

Responses of Tree Species to Climate Warming at Different Spatial Scales

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Abstract: Tree species respond to climate change at multiple scales, such as species physiological response at fine scale and species distribution (quantified by percent area) at broader spatial scale. At a given spatial scale, species physiological response and distribution can be correlated positively or negatively. The consistency of such correlation relationships at different spatial scales determines whether species responses derived from local scales can be extrapolated to broader spatial scales. In this study, we used a coupled modeling approach that coupled a plot-level ecosystem process model (LINKAGES) with a spatially explicit landscape model (LANDIS). We investigated species physiological responses and distribution responses to climate warming at the local, zonal and landscape scales respectively, and examined how species physiological response and distribution correlated at each corresponding scale and whether the correlations were consistent among these scales. The results indicate that for zonal and warming-sensitive species, the correlations between species physiological response and distribution are consistent at these spatial scales, and therefore the research results of vegetation response to climate warming at the local scale can be extrapolated to the zonal and landscape scales. By contrast, for zonal and warming-insensitive species the correlations among different spatial scales are consistent at some spatial scales but at other scales. The results also suggest that the results of azonal species at the local scale near their distribution boundaries can not be extrapolated simply to broader scales due to stronger responses to climate warming in those boundary regions.

Keywords: climate warming; vegetation response; local scale; zonal scale; landscape scale; LANDIS; Changbai Mountains

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1 Introduction

Forest ecosystem may change as a result of climate warming induced by increasing CO₂ and other greenhouse gases (Chris *et al.*, 2004). Tree species respond to climate change at multiple scales (Hansen *et al.*, 2001). At fine scale increased temperature and changed precipitation caused by climate warming, directly affect physiological processes of individual trees (Prentice *et al.*, 1992) and consequently alter the suitability of local environment to individual tree species. Such suitability

can be quantified by species establishment coefficient (SEC), a parameter measuring individual species response to environment. Due to spatial heterogeneity of environmental factors (such as climatic, topographic and edaphic factors), SECs can be variable spatially. Since spatial heterogeneity increases with increasing spatial resolutions (or the level of study detail), studying SECs on different spatial resolutions may allow extrapolating species physiological response from fine scale (plot) to broader spatial scales. At broader spatial scales, altered SEC due to climate warming may lead to different spe-

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cies composition and spatial distribution. Tree species distribution responding to climate warming is the result from complex of environment, competition, habitat and fragmentation. At a given spatial scale, species physiological response and distribution can be positively or negatively correlated. These response correlations are not always consistent across different spatial scales.

Numerous studies have investigated forest ecosystem response to climate change (Goulden *et al.*, 1996; Iverson and Prasad, 1998). Many studies were conducted at plot level (local, more experimentally tractable scales), whereas others focused at broad-scale including spatial processes such as species dispersal, migration (Hansen *et al.*, 2001; Iverson *et al.*, 2004), and disturbance (Lenihan *et al.*, 2003). Some researchers used statistical methods to identify the response of vegetation to atmosphere, and some focused on computer simulations in coupled vegetation-climate models (Notaro *et al.*, 2005; Liu *et al.*, 2006). Previous studies generally examined the forest response as a result of multiple-processes or single process at one spatial scale, whereas tree species responses to climate change are at multiple scales. Increasing attention has been paid to the researches on vegetation response to climate warming at different spatial scales (Pearson and Dawson, 2003; Opdam and Wascher, 2004).

We chose the Changbai Mountains Natural Reserve in Northeast China as the study area because of its sensitivity to climate change and the detailed data available in this area (Hao *et al.*, 2001; He *et al.*, 2005). The objective of this study is to investigate whether the correlation relationships of tree species physiology and distribution at different spatial scales are consistent in responding to climate change. Specifically, 1) we examined species physiological responses and distribution responses to climate warming at the local (equivalent to land cover type in this study), zonal (equivalent to elevation zone) and landscape (equivalent to study area) scales; 2) we investigated how the physiological response and distribution correlated at each spatial scale; and 3) we examined whether the correlations were consistent at the local, zonal, and landscape scales. Consistent relationships among different scales suggest that climate warming effects found at one scale may be extrapolated to another scale. We used a coupled modeling approach that coupled a plot-level ecosystem process model with a spatially explicit landscape model. Species

physiological response (quantified by SEC) was derived from the ecosystem process model that used the plot observational data (e.g., weather, soil, vegetation, *etc.*) as input. Species distribution (quantified as species percent cover) was derived from the landscape model that used SEC as an input.

2 Materials and Methods

2.1 Study sites

The Changbai Mountains National Natural Reserve (CMNNR) and its 8-km surrounding area (41°62'–42°49'N, 127°59'–128°38'E) was selected as the study area, with a total area of 4.1×10^5 ha (Fig. 1). The CMNNR is a dormant volcano site in the eastern Jilin Province of Northeast China. There are four vertical vegetation/elevation zones from 610 m at the lowest elevation to 2691 m at the summit of the Changbai Mountains. 1) Hardwood forest zone (lower than 750 m a. s. l.), where human activities have transformed the pine-hardwood forests into those mainly composed of hardwoods. 2) Korean pine hardwood forest zone (750–1100 m a. s. l.), including Korean pine (*Pinus koraiensis* Sieb. et Zucc), aspen (*Populus davidiana* Dode), birch (*Betula platyphylla* Suk), basswood (*Tilia amuresis* Rupr), ash (*Fraxinus mandshurica* Rupr), oak (*Quercus Mongolica* Fisch), maple (*Acer mono* Maxim) and elm (*Ulmus propingua* Koidz). 3) Spruce-fir forest zone (1100–1700 m a. s. l.), dominated by spruce (*Picea jezoensis* var. *domarovii*) and fir (*Abies nephrolepis* (Trautv.) Maxim), with characteristics typical of boreal forests. 4) Subalpine birch forest zone (1700–2000 m a. s. l.), dominated by mountain birch (*Betula ermanii* Cham) and larch (*Larix olgensis* Henry). There are tundra, bare rock and a volcanic lake above 2000 m a. s. l.

There are four long-term monitoring plots located in main elevation zones of the Changbai Mountains, and these plots cover four land cover types, including Korean pine hardwood forest at a lower elevation (located in Korean pine hardwood forest zone), Spruce-fir forest at a lower elevation (located in Spruce-fir forest zone near Korean pine hardwood forest zone), Spruce-fir forest at a higher elevation (located in Spruce-fir forest zone near Subalpine birch forest zone), and Subalpine birch forest (located in Subalpine birch forest zone) (Fig. 1). These four land cover types were used to examine species physiological responses and distribution re-

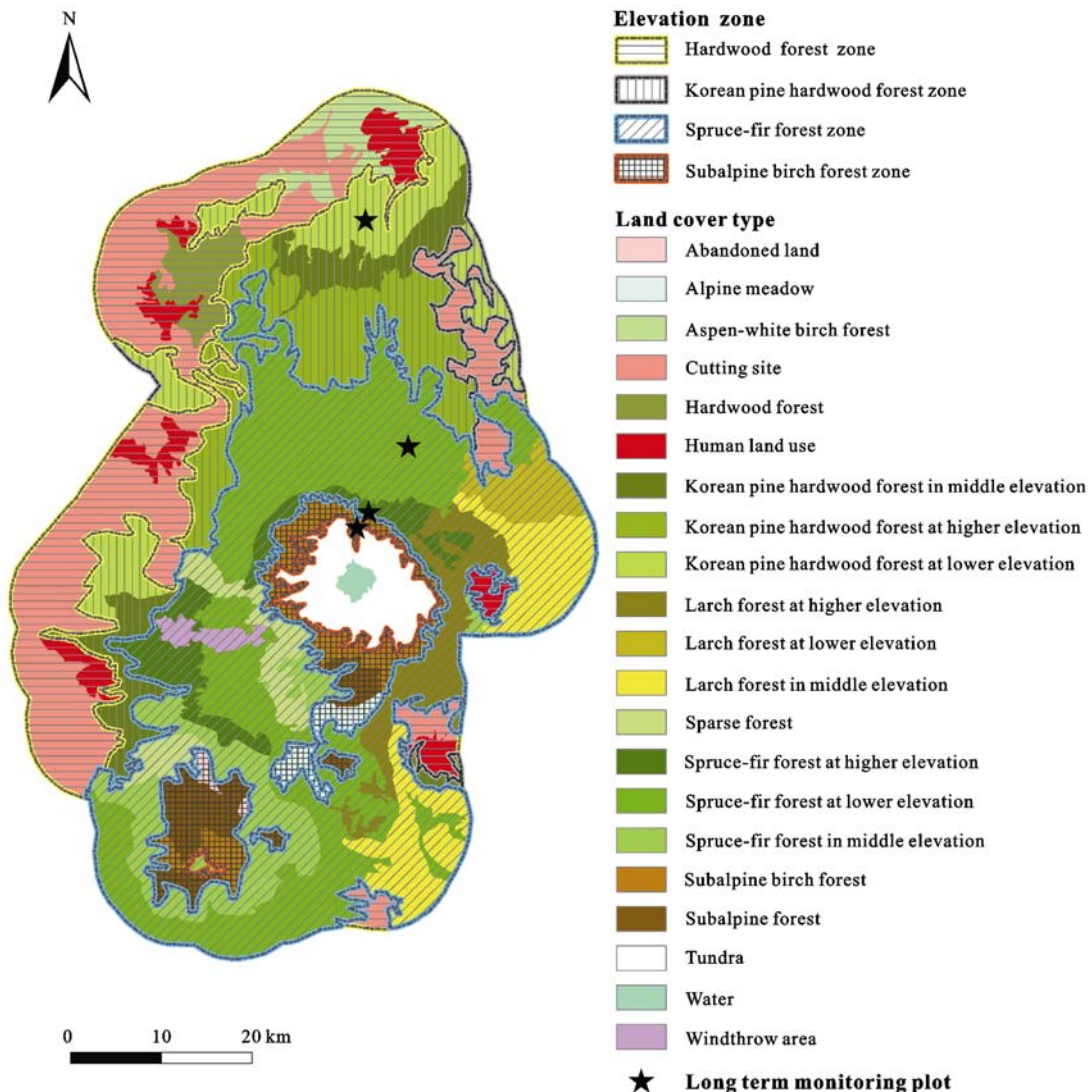
sponses to climate warming at the local scale. The three elevation zones where these four land cover types reside were used to examine species physiological responses and distribution at the zonal scale. The entire study area was used to examine these responses at the landscape scale.

2.2 Model simulation

For each land cover type, the current climate data were interpolated based on climate data recorded at meteorological stations using ArcGIS. The results were converted into 12 Arc/Info grids, which represent current temperature distribution from January to December (He *et al.*, 2005). The warming climate data were generated

from the second version of the Canadian Global Coupled Model (CGCM2) (Flato and Boer, 2001). The predicted result of temperature change between 1990 and 2090 is linear, indicating that warming will occur gradually over the next 100 years, as predicted by previous studies (Flato and Boer, 2001), and that resultant warmed conditions persist for the simulation years after 2090.

Within each land cover type, an ecosystem process model (LINKAGES) (Pastor and Post, 1985; Post and Pastor, 1996) was used to simulate the physiological responses of each species to both the current and the warming climate (Hao *et al.*, 2001; He *et al.*, 2005). To automate input of spatial environmental data sets re-



The land cover types were derived from a classified remote sensing image (Shao *et al.*, 1996)

Fig. 1 Major land cover types and elevation zones in study area

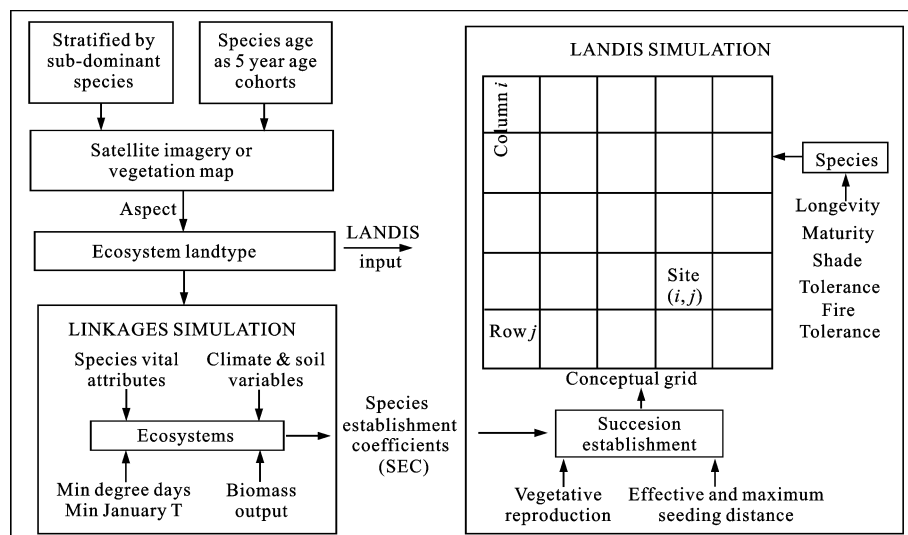
quired by LINKAGES, an ArcInfo AML (Arc Macro Language) program was written to assist in locating sample points. Sampling was stratified by land cover types. A total of 30–100 samples were randomly selected within each land cover type depending on its size, and the program then calculated the means of all the climatic and soil variables to represent the land cover type. These means were used as LINKAGES environmental input variables for every land cover type and equilibriums of individual species biomass were simulated under the current and warming climate scenarios. The biomasses were converted to two sets of species establishment coefficients for the current climate (SEC_c), and for the warming climate (SEC_w) using an approach described by He *et al.* (1999). Values of SEC range from 0 to 1, with high establishment coefficients having higher probabilities of establishment (Mladenoff and He, 1999). At the zonal or landscape scale, the SEC of a certain elevation zone or the entire study area was calculated by area-weighting SECs of all land cover types included in the elevation zone or study area.

The LINKAGES model was coupled with a spatially explicit forest landscape model (LANDIS), which used SECs as input parameters and simulated forest succession and landscape process (dispersal) for both the current climate and warming climate (He *et al.*, 2005) (Fig. 2). We used LANDIS 6.0 (www.missouri.edu/~landis.

htm), an expanded version of LANDIS 4.0 (He *et al.*, 2005), to simulate 12 most common tree species (*Pinus koraiensis*, *Picea jezoensis*, *Abies nephrolepis*, *Betula ermanii*, *Betula platyphylla*, *Larix olgensis*, *Quercus Mongolica*, *Fraxinus mandshurica*, *Acer mono*, *Populus davidiana*, *Tilia amuresis*, *Ulmus propingua*) from 1990 to 2190 at five years of time step. Each simulation run was replicated five times. All spatial data were initialized at the resolution of 100 m × 100 m, compatible with previous simulation studies, which yielded 960 rows and 647 columns (He *et al.*, 2005). Disturbance such as forest harvesting, fire, and wind were not simulated because our objective was to examine the natural successional trajectories of the main dominant species. The species percent areas at the local, zonal and landscape scales were derived from simulation results of LANDIS.

2.3 Data analysis

In a first step, we examined species physiological response to climate change by comparing SEC_c and SEC_w, and examined species distribution responses by comparing the differences of species percent areas between the two climate scenarios, for each of the three spatial scales (the local, zonal and landscape scales). LANDIS 6.0 statistics was used to process outputs of LANDIS (total areas of the simulated species) at three spatial scales. These statistical results were summarized



Species establishment coefficients can be derived from LINKAGES, which synthesizes individual species responses to various climate and environmental conditions

This figure is revised based on He *et al.*, 1999

Fig. 2 Major components of LANDIS model and link with LINKAGES model

as percentage cover (the number of pixels in which a species occurs divided by the total number of pixels) by forest ecosystem. Paired sample T test in SPSS 16.0 was used to analyze variance of species percent areas between the current and warming climate scenarios at the local, zonal and landscape scales. There was significant difference between the current and warming climate scenarios if p -value in Paired sample T test was lower than 0.05.

In a second step, we investigated how species physiological response and percent area correlated (positively or negatively) at each spatial scale. For example, for one species, the SEC increases after climate change (SEC_w is higher than SEC_c), and likewise, the mean of percent area under the warming climate is statistically higher than that under the current climate. This case is a positive correlation between species physiological response and distribution.

Finally, we investigated whether these correlation relationships were consistent among the local, zonal and landscape scales. We compared the consistency of correlations between species SEC and species percent area for Korean pine hardwood forest, spruce-fir forest and sub-alpine birch forest at the local, zonal, and study area scales.

3 Results

3.1 Correlations of species physiological response and distribution at local scale

At the local scale, SECs of *Pinus koraiensis* under the warming climate were higher than SECs under the current climate (SEC_c = 0.645 and SEC_w = 0.713 in Korean pine hardwood forest at lower elevation, SEC_c = 0.155 and SEC_w = 0.268 in spruce-fir forest at lower elevation). However, the increase of *Pinus koraiensis* percent areas under the warming climate was less than that under the current climate in both land cover types (Fig. 3a1 and 3a2; $p < 0.05$). This suggests that *Pinus koraiensis* physiological response and distribution response to climate warming showed negative correlations in the two land cover types.

For *Picea jezoensis* and *Larix olgensis*, SECs under the current climate were lower than SECs under the warming climate in spruce-fir forest at lower elevation, spruce-fir forest at higher elevation and subalpine birch forest. There was no significant difference in percent

areas of *Picea jezoensis* between the current and warming climate scenarios in spruce-fir forest at lower elevation (Fig. 3b1; $p > 0.05$). However, significant differences occurred in spruce-fir forest at higher elevation and subalpine birch forest ($p < 0.05$). Moreover, the means of *Picea jezoensis* percent area under the warming climate were higher than that under the current climate in the two land cover types (Fig. 3b2 and 3b3). This indicates that *Picea jezoensis* shows a negative correlation between physiological response and distribution in spruce-fir forest at lower elevation, while positive correlations in both spruce-fir forest at higher elevation and subalpine birch forest. By contrast, percent areas of *Larix olgensis* under the warming climate do not differ significantly with those under the current climate in both spruce-fir forest at lower elevation and spruce-fir forest at higher elevation (Fig. 3c1 and 3c2; $p > 0.05$), while the increase of *Larix olgensis* percent area under the warming climate is more dramatically than that under the current climate in subalpine birch forest (Fig. 3c3; $p < 0.05$). This demonstrates that for *Larix olgensis*, negative correlations between physiological response and distribution occurred in spruce-fir forest at higher elevation and spruce-fir forest at lower elevation, while positive correlation in subalpine birch forest.

SEC_w (0.062) of *Betula ermanii* was lower than SEC_c (0.344) in spruce-fir forest at higher elevation, while SEC_w (0.274) was higher than SEC_c (0.140) in subalpine birch forest. However, the means of percent area under the warming climate were lower than under the current climate in both land cover types (Fig. 3d1 and 3d2; $p < 0.05$). This suggests that positive correlation between *Betula ermanii* physiological response and distribution occurred in spruce-fir forest at higher elevation, while negative correlation in subalpine birch forest.

3.2 Correlations of species physiological response and distribution at zonal scale

At the zonal scale, SECs of *Pinus koraiensis* under the warming climate were higher than SECs under the current climate (SEC_c = 0.484 and SEC_w = 0.553 in Korean pine hardwood forest zone, SEC_c = 0.089 and SEC_w = 0.141 in spruce-fir forest zone). However, the increase of *Pinus koraiensis* percent areas under the warming climate was less than that under the current climate in both land cover types (Fig. 4a1 and 4a2; $p <$

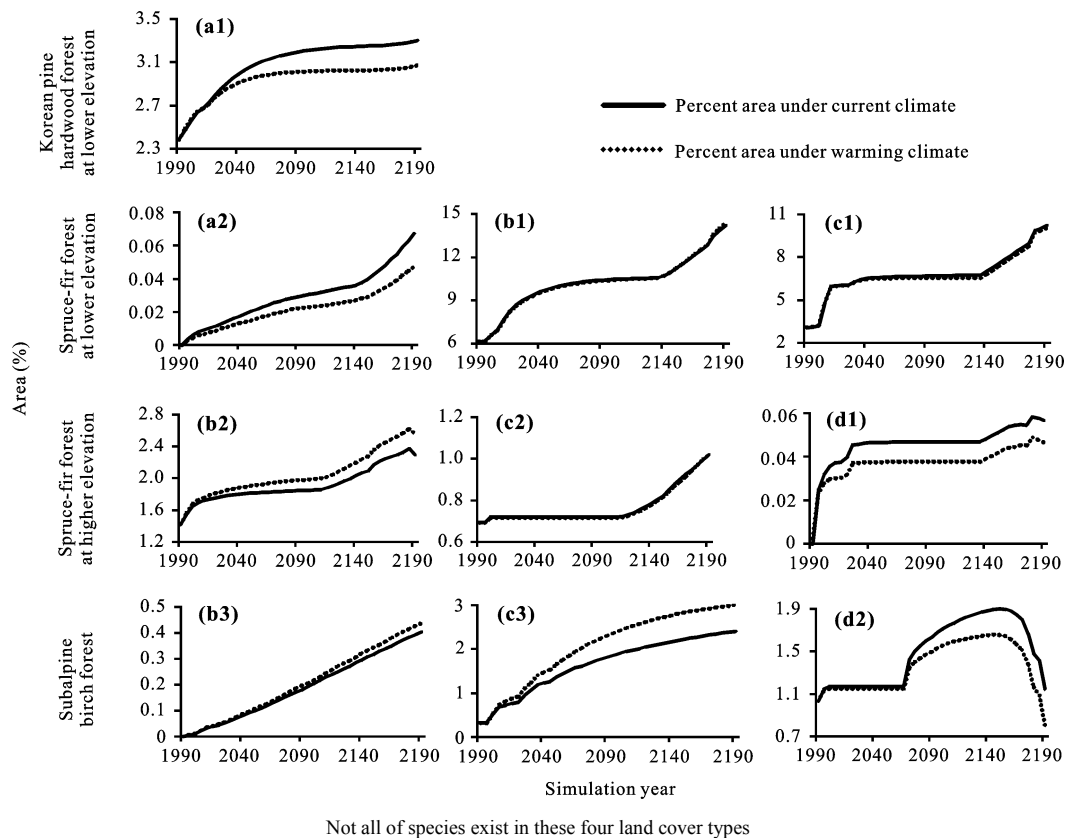


Fig. 3 Simulated percent areas of *Pinus koraiensis* (a), *Picea jezoensis* (b), *Larix olgensis* (c) and *Betula ermanii* (d) from 1990 to 2190 under current and warming climate scenarios at local scale

0.05). This illustrates that *Pinus koraiensis* also shows negative correlations between physiological response and distribution at the zonal scale.

SECs of *Picea jezoensis* and *Larix olgensis* under the current climate were lower than SECs under the warming climate in both spruce-fir forest zone and subalpine birch forest zone. No significant difference occurred in percent area of *Picea jezoensis* and *Larix olgensis* under two climate scenarios in spruce-fir forest zone (Fig. 4b1 and 4c1; $p > 0.05$), however, significant difference occurred in subalpine birch forest zone (Fig. 4b2 and 4c2; $p < 0.05$). This suggests that for *Picea jezoensis* and *Larix olgensis*, the relationships of physiological responses and distribution are positive correlations in subalpine birch forest zone, while negative correlations in spruce-fir forest zone.

Similar to the results of *Betula ermanii* at the local scale, SEC_w (0.164) was lower than SEC_c (0.310) in spruce-fir forest zone, and SEC_w (0.307) was higher than SEC_c (0.194) in subalpine birch forest zone. Percent area of *Betula ermanii* has no significant difference between the current and warming climate in spruce-fir

forest zone (Fig. 4d1; $p > 0.05$). However, in subalpine birch forest zone, the changes of *Betula ermanii* percent areas under warming were less than under the current climate (Fig. 4d2; $p < 0.05$). These results show that negative correlations between physiological response and distribution occurred in both land cover types.

3.3 Correlations of species physiological response and distribution at landscape scale

At the landscape scale, SECs of *Pinus koraiensis* and *Picea jezoensis* under the warming climate were higher than those under the current climate. Percent areas of *Pinus koraiensis* under two climate scenarios were increasing from 1990 to 2190 (Fig. 5a). However, the increase of *Pinus koraiensis* percent area under the warming climate was less than that under the current climate ($p < 0.05$). Trajectory of percent cover for *Picea jezoensis* suggested that its abundance increased significantly, from 11.6% to 26.8% under the current climate, and from 11.6% to 27.3% under the warming climate during the entire simulation period (Fig. 5b). Percent area of *Picea jezoensis* under the warming cli-

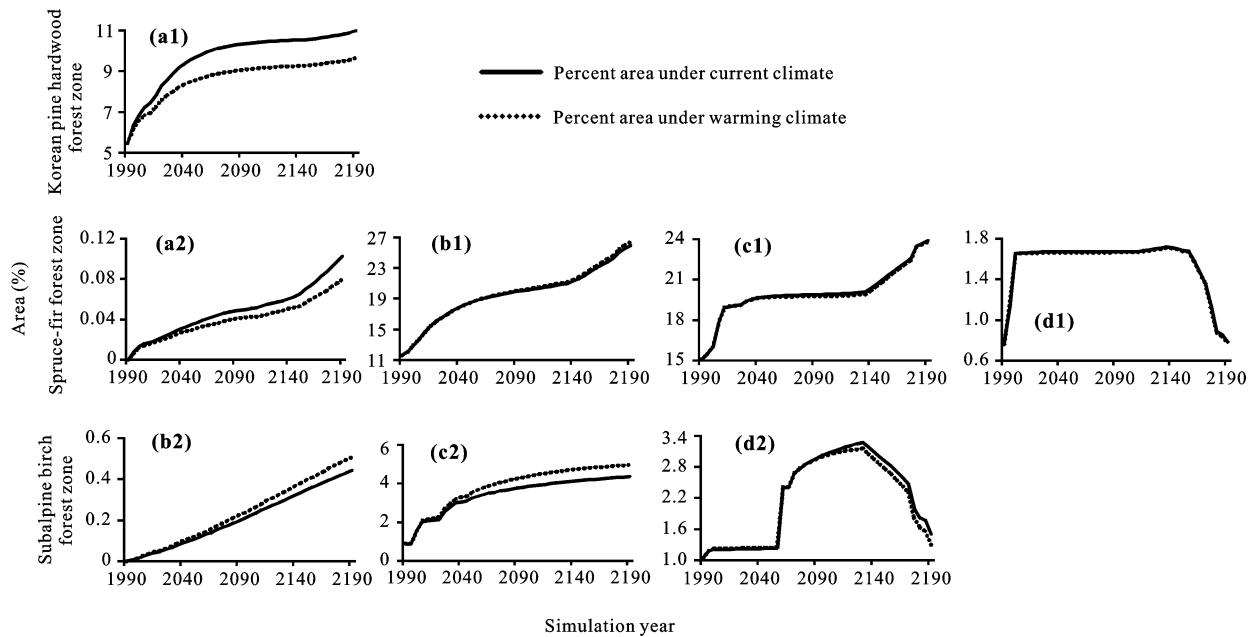


Fig. 4 Simulated percent areas of *Pinus koraiensis* (a), *Picea jezoensis* (b), *Larix olgensis* (c) and *Betula ermanii* (d) from 1990 to 2190 under current and warming climate scenarios at zonal scale

mate was not different significantly with that under the current climate at the landscape scale (Fig. 5b; $p > 0.05$), which illustrated that *Picea jezoensis* was an insensitive species to warming.

SECs of both *Larix olgensis* and *Betula ermanii* decreased with climate warming. Percent area of *Larix olgensis* was increasing with fluctuations under natural succession from 15.9% in 1990 to 29.4% in 2190. Under the warming climate, however, *Larix olgensis* increased more dramatically (Fig. 5c) because of the favorable conditions and relatively lower competition from other species. *Betula ermanii* is the dominant species in alpine forest. Starting in 1990, the percent cover of *Betula ermanii* was 1.8%; by 2190 it will reach 3.0% under the current climate and 2.8% under the warming climate. Statistical results indicates that there is no significant difference in the percent area between under the warming and current climate (Fig. 5d; $p > 0.05$), which illustrates that *Betula ermanii* is also a warming-insensitive species.

The above results indicate that for *Pinus koraiensis*, *Picea jezoensis*, *Larix olgensis* and *Betula ermanii*, the correlations between physiological responses and distribution responses to climate warming were all negative at the landscape scale.

3.4 Consistency among different scales

On the one hand, there were some situations that corre-

lation relationships of species physiological responses and distribution responses to climate warming were consistent among different scales. The correlation relationships of *Pinus koraiensis* physiological response and distribution were consistent among Korean pine hardwood forest at lower elevation (the local scale), Korean pine hardwood forest zone (the zonal scale) and study area (the landscape scale). Similarly, the correlations of *Pinus koraiensis*, *Picea jezoensis* and *Larix olgensis* were also consistent among spruce-fir forest at lower elevation (the local scale), spruce-fir forest zone (the zonal scale) and study area. Furthermore, for *Larix olgensis*, the correlations were consistent among spruce-fir forest at higher elevation (the local scale), spruce-fir forest zone (the zonal scale) and study area, and the correlations of *Betula ermanii* were consistent among sub-alpine birch forest (the local scale), sub-alpine birch forest zone (the zonal scale) and study area.

On the other hand, the correlation relationships were inconsistent among different scales. For *Picea jezoensis* and *Betula ermanii*, the correlations were inconsistent among spruce-fir forest at a higher elevation (the local scale), spruce-fir forest zone (the zonal scale) and study area. In addition, the correlations of *Picea jezoensis* and *Larix olgensis* were also inconsistent among sub-alpine birch forest (the local scale), sub-alpine birch forest zone (the zonal scale) and study area.

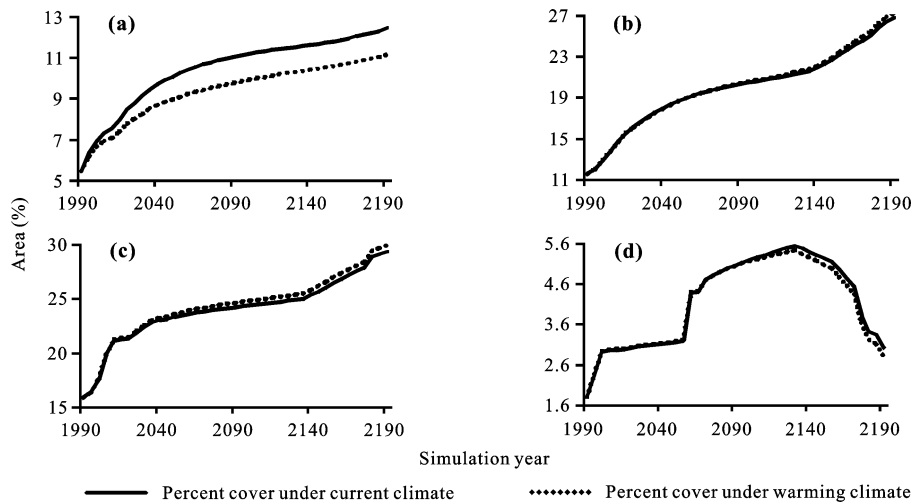


Fig. 5 Simulated percent areas of *Pinus koraiensis* (a), *Picea jezoensis* (b), *Larix olgensis* (c) and *Betula ermanii* (d) from 1990 to 2190 under current and warming climate scenarios at landscape scale

4 Discussion

The results in this study show that the correlations of species physiological response and distribution are not always consistent among the local, zonal and landscape scales. Our results demonstrate that zonal and warming-sensitive species show a consistent correlation of species physiological response and distribution among different spatial scales. For example, the correlations of *Pinus koraiensis* physiological response and distribution at the local, zonal and landscape scales are all negative. This negative correlation may be because strong inter-specific competitions from some species that initially occupy the higher elevation zone, such as *Picea jezoensis* and fir (He *et al.*, 2002). The correlation relationships among these scales are consistent, and therefore the research results of *Pinus koraiensis* response to climate warming at the local scale can be extrapolate to the zonal and landscape scales.

The results also show more complicated situations that for some species the correlations of species physiological response and distribution among different spatial scales are consistent at some scales but inconsistent at other scales. Most of these species are zonal and warming-insensitive species, such as *Picea jezoensis* and *Betula ermanii*. For example, *Picea jezoensis* is a zonal and climate insensitive species demonstrated by no significant difference in its percent areas between the current and warming climate scenarios (He *et al.*, 2005). At the local scale, the percent area of *Picea jezoensis* at the

bottom of spruce-fir forest zone shows no significant difference between the warming and current climate scenarios, while at the top of spruce-fir forest zone and subalpine birch forest the differences of percent area are significant. At the zonal scale, *Picea jezoensis* maintains a stable change between two climate scenarios in spruce-fir forest zone, while it experiences a more significant increase under the warming climate in subalpine birch forest zone. From what has been analyzed above, we may draw a conclusion that *Picea jezoensis* migrates upward after warming with variable migration rates both within the same scale and across different scales because of variable warming-insensitiveness spatially. *Picea jezoensis* finally shows no difference on percent area between two climate scenarios at the landscape scale because it migrates as a whole at this scale. Thus, the research results of *Picea jezoensis* response to climate warming in spruce-fir forest at a lower elevation can be extrapolated to spruce-fir forest zone and the entire study area, but the results derived from spruce-fir forest at higher elevation can not be extrapolated.

In addition, the above-mentioned more complicated situation also can be found in azonal species. For example, *Larix olgensis*, as an azonal and warming-sensitive species, spreads widely currently in the Changbai Mountains (Yan and Zhao, 1996; Zhao *et al.*, 1998), and almost spans all elevation zones. Our results indicate that the correlations of *Larix olgensis* physiological response and distribution among three scales are consistent at some scales, but inconsistent at others. This is

because species such as *Larix olgensis* near the upper boundary of its distribution (subalpine birch forest zone) is expected to have the strongest responses to climate warming (Pastor and Post, 1988; He *et al.*, 2005). Thus, for *Larix olgensis*, the results at the local scale near the upper boundary of distribution cannot be extrapolated to broader scales.

Although the results from this study might be different if the locations of monitoring plots are changed, they provide new insights into extrapolating the research results of vegetation response to climate warming at local scale to broader spatial scales.

5 Conclusions

We investigated whether the correlations of species physiological response and distribution response to climate warming are consistent at the local, zonal and landscape scales. The results indicate that for zonal and warming-sensitive species (e.g., *Pinus koraiensis*), the correlations between species physiological response and distribution response are consistent at these spatial scales, and therefore the research results of vegetation response to climate warming at the local scale can be extrapolated to the zonal and landscape scales. By contrast, for zonal and warming-insensitive species (e.g., *Picea jezoensis* and *Betula ermanii*), the correlations among different spatial scales are consistent at some spatial scales but inconsistent at others. The results in this study also suggest that the results of azonal species (e.g., *Larix olgensis*) at the local scale near their distribution boundary can not be extrapolated simply to broader scales due to stronger responses to climate warming.

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