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Resilience and Stability Associated with Conversion of Boreal Forest

Jacquelyn Kremper Shuman and Herman Henry Shugart
University of Virginia, Department of Environmental Sciences
 USA

1. Introduction

A clear understanding of boreal forest dynamics is critical to developing an accurate representation of the Earth's response to climate change. The Russian boreal forest is the largest continuous forest region on Earth and a tremendous repository of terrestrial organic carbon. The boreal forest has experienced significant warming over the past several decades and is expected to be impacted by global climate change (Chapin et al., 2000; McGuire et al., 2002; Soja et al., 2007). Siberian summers in the past century were warmer than any century in the past millennium, and future climate scenarios indicate that the region will continue warming, by some accounts between 2° and 10°C by 2100 (IPCC 2007; Soja et al., 2007). Warming climate will likely exert influence on species distributions and land cover types in the boreal forest regions (Ustin and Xiao 2001; Tchebakova et al., 2005; Tchebakova et al., 2009). In particular, these temperature increases have led to the shift of treelines northward or upslope of previous climate limits, and a reduction in cone and seed yield for *Larix sibirica* and *Pinus sylvestris* which changes forest composition and structure (Kharuk et al., 2009; Soja et al., 2007). These changes are important indicators of how Eurasian boreal forests may respond to, and ultimately amplify, increases in average global temperature.

These land cover changes can force alterations in regional climate through modifications in surface albedo and land/atmosphere energy fluxes (Bonan et al., 1992; Chapin et al., 2000; Baldocchi 2000; Amiro 2001; Beringer et al., 2005; Soja et al., 2007), as well as in global climate through changes in carbon sequestration and release patterns (Bonan 2008; Snyder et al., 2004). Global climate model (GCM) results have shown that clearing boreal forest alters surface albedo, and substantially cools the Earth, not only in the boreal region but across the Northern Hemisphere (Bonan et al., 1992), and has the greatest effect on global mean temperature when compared to the removal of other biomes (Snyder et al., 2004). Betts (2000) found surface albedo changes associated with the growth of coniferous evergreen trees led to significant increases in average global temperature large enough to overshadow the effect of carbon storage by growing evergreen forest in that region. Bioclimatic modeling predicts that by 2090 vegetation change across Siberia will create an albedo shift and increase overall net radiation, thereby producing enhanced warming above that already predicted for the high latitudes (Vygodskaya et al., 2007). Larch (*Larix* spp.) forest, dominated by both *L. sibirica* and *L. gmelinii*, covers extensive regions in Siberia. Field observations have documented shifts from larch to evergreen conifer forests, dominated by trees such as spruce (*Picea* spp.) or fir (*Abies* spp.) that are tolerant of higher temperatures

(Kharuk et al., 2007). Because larch is a deciduous conifer, this shift to evergreen dominance would lead to an albedo decrease, particularly in winter, when evergreen trees tend to mask laying snow relative to deciduous species (Betts and Ball 1997). The difference in summer albedo is smaller but also significant, with larch albedo measured at approximately 0.13 and evergreen species around 0.09 (Hollinger et al., 2010). This reduction of albedo associated with the shift in forest type indicates that increased temperatures may lead to a positive feedback response: a warmer climate accelerates the natural succession from larch to evergreen conifer forest and the resultant albedo promotes additional warming. Areas of southern Siberia identified as vulnerable to premature replacement of larch by evergreen conifers would undergo a local significant albedo shift of approximately 5.1 W m^{-2} following conversion from dominant larch to evergreen conifer stands (Shuman et al., 2011).

Identification of areas prone to vegetation change is crucial in efforts to mitigate the effects of potential forest type conversion. Remote sensing technology has advanced to a point which allows for estimation of biomass and detailed evaluation of land cover and land use change. Estimation of Russian forest biomass directly from Moderate Resolution Imaging Spectroradiometer (MODIS) data provided estimates of a distribution of biomass classes that correlated well to ground measured forest biomass with signatures from a minimum of training sites (Houghton et al., 2007). Detailed characterization of vegetation by remote sensing technology provides land cover maps for areas within Russia that are not easily accessible, and at a more frequent temporal resolution than is possible to obtain using field-based mapping techniques. A NOAA/AVHRR-derived vegetation map for a remote section of northern Siberia provides detailed information regarding latitudinal transition zones, vegetation differences inside each zone and variability along vertical transects for mountainous areas (Kharuk et al., 2003). This type of high quality map for a remote area provides land cover information essential to evaluating vegetation changes in response to climate change. Remotely sensed data can be used to identify areas undergoing a change in land cover type and assess the direction and magnitude of any albedo shift associated with such a change. Vegetation models can be used to provide information regarding the specific type of vegetation change and the location where this change is most likely to occur, and can thus inform vegetation monitoring efforts based on remotely sensed data.

In the past 20 years, individual-based models (IBMs) have been used to provide increasingly accurate predictions and simulations of forests (Mladenoff 2004; Scheller and Mladenoff 2007). The model used in this study, FAREAST, is in a class of IBMs called “gap models” (Shugart and West 1980) that simulate individual trees, specifically their growth, mortality, and decomposition into litter in a relatively small area, typically the size of a forest gap. Forest gap models established according to the approach of Botkin et al., (1972) and Shugart and West (1977) are based upon the concept of “gap phase” replacement (Watt 1947). Gap models account for competition among individuals of multiple tree species for light and other resources, with the outcome determining the composition and structure of the forest through aggregation of homogenous mosaic patches through time (Shugart 1984). Testing of gap models is divided into verification and validation (Mankin et al., 1977; Cale et al., 1983; Rykiel 1996; Sargent 1984), and involves evaluating the ability of the model to predict species successional dynamics and biomass accumulation for the region of model development. Gap models have been verified and validated for a variety of forests world-wide (Botkin et al., 1972; Shugart and West 1977; Shugart, 1984 and its reprinting 1998, 2003; Kienast 1987; Leemans and Prentice 1989; Kienast and Krauchi 1991; Bugmann 2001). The initial tests of the FAREAST

model included a simulation of forest composition and basal area at different elevations on Changbai Mountain in China, with statistical comparison to inventory data and then qualitative comparisons to observed forest type at 31 sites in the Russian Far East and Siberia (Yan and Shugart 2005). Further validation of the model using linear regression of model generated and independent forest inventory data indicated that FAREAST successfully captures the natural biomass dynamics of mixed-species forests across the vast geographic area and varied climatic conditions of Russia (Shuman and Shugart 2009; Shuman 2010).

The use of gap models allows for the evaluation of novel conditions or the addition of a new species for the purpose of evaluating the impact on existing vegetation. The impact that changing climate has on forests at local and regional scales has been explored with several different forest gap models (Shugart 1984; Solomon 1986; Pastor and Post 1988; Dale and Franklin 1989; Urban et al., 1993; Lasch and Lindner 1995; Bugmann 1996; Yan and Zhao 1996; Bugmann and Solomon 2000; Zhang et al., 2009). IBMs can be used to develop a vegetation “signature” for the response of ecosystems to change, especially climate change. Using a boreal forest gap model to assess climate change effects, Bonan (1989a,b) investigated the responses to several climate change predictions from global climate models along the north-facing and south-facing slopes of boreal forests near Fairbanks, Alaska. The black spruce forests growing on cold north-facing slopes were largely unaffected by the climatic warming, but white spruce forests on the relatively warmer south-facing slopes were strongly affected by the change in climate. Conditions predicted in the climate change scenarios for south-facing slopes were outside the ecological conditions under which the common tree species near Fairbanks are known to be able to persist. For white spruce, the limiting condition identified by the model results appeared to be moisture stress and not the direct effects of temperature change. A decade later, Barber et al., (2000) investigated tree ring data to determine the effect that several decades of warmer than usual temperatures in the Fairbanks area had had on white spruce stands and confirmed Bonan’s model predictions with evidence for moisture-stress effects in the tree ring dataset.

In this study, the FAREAST model is used to simulate forest composition and biomass at 372 sites across Siberia and the Russian Far East for the purpose of evaluating forest response to climate change. Climate sensitivity analysis is performed in order to assess the resilience and stability of forest structure and composition to altered climate at multiple spatial scales. The model was used to simulate the impact of changes in temperature and precipitation on both total and genus-specific biomass at sites across Siberia and the Russian Far East, and for six different regions representing areas of high and low diversity. Comparisons of regions within areas of high and low diversity provide a tool to evaluate the relationship between diversity and the response of the system to changing climate. Model runs with and without European Larch (*Larix decidua*) are compared in order to assess the potential for the introduction of this species to mitigate the effects of climate change, especially the positive feedback among temperature, forest type and surface albedo.

2. Methods

2.1 Model simulation across Siberia and Russian Far East

FAREAST was run at a total of 372 sites across Siberia and the Russian Far East (RFE) from the eastern coast to the western border of the range limits of *L. sibirica*. FAREAST uses monthly climate parameters derived from historical station data to compute daily

temperature and update soil water content. In particular, at each site, the model’s climate inputs are drawn from a statistical distribution of monthly values for minimum and maximum mean temperature and precipitation that is derived from 60 years of data recorded at local weather stations (NCDC 2005a, 2005b). The model also uses values for soil field capacity, and soil carbon and nitrogen from Stolbovoi and McCallum (2002) for each site.

The birth, growth, and eventual death of individual trees are determined in response to competition for light and local site parameters such as soil moisture and nutrient availability, which are updated annually with bio-environmental conditions and available nutrients. Complete model processing details are available in Yan and Shugart (2005). Fifty-eight different tree species are included in FAREAST simulations, and can be grouped into ten genera (*Abies* spp., *Betula* spp, *Larix* spp., *Picea* spp., *Pinus* spp. *Populus* spp., *Tilia* spp., *Quercus* spp., *Fraxinus* spp., and *Ulmus* spp.) and two collections of less common species (other deciduous and other coniferous). These species represent the genera that dominate Northern Eurasian forests, and include species that were added when the original geographic area of interest for the model in Yan and Shugart (2005) was expanded to cover all of Russia (Shuman and Shugart 2009). Twenty-five parameters describe each species and determine which species has an advantage in terms of competition for light or nutrients, or tolerance to lack of water. Tree growth and regeneration is limited by functions describing local light, temperature, nutrients and drought dynamics determined through interaction and annual update of soil water and available carbon and nitrogen. Tree mortality each year is a consequence of a Monte Carlo realization of individual species probability of mortality plus added probability of mortality on that individual from stress or disturbances. Successional dynamics are therefore a result of competition between tree species for light and nutrients, as well as limitations to growth imposed by local environmental conditions. Each site uses a unique species list drawn from species range information created in ESRI ArcGIS (2008) using range information adapted from Nikolov and Helmisaari (1992) and Hytteborn et al., (2005). At each site, 200 independent twelfth-hectare plots were simulated for 500 years and the modeled biomass values were averaged for each species in each year of the model run. This average produces a landscape-level approximation of succession, which includes the natural disturbance associated with the death of individual trees.

2.2 Climate sensitivity analysis

The authors evaluated biomass for the total forest, *Larix* spp., and evergreen conifers at 372 sites across Siberia in response to changes in temperature and precipitation, and to the inclusion of European Larch (*Larix decidua*) (Table 1).

Treatments used in climate sensitivity analysis	
Change in temperature	Base + 4 degrees
Change in precipitation	Base ± 10%
Introduction of <i>Larix decidua</i>	Base + <i>Larix decidua</i>

Table 1. A total of 12 treatments including the base condition, combinations of temperature and precipitation change and *Larix decidua* addition to the available species pool were used.

L. decidua has a higher tolerance for an increased number of warm days than do species of larch native to Siberia and the RFE. This gives *L. decidua* an advantage over other species of larch for establishing in areas with warmer temperatures. The climate scenarios used in this analysis are based on the moderate predictions of temperature and precipitation increase that are made by global climate models for portions of Eurasia (IPCC 2007). For the base scenario, no changes are made to the distributions of monthly temperature and precipitation values derived from historical records. The remaining climate scenarios employ a linear increase in temperature or precipitation or both from the start of simulation, year zero, to year 200 of the simulation. This is followed by an additional 300 years of simulation during which the climate stabilizes around the conditions attained in year 200. For each of the 12 treatments, biomass (tC ha^{-1}) values were summed across species to obtain values for the total forest, *Larix* spp., and evergreen conifers at each site.

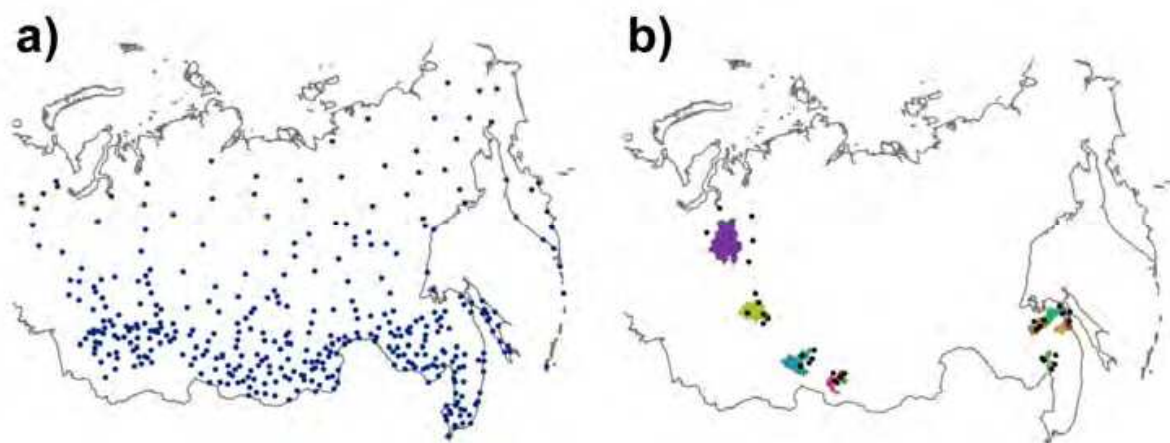


Fig. 1. Multi-scale analysis included data for 372 sites at the continental scale (a) and sub-sets from six regions (b) within northwest Siberia, the central border of Siberia, two sets from southern Siberia, and two eastern sets from high diversity areas in the Amur region of the Russian Far East

A non-parametric factorial ANOVA was performed at 10 year intervals and used to assess differences in total forest, *Larix* spp., and evergreen conifer biomass (tC ha^{-1}) between model runs that employed one of the 11 different climate and *L. decidua* treatments and the base climate scenario (SAS v. 9.1, SAS Institute Inc. 2002). This analysis was completed at the continental scale for a total of 372 sites (Figure 1a), and for six regional subsets (Figure 1b) including northwest Siberia (NW Siberia), the central border of Siberia (Central Siberia), two sets from southern Siberia (E Irkutsk, and W Irkutsk), and two sets from the Amur region of the Russian Far East (N RFE, and SW RFE). These regions represent areas with a broad range of climatic conditions and offer a representative sample of different forest types. Within the six regional subsets, local scale results were evaluated for changes in successional dynamics resulting from the climate or *L. decidua* treatments.

3. Results

3.1 Model simulation across Siberia and RFE

Overall biomass dynamics across Siberia and the RFE for the baseline climate scenario shows the highest values across the Amur region of the RFE, moderate biomass within

southern Siberia and low biomass across the northernmost sites. The successional dynamics across western Siberia in response to baseline climate feature a larch-dominated system persisting over time (Figure 2a). In the warmer southern portions of the region, larch forest undergoes a transition to mixed evergreen conifer and deciduous broad-leaved species beginning around year 230 (Figure 2b). This transition continues and by year 500, the southern portion of Siberia becomes a mixed larch and evergreen conifer forest (Figure 2c).

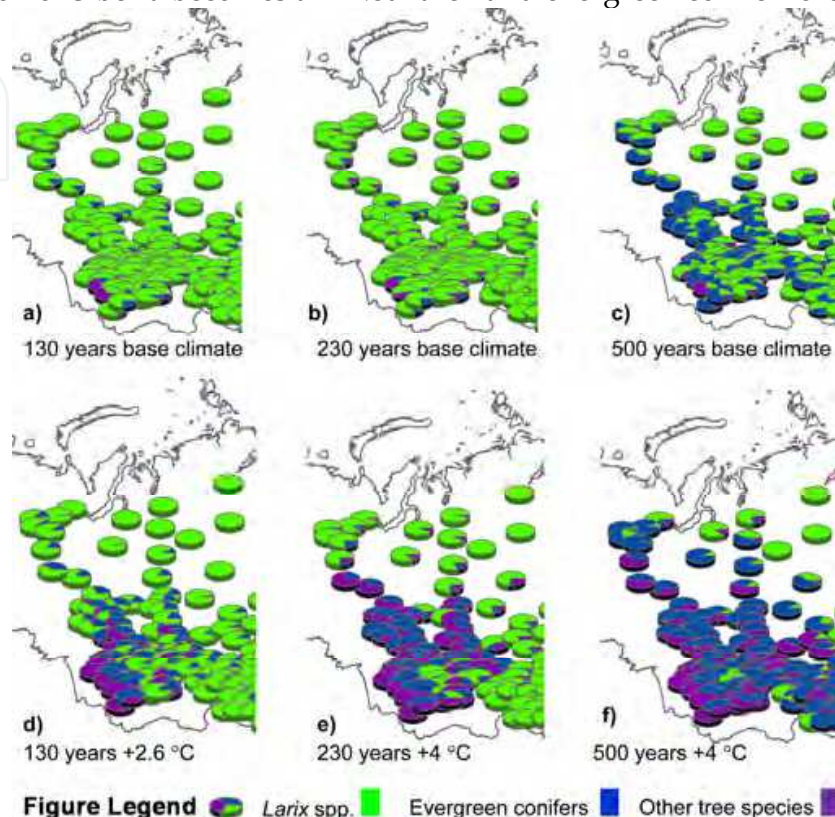


Fig. 2. Species distribution in western Siberia, a subset of the total area and dataset, for the baseline (a, b, c) and temperature increase (d, e, f) climates.

3.2 Climate sensitivity analysis

3.2.1 Continental scale results

Biomass response to the temperature treatment is significant ($p < 0.001$), continues to the end of simulation for total forest and *Larix* spp. biomass (Figure 3), and is reflected in the shift in species distribution over time (Figure 2). By year 130, the effects of the response to warming can already be seen when compared to the base climate (Figure 2a) in the shift of species dominance from larch to evergreen conifer and other species at sites in southwestern Siberia (Figure 2d). The presence of evergreen conifers and other species, in what was larch-dominated forest under the historical climate (Figure 2b), expands across more of southern Siberia by year 230 (Figure 2e), and by year 500 Siberia is no longer a larch-dominated forest under increased temperature conditions (Figure 2f).

At the continental scale non-parametric factorial ANOVA results for biomass (tC ha^{-1}) under the temperature, precipitation, and European Larch (*Larix decidua*) treatments indicated that all classes of biomass were affected ($p < 0.001$) (Figure 3). The temperature and *L. decidua* treatments have the strongest and most persistent effect on biomass throughout the simulation. *L. decidua* appears to be well-adapted to establishing across the region and

affects biomass in all groups (total forest, *Larix* spp., and evergreen conifer) at the continental scale for the entire simulation. There is an effect of precipitation change on biomass, but this effect occurs only later in succession, at year 140, and alters total forest and evergreen conifer biomass, not *Larix* spp. biomass (Figure 3).

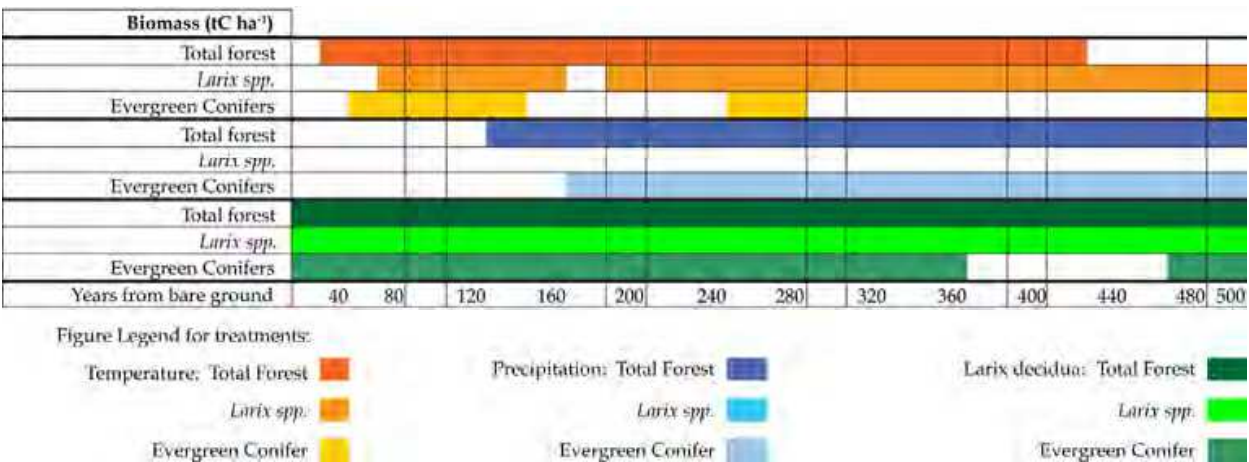


Fig. 3. Non-parametric factorial ANOVA results for climate sensitivity analyses for 372 sites across Siberia and Russian Far East. Shown in colors corresponding to figure legend are comparisons to baseline biomass values that were significant to $p<0.001$ for treatment effects of temperature, precipitation, and *Larix decidua* on total forest, *Larix* spp., and evergreen conifer biomass.

3.2.2 High diversity regional and local scale results

Sites in the Amur region of the Russian Far East (RFE) have an average of 38 individual tree species, and are classified for this analysis as high diversity. Within the high diversity regions, the non-parametric factorial ANOVA results showed a sporadic response ($p<0.001$) to the temperature and European Larch (*L. decidua*) treatments for the biomass classes measured (Figure 4). In contrast to the continental effect, the high diversity regions showed minimal response to the treatment effects of temperature increase and *L. decidua* addition, and no response to the effect of precipitation change.

Local results for the high diversity regions are variable depending on local climate conditions. The southwestern RFE (SW RFE) region under the base climate has mixed deciduous forests in the early successional stages which mature into mixed deciduous and evergreen conifer forests. Larch is present in SW RFE region, but is not a dominant species at any point during succession. Local scale analysis in SW RFE shows that the increased temperature alters the late successional dynamics by drastically reducing or replacing evergreen conifers with mixed deciduous species as early as year 150; this is reflected in the response ($p<0.001$) of evergreen conifer biomass from year 120 until the end of simulation (Figure 4). The *L. decidua* treatment does not significantly affect biomass in SW RFE region. With base climate conditions at sites in the northern RFE (N RFE) there is an initial pioneering stage dominated by *Larix* spp. which then transitions to evergreen conifer (*Picea* spp.) dominant forest (Figure 5a). The effect of temperature increase of 4°C across 200 years accelerates and alters the transition to a mixed-species forest dominated by *Pinus* spp. rather than *Picea* spp. (Figure 5b). This is reflected in the effect of the temperature treatment ($p<0.001$) on total forest biomass and *Larix* spp. biomass in late succession after year 200 for

sites in N RFE (Figure 4). Even with the increased biomass of the larch canopy created with the introduction of *L. decidua* the transition from larch to *Pinus* spp. in late succession still occurs under increased temperature conditions (Figure 5c), with strong similarity to the species shift seen without inclusion of *L. decidua* (Figure 5b).

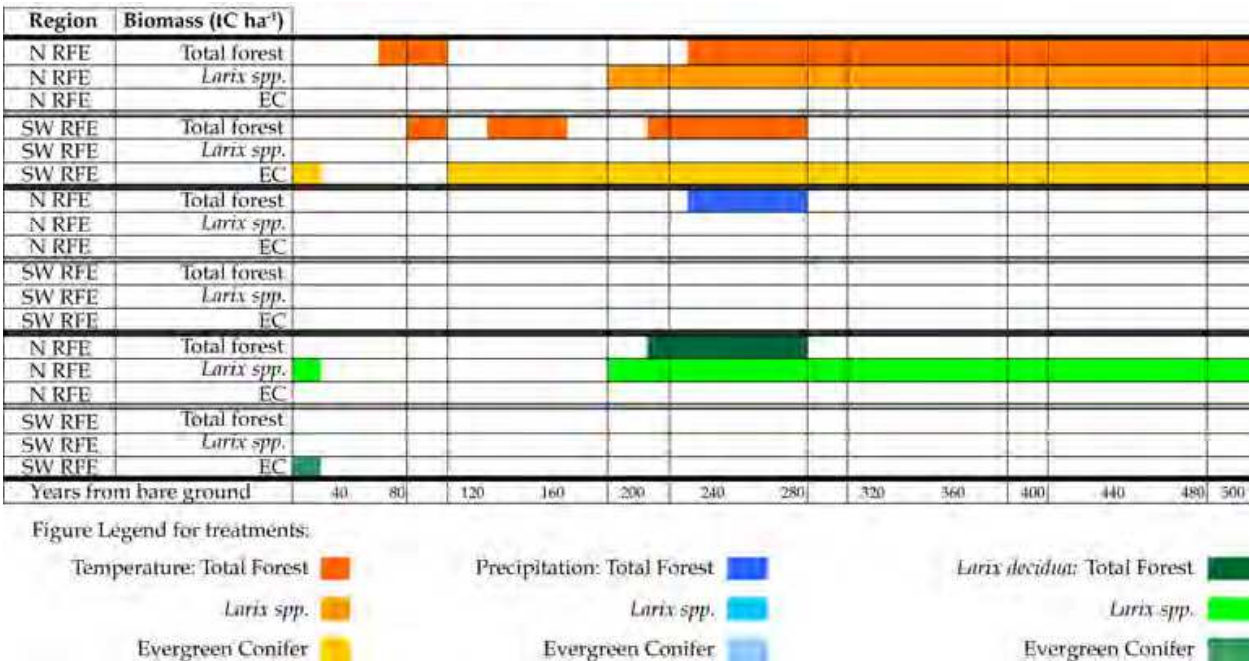


Fig. 4. Non-parametric factorial ANOVA results for climate sensitivity analyses in two high diversity sites of the Amur region in the Russian Far East: northern Russian Far East (N RFE) and southwestern Russian Far East (SW RFE). Shown in colors corresponding to figure legend are comparisons to baseline biomass values that were significant to $p<0.001$ for treatment effects of temperature, precipitation, and *Larix deciuda* on total forest, *Larix* spp., and evergreen conifer (EC) biomass.

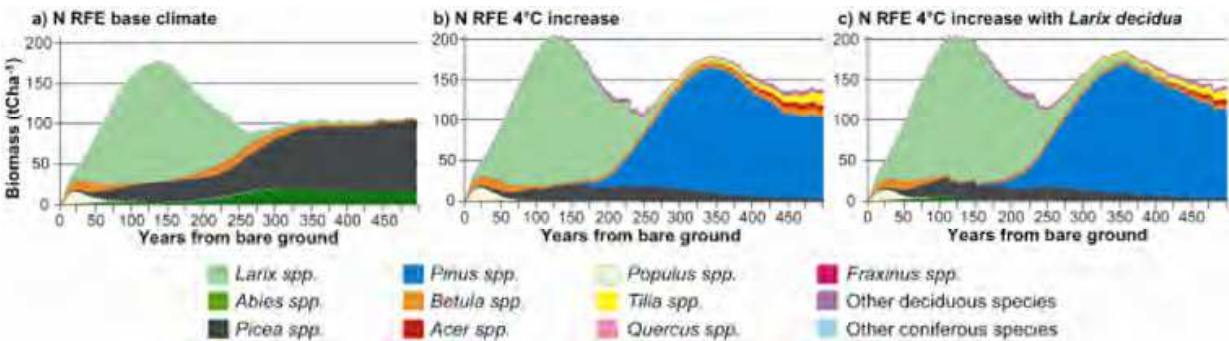


Fig. 5. Simulated species biomass dynamics (tC ha⁻¹) for high diversity Burukan site in northern Amur region of the Russian Far East (N RFE). Species composition by dominant genera is shown over 500 simulated years starting from bare ground for the base historical climate (a), temperature increase (b), and temperature increase with *Larix decidua* (c).

3.2.3 Low diversity regional and local scale results

The 279 sites across Siberia and the remainder of the RFE have an average of 9 individual tree species, and are classified as low diversity for this analysis. Similar to the continental response, within the low diversity regions the non-parametric factorial ANOVA results showed a consistent response ($p<0.001$) to temperature and *L. decidua* treatments for biomass of the total forest, *Larix* spp., and evergreen conifers when compared to baseline biomass values (Figure 6). Specifically the temperature increase in low diversity regions affects total forest and *Larix* spp. biomass early in succession and prior to year 200 (Figure 6). These regions also display a synchrony or lag response with total forest and *Larix* spp. biomass being closely connected in terms of the timing of the significant departure from baseline biomass. In all low diversity regions analyzed, except central Siberia, the response of evergreen conifer biomass to warming occurs after the response of total forest and *Larix* spp. biomass. The effect of the precipitation treatment was significant ($p<0.001$) in only one low diversity region analyzed, central Siberia.

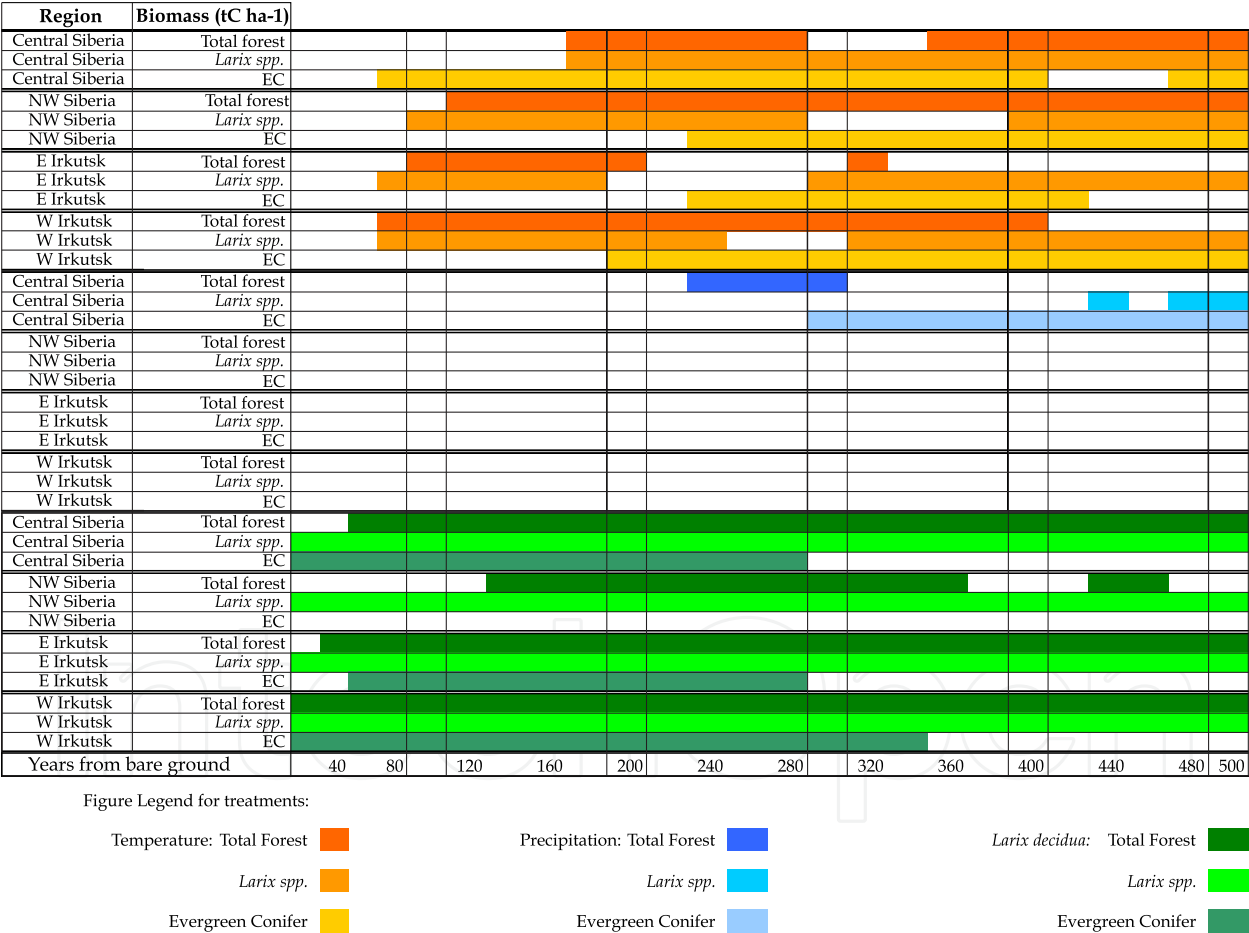


Fig. 6. Non-parametric factorial ANOVA results for climate sensitivity analyses in low diversity sites of Siberia. Shown in colors corresponding to figure legend are comparisons to baseline biomass values for treatment effects of temperature, precipitation, and *Larix decidua* that were significant to $p<0.001$ for total forest, *Larix* spp., and evergreen conifer (EC) biomass. NW Siberia is the northwestern Siberia region. E and W Irkutsk regions are in southern Siberia.

The low diversity regions under historical site conditions have a successional pattern of increasing *Larix* spp. biomass to year 200, followed by the slow establishment of evergreen conifers with *Larix* spp. maintaining a significant presence to the end of simulation (Figure 7a). The temperature treatment accelerates the establishment of evergreen conifers and at some sites causes a complete collapse of larch biomass in many of the low diversity sites around year 200 when the temperature has increased by 4°C (Figure 7b). Successional dynamics in northwestern Siberia represent an exception to this general pattern. The colder regional temperatures in northwestern Siberia do not promote transition from *Larix* spp. to evergreen conifer, rather there is persistent *Larix* spp. dominance (Figure 7d). Northwestern Siberia does not experience the collapse of larch that is seen at sites further south (Figure 7b), but does transition to forests dominated by evergreen conifers in late successional stages in response to warming (Figure 7e). This late successional transition is similar to the natural succession dynamics of central and southern Siberia under base climate conditions (Figure 7a). The effect of the *L. decidua* treatment on *Larix* spp. biomass is immediate and continues to the end of simulation in all low diversity regions (Figure 6), indicating that *L. decidua* easily establishes and contributes to overall biomass in these regions. The inclusion of *L. decidua* in the low diversity regions under base climate conditions delays and suppresses the transition to evergreen conifers. *L. decidua* acts to prevent the collapse of larch in response to warming that is observed in low diversity areas in central Siberia (Figure 7b,c).

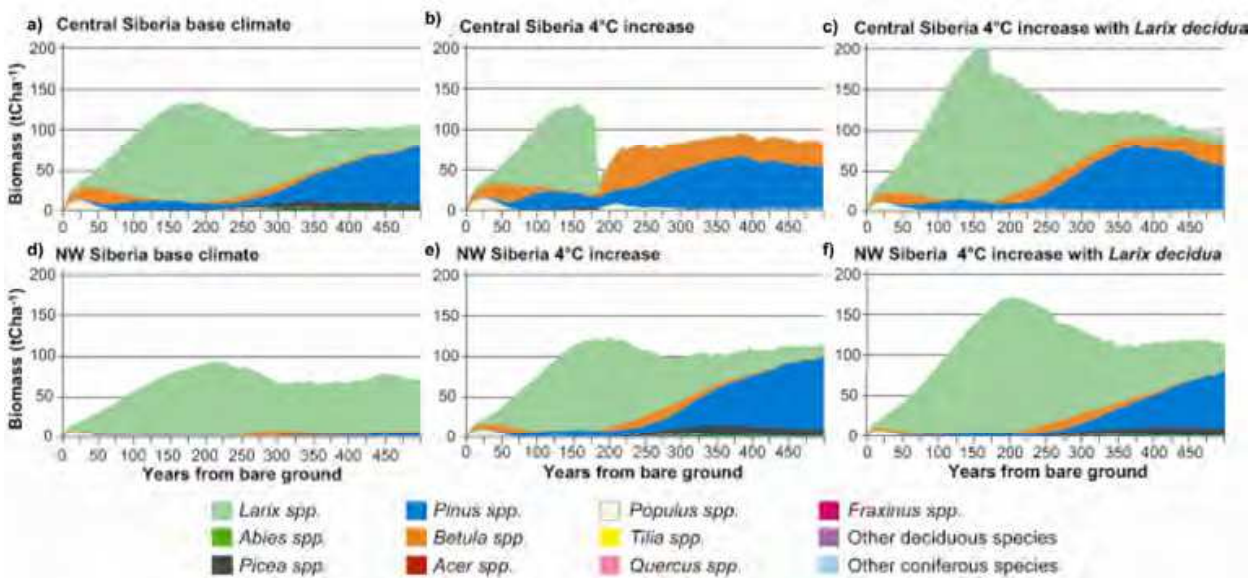


Fig. 7. Simulated mixed species biomass dynamics (tC ha-1) for low diversity sites in Siberia. Species composition by the dominant genera over 500 simulated years starting from bare ground for the base historical climate (a,d), temperature increase (b,e), and temperature increase with *Larix decidua* (c,f).

4. Discussion

4.1 Model simulation across Siberia and RFE

Biomass patterns from simulation of mature forest under historical climate conditions reflect the idea that areas with increased plant diversity have increased productivity (Tilman and Downing 1994; Chapin et al., 1997, Bengtsson et al., 2000), with areas of higher biomass located in the areas of increased diversity in the Amur region of the RFE. The 93 high diversity sites are all located in the Amur region of the RFE and have an average of 38 individual tree species. The remaining 279 sites have an average of 9 individual tree species. The Amur region of the RFE also has higher average temperatures and precipitation values than across Siberia and the remainder of the RFE which allows a more diverse group of species to actively compete and achieve optimal biomass without climate limitations. Similar biomass results from past simulations which allow 44 individual tree species to grow at all sites without range limitation across Siberia and the RFE suggest it is the severe climate, and not a decreased species diversity, which limits the amount of total biomass across the interior of Russia (Shuman and Shugart 2009).

Successional dynamics across the study area under base climate reflect fundamental competition dynamics among species. Larch (*Larix* spp.) is highly tolerant of cold temperatures, but is one of the most shade-intolerant genera in the region (Nikolov and Helmisaari 1992). As the forest matures, competition for light becomes a key factor in determining which species becomes dominant. In northwestern Siberia, the cold temperatures prevent many species from competing with the cold-tolerant larch. Central and southern Siberia do not experience the severely cold temperatures of northwestern Siberia, and evergreen conifers actively compete with larch. Due to the shade-intolerance of larch, these forests transition to evergreen dominance as seen in the base climate simulation (Figure 2a,b,c). The transition from larch to evergreen conifer is also a product of the lack of insect or wildfire disturbance in these simulations. At each site the results are a landscape-level approximation of succession, which includes the natural disturbance caused by the death of individual trees. Warming climate is expected to cause increases in total area burned, fire-season length, and the severity of fire (Overpeck et al., 1990; Kasischke et al., 1995; Stocks et al., 1998; Soja et al., 2004; Soja et al., 2007). Similarly, the incidence of insect disturbance is also expected to become more prevalent with warming conditions (Holling 1992, Volney and Fleming 2000; Logan et al., 2003). Understanding the intrinsic successional dynamics isolates the direct response of the system to changing climate. Establishing the response of the system without the added changes of disturbance provides a strong basis for deconstructing the complexities of the system response to climate change.

4.2 Climate sensitivity analysis

4.2.1 Continental scale discussion

Larch is shade-intolerant and, in all but the coldest regions, evergreen conifers naturally replace larch over time, especially when no disturbance occurs that can rejuvenate the larch by providing open gaps of sunlight (Nikolov and Helmisaari 1992). The shift from deciduous larch to evergreen conifer forest is accelerated across Siberia under warming conditions (Figure 2), and implies a significant change in albedo. Following 200 years of forest development, larch-dominated forests are replaced with evergreen conifer-dominated forests in areas across Siberia. In southern Siberia, where forests are vulnerable to early replacement of larch by evergreen conifer, there would be a local significant albedo shift of

approximately 5.1 W m^{-2} if the larch stands are replaced by evergreen conifers (Shuman et al., 2011). This represents a local increase in average annual absorbed surface radiation of between 2 and 7%. Albedo difference was the driver of the results of the modeling experiments completed by Bonan et al., (1992), Betts (2000), and Snyder et al., (2004) all of whom predicted the effects of such an albedo shift would extend beyond the boundaries of the boreal region. Chapin et al., (2000) documented similar albedo differences between forest and shrub tundra in Alaska with an increase in absorbed radiation leading to a warming trend that extends beyond the tundra. Similar to the modeling results for the boreal region, and the finding from the Alaskan tundra, the albedo shift implied by the successional dynamics shown in our forest simulations have the potential to increase temperatures across the region and create a positive feedback of regional warming. In particular, our results establish that there will be local shifts from larch to evergreen conifer. The resultant increase in the amount of absorbed incoming radiation has the potential to impact surrounding regions and set off a cascade of species shifts towards evergreen conifers, which in turn promote more warming. This positive feedback is of great concern across Siberia.

The response at the continental scale is most similar to the results for the low diversity regions for all treatments. This is not surprising given that 75% of the sites included in the continental-scale analysis are classified as low diversity, with an average of 9 tree species. Historically, this system maintains existing vegetation through cycles of predictable disturbance and succession, which support the regeneration of larch following fire (Chapin et al., 2004). The repetition of this successional sequence across the broad range of climatic conditions found in the boreal region creates a resilient vegetation composition with stable cycles of vegetation states (Chapin et al., 2004). The climate change scenarios considered here modify the vegetation composition in a new way, which in turn alters the successional history and reduces the resilience of vegetation, thereby forcing a new vegetation state to emerge. The larch-dominated forests appear sensitive to an increase in temperature very early in succession when the overall stand age is also young. The evergreen conifer dominated forests seem to be sensitive to changes in precipitation at mid-succession when there is a mix of stand ages from young to mature trees. Mid-succession is also the natural transition point, under base conditions, between larch and evergreen conifer, so the response to precipitation is likely connected with the emergence of evergreen conifers as the dominant species. The connection between precipitation and evergreen conifers is explored in more detail with the regional scale analysis.

At the continental scale, total forest and *Larix* spp. biomass are highly responsive to the *L. decidua* treatment and show a pattern similar to that of the forests in low diversity regions. These results suggest that low species diversity makes the system vulnerable to establishment by a new species, but highlight the potential of the introduction of *L. decidua* to be used in the mitigation or management of the albedo shift caused by transition to evergreen conifer dominance. *L. decidua* has the same characteristics as existing Siberian larch species, and thus forests dominated by this species have higher albedo, and decreased absorbed incoming radiation, when compared to stands of evergreen conifers in the same region. Maintaining larch-dominated stands across the region would delay the positive feedback triggered by the albedo shift that is associated with conversion from deciduous larch to evergreen forest.

4.2.2 High diversity regional and local scale discussion

The response to the temperature and *L. decidua* treatments in the high diversity regions highlights the importance of analysis of local climate and successional dynamics. The climate and *L. decidua* treatments do not have the strong effect on biomass in these high diversity regions of the RFE that is seen at the continental scale and in low diversity regions. Sites in the northern RFE (N RFE) region fall within larch's optimal growth ranges for both temperature and precipitation. Larch establishes strongly and competitively in N RFE in early succession followed by a transition to *Picea* spp. dominance under base climate conditions. The high diversity in the area indicates there is strong competition, and *L. decidua* does not have unique characteristics which allow it to establish in this region.

Under warmer conditions in the N RFE in late succession there is a transition, not to *Picea* spp., but to *Pinus* spp. dominance. This highlights the importance of genus-level analysis. These genera are typically combined into a single evergreen conifer group, both for the purposes of global climate models and for the regional scale analysis presented here. Such a grouping prevents the detection of this shift between the two evergreen conifer species. This shift has the potential for further exploration in association with altered albedo values. Measured in the boreal forest of Canada, the summer albedo difference between *Pinus* spp. (0.086) and *Picea* spp. (0.081) is negligible, but the winter albedo for *Pinus* spp. (0.150) and *Picea* spp. (0.108) is more significant (Betts and Ball 1997). The albedo values in the RFE are likely similar to these Canadian species, and there is potential, with the winter albedo difference, to alter total annual absorption of surface radiation in response to the shift from *Picea* spp. to *Pinus* spp. with warming. Unlike the low diversity regions, the successional dynamics resulting from including *L. decidua* as a species in simulation are similar to those observed in response to warming, with late successional dominance by *Pinus* spp. This result suggests that introduction of *L. decidua* would not be a useful strategy for mitigation of vegetation shifts in this region.

The response to the climate and *L. decidua* treatments in southwestern (SW) RFE is also a product of local climate conditions. The SW RFE region has a climate with temperatures which place it in the upper limit of tolerance for larch, creating a climate in which the native larch species cannot compete and establish. Under base climate conditions, it is difficult for larch to compete, so it is not surprising that larch continues to be absent under warmer conditions. Even with increased tolerance for warmer conditions, *L. decidua* cannot effectively compete with other species in the SW RFE, and does not have a significant impact on biomass. Under base climate conditions, the SW RFE has mixed evergreen and deciduous species in the mature forest late in succession. With warming temperatures, there is an increase in biomass of mixed deciduous trees, and a decrease in evergreen conifer biomass. The decrease of evergreen conifers is balanced by the increase of mixed deciduous trees, so the effect on total biomass is not consistent and lasts only 60 years.

The high diversity areas in the RFE have high ecological resilience and stability, which allow them to maintain basic ecosystem function following climate change and avoid irreversible shifts to another vegetation state. Stability is the ability of a system to return to equilibrium following temporary disturbance, and resilience is the persistence of a system and its ability to absorb change and disturbance without changing state (Holling 1973). In other terms, stability is a persistence of the system state and a consequence of interactions within the

system where the next state of the system is predictable from within the system (Margalef 1968; Lewontin 1969; Child and Shugart 1972). Ecological resilience is therefore related to the magnitude of disturbance or change that can be absorbed before the system transitions to another stability domain (Folke et al., 2004; Gunderson 2000, Peterson et al., 1998). In the N RFE, the successional cycle from larch-dominance to evergreen-dominance is the expected cycle between vegetation states, because this is the response for base climate conditions. Both N RFE and SW RFE respond to an increase in temperature with a shift in the dominant species during late succession, but these late successional groups are functionally similar to the assemblage of species that exist under the base climate. This is an indication that this group of high diversity regions in the Amur region of the RFE does not experience a change in vegetation state with in response to climate change, and is resilient to the perturbations associated with this amount of climate change.

The concept of response diversity adds to the conclusion that the system in the Amur region of the RFE is resilient by defining the range of reactions to environmental change among species contributing to the functioning of a given ecosystem (Elmqvist et al., 2003; Folke et al., 2004). The RFE region has high response diversity, which means that it has functionally similar species sets which respond differently to environmental change and provide a buffer that protects the system against failure and increases tolerance to disturbance or climate change (Elmqvist et al., 2003; Folke et al., 2004). In other words, there are species in the system capable of maintaining the original state of ecosystem function under the new conditions following change; a concept also known as the insurance hypothesis (Folke et al., 1996, Naeem and Li 1997). High response diversity within an ecosystem increases the chances of reorganization or restart of the system into the desired state after disturbance (Chapin et al., 1997; Bengtsson et al., 2000; Elmqvist et al., 2003). The altered climate disturbed the ecosystem, but because of the high diversity of the SW and N RFE, the species can reorganize and maintain the same vegetation state and ecosystem function that is observed throughout succession when the system is not disturbed by climate change. Therefore the diversity of species in this region allows for replacement of one species with another functionally similar one under new climate conditions. It is also the adaptability of the system under altered climate which prevents a substantial contribution to biomass from the introduction of *L. decidua*. Neither a change in climate, nor the addition of a single species (*L. decidua*) leads to a change in ecosystem function in this high diversity system.

It is important to note that the RFE regions analysed display ecological resilience and high response diversity for the both temperature increase and precipitation change treatments evaluated. There is a response to temperature in both regions, but not at the same magnitude as that of the low diversity areas. These results suggest that increased amounts of climate change may have a stronger impact on the system. Further analysis is necessary to determine if the RFE system is equally resilient when the temperature is increased by more than 4°C, or if it can restart under this altered climate condition following disturbance, such as fire or insect outbreak, that take the system back to bare ground. The results seen in this study indicate only a slight sensitivity of the mid- to late-successional stages, at and beyond year 200, which correspond to the time in the simulation when the temperature had increased to 4°C. The early successional stages are comprised of a different set of species which may not show the same high resilience or response diversity displayed by the mid- to late-successional stages in the RFE.

4.2.3 Low diversity regional and local scale discussion

The response of the low diversity regions to the altered climate treatment is similar to that observed at the continental scale. These low diversity regional scale responses, in conjunction with the low average diversity across the 372 sites considered at the continental scale, further emphasize the difference of the response in the high and low diversity areas. Similar to analysis at the continental scale, the response of the low diversity regions to treatments is connected to the transition from larch to evergreen dominance, which occurs across the southern and central portion of Siberia, and is accelerated by warming. Northwestern Siberia has the coldest temperatures compared to the other regions, and these cold temperatures naturally suppress evergreen conifer establishment during late succession under base climate. The patterns of successional dynamics in central Siberia under base conditions and in northwestern Siberia in response to warming climate suggest that the model is predicting consistent transitions. Under warming conditions, northwestern Siberia is exposed to temperatures more similar to those in the base condition in central Siberia. Thus, the forests in northwestern Siberia have similar dynamics under warming conditions to those seen in the central Siberia region for the base climate (Figure 7a,e). The temperature treatment results suggest that, with 4°C of warming, the larch-dominated system across southern and central Siberia will be prematurely replaced with evergreen conifer and other deciduous trees, and the forests of northwestern Siberia will warm enough that evergreen conifers will be able to effectively establish.

The lack of response in northwestern and southern Siberia, and the late response in central Siberia, to the effect of precipitation change suggests a connection between evergreen conifer presence and seasonal precipitation. The precipitation treatment is significant in only one of the low diversity regions analyzed (i.e., central Siberia). Within the central Siberia region there is a short-lived response of total forest biomass to precipitation change at year 240, and a longer period of response of evergreen conifer biomass from year 300 to 500. Of the six regions analyzed, central Siberia has one of the lowest average seasonal precipitation curves; it is closest to that of northwestern Siberia. Forests within central Siberia naturally transition from a larch-dominated to an evergreen-conifer dominated system, with larch as a secondary species (Figure 7a). This successional transition is similar to local dynamics at sites in both East and West Irkutsk, regions in southern Siberia that both have higher precipitation than central Siberia. Northwestern Siberia, which has similar precipitation to central Siberia, does not experience a natural shift from larch- to evergreen conifer-dominance. The colder regional temperatures in northwestern Siberia suppress evergreen conifer growth, thereby helping larch to maintain dominance (Figure 7d). These observations suggest that the precipitation treatment response in central Siberia is a result of both the lower seasonal precipitation, and the presence of evergreen conifers late in succession in this region. In other words, the transition from larch- to evergreen conifer-dominant in central Siberia, combined with the low annual precipitation, creates a region which is responsive to precipitation change (Figure 6). The variability across the low diversity regions suggests that differences in response to climate treatments are a result of local conditions and species composition over time. The continental scale analysis shows a response to precipitation for both total forest and evergreen conifer biomass. This suggests that many of the sites considered in this continental scale analysis have low seasonal precipitation, and are dominated by moisture-sensitive evergreen conifers later in succession.

There are marked differences between the results for the high and the low diversity regions, which demonstrate differences in the stability and resilience of these regions. The high diversity areas of the RFE have high ecological resilience and maintain basic ecosystem function as a result of similarly functioning species replacing one another following climate

change. The low diversity regions, however, have low resilience and cannot maintain basic ecosystem function following climate change, specifically temperature increase. This is shown by the collapse of dominant larch species following the 4°C increase in sites in central and southern Siberia, and the fact that the northwestern Siberia sites shift to an entirely new stable state, which is not seen under base conditions in this region, in response to warming climate conditions. The collapse of larch in southern regions in response to a temperature increase suggests that larch is particularly vulnerable, and that the systems' response threshold may be exceeded with the 4°C increase. With fewer species present, it is more likely that extinctions will alter ecosystem processes (Chapin et al., 1997). Furthermore, the diversity of the area is so low that there are no species capable of fulfilling the original ecosystem function under the new conditions following change. Additionally, differences in sensitivity among functionally different species, in this case larch and evergreen conifers, make the ecosystem vulnerable to change (Chapin et al., 1997).

Holling (1992) hypothesized that the vegetation of the boreal forest would buffer initial climate changes, but that there would be a limit to the buffering and an abrupt vegetation change would follow. These results follow Holling's hypothesis and suggest an abrupt shift in vegetation in response to temperature increase. This abrupt vegetation change is congruent with the identification of this system as having low resilience and stability when compared with the high diversity areas of the RFE. Chapin et al., (2004) suggested that vegetation within central portions of the boreal forest would remain stable for long periods followed by abrupt changes to a new state, which is what we see in the results for the low diversity areas in central Siberia. Low diversity areas do not have the appropriate pool of species to continue the cycle of succession and reorganization following change, thus the system in these areas is flipped into a different state (Bengtsson et al., 2000). The results presented here are consistent with field measurements documenting the shift of treelines northward or upslope of previous climate limits, and a reduction in cone and seed yield for *L. sibirica* (Kharuk et al., 2009; Soja et al., 2007). They are also consistent with bioclimatic model results predicting a replacement of taiga with forest-steppe or steppe environments across southern Siberia (Tchebakova et al., 2005; Vygodskaya et al., 2007; Tchebakova et al., 2009). These results also suggest that warming temperatures will lead to a shift in the ability of larch to establish and may signal a collapse of the species in this genus.

The introduction of *L. decidua* to the low diversity sites may help to buffer the perturbations associated with a warming climate. Unlike the high diversity regions in the RFE, the low diversity areas showed a strong response of biomass to the inclusion of *L. decidua*. Local scale analysis with warming conditions shows that the inclusion of *L. decidua* prevents the collapse of larch in central Siberia and delays transition to evergreen conifer dominance in northwestern Siberia. *L. decidua* is competitive in this low diversity area, and fills an important functional niche when temperatures are increased. Existing larch species cannot tolerate the warmer conditions, and their collapse opens functional space for the warm adapted *L. decidua*. These results, though theoretical, provide evidence that it is possible to address the issue of species replacement, and associated albedo shift, with techniques involving species management or introduction.

5. Conclusion

The FAREAST model was used to simulate forest successional dynamics across a region with broad geographic and climatic variability, and examine the behavior of forests at

different scales in response to altered climate. The model simulated forest growth at high diversity sites in the Amur region of the RFE and low diversity sites across Siberia and the remainder of the RFE. The model successfully captures the natural successional dynamics of forests for base climate conditions across the area.

Results of the climate sensitivity analysis indicate that a 4°C increase impacts the biomass of the total forest, *Larix* spp., and evergreen conifers at the continental scale, and in low diversity regions, early in succession. The effect of temperature is highly significant throughout most of the simulation in low diversity areas, whereas there is little effect of temperature in high diversity regions. Results at the continental scale suggest that the forests across much of Siberia and the RFE behave as a low diversity system. The early effect of temperature, across areas where larch is naturally dominant in early succession, suggests that larch is particularly vulnerable to temperature increase. In areas outside the cold northern portion of Siberia, larch is shown to abruptly collapse in response to warming. The effect of altered precipitation was significant at the continental scale, and in one low diversity region in central Siberia in mid- to late-succession following evergreen conifer establishment. Central Siberia, in addition to experiencing a late successional shift from larch- to evergreen conifer-dominance, has low seasonal precipitation. This suggests that sites that respond to the precipitation treatment have low annual precipitation, and are dominated by moisture-sensitive conifers. The precipitation effect was not significant in the high diversity regions, which have different dominant evergreen species in late succession.

Concepts of ecological stability and resilience are used to explain the variable response of the high and low diversity areas to altered climate. The high diversity regions showed high stability and resilience for they maintained overall species and biomass dynamics in response to changing climate, and had replacement of one species by a functionally similar species under new climate conditions. Unlike the high diversity regions, the low diversity regions across Siberia show low ecological stability and resilience. The low diversity areas displayed a strong response of biomass to the climate treatments, and locally showed the collapse of the dominant larch species under increased temperatures. It is this the lack of diversity in the response of functionally similar species to environmental change, and thus an inability to maintain ecosystem function with altered conditions, which creates the low ecological stability across the low diversity areas of Siberia.

L. decidua, the warmer adapted European larch, was added to the species list to gauge the potential of this species to prevent a premature shift to evergreen vegetation, and the associated albedo shift, in response to climate change. *L. decidua* established strongly in the low diversity system, but not in the high diversity areas of the RFE. Due to the increased diversity in the Amur region of the RFE, there are native species which can fill the same functional space under new climate conditions as the species which were dominant under base climate conditions, thereby creating high resilience and stability. It is this pool of locally available species which prevents *L. decidua* from significantly impacting biomass in the high diversity regions of the RFE. Within the low diversity regions, however, local scale results show that *L. decidua* becomes established and acts to prevent the collapse of larch in response to warming and delay the shift to an evergreen conifer-dominated forest. It is the low diversity which contributes to the lack of resilience and stability under altered climate, but also allows for strong establishment of *L. decidua*. Therefore *L. decidua* is uniquely adapted to establish in this low diversity system as well as to prevent the positive feedback associated with a premature shift to evergreen conifer-dominance.

This study establishes that larch-dominated forests across Siberia will transition to a different vegetation state, and have an altered species composition, in response to climate

change, especially increased temperature. *L. decidua* has been identified as a species capable of strong establishment across Siberia, and with the capacity to prevent the positive feedback associated with vegetation shift, from larch to evergreen conifer, in the region. These results deal with the response of the current system to controlled climate change. Future studies need to address the ability of the system to restart following disturbance, under altered climate conditions. Early successional species, such as larch may not be able to establish dominance in conditions, which have already warmed. In this case, the expected successional dynamics will be completely altered.

These results highlight potential for the use of remote sensing data in areas identified as vulnerable to vegetation change. Modeling studies offer the opportunity to identify a signature of climate change in vegetation dynamics in advance of those changes occurring on the ground. Remote sensing technology can be used to track land cover changes in areas identified by model results as vulnerable to vegetation shift. Furthermore, the results of this study identify a positive feedback cycle where warming creates vegetation shift, which then creates further warming. The detailed vegetation maps derived from remote sensing data offer a capability to evaluate locations where vegetation shift has occurred in an effort to track the progress of this positive feedback cycle and assess the direction and magnitude of any albedo shift associated with such a change. Vegetation monitoring informed by modeling efforts provide a robust tool in responding to and identifying vegetation changes due to climate change.

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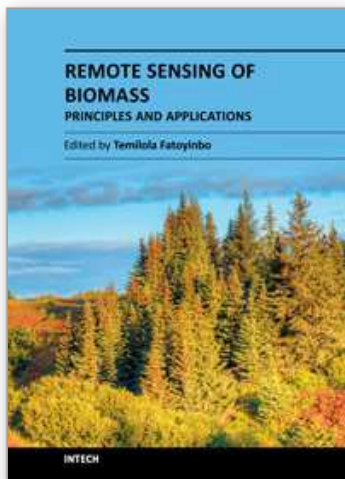
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Remote Sensing of Biomass - Principles and Applications

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The accurate measurement of ecosystem biomass is of great importance in scientific, resource management and energy sectors. In particular, biomass is a direct measurement of carbon storage within an ecosystem and of great importance for carbon cycle science and carbon emission mitigation. Remote Sensing is the most accurate tool for global biomass measurements because of the ability to measure large areas. Current biomass estimates are derived primarily from ground-based samples, as compiled and reported in inventories and ecosystem samples. By using remote sensing technologies, we are able to scale up the sample values and supply wall to wall mapping of biomass. Three separate remote sensing technologies are available today to measure ecosystem biomass: passive optical, radar, and lidar. There are many measurement methodologies that range from the application driven to the most technologically cutting-edge. The goal of this book is to address the newest developments in biomass measurements, sensor development, field measurements and modeling. The chapters in this book are separated into five main sections.

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51000 Rijeka, Croatia
Phone: +385 (51) 770 447
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Unit 405, Office Block, Hotel Equatorial Shanghai
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中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

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