	2.597	-0.236	-0.498	0.01	0.126	0.101	0.161
14	1.923	1.362	2.524	-0.06	-0.311	0.185	0.126	0.102	0.162
15	2.098	1.544	2.742	-0.204	-0.427	0.017	0.118	0.089	0.147
16	1.598	1.041	2.246	-0.221	-0.515	0.051	0.13	0.106	0.17
17	2.326	1.582	3.136	0.04	-0.193	0.268	0.128	0.103	0.165
18	1.705	1.203	2.317	-0.229	-0.474	0.014	0.121	0.096	0.15
19	1.733	1.245	2.292	-0.059	-0.297	0.173	0.116	0.084	0.144
20	1.689	1.068	2.386	0.17	-0.128	0.444	0.131	0.107	0.174
21	1.776	1.176	2.486	-0.409	-0.681	-0.144	0.135	0.112	0.178
22	1.662	1.196	2.198	-0.134	-0.376	0.103	0.116	0.085	0.143
23	2.169	1.522	2.945	-0.452	-0.687	-0.219	0.13	0.107	0.166
24	1.877	1.309	2.549	-0.602	-0.857	-0.333	0.127	0.104	0.162
25	1.803	1.189	2.488	0.098	-0.182	0.357	0.126	0.101	0.162
26	1.33	0.918	1.839	-0.255	-0.534	0.026	0.119	0.091	0.148
27	1.657	1.146	2.269	0.366	0.096	0.617	0.119	0.09	0.15
28	1.44	1.004	1.976	-0.065	-0.329	0.197	0.115	0.083	0.141
29	1.784	1.223	2.412	0.219	-0.039	0.459	0.124	0.098	0.158
30	1.863	1.314	2.488	-0.338	-0.592	-0.082	0.121	0.093	0.152
31	2.066	1.39	2.868	-0.227	-0.486	0.013	0.129	0.105	0.169
32	1.986	1.404	2.668	-0.336	-0.59	-0.09	0.126	0.102	0.162
33	2.207	1.512	2.978	-0.012	-0.255	0.218	0.129	0.105	0.168
34	2.172	1.498	2.976	-0.622	-0.872	-0.353	0.128	0.104	0.163
35	1.428	0.997	1.962	-0.065	-0.322	0.186	0.114	0.082	0.141
36	1.412	1.02	1.893	-0.277	-0.532	-0.02	0.115	0.084	0.141
37	2.381	1.704	3.226	-0.142	-0.375	0.067	0.129	0.103	0.17
38	1.564	1.128	2.08	-0.023	-0.27	0.217	0.116	0.086	0.143
39	1.724	1.208	2.343	-0.269	-0.522	-0.022	0.117	0.088	0.143
40	2.344	1.713	3.072	-0.032	-0.237	0.162	0.124	0.097	0.157
41	2.458	1.748	3.301	-0.102	-0.325	0.099	0.129	0.104	0.169
42	2.401	1.691	3.211	0.039	-0.177	0.241	0.127	0.1	0.167
43	1.196	0.841	1.628	-0.264	-0.543	0.013	0.115	0.085	0.141

44	1.701	1.114	2.415	-0.421	-0.7	-0.138	0.132	0.109	0.171
45	1.941	1.339	2.624	-0.114	-0.37	0.136	0.126	0.102	0.161
46	2.025	1.473	2.662	-0.161	-0.389	0.062	0.119	0.091	0.147
47	1.856	1.3	2.478	0.182	-0.062	0.412	0.119	0.089	0.148
48	1.804	1.249	2.457	-0.126	-0.375	0.111	0.123	0.095	0.156
49	1.695	1.074	2.409	0.172	-0.12	0.439	0.131	0.107	0.173
50	1.205	0.849	1.644	-0.263	-0.54	0.016	0.116	0.086	0.142
All	1.863	1.687	2.06	-0.157	-0.249	-0.067			

Supplementary Table 5.S8. 2012 PC *sGcc Betula* Model Output

ROI	Rate (95% CRI)			Inflection (95% CRI)			Sigma (95% CRI)		
	Mean	(lower, upper)		Mean	(lower, upper)		Mean	(lower, upper)	
1	3.145	2.269	4.333	-0.502	-0.628	-0.366	0.079	0.054	0.114
2	2.321	1.803	2.981	0.068	-0.062	0.195	0.077	0.054	0.108
3	3.832	2.939	4.963	-0.644	-0.727	-0.559	0.073	0.052	0.102
4	4.966	3.572	6.682	-0.891	-0.967	-0.806	0.08	0.058	0.11
5	2.107	1.61	2.733	-0.102	-0.228	0.028	0.084	0.062	0.115
6	2.288	1.661	3.147	-0.21	-0.347	-0.07	0.093	0.07	0.127
7	1.941	1.572	2.433	-0.332	-0.455	-0.205	0.074	0.057	0.098
8	2.644	2.07	3.347	-0.406	-0.51	-0.298	0.076	0.055	0.105
9	2.96	2.297	3.819	-0.329	-0.433	-0.221	0.079	0.059	0.106
10	3.045	2.42	3.755	-0.049	-0.141	0.037	0.069	0.048	0.097
11	2.749	2.271	3.298	-0.074	-0.155	0.004	0.059	0.038	0.085
12	3.555	2.562	4.872	-0.651	-0.755	-0.54	0.085	0.063	0.115
13	2.426	1.911	3.101	-0.294	-0.406	-0.177	0.072	0.054	0.097
14	1.955	1.615	2.367	0.373	0.254	0.487	0.059	0.04	0.084
15	2.799	2.184	3.551	-0.477	-0.585	-0.367	0.078	0.056	0.109
16	2.351	1.748	3.134	-0.393	-0.535	-0.244	0.092	0.069	0.126
17	2.141	1.823	2.53	-0.015	-0.099	0.068	0.055	0.039	0.076
18	2.596	2.096	3.211	-0.391	-0.486	-0.294	0.07	0.051	0.097
19	5.07	3.856	6.42	-0.784	-0.85	-0.719	0.066	0.044	0.097
20	2.165	1.772	2.659	-0.105	-0.221	0.011	0.071	0.051	0.096
21	2.161	1.753	2.671	0.307	0.211	0.401	0.065	0.048	0.087
22	1.611	1.331	1.923	0.231	0.11	0.346	0.07	0.052	0.093
23	2.04	1.457	2.83	-0.354	-0.506	-0.203	0.096	0.074	0.127
24	1.573	1.219	2.033	-0.275	-0.425	-0.128	0.084	0.065	0.111
25	1.645	1.136	2.366	0.083	-0.108	0.271	0.11	0.085	0.145
26	2.535	2.062	3.102	-0.181	-0.277	-0.086	0.067	0.048	0.092
27	2.134	1.808	2.51	-0.135	-0.234	-0.039	0.062	0.045	0.085
28	2.321	1.736	3.104	-0.441	-0.571	-0.307	0.083	0.061	0.113
29	3.613	2.749	4.672	-0.619	-0.715	-0.519	0.082	0.059	0.114
30	5.044	3.892	6.393	-0.851	-0.918	-0.781	0.068	0.047	0.098
31	5.217	3.653	7.224	-0.954	-1.037	-0.86	0.089	0.065	0.124
32	6.406	4.556	8.447	-0.981	-1.042	-0.915	0.077	0.053	0.109
33	5.64	4.072	7.452	-0.905	-0.976	-0.828	0.081	0.054	0.118
34	3.31	2.515	4.255	0.216	0.121	0.306	0.076	0.056	0.103
35	3.532	2.749	4.42	-0.091	-0.175	-0.01	0.068	0.046	0.099
36	2.589	2.067	3.238	-0.224	-0.333	-0.12	0.076	0.055	0.104
37	2.645	2.115	3.308	-0.276	-0.369	-0.182	0.069	0.053	0.089
38	6.557	4.088	9.266	-1.317	-1.41	-1.201	0.112	0.073	0.176
39	3.159	2.013	4.748	-0.558	-0.711	-0.395	0.114	0.089	0.148
40	5.746	4.208	7.466	-0.874	-0.94	-0.806	0.074	0.052	0.105
41	2.584	2.038	3.293	-0.566	-0.67	-0.461	0.077	0.057	0.104
42	2.253	1.529	3.379	-0.516	-0.683	-0.341	0.099	0.075	0.134
43	2.511	1.969	3.152	-0.132	-0.242	-0.025	0.076	0.054	0.106

44	2.463	1.896	3.175	-0.215	-0.337	-0.088	0.088	0.065	0.121
45	6.046	4.091	8.399	-0.986	-1.069	-0.894	0.098	0.065	0.146
46	3.241	2.49	4.185	-0.522	-0.625	-0.419	0.08	0.057	0.112
47	4.329	3.196	5.749	-0.66	-0.74	-0.576	0.074	0.054	0.103
All	3.192	2.75	3.704	-0.357	-0.47	-0.244			

Supplementary Table 5.S9. PC *sGcc* 2013 *Betula* Model Output

ROI	Rate (95% CRI)			Inflection(95% CRI)			Sigma (95% CRI)		
	Mean	(lower, upper)		Mean	(lower, upper)		Mean	(lower, upper)	
1	2.958	1.668	4.737	0.164	-0.017	0.365	0.145	0.108	0.2
2	3.309	2.056	4.97	-0.265	-0.4	-0.124	0.117	0.085	0.164
3	2.941	2.21	3.885	0.417	0.309	0.523	0.088	0.067	0.117
4	2.329	1.764	3.089	0.633	0.507	0.755	0.091	0.069	0.121
5	2.093	1.547	2.768	1.127	0.973	1.267	0.097	0.069	0.14
6	5.542	4.348	6.732	-0.061	-0.115	-0.006	0.059	0.035	0.097
7	4.175	3.615	4.794	0.267	0.227	0.306	0.038	0.024	0.058
8	3.453	2.795	4.284	0.258	0.187	0.33	0.062	0.043	0.091
9	2.587	2.179	3.079	0.497	0.421	0.572	0.058	0.043	0.08
10	3.87	2.674	5.364	-0.221	-0.322	-0.117	0.094	0.068	0.134
11	4.43	3.405	5.604	-0.115	-0.176	-0.042	0.049	0.026	0.087
12	4.788	3.638	6.103	-0.034	-0.105	0.043	0.078	0.053	0.12
13	3.063	2.348	4.053	-0.131	-0.224	-0.036	0.077	0.056	0.107
14	3.492	2.463	4.817	0.3	0.195	0.412	0.094	0.066	0.139
15	3.15	2.198	4.485	-0.12	-0.238	-0.004	0.097	0.071	0.134
16	4.388	3.194	5.821	0.062	-0.013	0.142	0.08	0.059	0.109
17	6.045	3.339	8.565	-0.674	-0.818	-0.273	0.155	0.098	0.26
18	4.024	3.019	5.269	0.189	0.113	0.263	0.071	0.049	0.101
19	2.12	1.745	2.649	0.087	-0.01	0.19	0.067	0.047	0.097
20	1.85	1.479	2.37	-0.08	-0.188	0.032	0.069	0.051	0.095
21	4.512	3.444	5.74	-0.019	-0.088	0.054	0.072	0.05	0.106
22	2.223	1.866	2.642	0.733	0.637	0.824	0.066	0.047	0.093
23	5.29	4.053	6.626	-0.058	-0.123	0.009	0.07	0.044	0.112
24	4.002	2.932	5.306	-0.058	-0.144	0.029	0.083	0.062	0.112
25	5.403	4.016	6.728	-0.189	-0.253	-0.122	0.07	0.04	0.118
26	4.868	4.075	5.714	-0.1	-0.146	-0.053	0.047	0.031	0.071
27	5.001	4.145	5.945	-0.176	-0.222	-0.132	0.048	0.033	0.071
28	4.717	3.754	5.825	-0.308	-0.369	-0.249	0.062	0.043	0.089
29	2.962	2.303	3.812	0.276	0.173	0.374	0.079	0.055	0.117
30	2.33	1.848	2.942	0.199	0.084	0.313	0.082	0.062	0.111
All	3.714	3.243	4.237	0.087	-0.058	0.232			

Supplementary Table 5.S10. 2012 PC *sGcc* Graminoid Model Output

ROI	Rate (95% CRI)			Inflection (95% CRI)			Sigma (95% CRI)		
	Mean	(lower, upper)		Mean	(lower, upper)		Mean	(lower, upper)	
1	2.883	2.301	3.491	0.06	-0.039	0.151	0.062	0.039	0.099
2	2.842	2.227	3.512	-0.576	-0.679	-0.466	0.078	0.054	0.115
3	1.822	1.584	2.124	0.151	0.057	0.241	0.055	0.039	0.078
4	2.101	1.701	2.572	0.116	-0.013	0.241	0.078	0.057	0.11
5	1.94	1.524	2.44	-0.876	-1.001	-0.749	0.074	0.053	0.106
6	1.996	1.544	2.575	-0.908	-1.039	-0.776	0.077	0.056	0.11
7	1.995	1.678	2.373	-0.247	-0.347	-0.148	0.059	0.041	0.086
8	2.583	2.123	3.103	0.411	0.317	0.502	0.063	0.044	0.093
9	0.977	0.668	1.412	-0.192	-0.544	0.155	0.137	0.104	0.186
10	2.621	2.261	3.025	0.021	-0.053	0.092	0.052	0.035	0.077
11	2.386	1.835	3.016	0.106	-0.042	0.254	0.088	0.061	0.13
12	1.972	1.508	2.576	-0.3	-0.455	-0.142	0.086	0.061	0.124
13	2.269	1.842	2.78	-0.051	-0.169	0.067	0.07	0.049	0.102
14	1.49	1.257	1.792	0.278	0.147	0.404	0.065	0.047	0.091
15	1.954	1.708	2.247	-0.435	-0.515	-0.357	0.049	0.035	0.07
16	2.394	2.1	2.717	-0.247	-0.313	-0.181	0.044	0.031	0.065
17	2.671	2.316	3.051	-0.347	-0.412	-0.281	0.047	0.032	0.07
18	2.727	2.351	3.138	0.249	0.187	0.31	0.044	0.031	0.064
19	2.234	1.853	2.692	-0.582	-0.677	-0.485	0.062	0.042	0.091
20	1.983	1.539	2.538	-0.575	-0.737	-0.403	0.101	0.075	0.139
21	2.457	2.172	2.79	0.816	0.756	0.873	0.04	0.028	0.058
22	1.549	1.346	1.792	1.073	0.968	1.174	0.055	0.041	0.074
23	1.75	1.306	2.32	0.12	-0.065	0.309	0.103	0.073	0.147
24	2.592	2.213	3.03	-0.091	-0.17	-0.013	0.055	0.038	0.079
25	2.117	1.781	2.516	0.007	-0.091	0.106	0.064	0.047	0.089
26	3.136	2.537	3.788	0.001	-0.081	0.085	0.058	0.041	0.084
27	1.713	1.483	1.991	0.765	0.667	0.86	0.054	0.04	0.075
28	2.726	2.151	3.338	-0.025	-0.133	0.081	0.076	0.053	0.113
29	2.716	2.3	3.185	0.47	0.399	0.542	0.053	0.038	0.075
30	1.616	1.228	2.193	-1.403	-1.601	-1.199	0.06	0.036	0.101
31	2.001	1.706	2.346	-0.221	-0.314	-0.127	0.056	0.041	0.078
32	3.152	2.633	3.674	0.02	-0.047	0.087	0.051	0.033	0.079
33	2.962	2.471	3.485	0.268	0.198	0.338	0.054	0.039	0.076
34	2.811	2.313	3.36	0.209	0.125	0.29	0.06	0.041	0.087
35	2.39	1.768	3.067	-0.986	-1.133	-0.827	0.098	0.067	0.146
36	3.051	2.613	3.506	0.09	0.033	0.148	0.045	0.033	0.064
37	2.191	1.935	2.5	0.083	0.011	0.155	0.046	0.032	0.067
38	2.09	1.902	2.299	0.027	-0.026	0.078	0.033	0.023	0.047
39	2.423	1.587	3.303	-0.331	-0.578	-0.079	0.166	0.117	0.241
40	2.532	2.197	2.9	-0.2	-0.267	-0.133	0.045	0.029	0.069
41	2.368	1.965	2.847	0.038	-0.064	0.141	0.069	0.05	0.097
42	2.377	1.909	2.929	0.292	0.182	0.399	0.075	0.055	0.103
43	2.197	1.888	2.578	0.026	-0.06	0.11	0.055	0.039	0.079

All	2.297	2.118	2.482	0.02	-0.153	0.193
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Supplementary Table 5.S11. PC *sGcc* 2013 Graminoid Model Output

ROI	Rate (95% CRI)			Inflection(95% CRI)			Sigma (95% CRI)		
	Mean	(lower, upper)		Mean	(lower, upper)		Mean	(lower, upper)	
1	2.059	1.703	2.491	1.028	0.926	1.123	0.068	0.052	0.092
2	1.395	1.102	1.777	0.799	0.634	0.965	0.091	0.07	0.121
3	2.075	1.406	2.988	-0.151	-0.332	0.034	0.117	0.085	0.164
4	3.342	2.951	3.789	-0.318	-0.366	-0.269	0.041	0.027	0.062
5	3.155	2.467	3.942	-0.171	-0.275	-0.064	0.088	0.061	0.131
6	2.77	2.322	3.305	0.46	0.381	0.542	0.062	0.046	0.084
7	2.586	2.246	2.997	-0.119	-0.182	-0.053	0.048	0.033	0.07
8	3.161	2.642	3.748	-0.015	-0.081	0.05	0.056	0.04	0.081
9	3.392	2.403	4.508	-0.018	-0.14	0.105	0.107	0.077	0.152
10	3.289	2.787	3.835	-0.158	-0.22	-0.094	0.054	0.036	0.081
11	2.73	2.182	3.428	0.134	0.045	0.225	0.073	0.054	0.099
12	2.919	2.645	3.235	-0.084	-0.124	-0.043	0.033	0.022	0.05
13	1.735	1.45	2.077	0.669	0.561	0.777	0.068	0.05	0.093
14	2.431	1.993	2.937	1.334	1.241	1.426	0.065	0.045	0.095
15	1.783	1.41	2.253	0.899	0.774	1.02	0.077	0.058	0.105
16	3.172	2.725	3.678	-0.168	-0.23	-0.106	0.052	0.036	0.076
17	1.776	1.614	1.96	0.596	0.536	0.656	0.038	0.027	0.054
18	2.782	2.397	3.223	0.742	0.669	0.814	0.057	0.041	0.079
19	2.873	2.47	3.323	0.917	0.854	0.981	0.051	0.037	0.072
20	4.22	3.119	5.496	0.072	-0.008	0.15	0.077	0.052	0.116
21	3.926	2.95	4.918	-1.056	-1.148	-0.962	0.08	0.051	0.128
22	2.708	2.23	3.272	0.621	0.534	0.708	0.069	0.051	0.093
23	2.721	2.397	3.107	0.348	0.291	0.405	0.045	0.031	0.065
All	2.571	2.241	2.918	0.404	0.168	0.641			

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CURRICULUM VITAE

EDUCATION

The Pennsylvania State University

Ph.D. Ecology 2015

The University of Richmond

B.S. Biology and Russian Studies 2007

SELECTED PUBLICATIONS

- Venkataraman, V., **Kerby, J.**, Fashing, P., Nguyen, N., Ashenafi, Z. (2015) Solitary wolves increase predation success upon rodents when among grazing monkey herds. *Journal of Mammalogy*, 96(1), 129-137.
- Fashing, P., Nguyen, N., Venkataraman, V., **Kerby, J.** (2014) Gelada feeding ecology in an intact ecosystem at Guassa, Ethiopia: variability over time and implications for theropit and hominin dietary evolution. *American Journal of Physical Anthropology*, 155(1), 1-16.
- Kerby, J.** & Post, E. (2013) Advancing plant phenology and reduced herbivore production in a terrestrial system associated with sea ice decline. *Nature Communications*, 4, 2514.
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SELECTED PRESENTATIONS

- Kerby, J.** Drones for Ecology. 1st Annual Environmental Biology Symposium, Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. (CICESE), 6 Nov 2014. (Invited talk)
- Kerby, J.** Ecological Consequences of Sea Ice Decline. University of Richmond, Global Environmental Speaker Series, November 2013 (Invited talk)
- Kerby, J.** & Post, E. Large Herbivore Reproductive Strategies in a Warming Arctic. Tundra Change – The Ecological Dimension, Aarhus, Denmark 2013 (Talk)
- Kerby, J.** & Post, E. Diminishing Arctic Sea Ice and Local Scale Plant Phenology in West Greenland. NPN Phenology Conference, Milwaukee 2012 (Talk)
- Kerby, J.** & Post, E. Large Herbivores in Changing Arctic: An Empirical Exploration of the Trophic Match/Mismatch Hypothesis. Smithsonian Conservation Biology Institute – 2012 (Invited Talk).
- Kerby, J.** & Post, E. Large Herbivore Reproductive Strategies in a Warming Arctic: Consequences of Climate Driven Trophic Match. American Geophysical Union – San Francisco 2011 (Talk)

AWARDS & GRANTS

National Geographic Society: Waitt Grant (\$15,000, 2015); Expeditions Council (\$15,000, 2015; \$8,000, 2014)

Arctic Institute of North America: Grant in Aid (\$1,000, 2014)

Pennsylvania State University Polar Day - Best Research Poster (2013)

National Science Foundation: Graduate Research Fellowship (2011 awarded, 2010 honorable mention)

PROGRAM SERVICE: Ecology Seminar Series Organizer, Recruiting Committee, Social Chair