Arctic Plant Migration by 2100: Comparing Predictions with Observations

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Abstract

Dahl Winters: Arctic Plant Migration by 2100: Comparing Predictions With Observations
(Under the direction of Dr. Aaron Moody)

Nowhere are the consequences of climate change greater than in the Arctic. The Arctic Climate Impact Assessment (ACIA, 2004) synthesized the potential impacts of climate change to Arctic ecosystems, including vegetation changes projected for 2100 using the BIOME4 dynamic vegetation model. In my research I synthesized empirical data from 30 studies of Arctic vegetation responses to climate change, and compared these data to the ACIA projected vegetation distribution for 2100. A general agreement between observed and projected changes was found, with exceptions due to regional variability and geographic clustering of the empirical data. There exist large areas of Siberia east of the Taymyr Peninsula and the Arctic Peninsula without empirical data, but are projected to undergo expansive change. Likewise, geographically limited empirical data have been published for large areas with no projected change in central Siberia and in the Yukon and Northwest Territories, Canada.

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If I could, I would also express my appreciation to all the young trees in the remote wildernesses of the Arctic forest-tundra ecotone that have served as the inspiration for this thesis. Year after year, they persevere in the face of harsh and lonely conditions, if only to make a minute increment of growth and progress. I am grateful my thesis progress has not been that slow in its maturation.

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1. Introduction

Although not always apparent, the global distributions of terrestrial biomes are dynamic, as are the ecosystem functions they fulfill. Given the rate and magnitude of anthropogenic climate change and expected ecosystem responses to it, it would appear that, on top of other human-caused ecosystem changes, we can expect changes in biome distributions over time scales of decades to centuries, with consequent implications for carbon storage and the provision of other ecosystem goods and services globally and locally (ACIA 2004). Nowhere are the implications of these trends greater than in the Arctic, which contains a major portion of Earth's terrestrial ecosystem carbon storage (Soja *et al.* 2007) distributed throughout vast and largely intact forests, peatlands, and tundra (ACIA 2004, Soja *et al.* 2007). In the Arctic, temperature increases have already been large relative to other global regions (IPCC 2007) and this trend is projected to continue (IPCC 2007, Soja *et al.* 2007). The net carbon balance of Arctic ecosystems is highly sensitive to climate change, and may be affected by changing biome distributions, such as forest encroachment into tundra (ACIA 2004).

The Arctic Climate Impact Assessment (ACIA) produced by the Arctic Council and the International Arctic Science Committee (IASC) includes predicted changes to Arctic ecosystems resulting from anthropogenic climate change by 2100 based on state-of-the-art climate and ecosystem forecasting models (ACIA 2004). This document is the most recent evaluation and synthesis of knowledge regarding Arctic climate change and its

impacts on Arctic ecosystems. In the ACIA report, several climate change scenarios and dynamic vegetation models were used to predict changes in Arctic biome distributions, which will be critical to energy and carbon budgets in the Arctic. The relationship of these biome projections to empirical data on contemporary changes in the Arctic remains unexamined, leaving several open questions: Do ground data corroborate the patterns and types of change projected in the ACIA report? Which geographic areas are projected to undergo major changes, but contain particularly limited empirical data? Are there geographic areas where biome projections are counter-indicated by empirical data?

I address these questions by assessing the correspondence between the geographic distributions and types of change predicted in the ACIA report, and changes observed on the ground as determined through a survey of published data on modern biome responses to climate change in the Arctic.

2. Background

2. 1. *Ecological Importance of the Arctic*

Although the Arctic has been defined in many ways for different purposes (Olson *et al.* 2001) one definition, adopted by the Arctic Climate Impact Assessment (ACIA 2004) defines the Arctic as the region above 55°N latitude (Fig. 1). This region covers over 1.2 billion hectares, two-thirds of which lies in Eurasia, and the remainder in Canada and Alaska (Soja *et al.* 2007). Arctic forests vary regionally depending on climatology and biogeographic history. Depending on region they may be dominated by larch (*Larix*), pine (*Pinus*), spruce (*Picea*), or fir (*Abies*) or birch (*Betula*), and more locally interspersed with aspen (*Populus*), willow (*Salix*) and alder (*Alnus*) following topographic insulae and disturbance. At the forest-tundra ecotone, where large trees give way to krummholz form and intergrade into tundra, larch, spruce, and pine are the dominant tree species found.

In addition to the carbon stored and assimilated by the vast expanses of Arctic forest, low temperatures and slow decomposition of organic matter breakdown result in large carbon stores on the ground and below the surface (Soja *et al.* 2007). Arctic regions have also experienced the largest temperature increases due to climate change in the 20th century, warming by 0.6-1.0°C (Beltrami and Mareschel, 1991; Chapman and Walsh, 1993; Kattenberg *et al.*, 1996; Overpeck *et al.*, 1997; Everett and Fitzharris, 1998; Mann *et al.*, 1999). The IPCC (Intergovernmental Panel on Climate Change) has more recently

estimated a global-scale warming of 0.56-0.92°C between 1906 and 2005 (IPCC 2007). Climate predictions indicate that the Arctic will continue to experience more rapid warming than other regions of the globe (IPCC 2007, Soja *et al.* 2007).

Climate change is known to cause changes in the distribution of vegetation types and biomes, with consequent change in ecosystem function, including carbon storage, which are increasingly valued by society. Although the sensitivity of global temperatures to atmospheric CO_2 concentration is uncertain, models accounting for a range of sensitivities have predicted increases of 1.1 to 6.4°C in global average temperature by the year 2100 (IPCC 2007). In the Arctic, the predicted increase in average annual temperature is even greater, at 2.8 to 7.8 °C, with a winter warming of between 4.3 and 11.4 °C (IPCC 2007).

Some ecosystem changes have already resulted from recent Arctic warming. Vegetation throughout the northern high latitudes greens earlier today than it did a century ago (Myneni *et al.* 1997), and climate envelopes characteristic of particular biomes have shifted, allowing for new establishment in previously cooler areas (Tape *et al.* 2006, Kapralov *et al.* 2006, Shiyatov *et al.* 2007). A major type of biome transition expected across much of the Arctic is from tundra to forest (ACIA 2004).

2. 2. *The Arctic Climate Impact Assessment (ACIA)*

The Arctic Climate Impact Assessment is an international project of the Arctic Council, a high-level intergovernmental forum comprised of Canada, Denmark, Finland, Iceland, Norway, the Russian Federation, Sweden, and the US, and the International Arctic Science Committee (IASC), a non-governmental organization that facilitates

cooperation in all aspects of Arctic research in all regions of the Arctic. The project's stated goal was to evaluate and synthesize knowledge on climate variability, climate change, and increased ultraviolet radiation and their consequences. The results of the assessment were released at the November 2004 ACIA International Scientific Symposium in Reykjavik, Iceland. The assessment is online at http://www.acia.uaf.edu/pages/scientific.html.

Much research has been done to predict the effects of warming climate on Arctic vegetation this century by developing dynamic vegetation models (ACIA 2004). There has also been an effort to document signs of plant migration, or the increased growth and stand density increases that may be precursors to migration (Table A. 1. 1). However, to our knowledge there has not been an attempt to compare a comprehensive set of these empirical observations with dynamic vegetation model projections. In its description of projected vegetation changes for the year 2100, ACIA featured the use of two dynamic vegetation models. In this paper, I compare one of these models to a set of 30 published studies on Arctic vegetation response to climate change.

2. 3. *Research Objectives*

This thesis research was prompted by a desire to know whether plant migration might already be occurring in places where models predict a more favorable climate for growth and establishment over this next century. For example, if a location on the Alaskan tundra is predicted to have a warmer, wetter climate suitable for rapid tree migration in 2100, are there already signs at that location of increased tree growth and establishment? If there are, this would lend the model some validity because it predicted a migration of

forest into tundra, which would only occur if temperatures at the range boundary promoted increased growth and establishment. If there are no signs, then either the model needs improvement, the observation lacked enough spatial resolution or temporal scope to observe change, or there may be time lags between climate forcing and vegetation change. If changes are occurring in places where the model did not predict change, then again this indicates opportunities for model improvement. All three cases provide opportunities to assess our understanding of plant migration, by comparing where models predict change and where observations show it has already begun.

Performing this model validation research has required the assembly of as many observations as possible of recent plant spatial responses linked to Arctic climate change, so that these observations can be compared with model predictions. The observations are described in the upcoming literature review, along with a synthesis of their important points. Following this is a description of how these observations will be treated as data points for the purpose of assessing the accuracy of a key model from the Arctic Climate Impact Assessment, as well as an explanation for why this model was selected for this assessment.

The objective of this thesis, besides providing an extensive literature review and synthesis, is to validate a key ACIA vegetation model using a set of empirical observations. The primary research results will be the comparison of migration observations with model predictions, a discussion of the resulting matches, and a discussion of potential reasons for the non-matches. The hypothesis is that the model predictions will be able to stand up to observations made by numerous researchers throughout the Arctic region. If there is close agreement, then we are likely on the right

track as far as understanding how warming temperatures will influence plant migration in the Arctic. However, if there is poor agreement, then this work should serve as an incentive for further research into the processes that control plant migration in the Arctic so that we can improve our existing models.

3. Methods

3. 1. *Study System*

Our study region includes land areas above 55°N latitude. This area contains Arctic treeline, as well as the study sites providing empirical data used in this research. The study region (Fig. 1) covers over 1.2 billion hectares of land area, two-thirds of which lies in Eurasia, with the remainder in Canada and Alaska (Soja *et al*. 2007). This area contains most of the boreal forests, giving way to taiga and eventually tundra north of treeline, although there is interstitial mixing across these ecotones.

Arctic forests are dominated by coniferous genera, including the pines (*Pinus* spp.), spruces (*Picea* spp.), firs (*Abies* spp.), and larches (*Larix* spp.), and less frequently by deciduous broadleaved genera including the aspens (*Populus* spp.), birches (*Betula* spp.), willows (Salix spp.), and alders (*Alnus* spp.). In some conditions one or two of these taxa dominate over large areas, and in other places several taxa sort themselves into intergrading or interspersed stands according to locally varying conditions. Under the harsher conditions near treeline, taiga or dwarf thicket forests form over extensive areas or in small pockets, sometimes creating island outposts of forest embedded in the tundra biome far north of treeline, as has been reported for Quebec and frequently in Siberian tundra in mid-century Russian reports (Maycock and Matthews 1966).

The Arctic biomes cover a vast, nearly continuous, and relatively untrammeled expanse of Earth's surface relative to other global biomes. These ecosystems play a huge role in Earth's carbon budget in terms of both seasonal uptake, and in terms long-term storage of carbon on and below the ground surface due to low temperatures and slow decomposition of organic matter (Soja *et al.* 2007). For example, boreal forests contain approximately 30-35% of global terrestrial ecosystem carbon storage (Soja *et al*. 2007). In addition, although sparsely populated, many inhabitants of the Arctic are highly dependent on the goods and services Arctic ecosystems provide (ACIA 2004), as is the earth system at large.

Arctic regions have also experienced the largest temperature increases due to climate change, with annual temperature increases up to 0.6-1.0°C (Beltrami and Mareschel 1991, Chapman and Walsh 1993, Kattenberg *et al.* 1996, Overpeck *et al.* 1997, Everett and Fitzharris 1998, Mann *et al.* 1999). Climate predictions indicate that the Arctic will continue to experience more rapid warming than other regions of the globe (Soja *et al.* 2007). Models accounting for a range of sensitivities have predicted an increase in average annual temperature of 2.8 to 7.8 °C, with a winter warming of between 4.3 and 11.4 °C (IPCC 2007).

3. 2. *The ACIA Biome Model*

The Arctic Climate Impact Assessment made use of two dynamic vegetation models to project future changes in the areas of tundra and polar desert: LPJ and BIOME4. The BIOME4 projection was used for our analysis because it has a greater number of vegetation types, providing a finer resolution of potential vegetation change in the Arctic.

This model was run under a relatively conservative equilibrium sensitivity of 2.5°C using the global climate model HadCM2-SUL, compared with a value of 3.3°C for HadCM3 which was used to provide climate data for the LPJ model. The GCM runs used to parameterize BIOME4 were forced using the IS92a greenhouse gas and sulfate aerosol concentration scenario for the 21st century (Kaplan *et al.* 2003) a widely adopted, but also relatively conservative emissions scenario.

BIOME4 is a coupled carbon and water flux model that predicts global steady-state vegetation distribution, structure, and biogeochemistry, and accounts for interactions between these aspects (Kaplan *et al.* 2003). Since it is a biome-level model and does not include species-specific demographics and dispersal, its predictions are of equilibrium vegetation distributions at any given time. The model receives as inputs long-term averages of monthly mean temperature, insolation, and precipitation, which can be provided by a GCM. Percolation rates and water-holding capacity are constrained using soil texture and depth.

3. 3. *Empirical Data*

We searched for and compiled 66 studies to date that document contemporary range shifts, stand density changes, growth changes, or the lack of any or all such changes in vegetation (Tables A. 1. 1 and A. 1. 2). We excluded from our Arctic-based analysis 31 studies (Table A. 1. 2) that were either located in Antarctica or lower-latitude alpine systems, that involved non-woody vegetation such as grasses, herbs, mosses, and lichens, or that described confounding factors like grazing or other major anthropogenic land disturbances that were not included in the ACIA model projections. An additional five

studies were excluded from this analysis because they reported generalized findings among multiple study sites, but no geo-coordinates for those sites (Wilmking *et al.* 2004, Sturm *et al.* 2001, Kullman 1989, Kharuk *et al.* 2005, Payette and Filion 1985). Of the remaining 30 studies, 12 included multiple study sites, totaling 76 sites all together. As a result, we had 95 geographic data points available for our analysis from the thirty studies. The analysis is based on these 95 study sites.

In order to standardize the varying information presented for different sites in the 30 papers, we developed a rubric for scoring study sites in terms of type and direction of change observed. Each study site was assigned a score in each of the following change categories: altitudinal migration, latitudinal/horizontal migration, tree growth, and stand density/abundance increase. For each category a +1 signifies migration in the direction expected from warming temperatures. A -1 signifies change in the direction opposite to that expected, and 0 is assigned when no change is reported.

These scores represent types of observed vegetation change that may indicate or are precursors to climate-driven changes in biome distributions. An additional score was also generated for each site to provide a summary index of change across the four categories of change for comparison with the 2100 biome distribution. This index also takes on values of -1, 0, or +1. Most study sites reported just one instance of a positive or negative change out of the 4 categories, and were scored with an overall change value of +1 or -1. For sites that reported unequal numbers of signs (e.g. 2 positives and a negative), the majority value (e.g. +1) was recorded as the change value. A change value of 0 only resulted when there was a 0 in all four vegetation change categories. There were no cases where positive and negative changes among the four categories cancelled each other out.

There also were no study sites with both positive and negative changes in these four categories.

3. 4. *Comparison of Data to Model Predictions*

Model predictions at study-site locations were also coded using the -1, 0, +1 scheme to determine where matches existed between predictions and observations. Of the nine possible combinations of data and model predictions, only three constitute matches (Table 1).

Table 1. Judging Matches from Possible Combinations of Data and Model Findings

For empirical data, evidence of forest range expansion, including observed increases in growth or density, or treeline migration, are indicated as 1. Evidence of range contraction (decreased growth or density, or treeline recession) is indicated as -1, and no change is indicated as 0. For model predictions, predicted forest advance is indicated as 1, forest contraction as -1, and no change is indicated as 0. A match between the empirical observations at a study location and the projected change by 2100 occurs where empirical and projected indicators agree.

Data (Overall change)	1	1	1	0	0	0	-1	-1	-1
Model Prediction	1	0	-1	1	0	-1	1	0	-1
Match	1	0	0	0	1	0	0	0	1

The model and data are judged to match only if they both predict no change, or the same direction of change. A match validates the model, indicating that observations at a study site suggest a change trend consistent with its predicted biome type in 2100. Non-matches occur when the model and data disagree on the presence and/or direction of change. This can happen in one of two ways: change is observed in the data but not predicted by the model (false negative), or change is predicted by the model but not

observed in the data (false positive). The presence of a non-match at a study site would invalidate the model there, and too many such results throughout the Arctic would invalidate the model entirely.

As noted previously, twelve of the studies reported multiple findings for separate study sites, thus producing a nested data structure, where not all studies were well represented by a single match value, and where different sites within a study site were not spatially independent. In these cases, to account for the nested data structure in the comparison procedure we used the proportion of matches out of all the sites within the study. We also did a second comparison by fitting a multilevel model that accounts for the nesting of multiple study sites within some of the 30 studies and that takes advantage of the fact that the match variable is binary. This will generate a single value between 0 and 1 that describes how well BIOME4 has performed in predicting the direction of change (if any) at all 30 study sites throughout the Arctic.

Since the match variable is binary and the study sites that contain match variables are nested within their respective studies, a generalized linear mixed effects model can be fit in order to give a probability that all study sites will yield perfect validation (a 1, vs. 0 for no validation). This probability can be treated as a measure of how well the model has performed across all study sites, taking into account the nested data structure.

In a GIS I projected the geographic locations of the empirical studies into the WGS1984 geographic coordinate system and a North Pole Orthographic projection. Maps of present-day and predicted biome distributions for 2100 were obtained from Kaplan *et al.* (2003) at 0.5-degree resolution and geo-referenced to this same projection.

4. Results

4. 1. Summary of Empirical Studies

Of the 30 empirical studies included in this analysis, 25 reported one or more Arctic vegetation changes consistent with a warming-induced conversion from tundra to forest or shrubland (Table A. 1. 4). The most commonly observed type of change for all sites in these 30 studies was increased stand density, present at 41 of the 95 study sites (43%) (Table 2). The second most common change was increased tree growth, observed at 27 sites (28%). Upward altitudinal shift and northward latitudinal shift occurred at 16 and 8 of the study sites respectively (17% and 8%). The only negative changes were decreased tree growth at 14 study sites (15%), and a lowering of altitudinal treeline at 1 study site (1%).

Table 2. Frequency of Change Observations by Geographic Region

Summary of change observations by change type and geographic region indicating the frequency and percentage of studies reporting evidence consistent with forest range expansion, contraction, or no change. The last row shows the frequency of agreement between empirical observations and model predictions by region.

	Canada	**Alaska**	**Europe**	**Siberia**	**Total**
Altitudinal shift (+)	1/28 (4%)	7/47 (15%)	2/5 (40%)	6/15 (40%)	16/95 (17%)
Altitudinal shift (-)	1/28 (4%)	None	None	None	1/95 (1%)
Latitudinal shift (+)	4/28 (14%)	2/47 (4%)	None	2/15 (13%)	8/95 (8%)
Tree growth (+)	10/28 (36%)	4/47 (9%)	1/5 (20%)	12/15 (80%)	27/95 (28%)
Tree growth (-)	1/28 (4%)	11/47 (23%)	2/5 (40%)	None	14/95 (15%)
Stand density (+)	8/28 (29%)	29/47 (62%)	1/5 (20%)	3/15 (20%)	41/95 (43%)
Frequency of (+) change	21/28 (75%)	34/47 (72.3%)	3/5 (60%)	15/15 (100%)	73/95 (77%)
Frequency of (-) change	1/28 (4%)	11/47 (23%)	2/5 (40%)	None	14/95 (15%)
Frequency of no change	6/28 (21%)	2/47 (4%)	None	None	8/95 (8%)
Sites validating model	21/28 (75%)	33/47 (70%)	3/5 (60%)	12/15 (80%)	69/95 (73%)

The BIOME4 model predicts major northward shifts of treeline and shrub-dominated tundra (Fig. 2). These changes result in large reductions in area of *cold deciduous forest* (larch-dominated) due to replacement by evergreen forests, and reductions in the area of *cushion forb, lichen, and moss tundra* and *graminoid and forb tundra*. These predictions are consistent with the direction of change already observed at 64 of the 95 study sites (67%), which validate the model. The multilevel model used to account for all studies simultaneously, given the nested data structure, yielded a correspondence rate of 72.1 +/- 7% agreement between observed and predicted change (see Appendix 2 for complete model results and explanation).

4. 1. 1. North America

Two studies from Yukon Territory occurred at sites predicted by BIOME4 to undergo no vegetation change (Fig. 2). Of these studies, one (Szeicz and MacDonald 1995) reported no change, corresponding to the model prediction. The other (Danby and Hik 2007) found both canopy-cover and stand-density increases for *P. glauca* in the Yukon, with a limited amount of altitudinal shift compared to the other two changes. The model did predict vegetation change for a cluster of study sites in southern Nunavut, where abundance increases were found for *P. glauca* (MacDonald *et al.* 1998).

Seven studies were located on the eastern coast of Hudson Bay, at sites where BIOME4 projected vegetation changes from *low- and high shrub tundra* to *cold needleleaf evergreen forest*. Five of these studies reported change consisten with model predictions, demonstrating vegetation changes in the direction of model predictions. One study (Gamache and Payette 2004) demonstrated vegetation changes in the direction of

model predictions at only 3 of its 5 study sites. The last study (Masek 2001) was both observed and predicted to undergo no change, thus also validating the model. However, the lack of observed latitudinal shift or other vegetation change was likely due to the coarse resolution of the satellite imagery used in that study. The other six studies were implemented at finer, ground-level resolution.

Of the seven Hudson Bay studies, five reported either latitudinal shifts (Lavoie and Payette 1994, 1996; Lescop-Sinclair and Payette 1995), increased stem initiation (Lavoie and Payette 1992), or increased krummholz growth of *P. mariana* (Gamache and Payette 2004, Lescop-Sinclair and Payette 1995, Lavoie and Payette 1996). One study in this area, excluded from analysis due to insufficient geolocation information (Payette and Filion 1985) found an altitudinal shift of *P. glauca* treeline by several tens of meters over the past century. A neighboring six-site study of *P. glauca* in the northeastern Quebec-Labrador area (Payette 2007) found positive vegetation changes at 2 sites, no change at 3 sites, negative change at one site, and yielded only 50% agreement with model predictions.

Sturm *et al.* (2001) and Tape *et al.* (2006) have documented widespread increases in shrub abundance, size, and extent on what is presently part of the *erect dwarf shrub tundra* of northern Alaska. These changes are consistent with the BIOME4 prediction of widespread conversion of *erect dwarf shrub tundra* across northern Alaska to *cold needleleaf evergreen forest*. Sturm *et al.* (2001) also found increases in density and extent of *P. glauca* this region. Findings of forest expansion at another N. Alaska study site in *low-* and *high shrub tundra* are also consistent with this prediction (Wilmking *et al.* 2006). Increases in growth and density, and altitudinal migration of *P. glauca* at several

sites in the White Mountains and Alaska Range are also consistent with the transition from *cold* to *cool evergreen needleleaf forest* predicted by BIOME4 in these areas (Lloyd and Fastie 2002, 2003).

Reduced growth of *P. glauca* due to drought stress, reported by Barber *et al.* (2000) in the Alaskan interior, was considered a negative response to warming temperatures, inconsistent with model predictions of a change from *cold* to *cool evergreen needleleaf forest*. Nevertheless, a growth decline in *P. glauca* is not necessarily inconsistent with this model prediction, if it leads to future opportunities for increased establishment of *cool evergreen needleleaf forest* species.

4. 1. 2. Europe

Vegetation changes were predicted for 3 of the 5 European studies, all located along the Scandinavian Mountains. These sites are predicted to change from *cold needleleaf evergreen forest* to *cool mixed forest*, with some temperate deciduous trees able to survive warmer temperatures. Altitudinal migration and density increases in response to warmer temperatures reported in two of these three studies (Kullman 2001, Klanderud and Birks 2003) may signal the beginning of transition to *cool mixed forest*. Increased growth after severe previous cold damage documented by Hofgaard *et al.* (1991) is also consistent with model predictions. The two studies finding growth decline and recession in old-growth *Picea abies*, apparently due to a series of cold winters, are not consistent with an eventual transition into *cool mixed forest* (Kullman 1991, 1996).

4. 1. 3. Siberia

For 6 of the 7 studies in Siberia, BIOME4 predictions indicated changes from *low- to high shrub tundra* to *cold needleleaf evergreen forest*. However, migration of deciduous *Larix* forests into tundra was almost universally found among these eight studies, and larch is often the only tree species at treeline. Nevertheless, we considered observations of these studies to be consistent with the direction of change predicted for these locations.

Larix species were reported advancing into *low- and high shrub tundra* in a series of studies across eastern Siberia (Esper and Schweingruber 2004, Kapralov *et al.* 2006, Kharuk *et al.* 2006, Shiyatov *et al.* 2007, Devi *et al.* 2008). There was also greater tree establishment (Esper and Schweingruber 2004, Hantemirov *et al.* 2008), increased stand density (Mazepa 2005, Hantemirov *et al.* 2008), and increased tree growth (Kapralov *et al.* 1996, Mazepa 2005, Devi *et al.* 2008) in some areas. These are all positive responses suggestive of continuing advancement of the *Larix*-dominated *cold deciduous forest* into the tundra.

Although *cold needleleaf evergreen forest* is predicted as the future vegetation type for all but one study site (Kapralov *et al.* 1996), only two studies found increased growth or migration of any evergreen species (Esper and Schweingruber 2004, Kapralov *et al.* 1996). In a study documenting evergreen conifer invasion into the Siberian larch-dominated zone (Kharuk *et al.* 2005), fire played a crucial role in facilitating the invasion of evergreen trees. Climate scenarios predict that boreal climate change will result in increased lightning ignitions, fire season length, and fire weather severity, and those scenarios from the Canadian Climate Center predict spatial and temporal increases in fire weather severity across Russia, Alaska, and Canada (Soja *et al.* 2007). Fire can facilitate

the invasion of evergreen conifers into larch forest, and an increase in fire frequency and severity across Siberia would contribute to the conversion of larch to evergreen forests as predicted in the region.

5. Discussion

There are several plausible explanations for lack of observable change in locations that are predicted to have changed by 2100. The simplest is that predicted changes have not begun yet to appear. Secondly, the model predictions are at a crude resolution relative to data collected for the field studies, and completely ignore local processes that can influence the vegetation found at particular sites. At half-degree resolution, geolocation errors ranged from zero to potentially half a degree, which could cause poor agreement between model and data near biome boundaries. In some cases change may be occurring but has gone undetected in the field, and treeline areas that are experiencing stand density increases could be in the first stages of migration, and will do so if suitable climatic conditions persist long enough for dispersal, germination and survival in suitable sites. Lastly, there can be some factor preventing change, such as warming-induced drought stress or time lags between climate forcing and migration, or transition episodes may require trigger events such as fire.

5. 1. *Water Availability*

While there is much evidence for new plant establishment and density increases reported in the studies surveyed, growth declines have also occurred, suggesting that the location and timing of vegetation transitions in the direction predicted by the model may vary according to water availability. Studies finding growth decreases at the Arctic forest-tundra ecotone since the 1970s suggest that drought stress caused by warming with

insufficient precipitation may be a cause (Briffa *et al.* 1998, Barber *et al.* 2000, D'Arrigo *et al.* 2004, Piao *et al.* 2006).

In the Alaskan interior, Barber *et al.* (2000) found a drought stress-linked growth decline in *P. glauca*, which may be an important factor in boreal forest CO_2 uptake, given the widespread distribution of this species. Using tree-ring data from a pan-Arctic network of sites, Briffa *et al.* (1998) found growth suppression in the second half of the 20th century across the Arctic, with the exception of Alaska and northern Europe. Between the periods 1935-45 and 1975-85, they found a sudden decoupling of tree ring density and air temperatures across hundreds of Arctic study sites (Briffa *et al.* 1998). Although the authors argue against a simple soil moisture-related explanation for reduced tree growth they did not rule out summer drought sensitivity. The pan-Arctic synchronicity of tree growth declines argues against local-scale influences such as disease as primary mechanisms of this phenomenon. Briffa *et al.* (1998) also suggest higher UV-B levels, decreased solar radiation, increased acidic deposition, and increased tropospheric ozone as potential causes of declines in tree growth.

Growth declines could also be caused by warming temperatures exceeding optimal physiological conditions. However, warmer temperatures have been found to have little effect on plant survival as long as ample water is available (Woodward 1988). Transplant experiments have also shown that cold-adapted plants such as boreal tree species can survive and thrive under warmer temperatures, but only if there is adequate rainfall (Wright 1976).

D'Arrigo *et al.* (2004) also found a post-1960s weakening in the relationship between *P. glauca* tree ring width and temperature, and a concurrent decline in tree growth. They suggest that even at tree line, tree growth may decline when temperatures warm beyond a physiological threshold without significant gains in precipitation. This may lead to a reversal of the large-scale greening seen in recent decades, and the resulting browning could slow or reverse boreal forest carbon uptake.

Piao *et al.* (2006) conducted a modeling study that lends support and insight to possible drought impacts on Arctic biome transitions. Their analysis incorporated a dynamic global vegetation model (ORCHIDEE) that simulates global carbon and water cycles. The LAI trends of their model over the past 20 years were consistent with widespread reports of enhanced Arctic plant growth during that time, and demonstrate that warming temperatures were the likely drivers of this greening trend at high latitudes (Piao *et al.* 2006). However, subsequent calculations based on their model results indicated that the effects of warmer temperatures on vegetation growth depend partly on the balance between the positive effect of growing season extension and the negative effect of soil moisture stress. Piao *et al.* (2006) suggest that under increasing temperatures, dry, warm conditions will lead to growth decline whereas wet and cool areas will tend to have the largest increases in vegetation growth.

Warming-induced drought stress could potentially cause the Arctic to switch from a carbon source to a sink. Between 1985 and 1991, Angert *et al.* (2005) found an accelerated springtime net CO_2 uptake in the Northern Hemisphere, and again from 1994 to 2002. However, spring increases were negated by lower summer uptake, which was likely the result of hotter and drier summers in both the mid and high latitudes.

5. 2. *Time Lags*

Climate limitations exist for all plants, and in part define the boundaries of their fundamental niche. If suitable conditions for a plant's recruitment and survival exist within the dispersal field of the plant's present range boundary, the null expectation is that migration and range changes would take place. However, there are many factors that introduce time lags between climate forcing and migration, possibly explaining why migrations are not presently observable in some locations despite a century-long history of global warming.

Time lags between contemporary climate forcing and boreal tree migration of up to 150 years (Masek 2001, MacDonald *et al.* 1993) are known, and longer-lived trees are expected to respond more slowly and indirectly to climate changes compared to shorter-lived plant species (Clark 1991, Zasada *et al.* 1992, Graumlich and Brubaker 1995, and Sirois 1997). Cold temperatures at treeline also limit the production of viable seeds, so that when warmer years come, insufficient seed may be available to support increases in tree establishment (Lloyd and Fastie 2002).

Perhaps most importantly, it takes time for the suitable conditions for dispersal and recruitment to come together in sufficient density to form migration. For example, the environmental conditions necessary for germination and juvenile survival may be different from the requirements for adult survival and reproduction. Thus, site limitations such as soil-nutrient deficiency can delay or prevent seedling establishment (Billings 1987), as has been argued for shrubland migrating into colder tundra in northern Alaska and throughout the Arctic (Tape *et al.* 2006). As a result, there may be patterns of

ecological assembly at play that delay migration. For example, nitrogen-fixing species may need to recruit into nutrient poor sites such as newly deglaciated tundra before trees can colonize.

The level of soil development and water-retaining capacity can also delay migration (Pennington 1986). For example, in areas underlain by permafrost, there may be a delay in tree establishment until air temperatures warm enough to thaw sufficient permafrost for root activity (Lloyd and Fastie 2002).

In other cases, migration may be dispersal limited. For example, Shiyatov *et al.* (2007) showed that larch seeds at a site in the Polar Urals are carried by wind no farther than 40-60 m from maternal plants due to their heaviness, and are retained in the soil litter after settling. Thus, in distant tundra areas with few trees, larch establishment into denser tree stands takes time. Complex topography is another dispersal-limiting factor. In a modeling study, Rupp *et al.* (2001) found that white spruce would take 3000-4000 years to disperse across the Brooks Range to the currently treeless North Slope of Alaska, in response to a climate warming of 6°C. Glacial lakes and ridges, and thermokarsts, the physiographic transformations associated with melting of frozen ground, are other barriers to dispersal related to terrain, as described by Masek (2001) during his work in northern Canada. Human-modified, fragmented landscapes also potentially constrain dispersal (Honnay *et al.* 2002).

5. 3. *Episodic Events*

The suitability of conditions for migration are also likely episodic. For example, as described above, warmer temperatures and abundant humidity throughout much of the

Arctic created optimal conditions for mid-20th century tree establishment, but in the latter half of the 20th century drought stress slowed establishment in some areas (Briffa *et al.* 1998, Barber *et al.* 2000, D'Arrigo *et al.* 2004, Piao *et al.* 2006).

Migration episodes may also be triggered by events that remove ecological constraints, such as resource competition, that interfere with range expansion. For example, trees at treeline may respond slowly to warming if they face competition from faster-responding tundra plants that limit successful tree seedling establishment (Lloyd and Fastie 2002). Given a sufficient disturbance, the treeline may experience competitive release and migration may then proceed rapidly (Lloyd and Fastie 2002). Disturbance events of many kinds are known to trigger competitive release by temporarily relaxing ecological constraints to successful establishment. This has been shown for gap formation from windthrow or disease, fire, drought, wetness anomalies, or other extreme weather or climate events that can remove competitors from part of the landscape (Racine *et al.* 1987) or change the competitive balance (Landhausser and Wein 1993, Cater and Chapin 2000) Such events have been important in past episodes of climate change-driven plant migration (Parshall 2002, Szeicz and MacDonald 1995, Pearson 2006) and they are likely also to be important in the present episode.

5. 4. *Regional Variability*

Although most of the studies corresponded with the direction of predicted change, several mismatches indicate the possibility of regional differences between predicted biome transitions and what may actually occur. Disturbance from fire was not accounted for in the BIOME4 predictions, but there is evidence that fire may be necessary for the

transition from larch-dominated *cold deciduous forest* to the *cold needleleaf evergreen forest* type in Siberia (Soja *et al.* 2007). Fire is likely to increase in boreal forests with climate warming (Soja *et al.* 2007), so this mechanism may promote the migration of evergreen needleleaf forest into the deciduous needleleaf forest which is presently encroaching into tundra across western Siberia (Kharuk *et al.* 2005).

Areas in the Yukon and Labrador regions of Canada (Danby and Hik 2007, Payette 2007) are undergoing apparent climate-related changes in areas where none are predicted, while areas in the Alaskan interior (Barber *et al.* 2000, Lloyd and Fastie 2002) are undergoing apparent drought induced changes that are contrary to expected trajectories of change. Both of these scenarios imply that models of biome change are not accounting for, or are not capturing regional scale variability, in certain forcing mechanisms.

The eastern coast of Hudson Bay, northwestern Canada, montane and northern Alaska, the Scandes Mountains of Europe, and the Polar Ural Mountains have been focal areas for studies of plant migration (Fig. 2). However, there are two regions where major changes are predicted, but field studies are few or absent (Fig. 3). Eastern Siberia is currently dominated by *low- and high shrub tundra*, where isolated pockets of larch forest could exist and could be expanding. This region is predicted to transition to *cold evergreen needleleaf forest*. The area largely encompassed by Nunavut, which contains the Arctic Archipelago extending through the Northwest Passage between mainland Canada and northern Greenland, is predicted to experience a major northward translocation of tundra types (for example from a forb or cushion tundra type into *low- and high shrub tundra*), and expansion of *cold evergreen needleleaf forest* (Fig. 2). These

locations are extremely remote and relatively inaccessible, but studies by satellite or aerial photography are possible.

5. 5. *Rates of Migration*

Estimates of migration rates of 0.1-5 km/year have been suggested as necessary for plants to geographically track their changing climate envelopes (Davis and Zabinski 1992, Davis & Shaw 2001, Iverson and Prasad 2002). The ability of plants to do this will clearly vary. In some instances, recorded migration rates are in this order of magnitude. For example, *Picea mariana* along the eastern coast of Hudson Bay in Canada has migrated 4 km through new tree establishment (Lavoie and Payette 1994), and 12 km westward through krummholz growth since the late 1800s (Lescop-Sinclair and Payette 1995). *Picea glauca* in the Alaskan interior has moved 120 m upward and 10 km northward during the same time period (Lloyd and Fastie 2003). In other cases, much slower migration rates have been reported. For example, Kullman *et al.* (2001) found northward migration rates of only 30-165 m during the last century for a treeline dominated by *Betula pubescens* ssp. *tortuosa*, *Picea abies*, and *Pinus sylvestris* in the southern Swedish Scandes. Although some of these findings are in the general range of expected migration rates, the high end of the latitudinal migration rates falls short of the lowest estimate needed for plants to track climate change. Growth declines would be expected in locations where migration rates stay below rates required to track climate change.

6. Conclusion

It is inevitable that the ability of plants to track climate change will vary both geographically and taxonomically, and in some cases will be contingent upon trigger events such as humid periods or fire. It is not expected that ecosystems will shift *en toto*, nor that predicted patterns at the global scale would necessarily match those found on the ground now or in 2100. In many cases actual changes may constitute a reordering from within and across existing ecosystems to produce novel ecosystems whose composition and function differ from current ecosystems (Williams and Jackson 2007). Such reorganization could place evolutionarily significant selective pressure on some taxa at shifting ecotones (Thomas *et al.* 2004).

Improved information on water availability and water use efficiency, and more detailed understanding of time lags related to recruitment, dispersal, and barriers will improve prognostic capabilities. Likewise, potential feedback mechanisms between warmer temperatures, fire and insect disturbances, and biome transitions represent major areas of uncertainty in understanding biome responses to climate change in the Arctic. There is a lack of studies from the Arctic Archipelago and the eastern half of Siberia, both areas that are predicted to undergo widespread northward biome shifts. Studies based on aerial photographs should be readily feasible in these areas if historical data are accessible.

Appendix 1: Supplementary Tables

Table A. 1. 1. Empirical Observations of Arctic Plant Migration and Related Changes

Asterisks indicate the 5 of 35 studies that were excluded from analysis because they offered generalized findings among multiple study sites without geo-coordinates for those sites.

Alaska – 8 studies, 2 excluded

Study	Location	Species	Shift	Amount	Time	Cause Suggested
Barber *et al.* 2000	Interior Alaska	*Picea glauca*	Reduced growth	--	20th century	Temperature-induced drought stress
Lloyd and Fastie 2002	Twelve sites in the White Mtns, Alaska Mtns, and Seward Peninsula (map in article)	*Picea glauca*	Tree growth changes	Increased tree growth on 9 of 12 sites prior to 1950	Reconstruction since 1800	Warmer temperatures after 1950 associated with decreased tree growth in all but the Alaska Range sites; water stress believed to be a cause for the growth decline
Lloyd and Fastie 2003	Seven sites in the White and Alaska Mountain ranges, interior Alaska (map in article)	*Picea glauca*	Stand density increases and altitudinal migration at most sites	Density increases from <5 trees/ha to >15 trees/ha	Reconstruction since 1800	>1.5 degree C warming since mid 1800s. Positive stand density-summer temperature relationship at all Alaska Range sites; at White Mountains sites, all positive correlations except one site with zero and one with inverse correlation.
*Sturm *et al.* 2001	Alaskan Arctic, between the Brooks Range and the Arctic coast.	*Betula nana*, *Salix* spp., *Alnus crispa*, *Picea glauca*	Shrub abundance increase; extent and density increases of white spruce forest	--	1948-50 to 1999-2000	Warming over past 150 years that has accelerated in the past 30
Suarez *et al.* 1999	Noatak National Preserve, NW Alaska	*Picea glauca*	Latitudinal shift and increased stand densities	80-100 m	Past 150 years	Warmer climate
Tape *et al.* 2006	Northern Alaska and Pan-Arctic	*Betula, Salix, Alnus* spp.	Shrub expansion in size, abundance, and extent	Varies by landscape type	1983-2004	Warming Arctic climate
*Wilmking *et al.* 2004	Brooks and Alaskan Ranges	*Picea glauca*	Variable growth responses to climate warming	Warming increases growth of	20th century	Growth response varies for higher spring and summer temperatures
Wilmking *et al.* 2006	NW Alaska (68°060'N, 161°400'W)	*Picea glauca*	Forest area expansion	62-72% expansion	1949-2004	Warming temperatures

Canada – 13 studies, 1 excluded

Study	Location	Species	Shift	Amount	Time	Cause Suggested
Danby and Hik 2007	Kluane Ranges, SW Yukon, Canada	*Picea glauca*	Mostly canopy cover and stand density increases, limited altitudinal shift	--	1947-48 to 1989	Warmer temperatures (0.5 degrees C over past 100 years)
Gamache and Payette 2004	East coast of Hudson Bay, Canada	*Picea mariana*	Acceleration in height growth of trees <2.5 m	0.5-1 m above previous levels	1970s to 1998	Primarily longer growing degree days, secondarily an earlier snowmelt.
Lavoie and Payette 1992	Boniface River area (57°45'N, 76°20'W) , in subArctic Quebec, Canada	*Picea mariana*	Increased stem initiation	Supranival stem number increase from 1880, peaking in 1930-35, decreasing after 1955	Study done in 1989; reconstruction of past 400 yr	Warmer summers, milder and snowier winters (snow provides increased insulation from freezing winds)
Lavoie and Payette 1994	East coast of Hudson Bay, Canada	*Picea mariana*	Latitudinal	4 km northward	since late 1800s	milder winter conditions
Lavoie and Payette 1996	East coast of Hudson Bay, Canada	*Picea mariana*	Latitudinal shift from krummholz growth	Approx. 4 km	Little Ice Age to 1990s	Recent warming temperatures
Lescop-Sinclair and Payette 1995	Eastern coast of Hudson Bay, Canada, from 56°52'46N 76° 17'04W to 57° 55'18N 76°41'46W	*Picea mariana*	Latitudinal, toward Hudson Bay; krummholz growth, no establishment	12 km toward Hudson Bay	1992; tree establishment from late 1800s (Little Ice Age)	Warming temperatures
MacDonald *et al.* 1998	Central Canada (NW Territories)	*Picea glauca, Picea mariana*	No latitudinal shift but abundance increase	none	1880-1987	warming temps help recruitment, but seed dispersal of spruces limited
Masek 2001	Canada - east coast of Hudson Bay; Great Slave Lake, NW Territories	*Picea mariana*	No latitudinal shift	< 200-300 m/century	1972-2001	--
Payette 2007	Northern Labrador, Canada	*Picea glauca*	Altitudinal/latitudinal shifts, growth declines at some sites	--	Last half of 20th century	Warmer growing season temperatures
*Payette and Filion 1985	East coast of Hudson Bay, Canada	*Picea glauca*	No latitudinal but altitudinal shift	Several tens of meters	Last century	--
Pereg and Payette 1998	East of Hudson Bay, Canada (57°45'N; 76°20'W) (map in article)	*Picea mariana*	Increased krummholz growth	Increases in stem initiation began in 1940s, peaking during the 1970s	Since 1890s	Warmer winters, more precipitation
Scott *et al.* 1987	Northern Manitoba, Canada	*Picea glauca*	Latitudinal migration and density increases	--	Little Ice Age to 1980s	Climatic warming
Szeicz and MacDonald 1995	NW Canada	*Picea glauca*	No latitudinal shift or re-establishment of old stands	--	200 years ago to present	--

Europe – 6 studies, 1 excluded

Study	Location	Species	Shift	Amount	Time	Cause Suggested
Hofgaard *et al.* 1991	Mt. Blaikfjället, east of the Scandes Mtns in N. Sweden (64°40'N, 15°50'E)	*Picea abies*	Increased growth after pronounced cold damage	69% of tops had increased regernation (2% unchanged, 29% shorter)	1938-1988	Warming temperatures
Klanderud and Birks 2003	Jotunheimen Mountains, Central Norway (61°N)	All vascular plants (~100)	Altitudinal	73.2% of all species recorded had range expansions	1930-31 to 1998	Recent climatic changes, specifically warming (0.4-1.2 degrees C in past 100 years)
*Kullman 1989	Southern Swedish Scandes	*Betula pubescens* ssp. *tortuosa*	Growth decline, recession	16% decline in trees >2m, trees to krummholz	1972-1986	Recent climatic cooling and delayed thawing
Kullman 1991	Mt. Välliste in the Northern Swedish Scandes (63°17'N, 13°14'E)	*Pinus sylvestris*, *Picea abies*	Growth decline, recession	--	1949-1987	Recent climatic cooling
Kullman 1996	Handolan Valley of the southern Swedish Scandes (63°12'N, 12°23'E)	Old-growth *Picea abies*	Growth decline, recession	Rate of needle loss is 2.69% per year.	1974-1994	Cooler climate since the late 1930s followed by very cold winters after the 1960s; complete stem loss projected for 2003 if temperatures do not warm)
Kullman 2001	Swedish Scandes	*Betula pubescens* ssp. *tortuosa*, *Pinus sylvestris*, *Picea abies*, and the grass *Deschampsia flexuosa*	Altitudinal migration and density increases	Mostly 30-50 m; at most 120-165 m	Between late 19th and 20th centuries	Earlier, more complete snowmelt due to 0.8°C / century warming, soil chemical changes

Siberia – 8 studies, 1 excluded

Study	Location	Species	Shift	Amount	Time	Cause Suggested
Devi *et al.* 2008	Polar Urals treeline (map in article)	*Larix sibirica*	Expanding forests, taller growth forms	Upward by 20-60 m; 90% new seedlings after 1950 upright in growth form	1960 to 2007	0.9 degree C summer warming and doubling of winter precipitation
Esper and Schweingruber 2004	Nine trans-Siberian study sites (map in article)	*Larix species, Pinus sibirica, Picea obovata*	Altitudinal migration and greater tree establishment	Pulses of tree establishment in 1940s-50s and again in 1970s	1940s and 1950s and after the early 1970s	Warming temperatures, suggested to be part of a circumpolar trend based on comparisons with other studies
Hantemirov *et al.* 2008	Northern timberline of Yamal Peninsula, Russia	*Larix sibirica*	Greater tree establishment	Pulses of tree establishment in 1900-1935 and 1950-1970	1880-1980	Warmer July air temperatures
Kapralov *et al.* 2006	Northern Ural Mountains (59°30'-59°40'N, 59°00'-59°20'E)	Variety of tree species (*L. sibirica, P. sibirica, B. tortuosa*)	Altitudinal and horizontal range expansions; crown density increase, tree species changing in land area dominance	Average of 31 m altitudinal shift, 113 m horizontal shift, and 11% increase in crown density	1956-2005	Climate warming and increased humidity: over the past 40 years, summer temperature and precipitation increases have been 0.4°C and 72 mm, respectively, and the winter temperature and preciptation increases have been 2.0°C and 105 mm, respectively.
*Kharuk *et al.* 2005	Middle Siberian Plateau, near Yenisei Ridge (map in article)	Evergreen conifers (primarily *P. sibirica*) into larch zone	Range expansion via new establishment; stand density increases in forest/tundra ecotone; larch spreading into the tundra zone	70 years post fire, larch abundance went from 100% to 10%; P. *sibirica* abundance from 0 to nearly 80%	2001-2003	Warming temperatures
Kharuk *et al.* 2006	Ary-Mas forest, northern Siberia (from 72°02'-72°40'N to 101°15'-102°06'E)	larch forest (*Larix gmelinii, Larix sibirica*)	Increased canopy cover; 65% abundance increase; altitudinal shift	65% increase in closeness of larch canopy; larch into tundra expansion by 3-11 m/year	1973-2000	Primarily warmer winter temperatures (cold from 1948-1972, but then warmed, which later increased seedling survival). Correlation between density of young tree growth and summer air temperature.
Mazepa 2005	25 mapped sites in the Polar Ural Mountains (66°48'57"N, 65°34'09"E)	*Larix sibirica*	Stand density and stem growth increases	2-5x increase in stem growth volume; up to 1-3.5x increase in stand density	1960-62 to 1999-2001	Warmer summer temperatures and earlier growing seasons
Shiyatov *et al.* 2007	Polar Urals	*Larix sibirica*	Altitudinal and latitudinal	26-35 m rise in elevation; 290-520 m horizontal shift	20th century (1910s-2000s)	Climate warming and increased humidity observed since the 1920s

Table A. 1. 2. Non-Arctic Observations of Plant Migration and Related Changes

These 31 studies were not used in the analysis presented in this paper, but are listed to provide a more global view of vegetation changes.

Study	Location	Species	Shift	Amount	Time	Cause Suggested
Alward *et al.* 1999	Northeast Colorado	exotic forb and C3 grass *Sitanion hystrix* increase; dominant C4 grass and C3 forbs decrease	Abundance increases and decreases	--	1983-1999	Seasonal increases in T_{min}, decline of dominant species
Brink 1959	Garibaldi National Park, British Columbia coast	*Abies lasiocarpa* and *Tsuga mertensiana*	Altitudinal	n/a	~1900-1959	diminished snow cover (warmer temps)
Camarero and Gutierrez 2004	Spanish Pyrenees	*Pinus uncinata*	increased tree size and density; variable altitudinal shift with time	n/a	data from 1750-1997	warmer mean annual temperatures, warmer springs; interannual variability in mean temperature
Cannone *et al.* 2007	Italian Alps	alpine grasslands and shrub communities	Altitudinal	1.9% cover increase per decade	1950-2003	1°C regional temperature increase, variable precipitation increase, and decrease in snow cover duration/thickness
Coop and Givnish 2007	Valles Caldera, New Mexico	multiple tree species; mostly *Pinus ponderosa*	Range expansion into meadow	18% decline in grassland area	1935-1996	warmer minimum summer temperatures
Franklin *et al.* 1971	Cascade Range, Washington-Oregon	*Abies lasiocarpa, Tsuga mertensiana, Larix lyalli*	Range expansion into meadow	--	Establishment in 1923-1944	--
Grabherr *et al.* 1994	Austrian and Swiss Alps	multiple plant species	Altitudinal	Average of 0.4 m/yr for 9 alpine plants	20th century	0.7°C increase in mean annual temperature
Hamburg and Cogbill 1988	Central New Hampshire	Red spruce	Abundance decline	n/a	Past 180 years	Warmer mean annual and summer temperatures
Hampe 2005	Southern Spain	*Frangula alnus*	Reproductive decline near southern range limit	--	Years 2000 and 2001	Warmer and drier conditions over the past century affecting a critical late-season reproductive period
van Herk *et al.* 2002	Netherlands	329 lichen species	Abundance decline and range expansion	Decline in 50% of alpine spp, expansion in 83% of subtropical spp.	1979-2001	Temperature, pollution, nutrient demand
Hessl and Baker 1997	Rocky Mountain National Park, Colorado,	*Picea engelmannii*, *Abies lasiocarpa*	Altitudinal	n/a	1930-1997	intermediate (optimal) warmer/wetter conditions - too warm and no establishment occurs
Holzinger *et al.* 2008	Eastern Swiss Alps	70 plant species	Altitudinal	11% increase in species richness per decade	Past 120 years	Warming temperatures
Jakubos and Romme 1993	Yellowstone National Park, Wyoming	*Pinus contorta*	Range expansion into meadow	n/a	1865-present	regional climatic trend toward warmer/wetter conditions since end of Little Ice Age (1870s) - not much correspondence for mesic meadows though
Jump *et al.* 2006	Mediterranean region of	*Fagus sylvatica*	Growth decline at southern	Basal area increment	1975-2003	Regional warming trend

	Spain		range limit	decline of 49% at lower elevations; higher elevations unaffected		
Kearney 1982	Jasper National Park, Canada	*Abies lasiocarpa, Picea engelmannii, Pinus contorta*	Altitudinal	--	Establishment in 1965-1973	Above average mean summer temperature
Klasner and Fagre 2002	Glacier National Park, Montana	*Abies lasiocarpa*	Altitudinal, krummholz growth, increased tree density	3.4% increase in forest area over 46 years	1945-1991	--
Lavergne *et al*. 2006	Mediterranean region of France	2100 plant species	Abundance declines	Regression or extinction of Eurosiberian species	1886-2001	Regional warming negatively affecting southern range limits of Eurosiberian spp.
Millar *et al*. 2004	upper elevation forests of the central Sierra Nevada, California	*Pinus* spp.	Altitudinal migration and krummholz growth	n/a	between 1880 and 2002	minimum temp increase
Meshinev *et al.* 2000	Bulgaria	*Pinus peuce*	Altitudinal	Establishment 300 m above previous treeline	1970-1999	Warming
Parolo and Rossi 2008	Rhaetian Alps, Northern Italy	166 plant species	Altitudinal	Species richness increase from 153 to 166; median migration rate of 23.9 m/decade.	1926-2003	mean air temperature increase of 1.6°C in summer and 1.1°C in winter during the last 50 years
Pauli *et al*. 2007	Austrian Alps	54 plant species	Altitudinal	11.8% mean increase in species richness	1994-2004	Warming of 0.8°C between 1980-2004
Peñuelas *et al.* 2007	Montseny Mountains (Catalonia, NE Spain)	*Fagus sylvatica, Quercus ilex,*	Altitudinal	Beech migration 70 m upward; replacement by oak at lower range limit	1910-2003	~1.5°C average annual temperature increase since 1950
Peñuelas and Boada 2003	Montseny Mountains (Catalonia, NE Spain)	*Fagus sylvatica, Quercus ilex,*	Altitudinal	Beech migration 70 m upward in the past 55 yrs	1940-2001	1.2-1.4°C temperature increase since 1950
Peterson *et al.* 1994	North Cascade Mountains, Washington	*Abies lasiocarpa, Picea engelmannii, Larix lyallii*	Increased growth	--	--	Warming
Sanz-Elorza *et al.* 2003	central Iberian Peninsula	Subtropical shrubs *Juniperus communis* ssp. *alpina* and *Cytisus oromediterraneus*	Altitudinal	--	1957-1991	significantly higher T_{min} and T_{max}, fewer snow cover days, redistributions in monthly rainfall
Smith 1994, Fowbert and Smith 1994	Antarctica	only two native Antarctic vascular plant species	Range expansion, abundance increase	5-fold rise in *C. quitensis*, 25-fold rise in *D. antarctica*	1964-1990	Warming summer temperatures and longer growing seasons since late 1940s
Taylor 1995	Lassen Volcanic National Park, California	*Tsuga mertensiana*	Abundance increase	n/a	since mid 1800s	longer snow-free growing season length; warmer annual and summer temperatures
Walther *et al.* 2005	Swiss Alps	Multiple plant species	Altitudinal	Accelerating altitudinal shift; mean shift of 27.8 ± 14.6 m/decade	1905-2003	Warming
Wardle and Coleman 1992	New Zealand	4 native tree species	Altitudinal	--	1930-1991	Warming
Woodward *et al.* 1995	Olympic Mountains, Washington	*Abies lasiocarpa, Tsuga mertensiana*	Range expansion into meadow	--	1901-1990	Wetter or drier conditions than average, dependent on species

Table A. 1. 3. Correspondence between Predictions and Observations, by Study Site

This table provides correspondences between BIOME4 2100 predictions and observed changes in the 95 study sites included in the 30 studies analyzed, by study site. See Methods for more detailed scoring information about how change values for sites were determined. For studies with multiple sites, the final column provides a summary of the match information over all sites in the study.

Region	Study	Type	Species	Site #	Site Name	Alt Mig	Lat Mig	Growth	Density	Change	Model	Match	Study Result
Alaska	Barber *et al.* 2000	M	*Picea glauca*	1	Barber *et al.* 2000	0	0	-1	0	-1	0	0	0.00
Alaska	Barber *et al.* 2000	M	*Picea glauca*	2	Barber *et al.* 2000	0	0	-1	0	-1	0	0	"
Alaska	Barber *et al.* 2000	M	*Picea glauca*	3	Barber *et al.* 2000	0	0	-1	0	-1	0	0	"
Alaska	Barber *et al.* 2000	M	*Picea glauca*	4	Barber *et al.* 2000	0	0	-1	0	-1	1	0	"
Alaska	Barber *et al.* 2000	S	*Picea glauca*	0	Barber *et al.* 2000	0	0	-1	0	-1	0	0	0.00
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	1	AR-Canyon Creek	0	0	1	0	1	1	1	0.50
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	2	AR-Monahan Flats	0	0	1	0	1	1	1	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	3	AR-Usibelli-Treeline	0	0	0	0	0	1	0	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	4	AR-Usibelli-Below	0	0	1	0	1	1	1	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	5	SP-Bank	0	0	-1	0	-1	-1	1	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	6	SP-Grasshopper Hill	0	0	-1	0	-1	-1	1	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	7	WM-Eagle Summit-T	0	0	1	0	1	1	1	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	8	WM-Eagle Summit-B	0	0	-1	0	-1	1	0	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	9	WM-Nome Creek-T	0	0	0	0	0	1	0	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	10	WM-Nome Creek-B	0	0	-1	0	-1	1	0	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	11	WM-Twelvemile Summit-T	0	0	-1	0	-1	0	0	"
Alaska	Lloyd and Fastie 2002	M	*Picea glauca*	12	WM-Twelvemile Summit-B	0	0	-1	0	-1	0	0	"
Alaska	Lloyd and Fastie 2003	M	*Picea glauca*	1	WM-Eagle Summit	1	0	0	1	1	1	1	0.86
Alaska	Lloyd and Fastie 2003	M	*Picea glauca*	2	WM-Twelvemile Summit	1	0	0	1	1	0	0	"
Alaska	Lloyd and Fastie 2003	M	*Picea glauca*	3	WM-Nome Creek	1	0	0	1	1	1	1	"
Alaska	Lloyd and Fastie 2003	M	*Picea glauca*	4	AR-Usibelli	1	0	0	1	1	1	1	"
Alaska	Lloyd and Fastie 2003	M	*Picea glauca*	5	AR-Monahan Flats	1	0	0	1	1	1	1	"

Alaska	Lloyd and Fastie 2003	M	*Picea glauca*	6	AR-Canyon Creek	1	0	0	1	1	1	1	"
Alaska	Lloyd and Fastie 2003	M	*Picea glauca*	7	AR-Wrangell View	1	0	0	1	1	1	1	"
Alaska	Suarez *et al.* 1999	S	*Picea glauca*	0	Suarez *et al.* 1999	0	1	0	1	1	1	1	1.00
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	1	Anaktuvuk S	0	0	0	1	1	1	1	0.67
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	2	Anaktuvuk N	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	3	Atigun Gorge	0	0	0	1	1	0	0	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	4	Ayiyak	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	5	Chandler	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	6	Colville W	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	7	Colville	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	8	Colville E	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	9	Itigaknit	0	0	0	1	1	0	0	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	10	Ivishak	0	0	0	1	1	0	0	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	11	Killik	0	0	0	1	1	0	0	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	12	Kokolik	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	13	Kugururok	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	14	Kurupa	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	15	Lupine	0	0	0	1	1	-1	0	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	16	Nanushuk S	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	17	Nanushuk N	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	18	Nigu	0	0	0	1	1	0	0	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	19	Namiuktuk	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	20	Oolamnagavik	0	0	0	1	1	1	1	"
Alaska	Tape *et al.* 2006	M	*Betula, Salix, Alnus* spp.	21	Sagavanirktok	0	0	0	1	1	-1	0	"
Alaska	Wilmking *et al.* 2006	S	*Picea glauca*	0	Wilmking *et al.* 2006	0	1	0	0	1	1	1	1.00
Canada	Danby and Hik 2007	S	*Picea glauca*	0	Danby and Hik 2007	0	0	1	1	1	0	0	0.00
Canada	Gamache and Payette 2004	M	*Picea mariana*	1	PB	0	0	1	0	1	0	0	0.60
Canada	Gamache and Payette 2004	M	*Picea mariana*	2	EC	0	0	1	0	1	0	0	"
Canada	Gamache and Payette 2004	M	*Picea mariana*	3	LM	0	0	1	0	1	1	1	"
Canada	Gamache and Payette 2004	M	*Picea mariana*	4	RI	0	0	1	0	1	1	1	"
Canada	Gamache and Payette 2004	M	*Picea mariana*	5	LC	0	0	1	0	1	1	1	"
Canada	Lavoie and Payette 1992	S	*Picea mariana*	0	Lavoie and Payette 1992	0	0	1	0	1	1	1	1.00
Canada	Lavoie and Payette 1994	S	*Picea mariana*	0	Lavoie and Payette 1994	0	0	1	0	1	1	1	1.00
Canada	Lavoie and Payette 1996	S	*Picea mariana*	0	Lavoie and Payette 1996	0	1	0	0	1	1	1	1.00
Canada	Lescop-Sinclair and Payette 1995	S	*Picea mariana*	0	Lescop-Sinclair and Payette 1995	0	1	1	0	1	1	1	1.00
Canada	MacDonald *et al.* 1998	S	*Picea glauca, Picea mariana*	0	MacDonald *et al.* 1998	0	0	0	1	1	1	1	1.00

Canada	MacDonald *et al.* 1998	S	*Picea glauca, Picea mariana*	0		0	0	0	1	1	1	1	1.00
Canada	MacDonald *et al.* 1998	S	*Picea glauca, Picea mariana*	0		0	0	0	1	1	1	1	1.00
Canada	MacDonald *et al.* 1998	S	*Picea glauca, Picea mariana*	0		0	0	0	1	1	1	1	1.00
Canada	MacDonald *et al.* 1998	S	*Picea glauca, Picea mariana*	0		0	0	0	1	1	1	1	1.00
Canada	MacDonald *et al.* 1998	S	*Picea glauca, Picea mariana*	0		0	0	0	1	1	1	1	1.00
Canada	MacDonald *et al.* 1998	S	*Picea glauca, Picea mariana*	0		0	0	0	1	1	1	1	1.00
Canada	Masek 2001	M	*Picea mariana*	1	Richmond Gulf Region, Quebec	0	0	0	0	0	0	1	1.00
Canada	Masek 2001	M	*Picea mariana*	2	Great Slave Lake, NWT	0	0	0	0	0	0	1	‘’
Canada	Payette 2007	M	*Picea glauca*	1	Napaktok	0	1	0	0	1	1	1	0.50
Canada	Payette 2007	M	*Picea glauca*	2	Okak	1	0	0	0	1	0	0	‘’
Canada	Payette 2007	M	*Picea glauca*	3	Eli-Vincent	0	0	0	0	0	0	1	‘’
Canada	Payette 2007	M	*Picea glauca*	4	Hutte-Sauvage	0	0	0	0	0	0	1	‘’
Canada	Payette 2007	M	*Picea glauca*	5	Pyramid Sites	-1	0	-1	0	-1	1	0	‘’
Canada	Payette 2007	M	*Picea glauca*	6	Qairajutait	0	0	0	0	0	1	0	‘’
Canada	Pereg and Payette 1998	S	*Picea mariana*	0	Pereg and Payette 1998	0	0	1	0	1	1	1	1.00
Canada	Scott *et al.* 1987	S	*Picea glauca*	0	Scott *et al.* 1987	0	1	0	1	1	0	0	0.00
Canada	Szeicz and Macdonald 1995	M	*Picea glauca*	0	Szeicz and Macdonald 1995	0	0	0	0	0	0	1	1.00
Europe	Hofgaard *et al.* 1991	S	*Picea abies*	0	Hofgaard *et al.* 1991	0	0	1	0	1	1	1	1.00
Europe	Klanderud and Birks 2003	S	All vascular plants	0	Klanderud and Birks 2003	1	0	0	0	1	1	1	1.00
Europe	Kullman 1991	S	*Pinus sylvestris, Picea abies*	0	Kullman 1991	0	0	-1	0	-1	0	0	0.00
Europe	Kullman 1996	S	Old-growth *Picea abies*	0	Kullman 1996	0	0	-1	0	-1	0	0	0.00
Europe	Kullman 2001	S	*Betula pubescens* ssp. *tortuosa*, Pinus sylvestris	0	Kullman 2001	1	0	0	1	1	1	1	1.00
Siberia	Devi *et al.* 2008	S	*Larix sibirica*	0	Devi *et al.* 2008	1	0	1	0	1	0	0	0.00
Siberia	Esper and Schweingruber 2004	M	*Larix species, Pinus sibirica, Picea obovata*	1	URA1	1	0	1	0	1	1	1	0.89
Siberia	Esper and Schweingruber 2004	M	*Larix species, Pinus sibirica, Picea obovata*	2	URA2	1	0	1	0	1	1	1	‘’
Siberia	Esper and Schweingruber 2004	M	*Larix species, Pinus sibirica, Picea obovata*	3	MOR	0	0	1	0	1	1	1	‘’
Siberia	Esper and Schweingruber 2004	M	*Larix species, Pinus sibirica, Picea obovata*	4	ADZ	0	0	1	0	1	1	1	‘’
Siberia	Esper and Schweingruber 2004	M	*Larix species, Pinus sibirica, Picea obovata*	5	NOR	0	0	1	0	1	1	1	‘’
Siberia	Esper and Schweingruber 2004	M	*Larix species, Pinus sibirica, Picea obovata*	6	PUT	0	0	1	0	1	0	0	‘’
Siberia	Esper and Schweingruber 2004	M	*Larix species, Pinus sibirica, Picea obovata*	7	BOJ	0	0	1	0	1	1	1	‘’
Siberia	Esper and Schweingruber 2004	M	*Larix species, Pinus sibirica, Picea obovata*	8	ANA	0	0	1	0	1	1	1	‘’

Siberia	Esper and Schweingruber 2004	M	*Larix species, Pinus sibirica, Picea obovata*	9	ARE	0	0	1	0	1	1	1	‘’
Siberia	Hantemirov *et al.* 2008	S	*Larix sibirica*	0	Hantemirov *et al.* 2008	0	0	0	1	1	1	1	1.00
Siberia	Kapralov *et al.* 2006	S	*L. sibirica, P. sibirica, B. tortuosa*	0	Kapralov *et al.* 2006	1	1	1	0	1	1	1	1.00
Siberia	Kharuk *et al.* 2006	S	*Larix gmelinii, Larix sibirica*	0	Kharuk *et al.* 2006	1	0	0	1	1	1	1	1.00
Siberia	Mazepa 2005	S	*Larix sibirica*	0	Mazepa 2005	0	0	1	1	1	0	0	0.00
Siberia	Shiyatov *et al.* 2007	S	*Larix sibirica*	0	Shiyatov *et al.* 2007	1	1	0	0	1	1	1	1.00
					Total Positive	16	8	27	42				
					Total No Change	77	86	53	52				
					Total Negative	1	0	14	0				

Table A. 1. 4. Comparison of Present and Predicted Biome Types, By Study

Described here are comparisons of the dominant biome type across each study's sites with the type predicted by BIOME4 for the year 2100. Only six biome types applied to the 30 studies. Biome abbreviations are:

Tundra: LHST = low and high shrub tundra, EDST = erect dwarf shrub tundra
Forest: NEF = needleleaf evergreen forest (cold or cool), CDF = cold deciduous forest, CMF = cool mixed forest

Alaska – 6 studies

Study	Location	Species	Shift	Amount	Time	Predicted Change?	Present Type	Future Predicted Type
Barber *et al.* 2000	Alaska	*Picea glauca*	Reduced growth	--	20th century	yes	Cold NEF	Cool NEF
Lloyd and Fastie 2002	Twelve sites in the White Mtns, Alaska Mtns, and Seward Peninsula (map in article)	*Picea glauca*	Tree growth changes	Increased tree growth on 9 of 12 sites prior to 1950	Reconstruction since 1800	yes	Cold NEF	Cool NEF
Lloyd and Fastie 2003	Seven sites in the White and Alaska Mountain ranges, interior Alaska (map in article)	*Picea glauca*	Stand density increases and altitudinal migration at most sites	Density increases from <5 trees/ha to >15 trees/ha	Reconstruction since 1800	yes	Cold NEF	Cool NEF
Suarez *et al.* 1999	Noatak National Preserve, NW Alaska	*Picea glauca*	Latitudinal shift and increased stand densities	80-100 m	Past 150 years	yes	LHST	Cold NEF
Tape *et al.* 2006	Northern Alaska and Pan-Arctic	*Betula, Saliz, Alder spp.*	Shrub expansion in size, abundance, and extent	Varies by landscape type	1983-2004	yes	EDST, LHST	Cold NEF
Wilmking *et al.* 2006	NW Alaska (68°060'N, 161°400'W)	*Picea glauca*	Forest area expansion	62-72% expansion	1949-2004	yes	LHST	Cold NEF

Canada – 12 studies

Study	Location	Species	Shift	Amount	Time	Predicted Change?	Present Type	Future Predicted Type
Danby and Hik 2007	Kluane Ranges, SW Yukon, Canada	*Picea glauca*	Mostly canopy cover and stand density increases, limited altitudinal shift	--	1947-48 to 1989	no	Cold NEF	Cold NEF
Gamache and Payette 2004	East coast of Hudson Bay, Canada	*Picea mariana*	Acceleration in height growth of trees <2.5 m	0.5-1 m above previous levels	1970s to 1998	yes	LHST, some cold NEF	Cold NEF
Lavoie and Payette 1992	Boniface River area (57°45'N, 76°20'W) , in subArctic Quebec, Canada	*Picea mariana*	Increased stem initiation	Supranival stem number increase from 1880, peaking in 1930-35, decreasing after 1955	Study done in 1989; reconstruction of past 400 yr	yes	LHST	Cold NEF
Lavoie and Payette 1994	East coast of Hudson Bay, Canada	*Picea mariana*	Latitudinal	4 km northward	since late 1800s	yes	LHST	Cold NEF
Lavoie and Payette 1996	East coast of Hudson Bay, Canada	*Picea mariana*	Latitudinal shift from krummholz growth	Approx. 4 km	Little Ice Age to 1990s	no	Cold NEF	Cold NEF
Lescop-Sinclair and Payette 1995	Eastern coast of Hudson Bay, Canada, from 56°52'46N 76° 17'04W to 57° 55'18N 76°41'46W	*Picea mariana*	Latitudinal, toward Hudson Bay; krummholz growth, no establishment	12 km toward Hudson Bay	1992; tree establishment from late 1800s (Little Ice Age)	yes	LHST	Cold NEF
MacDonald *et al.* 1998	Central Canada (NW Territories)	*Picea glauca, Picea mariana*	No latitudinal shift but abundance increase	None	1880-1987	no	Cold NEF	Cold NEF
Masek 2001	Canada - east coast of Hudson Bay; Great Slave Lake, NW Territories	*Picea mariana*	No latitudinal shift	< 200-300 m/century	1972-2001	yes	LHST	Cold NEF
Payette 2007	Northern Labrador, Canada	*Picea glauca*	Altitudinal/latitudinal shifts, growth declines at some sites	--	Last half of 20th century	yes	LHST, some cold NEF	Cold NEF
Pereg and Payette 1998	East of Hudson Bay, Canada (57°45'N; 76°20'W) (map in article)	*Picea mariana*	Increased krummholz growth	Increases in stem initiation began in 1940s, peaking during the 1970s	Since 1890s	yes	LHST	Cold NEF
Scott *et al.* 1987	Northern Manitoba, Canada	*Picea glauca*	Latitudinal migration and density increases	--	Little Ice Age to 1980s	no	Cold NEF	Cold NEF
Szeicz and MacDonald 1995	NW Canada	*Picea glauca*	No latitudinal shift or re-establishment of old stands	--	200 years ago to present	no	Cold NEF	Cold NEF

Europe – 5 studies

Study	Location	Species	Shift	Amount	Time	Predicted Change?	Present Type	Future Predicted Type
Hofgaard *et al.* 1991	Mt. Blaikfjallet, east of the Scandes Mtns in N. Sweden (64°40'N, 15°50'E)	*Picea abies*	Increased growth after pronounced cold damage	69% of tops had increased regernation (2% unchanged, 29% shorter)	1938-1988	yes	Cold NEF	CMF
Klanderud and Birks 2003	Jotunheimen Mountains, Central Norway (61°N)	All vascular plants (~100)	Altitudinal	73.2% of all species recorded had range expansions	1930-31 to 1998	Yes, though resolution is poor	Cold NEF	CMF
Kullman 1991	Mt. Välliste in the Northern Swedish Scandes (63°17'N, 13°14'E)	*Pinus sylvestris*, *Picea abies*	Growth decline, recession	--	1949-1987	no	Cold NEF	Cold NEF
Kullman 1996	Handolan Valley of the southern Swedish Scandes (63°12'N, 12°23'E)	Old-growth *Picea abies*	Growth decline, recession	Rate of needle loss is 2.69% per year.	1974-1994	yes	Cool NEF	CMF
Kullman 2001	Swedish Scandes	*Betula pubescens* ssp. *tortuosa*, *Pinus sylvestris*, *Picea abies,* and the grass *Deschampsia flexuosa*	Altitudinal migration and density increases	Mostly 30-50 m; at most 120-165 m	Between late 19th and 20th centuries	yes	Cold NEF	CMF

Siberia – 7 studies

Study	Location	Species	Shift	Amount	Time	Predicted Change?	Present Type	Future Predicted Type
Devi *et al.* 2008	Polar Urals treeline (map in article)	*Larix sibirica*	Expanding forests, taller growth forms	Upward by 20-60 m; 90% new seedlings after 1950 upright in growth form	1960 to 2007	yes	LHST	Cold NEF
Esper and Schweingruber 2004	Nine trans-Siberian study sites (map in article)	*Larix species, Pinus sibirica, Picea obovata*	Altitudinal migration and greater tree establishment	Pulses of tree establishment in 1940s-50s and again in 1970s	1940s and 1950s and after the early 1970s	yes	LHST in west, CDF in east	Cold NEF, some remaining eastern CDF
Hantemirov *et al.* 2008	Northern timberline of Yamal Peninsula, Russia	*Larix sibirica*	Greater tree establishment	Pulses of tree establishment in 1900-1935 and 1950-1970	1880-1980	yes	LHST	Cold NEF
Kapralov *et al.* 2006	Northern Ural Mountains (59°30'-59°40'N, 59°00'-59°20'E)	Variety of tree species (*L. sibirica, P. sibirica, B. tortuosa*)	Altitudinal and horizontal range expansions; crown density increase, tree species changing in land area dominance	Average of 31 m altitudinal shift, 113 m horizontal shift, and 11% increase in crown density	1956-2005	yes	Cold NEF	Cool NEF
Kharuk *et al.* 2006	Ary-Mas forest, northern Siberia (from 72°02'-72°40'N to 101°15'-102°06'E)	larch forest (*Larix gmelinii, Larix sibirica*)	Increased canopy cover; 65% abundance increase; altitudinal shift	65% increase in closeness of larch canopy; larch into tundra expansion by 3-11 m/year	1973-2000	yes	LHST	Cold NEF
Mazepa 2005	25 mapped sites in the Polar Ural Mountains (66°48'57"N, 65°34'09"E)	*Larix sibirica*	Stand density and stem growth increases	2-5x increase in stem growth volume; up to 1-3.5x increase in stand density	1960-62 to 1999-2001	yes	LHST, some cold NEF	Cold and cool NEF
Shiyatov *et al.* 2007	Polar Urals	*Larix sibirica*	Altitudinal and latitudinal	26-35 m rise in elevation; 290-520 m horizontal shift	20th century (1910s-2000s)	yes	LHST	Cold NEF

Table A. 1. 5. Correspondence between Site Vegetation and Present Vegetation Map

Comparison of the vegetation description at the 30 study sites to the biome type at the study sites taken from the present-day vegetation map (from Kaplan *et al.* 2003). Biome abbreviations are as follows:

Tundra: LHST = low and high shrub tundra, EDST = erect dwarf shrub tundra
Forest: NEF = needleleaf evergreen forest (cold or cool), CDF = cold deciduous forest

Region	Study	Actual Type (Site Description)	Mapped Type	Match	Comments
Alaska	Barber *et al.* 2000	Mature and old white spruce stands representative of the Alaskan boreal forest, in contrast to the forest-tundra treeline	Cold NEF, Cold NEF/LHST border	Good	
	Lloyd and Fastie 2002	White spruce-dominated treeline, adjacent to primarily low shrub (*Salix*, *Vaccinium*) and herb tundra	LHST, Cold NEF, EDST	Good	
	Lloyd and Fastie 2003	White spruce-dominated treeline, low shrub/herb tundra	LHST, Cold NEF, EDST	Good	
	Suarez *et al.* 1999	White spruce adjacent to shrub and tussock tundra	Cold NEF/LHST border	Good	
	Tape *et al.* 2006	Sedge tussock/deciduous shrub tundra (birch, willow, alder) – low and high shrubs	LHST, EDST	Good	
	Wilmking *et al.* 2006	Mosaic of tussock tundra, shrub tundra, and patches of white spruce forests	LHST	Good	
Canada	Danby and Hik 2007	White spruce alpine treeline	Cold NEF	Good	
	Gamache and Payette 2004	Open-crown boreal forest to shrub tundra	LHST, Cold NEF	Good	
	Lavoie and Payette 1992	Border between forest-tundra and shrub-tundra	LHST	Good	
	Lavoie and Payette 1994	Border between forest-tundra and shrub-tundra	LHST	Good	
	Lavoie and Payette 1996	Forest-shrub tundra ecotone composed of moss-shrub black spruce forests and krummholz, lichen-heath communities on well-drained sites, and tundra peatlands	LHST	Good	
	Lescop-Sinclair and Payette 1995	Treeline of black spruce and shrub tundra; treeline located between the forest limit and species limit	LHST	Good	
	MacDonald *et al.* 1998	Tundra side of boreal forest-tundra ecotone; krummholz of black and white spruce	LHST	Fair	no specific tundra types mentioned in study description
	Masek 2001	Forest-tundra and shrub-tundra ecotones	Cold NEF, LHST	Good	
	Payette 2007	Coastal tundra with open treeline	LHST, Cold NEF	Good	

	Pereg and Payette 1998	Black spruce krummholz, lichens, shrubs	LHST	Good	
	Scott *et al.* 1987	White spruce forest-tundra ecotone	Cold NEF	Good	
	Szeicz and MacDonald 1995	White spruce-dominated altitudinal treeline	Cold NEF	Good	
Europe	Hofgaard *et al.* 1991	Mosaic of *Picea abies*-dominated forest and mire, but birch more dominant near treeline	Cold NEF	Good	
	Klanderud and Birks 2003	Alpine dwarf shrubs (*Salix*, *Vaccinium*), herbs, grasses; no mention of boreal tree species	Cold NEF, LHST	Fair	Site vegetation only partially described by map; topography likely a problem for map resolution
	Kullman 1991	Forest plot with a dense stand of pine, scattered spruces, a few birches, and some low-growing junipers; a field-layer of dwarf shrubs, herbs, and mosses	Cold NEF	Good	
	Kullman 1996	Alpine spruce krummholz mixed with birch; treeless heaths with ericaceous dwarf-shrubs	Cold NEF	Fair	Site vegetation only partially described by map; topography likely a problem for map resolution
	Kullman 2001	Alpine treeline ecotone of mountain birch, Norway spruce, and Scots pine, 50-300 m above the coniferous forest	Cold NEF	Good	Study description applies to the map type, but topography may still be an issue
Siberia	Devi *et al.* 2008	Alpine treeline ecotone dominated by larch in association with spruce and mountain birch; understory of shrubs (*Betula*, *Salix*, *Vaccinium*) and herbs; ground layer of mosses	Cold NEF	Fair	Site vegetation only partially described by map; topography likely a problem for map resolution
	Esper and Schweingruber 2004	Sapling/krummholz-tundra ecotones: *Pinus sibirica* in N. Urals, *Picea obovata* in W. Urals, and *Larix* spp. east of the Urals	Cold NEF, LHST, EDST, Cold/Cool NEF border	Fair	no specific tundra types mentioned in study description
	Hantemirov *et al.* 2008	Northern timberline ecotone; sparse larch stands only in valleys of small rivers	LHST	Fair	no specific tundra types mentioned in study description
	Kapralov *et al.* 2006	Foothill conifer forests dominated by Siberian spruce, fir, and stone pine; birch and larch at higher elevations	Cool NEF	Good	map resolution still a potential problem in resolving alpine vegetation types well due to topography
	Kharuk *et al.* 2006	Ary-Mas larch forest-tundra ecotone	EDST, LHST, and CDF border	Fair	no specific tundra types mentioned in study description
	Mazepa 2005	Treeline ecotone dominated by larch stands of varying density, in association with Siberian spruce and mountain birch; closed larch-spruce forests at lower elevations; tall shrubs also present	Cold NEF	Fair	Site vegetation only partially described by map; topography likely a problem for map resolution; site should ideally be represented as cold deciduous forest
	Shiyatov *et al.* 2007	Pure larch open and closed forests	Cold NEF	Poor	map should represent this area as cold deciduous forest

Appendix 2: Multi-Level Model

The main statistical output from the multi-level model includes the following:

```
m1<-lmer(Match~1+(1|Study), dat, family="binomial")

> m1
Generalized linear mixed model fit using Laplace
Formula: Match ~ 1 + (1 | Study)
   Data: dat
 Family: binomial(logit link)
   AIC   BIC logLik deviance
 120.9 126.0 -58.43    116.9
Random effects:
 Groups Name Variance Std.Dev.
 Study       1.1274   1.0618
number of obs: 95, groups: Study, 30

Estimated scale (compare to  1 )  0.9284766

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   0.9519     0.3539    2.69  0.00715 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

The intercept is significant (p-value = 0.00715, < 0.05). To convert to a percentage agreement we apply the logit canonical link function, defined as $\log\left(\frac{p}{1-p}\right)$, to the parameter estimate from the binomial GLM, giving p = 0.721.

$$p = \frac{e^{\theta}}{1+e^{\theta}} = e^{0.9519} / (1+e^{0.9519}) = 0.721$$

Subtracting and adding the standard error, 0.3539, before the logit inversion gives the expected range of agreement values. θ is set to 0.9519 + 0.3539 = 1.3058 and 0.9519 - 0.3539 = 0.5980. This gives probability values of 0.7868 and 0.6452, which are +0.0658 and -0.0758 from p.

Figures

Figure 1

Different definitions of the Arctic, including the region above the Arctic Circle, high-, low-, and sub-arctic regions, 10° C isotherm, and the region north of 55°N latitude, as done by Kaplan *et al.* 2003, and as adopted for this study. Arctic treeline is also shown.

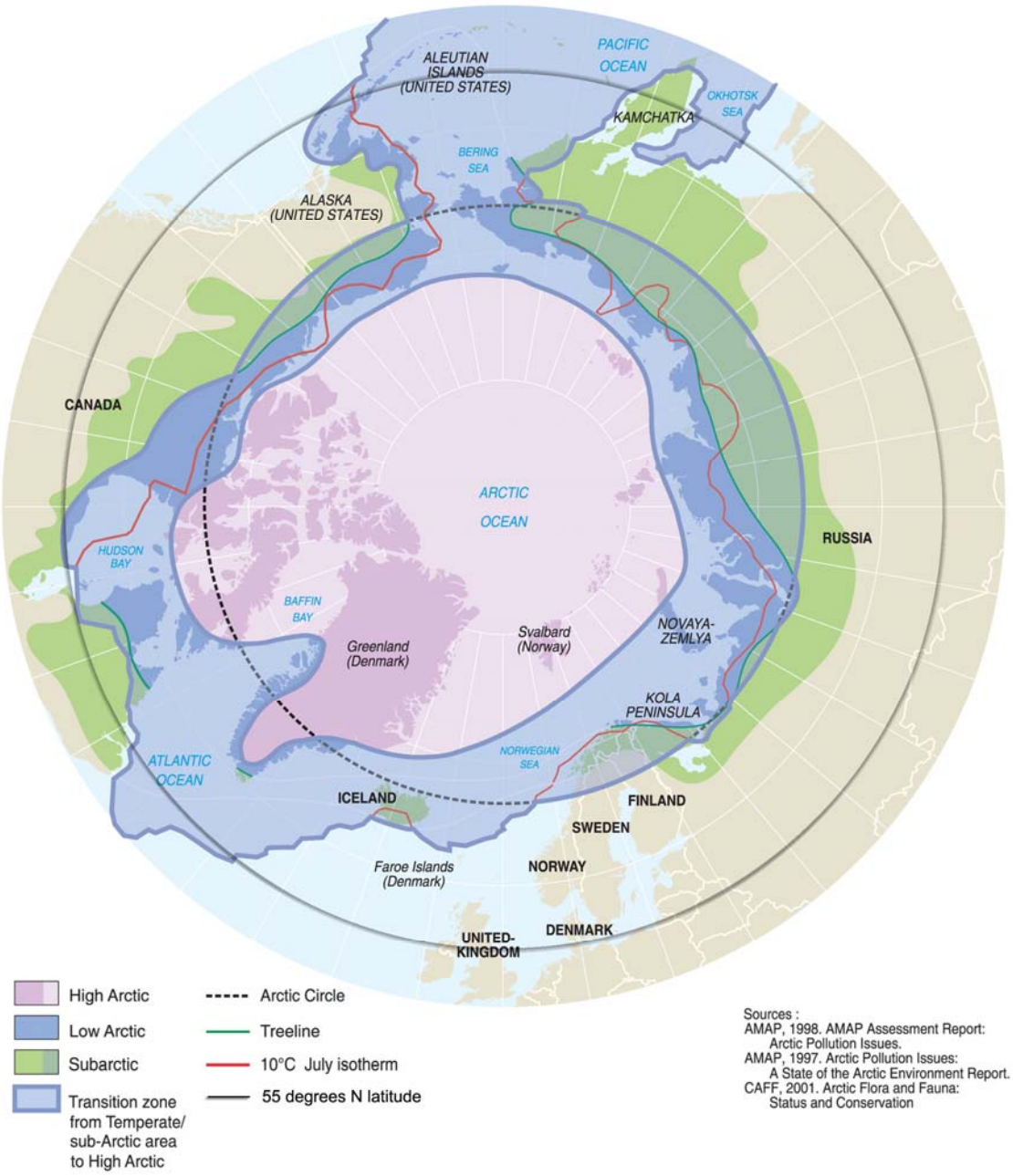
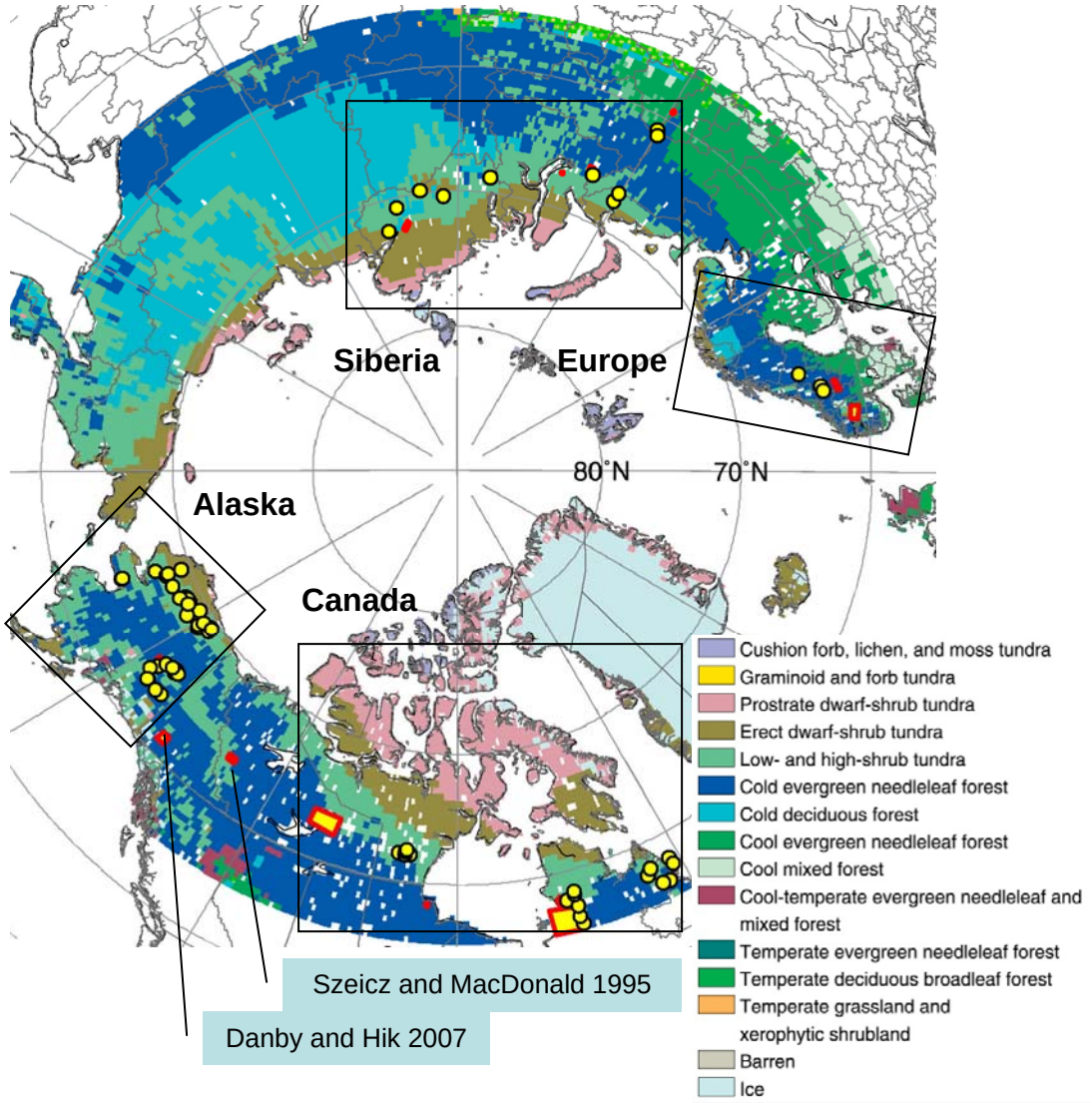


Figure 2

Study site locations of the 30 studies used in this analysis, geolocated on a) present-day biome distribution, and b) projected biome distribution for 2100 (Kaplan *et al.* 2003). Points with geocoordinate information are shown in yellow; polygons are shown in red. See Figure 4 for increased regional detail showing comparisons between empirical observations and model projections.

2a)



2b)

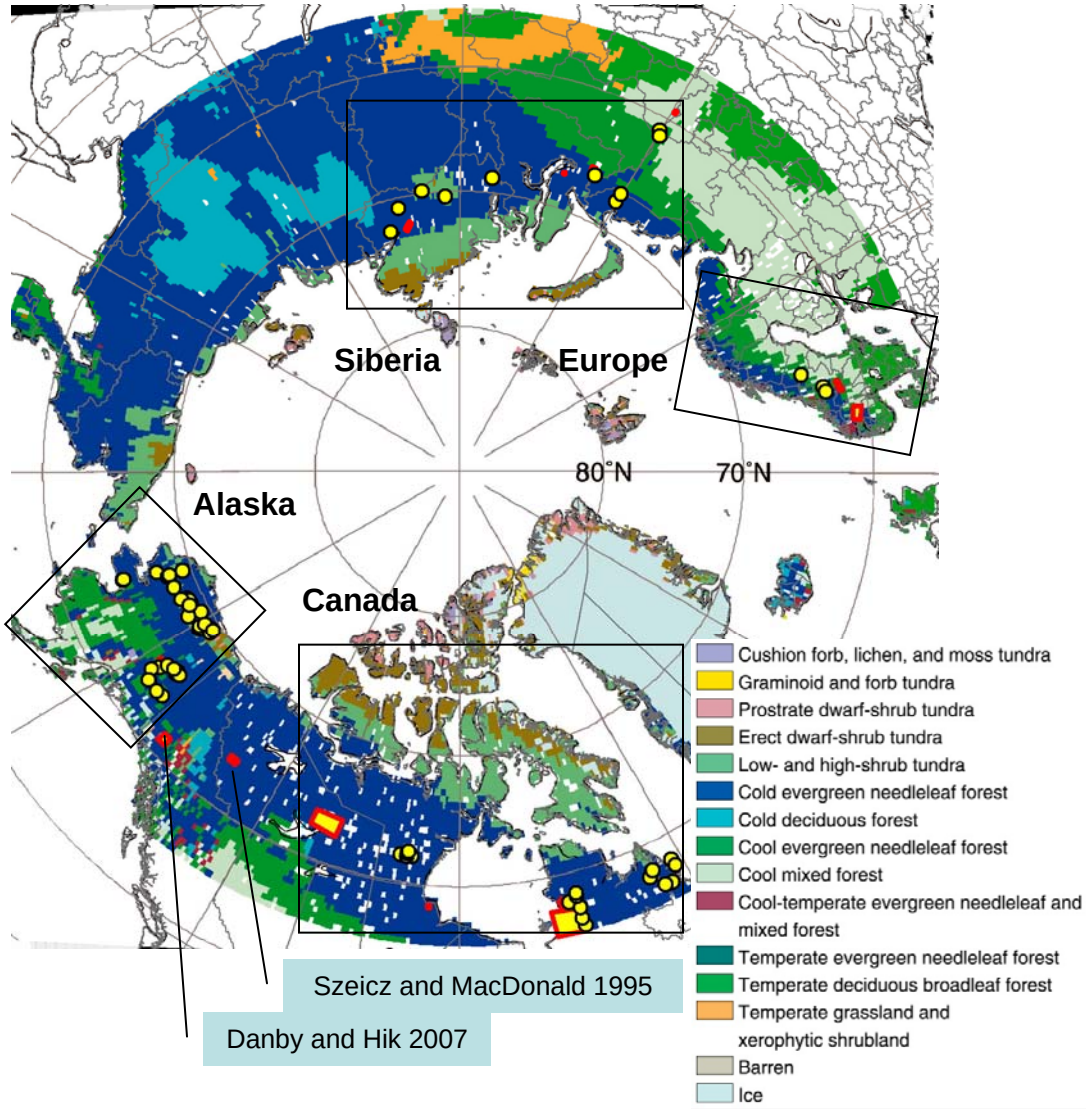

Siberia
Europe
80°N
70°N
Alaska
Canada
Szeicz and MacDonald 1995
Danby and Hik 2007
Cushion forb, lichen, and moss tundra
Graminoid and forb tundra
Prostrate dwarf-shrub tundra
Erect dwarf-shrub tundra
Low- and high-shrub tundra
Cold evergreen needleleaf forest
Cold deciduous forest
Cool evergreen needleleaf forest
Cool mixed forest
Cool-temperate evergreen needleleaf and mixed forest
Temperate evergreen needleleaf forest
Temperate deciduous broadleaf forest
Temperate grassland and xerophytic shrubland
Barren
Ice

Figure 3

Study site locations of the 30 studies used for this analysis, geolocated on the distribution of projected change (blue). All study sites are in or near areas predicted to undergo vegetation change due to warming temperatures. Study sites are color-coded according to level of agreement between study data and model predictions. Red indicates agreement between data and prediction; yellow indicates a mismatch.

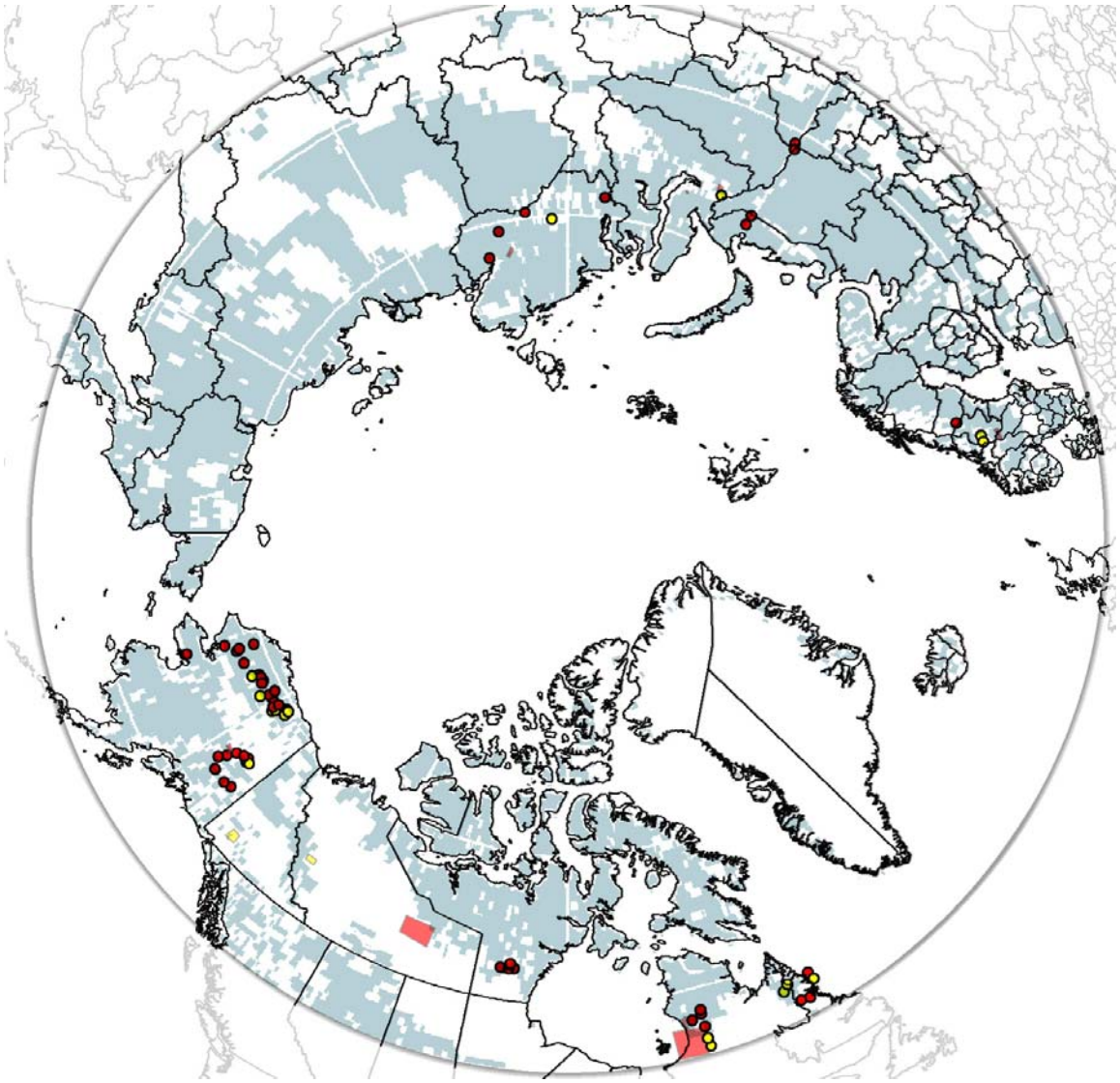
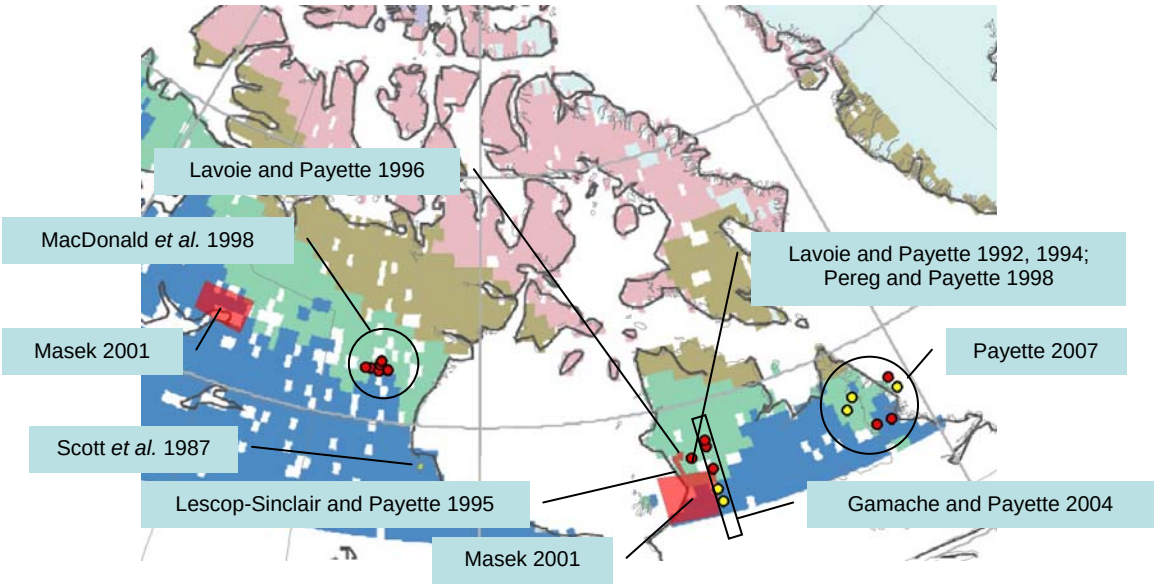


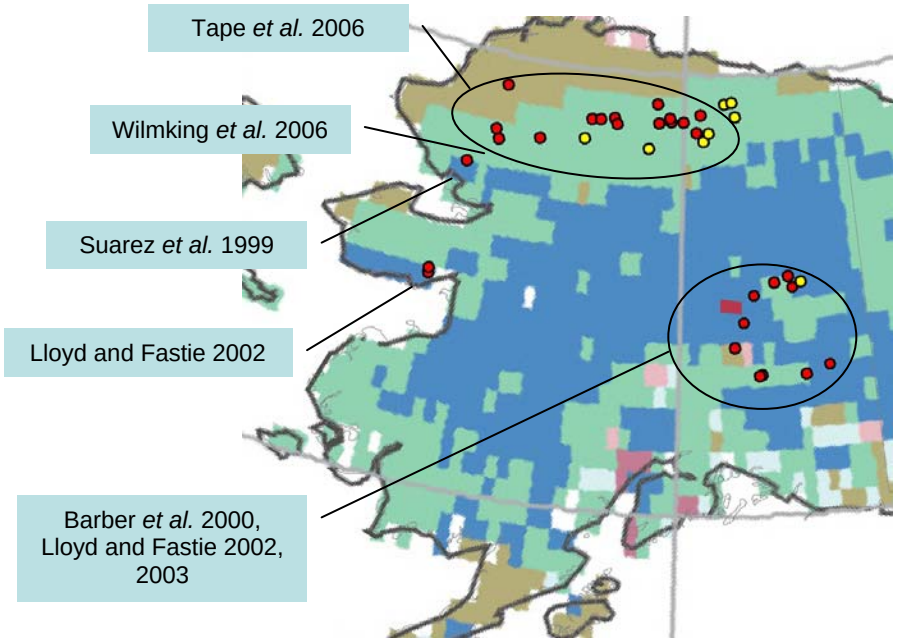
Figure 4

Inset maps for a) eastern Canada, b) Alaska, c) Europe, and d) Siberia, showing locations of the study sites, labeled by study and color-coded according to level of agreement between study data and model predictions. Red indicates agreement between data and prediction; yellow indicates a mismatch. Locations are superimposed on the present-day vegetation distribution from Kaplan et al. (2003).

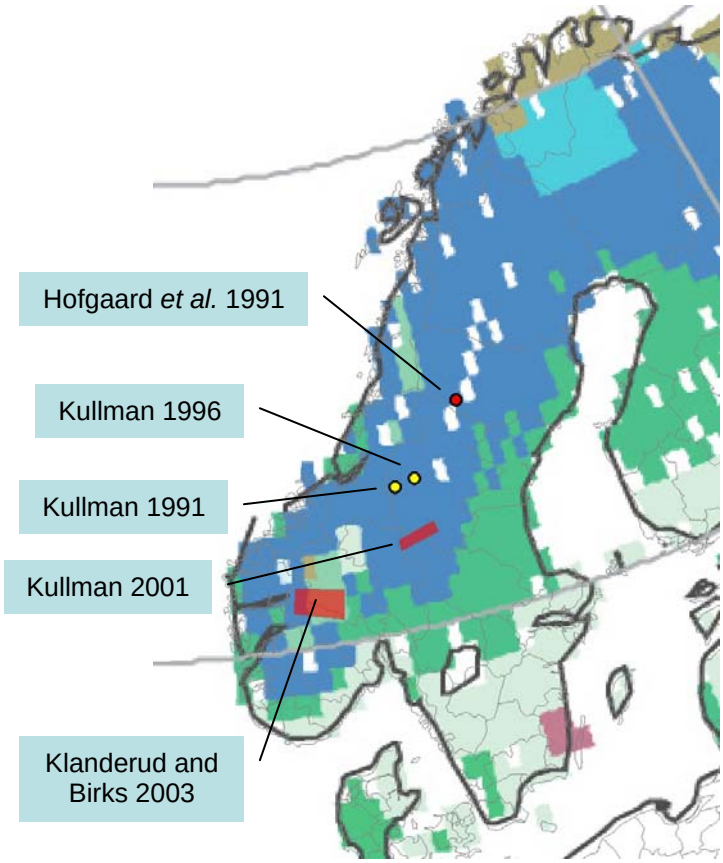
4a) Eastern Canada



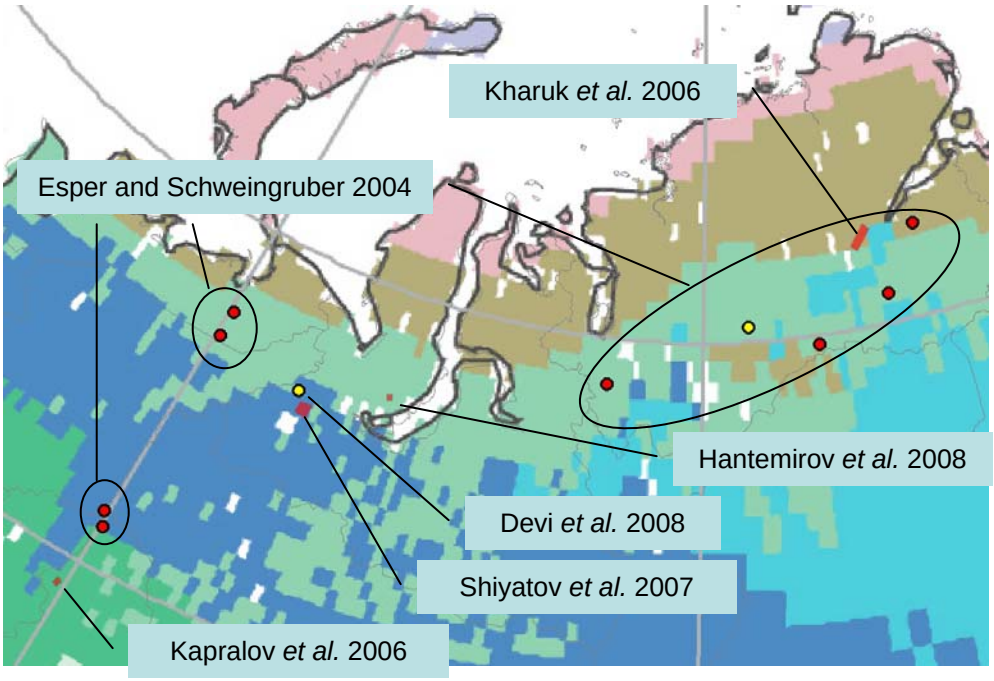
4b) Alaska



4c) Europe



4d) Siberia



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