



Simulating forest ecosystem response to climate warming incorporating spatial effects in north-eastern China

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ABSTRACT

Aim Predictions of ecosystem responses to climate warming are often made using gap models, which are among the most effective tools for assessing the effects of climate change on forest composition and structure. Gap models do not generally account for broad-scale effects such as the spatial configuration of the simulated forest ecosystems, disturbance, and seed dispersal, which extend beyond the simulation plots and are important under changing climates. In this study we incorporate the broad-scale spatial effects (spatial configurations of the simulated forest ecosystems, seed dispersal and fire disturbance) in simulating forest responses to climate warming. We chose the Changbai Natural Reserve in China as our study area. Our aim is to reveal the spatial effects in simulating forest responses to climate warming and make new predictions by incorporating these effects in the Changbai Natural Reserve.

Location Changbai Natural Reserve, north-eastern China.

Method We used a coupled modelling approach that links a gap model with a spatially explicit landscape model. In our approach, the responses (establishment) of individual species to climate warming are simulated using a gap model (LINKAGES) that has been utilized previously for making predictions in this region; and the spatial effects are simulated using a landscape model (LANDIS) that incorporates spatial configurations of the simulated forest ecosystems, seed dispersal and fire disturbance. We used the recent predictions of the Canadian Global Coupled Model (CGCM2) for the Changbai Mountain area (4.6 °C average annual temperature increase and little precipitation change). For the area encompassed by the simulation, we examined four major ecosystems distributed continuously from low to high elevations along the northern slope: hardwood forest, mixed Korean pine hardwood forest, spruce-fir forest, and sub-alpine forest.

Results The dominant effects of climate warming were evident on forest ecosystems in the low and high elevation areas, but not in the mid-elevation areas. This suggests that the forest ecosystems near the southern and northern ranges of their distributions will have the strongest response to climate warming. In the mid-elevation areas, environmental controls exerted the dominant influence on the dynamics of these forests (e.g. spruce-fir) and their resilience to climate warming was suggested by the fact that the fluctuations of species trajectories for these forests under the warming scenario paralleled those under the current climate scenario.

Main conclusions With the spatial effects incorporated, the disappearance of tree species in this region due to the climate warming would not be expected within the 300-year period covered by the simulation. Neither Korean pine nor spruce-fir was completely replaced by broadleaf species during the simulation period. Even for the sub-alpine forest, mountain birch did not become extinct

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under the climate warming scenario, although its occurrence was greatly reduced. However, the decreasing trends characterizing Korean pine, spruce, and fir indicate that in simulations beyond 300 years these species could eventually be replaced by broadleaf tree species. A complete forest transition would take much longer than the time periods predicted by the gap models.

Keywords

Climate warming, fire, forest response, gap model, landscape model, LANDIS, north-eastern China, result validation, seed dispersal, spatial configuration.

INTRODUCTION

Forest ecosystems are expected to change as a result of climate warming induced by increasing levels of CO₂ and other greenhouse gases (Intergovernmental Panel on Climate Change, 2001). Climate warming directly affects tree ecophysiology (Hansen *et al.*, 2001) and water availability (Weltzin *et al.*, 2003). Increased temperatures can alter ecosystem processes such as soil nutrient regimes by affecting organic matter mineralization dynamics (Pastor & Post, 1986; Running & Nemani, 1991). These local effects have been taken into consideration in most studies of the impact of climate warming on forest ecosystems (see Bugmann, 2001).

Recently, increasing attention has been paid to broad-scale, spatial processes that may be altered by climate warming. These include disturbance regimes (Dale *et al.*, 2001; Flannigan *et al.*, 2001; Lenihan *et al.*, 2003) and species dispersal and migration (Pitelka & the Plant Migration Workshop Group, 1997; Hansen *et al.*, 2001; Iverson *et al.*, 2005). A warming climate may increase both fire severity and burning area by more than 40% in Canada (Flannigan & Van Wagner, 1991). Some of the warmer and drier climate change scenarios suggest an increase in fire intensity and a 25–50% increase in the area burned in the United States (Dale *et al.*, 2001). The effects of disturbances on forest ecosystems include the loss of biomass (Scheller & Mladenoff, 2005) and change in species composition. He *et al.* (2002) found that increased fire frequency can accelerate the decline of shade-tolerant species and accelerate the northward migration of southern species. Seed dispersal is an important agent linking climate change and species distribution. The lag between the rapid rate of climate change predicted and the rate of the seed dispersal is often the cause of a particular species disappearing in a region (Iverson *et al.*, 2004). Seed dispersal becomes critical when the forest ecosystem is fragmented due to human land uses, including timber harvesting, and climate warming itself (Iverson *et al.*, 2005).

Predictions of ecosystem response to climate warming are often made using gap models, which are among the most effective tools for assessing the effects of climate change on forest composition and structure (Shugart, 1998). Gap models do not generally account for broad-scale effects such as the spatial configuration of the simulated forest ecosystems, disturbance, and seed dispersal, that extend beyond the simulation plots and are important under changing climates (Carcaillet *et al.*, 2001; Higgins *et al.*, 2003; Lenihan *et al.*,

2003; Lyford *et al.*, 2003; Malanson, 2003; Iverson *et al.*, 2004). Recent studies have increasingly discussed the limitations of using gap models under new climate conditions (Bugmann, 2001; Shao *et al.*, 2001; Reynolds *et al.*, 2003). In gap models, the effects of warming on vegetation types and species composition are usually aggregated from the non-interacting simulation plots to represent the much larger landscape, and ecosystem resilience to changing climate has not been fully incorporated within such models.

In this study we incorporate the broad-scale spatial effects in simulating forest responses to climate warming. We chose the Changbai Natural Reserve as our study area because our simulation studies of forest landscape dynamics under the current climate conditions were conducted for the Reserve. Furthermore, various predictions have been made for forest responses to climate warming (Zhao *et al.*, 1998; Hao *et al.*, 2001; Shao *et al.*, 2003). The previous results provide an ideal basis upon which this study builds. In addition, the Changbai Natural Reserve is one of the largest biosphere reserves in China and has been spared from logging and other severe human disturbances due to its remote location and relatively high elevation. The original forest types along the elevational gradients provide a condensed picture of the array of temperate and boreal forests found across north-eastern China. Because of its uniqueness, scientists have focused on this area in north-eastern China – particularly the pine-hardwood mixed forests – when studying forest responses to climate warming (e.g. Burger & Zhao, 1988; Barnes *et al.*, 1993; Shao, 1996; Yan & Zhao, 1996; Zhao *et al.*, 1998; Shao *et al.*, 2001).

Earlier studies predicted forest change under warming climate in this region using gap models. These studies predicted drastic changes in major forest types where dominant species became extinct or were replaced within a relatively short time period by species better adapted to the new climate conditions. For example, the extinction of Korean pine (*Pinus koraiensis* Sied. et Zucc) within 80 years, followed by a complete dominance by oak (*Quercus mongolica* Fisch), was predicted in Korean pine-hardwood forests (Zhao *et al.*, 1998; Hao *et al.*, 2001). In the results of other simulations, spruce (*Picea koraiensis* Nakai)-larch (*Larix olgensis* Henry) forests were completely replaced by deciduous species such as oak and elm (*Ulmus propinqua* Koidz) in *c.* 100 years in the Changbai Mountain (Hao *et al.*, 2001) and Daxinganling areas (Deng *et al.*, 2000).

Our goal was to incorporate spatial effects in making new predictions for this region using a coupled modelling approach and to compare our simulation results with those predicted using gap models. We used a coupled modelling approach that links a gap model with a spatially explicit landscape model. In our approach, the responses (establishment) of individual species to climate warming are simulated using a gap model that was previously used for making predictions in this region, and the spatial effects are simulated using a landscape model that incorporates spatial configurations of the simulated forest ecosystems, seed dispersal and fire disturbance. Incorporation of spatial configurations of various forest ecosystems can simulate that large, mature forest ecosystems may act as hostile environments for exotic species, thus preventing ecosystems from undergoing rapid transformations due to the invasion and establishment of exotic species. Tracking both seed source and location and modelling seed dispersal can be used to simulate directly the agents of change within the forest ecosystems (He & Mladenoff, 1999b).

We do not anticipate that the new predictions will differ from those of the gap models, as to the direction of forest ecosystem change under warming, because in the coupled modelling approach the responses of individual species are simulated using the gap model. However, by comparing our results with gap model predictions we will be able to demonstrate the effects of incorporating the spatial processes. In doing so, we anticipate that ecosystem transitions under the warming climate will be more prolonged than those predicted by the gap models.

METHODS AND APPROACHES

Study area

The study area is the Changbai Nature Reserve and the 8-km surrounding area. The reserve is located along the border of China and North Korea (Fig. 1) extending from 127°42' to

128°17' E and 41°43' to 42°26' N. The reserve is 200,000 ha in size with an elevation ranging from 740 m at the lowest part to 2691 m at the summit of Changbai Mountain. Changbai Mountain is the highest mountain in north-eastern China and is the head of three large rivers (the Songhua, Yalu and Tumen) in the north-eastern provinces. Topographic features differ on the four slopes of the mountain, with the northern slope being relatively moderate (average slope < 3%) and other slopes being relatively steep (average 10%). The area has a temperate, continental climate, with long, cold winters and warm summers. Annual mean temperatures vary from 7.3 °C in the lowest reaches of the reserve to 2.8 °C near Sky Lake (the volcanic Crater Lake) on the mountaintop, and annual mean precipitation varies from 750 to 1340 mm. Even before the reserve was established in the 1950s, forest harvesting and other human disturbances inside the reserve had been minor compared to those at areas of lower elevation. This is partly due to the reserve's difficult access. A major volcanic eruption occurred between 1000 and 1410, while more recent eruptions occurring in 1597 and 1668 were not broadly destructive (Zhao, 1981; Liu *et al.*, 1992). Forest vegetation inside the reserve is largely the result of natural succession (Zhao, 1981).

Topographic and climatic variations result in a vertical zonation of major forest types that is especially distinct along the northern slope (Fig. 1). From an elevation of 750 to 1100 m a typical temperate forest, composed of Korean pine and hardwood species is found. Common hardwood species include aspen (*Populus davidiana* Dode), birch (*Betula platyphylla* Suk), basswood (*Tilia amurensis* Rupr), oak, maple (*Acer mono* Maxim), and elm. From 1100 to 1700 m, the evergreen coniferous forest occurs, dominated by spruce and fir (*Abies nephrolepis* (Trautv.) Maxim), with the typical characteristics of boreal forests. From 1700 to 2000 m, is the sub-alpine forest, dominated by mountain birch (*Betula ermanii* Cham) and larch. Above 2000 m, are tundra, bare rock, and a volcanic lake. Hardwoods are located in the temperate forest zone areas that extend *c.* 8 km outside the nature reserve (lower than

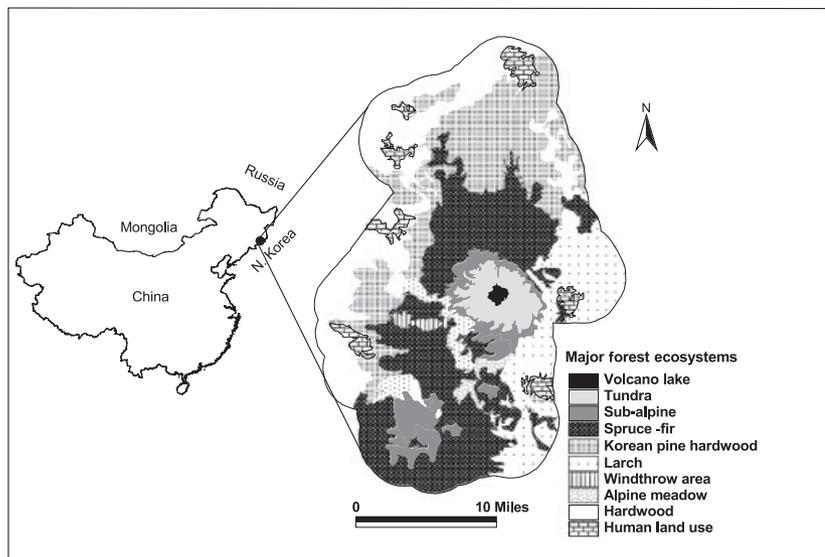


Figure 1 Location of The Changbai Nature Reserve and the major forest types, which were derived from a classified remote sensing image (Shao *et al.*, 1996).

750 m in elevation) where human activities have transformed the pine-hardwood forests into those mainly composed of hardwoods (Shao *et al.*, 1996).

The coupled modelling approach

This study adopted a coupled modelling approach (Fig. 2). For each of the forest ecosystems in the Changbai Natural Reserve we used the gap model (LINKAGES) to simulate the physiological response of each species to current and warming climate conditions. The results were summarized in the form of two sets of species establishment coefficients (SEC), one for the current climate and the other for the warmed climate (see the LINKAGES section for details). We then used the landscape model (LANDIS) to simulate species establishment, successions, and the landscape effects using the SECs derived from LINKAGES under the two climate scenarios as an inputs. The effects of climate warming on each forest ecosystem are derived from the comparisons of LANDIS simulation results (species composition, age structure, and species abundance) for the two climate scenarios. A key reason for employing the LINKAGES model was that it has been parameterized and used to predict the response of major forests to climate warming in the Changbai National Reserve (Hao *et al.*, 2001). Thus, it provides a reference to which the results of this study, incorporating the spatial effects may be compared.

Climate warming scenarios

We used predictions generated by the second version of the Canadian Global Coupled Model (CGCM2), which has a surface grid resolution of 3.7° × 3.7° and has been re-gridded to a 0.5° × 0.5° grid resolution (Flato & Boer, 2001). We acquired the prediction at 127.5° E 43° N, a point that is closest to the Changbai Natural Reserve from the Canadian Centre for Climate Modelling and Analysis. The average annual temperature increase predicted by CGCM2 over the next 100 years

(from 1990s to 2090s) is 4.6 °C. The temperature increase varies by months, with the largest (10.7 °C) increase in December and the smallest increase in March (0.07 °C). June and July temperature increases are also substantial (8.0 and 7.8 °C, respectively). The model predicts precipitation changes of <0.1% from 1990 to 2090. Monthly change is also small, with the largest change in April (-0.4%).

To process temperature data for the current and warming scenarios, we first used data from four weather stations distributed at altitudes from 760 to 2760 m to linearly interpolate temperature gradients along the altitudes of the northern slope of Changbai Mountain. This result was converted into 12 Arc/Info grids, representing current temperature distributions from January through December. These grids captured monthly temperature variations with altitude. However, since the temporal resolution of the LINKAGES model is 1 year, we did not process seasonal temperature variation. To derive the warming climate data scenario, we first calculated the monthly temperature differences between the warming and current climate predicted by CGCM2, using the following method:

$$\Delta T_{i,j} = Tw_{i,j} - Tc_{i,j}$$

where *Tw* represents warming temperature, *Tc* represents current temperature from CGCM2, *i* represents year (1990 ≤ *i* ≤ 2090) and *j* represents month (1 ≤ *j* ≤ 12). Δ*T*_{*i,j*} is, therefore, the temperature change for year *i* and month *j*. Δ*T*_{*i,j*} was added to the monthly temperature grids of current temperature to derive the warmed monthly temperature grids for years from 1990 to 2090. The predicted temperature change between 1990 and 2090 is linear and indicating that warming will occur gradually over the next 100 years as previous studies (Flato & Boer, 2001) and that resultant warmed conditions will persist for the simulation years after 2090.

Other comparable climate change predictions include HadRM3 from the Hadley Centre for Climate Prediction in

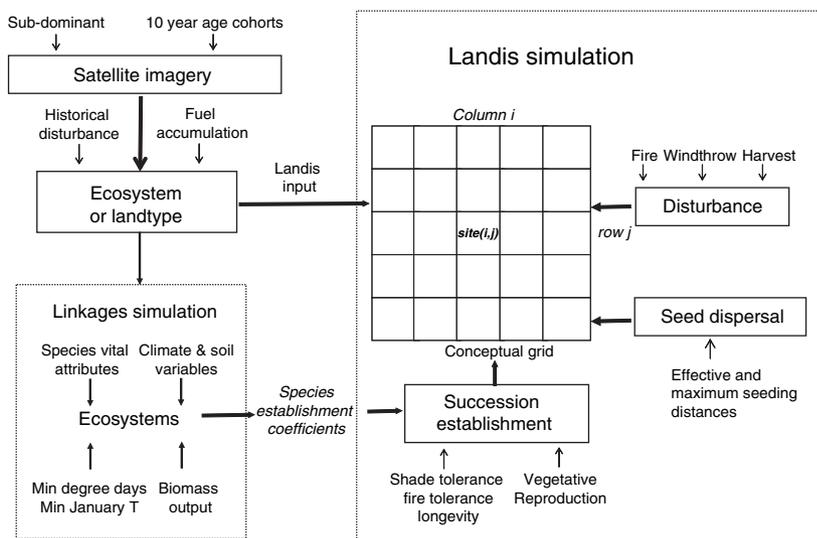


Figure 2 Major components of the LANDIS model and the link with the LINKAGES model. In LANDIS, a landscape is divided into equal-sized individual cells or sites. Each site (*i, j*) on a certain land type (ecosystem), records a unique species list and age cohorts of species. These species data change via establishment, succession, and seed dispersal, and interact with disturbances. Species establishment coefficients can be derived from LINKAGES, which synthesizes individual species responses to various climate and environmental conditions.

the United Kingdom. Unfortunately, no predictions from HadRM3 are currently available for China. Climate change predictions from the older generation of General Circulation Models (e.g. OSU and GFDL) have been used in previous studies in China. However, we did not use these predictions in our study because they either lacked the monthly data or used approaches (equilibrium or static) that are not comparable with those used in the new generation GCM.

LINKAGE model simulations

LINKAGES (Pastor & Post, 1986; Post & Pastor, 1996) is a derivative of the JABOWA/FORET class of gap models. Input data for LINKAGES include 12-month mean temperature and precipitation, and their standard deviations; growing season degree-days; soil organic matter (total C); soil nitrogen (total N); and soil moisture, including wilting point and field water capacity. Vegetation input data include the site (ecosystem) level data (number, age, and DBH of tree stems per species) and species' vital attributes (longevity, shade tolerance, drought tolerance, etc). These data were compiled based upon previous studies in the reserve or derived from forest inventory data (Wang *et al.*, 1980; Xu, 1992; Yan & Zhao, 1996; Hao *et al.*, 2001).

Species establishment in LINKAGES was simulated as a stochastic process using soil variables, the annual sum of degree-days and species coldness tolerance compared with the simulated degree-days, and January temperature. Since low temperature rather than precipitation is the limiting factor for tree species establishment in the Changbai Natural Reserve and maximum degree-day was not used in the model, there were no 'too warm' constraints for species establishment under the warming climate scenario.

To estimate species establishment for each forest ecosystem we simulated one species at a time in LINKAGES, planting the same number of trees (200 saplings/ha) for each forest ecosystem. The model was first iterated to generate a forest floor with environmental and species inputs for each ecosystem. When carbon and nitrogen in the forest floor reached a steady state, we ran the model to 10 iterations (years). If the stand exhibited positive biomass growth during the first 10 years, then this would be considered as a successful establishment. One hundred replications were used for each species. We used a method described by Scheller *et al.* (2005) to calculate a species establishment coefficient (SEC), which equals the number of successful establishments divided by the total number of replications (100). Individual runs were conducted for each of the 12 species \times 20 ecosystems \times 100 replications. Excluding replications, there were 240 (12 species \times 20 ecosystems) independent LINKAGES runs. A parallel set of 240 \times 20 LINKAGES runs was conducted for the warming climate scenario. A difference in species establishment coefficients under current and warming climate thus reflects the species establishment response to climate warming.

LANDIS model description

LANDIS is a spatially explicit, raster-based succession and disturbance model (Mladenoff *et al.*, 1996; Mladenoff & He, 1999). In LANDIS, a heterogeneous landscape can be delineated into various forest ecosystems (land types or ecoregions, depending on the study scale). At a given focal resolution, such as within each forest ecosystem, environmental conditions such as climate and soils are assumed to be homogeneous, as is species establishment (He *et al.*, 1999; Mladenoff & He, 1999; He & Mladenoff, 1999). Each raster unit or cell is a spatial object that tracks: (1) the presence or absence of age cohorts of individual species parameterized from satellite data and forest inventory data, (2) the forest ecosystem a cell encompasses, (3) the establishment coefficients of all species in this cell, and (4) disturbance and harvest history if simulated. For each cell, non-spatial processes such as vegetation dynamics, including species birth, growth, death, regeneration, random mortality, and vegetative reproduction, are simulated using species vital attributes (Table 1). 'Birth' simulates a new species seeding in from another site, or on-site species seeding. For some species that can reproduce by sprouting, 'birth' simulates the vegetative reproduction based on vegetative reproduction probability and minimum age required for such reproduction (Table 1). 'Death' typically simulates species reaching their maximum longevity and applies only to the particular age cohort that reaches species longevity. 'Growth' simulates species age-class increments during each model iteration.

At a landscape scale, spatial processes such as seed dispersal are simulated for each time-step. The seed dispersal process is comprised of three distinct steps: seed travel, on-site checking, and seedling establishment. Firstly, the seed travels based on the exponential function of the effective and maximum seeding distances for a given species. Seed has a higher probability of reaching a site within the species effective seeding distance than beyond this distance (He & Mladenoff, 1999b). Secondly, when seed successfully arrives at a given site, the on-site checking procedure determines whether the species is able to establish itself based on other species that occur on the site and the shade tolerance rank of the seeding species relative to the species occupying the site. For example, aspen cannot seed into a site where Korean pine is established because the latter has a higher shade tolerance. Finally, once a species is allowed to seed into the site, a uniform random number from 0 to 1 is drawn for comparison with the SEC to decide if seed can become established. A species can establish only when its establishment coefficient is greater than the random number drawn. Therefore, species with high establishment coefficients have higher probabilities of establishment (Mladenoff & He, 1999).

LANDIS input data and simulation

In LANDIS, succession and dispersal are driven by species' vital attributes. For our study these were compiled from existing studies in the reserve (Table 1) (Wang *et al.*, 1980; Xu, 1992;

Table 1 LANDIS species life history parameters for The Changbai Nature Reserve

Species	Longevity (years)	Mean maturity (years)	Shade tolerance (class)	Fire tolerance (class)	Effective seeding distance (m)	Max seeding distance (m)	Vegetative reproduction probability	MVP (years)
<i>Abies nephrolepis</i>	200	30	5	5	20	100	0	0
<i>Acer mono</i>	200	30	4	3	100	200	0.3	60
<i>Betula armanii</i>	200	30	1	2	100	300	0.5	60
<i>Betula platyphylla</i>	150	20	1	1	200	4000	0.8	50
<i>Fraxinus mandshurica</i>	300	30	4	2	50	150	0.1	80
<i>Larix olgensis</i>	300	30	2	5	100	400	0	0
<i>Picea koraiensis</i>	300	30	4	4	50	150	0	0
<i>Pinus koraiensis</i>	400	40	4	4	50	100	0	0
<i>Populus davidiana</i>	150	30	2	1	-1	-1	1	0
<i>Quercus mongolica</i>	350	40	2	3	20	200	0.9	60
<i>Tilia amuresis</i>	300	30	4	2	50	100	0.1	60
<i>Ulmus propinqua</i>	250	30	3	3	300	1000	0.7	60

MVP: minimum age of vegetative reproduction; '0' signifies no vegetative reproduction. '-1' in effective and maximum seeding distance means unlimited dispersal distance used in the model. The species life history parameters were compiled from existing studies in the reserve (Wang *et al.*, 1980; Xu, 1992; Yan & Zhao, 1996; Hao *et al.*, 2001).

Yan & Zhao, 1996). Forest ecosystems in the study area were delineated based on a classified TM imagery (Shao *et al.*, 1996), elevation, and landform data using GIS software (Fig. 1). To populate each pixel with species and age cohorts for LANDIS simulations, we combined the dominant forest types derived from Thematic Mapper data (Shao *et al.*, 1996) with field inventory data describing species/age cohort distributions to derive a forest composition map containing individual species/age class distributions for the study area. To reduce computational loads for model simulations, the forest composition map was derived at a 100 × 100 m cell size resolution, which yielded 960 rows × 647 columns for the study area. The cell size was a compromise between the classified TM imagery (30 m), computation efficiency, and LANDIS model simulations for the current climate in this area (He *et al.*, 2002). We parameterized fire disturbance-related parameters including mean return interval (MRI) and mean fire size (MFS) for each forest ecosystem. Mean fire return intervals are substantially longer than the historical regime because of the extensive fire suppression efforts in the reserve. MRI was estimated at 800 years in the mixed Korean pine hardwood and hardwood forests, 500 years for the spruce fir forest, and 1000 years for the sub-alpine forest. Fire typically occurs in small patches (< 0.5 ha) with MFS equal to 1.0 ha. Forest harvesting was not simulated because we were interested in examining the natural successional trajectories of the main dominant species. In addition, harvesting does not reflect the management activities being carried out on the reserve.

To conduct the LANDIS (v 3.7) simulations, we started with the forest composition map with species/age classes representing the initial configuration in the 1990s. We simulated the entire study area for 300 years (up to year 2290) and examined species composition, age structure, and spatial distribution of all major tree species under both current and warming climate scenarios. Results from the simulation are summarized as

percentage cover (the number of pixels in which a species occurs divided by the total number of pixels) by forest ecosystem.

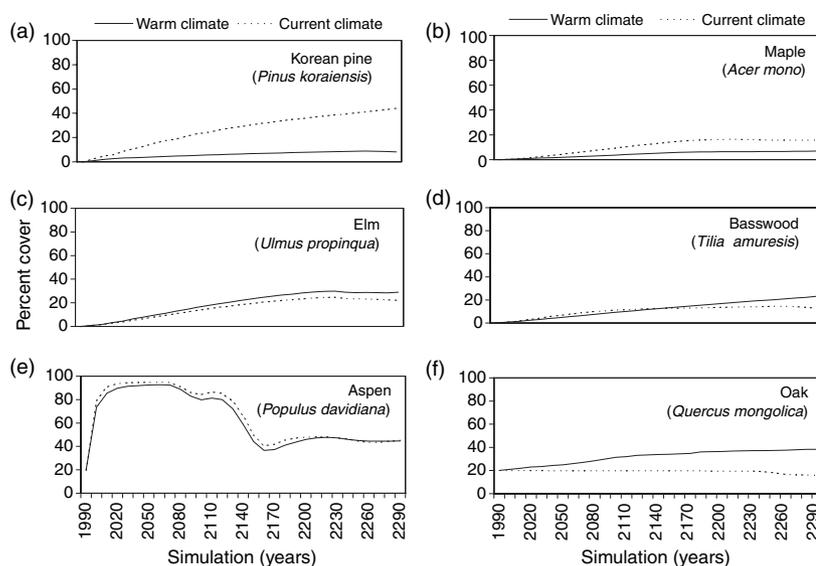
RESULTS

Hardwood forests

Hardwood forests occupy areas below 750 m in elevation. Historically, this is the lowest elevation at which typical mixed pine-hardwoods may occur. Human harvesting for pines has made Korean pine disappear from this ecosystem and transformed the pine-hardwood forests into secondary generation hardwoods comprised primarily of aspen, birch, and oak. Under the current climate scenario without simulating forest harvesting, a steady recovery in Korean pine (Fig. 3a), maple (Fig. 3b), elm (Fig. 3c), and basswood (Fig. 3d) is predicted from the simulation. Early successional species such as aspen and birch show more periodic dynamics with their abundances decreasing after year 2150 (Fig. 3e) as the abundances of mid- to late-succession species increase. A decline in oak is predicted (Fig. 3f) due to competition from Korean pine and other species (He *et al.*, 2002).

The results of the coupled modelling approach show that most broadleaf hardwood species responded positively to the warming scenario while coniferous species (e.g. Korean pine) declined. Although Korean pine does show some recovery from levels of low abundance due to historical cutting, it recovers to a substantially lower abundance relative to that seen predicted the current climate scenario (Fig. 3a). By the year 2290, Korean pine abundance is simulated at 10% under the warming climate scenario compared to 44.5% under the current climate. On the other hand, oak shows significant, positive response to the warming. Oak abundance increases steadily from 20% in the 1990s to almost 40% in 2290

Figure 3 The abundance of (a) Korean pine, (b) basswood, (c) aspen, (d) maple, (e) oak and (f) elm is simulated from 1990 to 2290 for the mixed hardwood ecosystem using the coupled modelling approach. The warming climate scenario is from the Canadian Global Coupled Model (CGCM2). Summation of percent cover may exceed 100% because each pixel may contain more than one species.



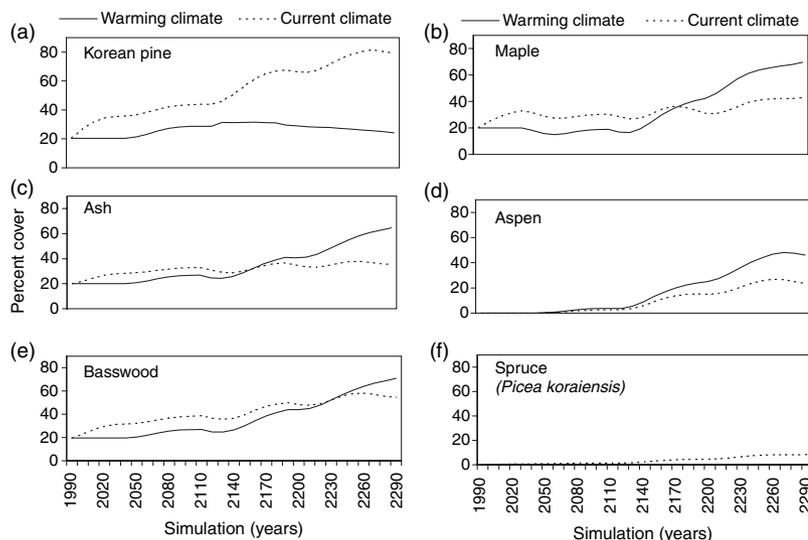
(Fig. 3f). Broadleaf species also show positive responses with abundances increasing by 7% for maple, 3% for elm and basswood, and 2% for aspen by year 2290. These results are consistent with those predicted by LINKAGES and other gap models (Shao, 1996; Yan & Zhao, 1996; Zhao *et al.*, 1998; Hao *et al.*, 2001). However, the persistence of Korean pine under the warming climate scenario shown in this study suggests that a mixed hardwood and pine forest dominated by oak could still persist under the warming climate scenario. This result differs from predictions generated by use of gap model alone.

Mixed Korean pine hardwood forests

Mixed Korean pine hardwood forests are mainly distributed across elevations from 750 to 1100 m. Under the current climate scenario, Korean pine abundance increases (Fig. 4a), reflecting a natural recovery from historical human influence.

Results of the coupled modelling approach show a complicated response of Korean pine to climate warming. Initially Korean pine abundance increases until 2120. This is because the simulated warming occurs gradually over the next 100 years and the initial decades of warming do not cause the Korean pine decline. After 120 years, a gradual decline of Korean pine was simulated (Fig. 4a). Hardwood species increase in their percentage cover under the warming climate scenario, because they move up from the adjacent hardwood forests in the lower elevation areas. In the year 2290 under the warming climate scenario, sugar maple percent area reaches over 70% of the forest ecosystem, 20% higher than that under the current climate scenario (Fig. 4b); ash reaches 60%, 30% higher than that under the current climate scenario (Fig. 4c). Aspen and basswood also have positive responses to warming with their percentage area under the warming climate scenario higher than those under the current climate scenario (Fig. 4d,e). Thus, the broadleaf species overtake Korean pine

Figure 4 The abundance of (a) spruce, (b) maple, (c) spruce, (d) ash, (e) aspen and (f) basswood is simulated from 1990 to 2290 for the mixed Korean pine hardwood ecosystem using the coupled modelling approach. The warming climate scenario is from the Canadian Global Coupled Model (CGCM2). Summation of percentage cover may exceed 100% because each pixel may contain more than one species. Refer to Fig. 3 for other scientific names.



to become the dominant species in this forest. Spruce, which has a minor presence (5%) under the current climate, is shown as not being able to establish itself and thus disappearing under the warmer climate condition for this forest (Fig. 4f).

Spruce–fir forests

The spruce–fir ecosystem, which occupies an elevation zone from 1110 to 1700 m, is the largest forest ecosystem in the study area. Species dynamics under the current climate scenario shows a significant increase in spruce, from 30% to 60% of forest cover (Fig. 5a); a significant increase in larch, from 16% to 40% of forest cover (Fig. 5c), and a slight decline in fir, from 40% to 30% of forest cover (Fig. 5b).

The results of the coupled modelling approach show that warming does indeed have negative impacts on these coniferous

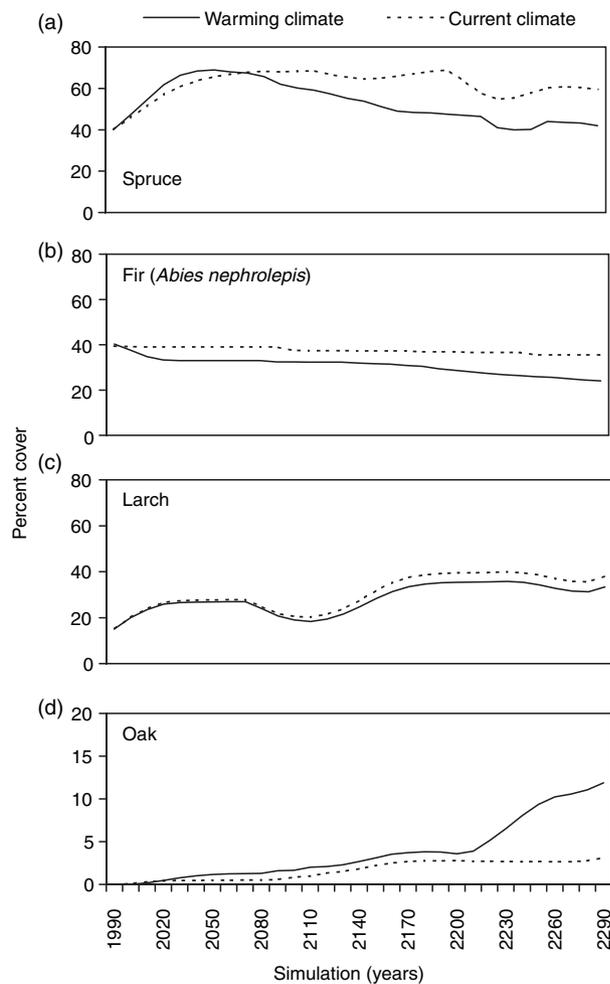


Figure 5 The abundance of (a) spruce, (b) fir, and (c) larch is simulated from 1990 to 2290 for the mixed Korean pine hardwood ecosystem using the coupled modelling approach. The warming climate scenario is from the Canadian Global Coupled Model (CGCM2). Summation of percentage cover may exceed 100% because each pixel may contain more than one species. Refer to Fig. 3 for other scientific names.

species (Fig. 5a–c). Species trajectories of spruce, fir and larch are 5–20% lower than that under the current climate scenario (Fig. 5a–c), while broadleaf species such as oak increase substantially in abundance (Fig. 5d). However, spruce and fir remain as dominant species in this forest during the 300-year simulation period.

Stand-replacing fire is more common in this forest than in the other forest ecosystems. Fire can enhance the establishment success of some broadleaf species. Birch and larch are two species that initially occupy the openings created by fire and they are succeeded by oak and maple in the 60–80 years.

Sub-alpine forests

The sub-alpine forests occur in the elevation zone from 1700 to 2000 m. Mountain birch and larch are two major tree species in these forests, with mountain birch having higher percentage cover (90%) than larch (10%) in this forest [Fig. 6a (year 1990)]. Without climate warming, simulations of natural succession for this forest ecosystem suggest a cyclic pattern in which larch replaces the ageing mountain birch and becomes more dominant and then mountain birch recovers over the next 300 years (He *et al.*, 2002). In Fig. 6a, for example, the percentage area of mountain birch decreases from over 90% of the forest ecosystem in 1990 to below 40% in year 2150 and then rebounds to cover 70% of the forest ecosystem by the year 2290.

No previous gap model predictions have been made for this forest for the warming climate scenario. Results from the coupled modelling approach show that mountain birch would no longer re-establish itself effectively in this forest. After the first generation of mountain birch reaches longevity and dies at around year 2150, the species never recovers in this forest as it does under the current climate scenario and its percentage cover drops below 20% (Fig. 6a). At the same time, a positive response of larch to climate warming in the sub-alpine forest is simulated. Under the current climate scenario, larch is projected to increase from 10% of the area to over 20% in year 2290 (Fig. 6b). Under the warming climate scenario, however, larch percentage area increases dramatically because of the favourable conditions and relatively less competition from other species. The percentage area of larch increases to nearly 80% of the forest ecosystem at the year 2080 and remains relatively stable for the next 150 years (2230) before a decline is observed (Fig. 6b). The persistence of high larch abundance before 2230 is largely due to the diminished competition from mountain birch and the decline after 2230 is due to the competition from spruce, a more shade tolerant species, that eventually moves higher into this forest under the warming climate scenario. Spruce is initially absent and remains absent in this sub-alpine forest under the current climate scenario (Fig. 6c). Under the warming climate scenario, spruce gradually increases in percentage area to c. 50% of this forest ecosystem (Fig. 6c).

Examining the distributions and age structures of the simulated mountain birch, larch, and spruce provides greater

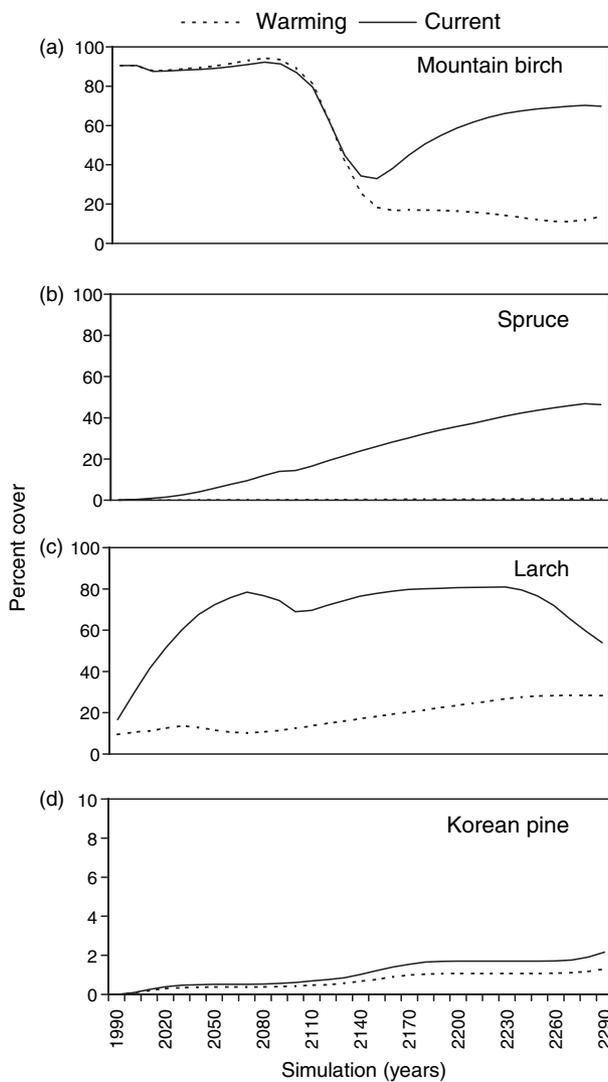


Figure 6 The abundance of (a) mountain birch, (b) spruce, (c) larch and (d) Korean pine is simulated from 1990 to 2290 for the sub-alpine ecosystem using the coupled modelling approach. The warming climate scenario is from the Canadian Global Coupled Model (CGCM2). Summation of percentage cover may exceed 100% because each pixel may contain more than one species. Refer to Fig. 3 for other scientific names.

details in a spatial context. For the year 2290, mountain birch is obviously less abundant in the sub-alpine forest surrounding the volcanic Crater Lake under the warming climate scenario (Fig. 7a,b). Mountain birch appears to be sparser and their age structure is simpler than that simulated under the current climate. Under the warming climate scenario, larch shows both higher abundance and more diverse age structure than that under the current climate scenario (Fig. 7c,d). It is seen that the second generation of larch is able to establish well and grows to over 200 years of age under the warming climate scenario (Fig. 7d). Spruce is seen clearly moving from lower spruce-fir forest to higher sub-alpine forest with younger age cohorts of spruce (< 40) establishing at the frontier encroaching into the sub-alpine forest (Fig. 7e,f).

The change of species composition under the warming climate scenario could eventually transform the sub-alpine forest into a spruce-larch forest similar to that which is now widely distributed in the further north Daxinganling mountainous areas. Results suggest that the transition will occur gradually between 2110 and 2150. Sub-alpine forests could move to higher and colder areas, which are currently tundra. However, we do not have the soil data needed to simulate mountain birch establishment in the tundra area.

DISCUSSION

Validation of our result presents a challenge, just as it does for gap models. Validation in the traditional sense involves acquiring independent data at a particular time and place to compare with model predictions. Since long time series vegetation data do not exist for the warming climate, it is unfeasible to conduct model validation in the traditional sense (Rykiel, 1996). Thus, verifying the simulation results by comparing them with the empirical knowledge (as described below) is a reasonable way to increase confidence in our simulation results (Bugmann, 2001), in addition to the evaluation of model behaviours and internal model formulations (see Mladenoff & He, 1999).

Effects of seed dispersal

The unique aspect of this study is the incorporation of spatial effects, which include seed dispersal, spatial configuration, and fire disturbance, within the simulation framework. The general time requirement for the forest transition can be verified using these spatial components. In our approach, seed sources (based on the presence of mature trees) were parameterized from satellite imagery and forest inventory data, and seed dispersal was simulated based on species effective and maximum seeding distances in a spatially explicit manner, in which the probability of seed reaching a site is negatively related to its dispersal distance (He & Mladenoff, 1999b). For example, spruce-fir forest has an average width of 12,800 m (8 miles) and oak does not exist under the current climate scenario in this forest. Since the maximum seeding distance of oak is 200 m per year and oak needs 30 years to mature and produce seed, we can estimate that it takes 30 years for oak to migrate 200 m and more than 200 years to percolate the spruce-fir system. Based on its longevity, oak may take an additional 50 years to become dominant after the establishment. Thus, the hypothetically shortest time for oak to replace a spruce-fir forest is at least 250 years, assuming there is no competition from other species and optimal conditions exist for oak seedling establishment. If other factors such as competition, shorter dispersal distances (as apposed to maximum distance), and actual establishment probabilities are considered, we can assert that it would take over 300 years for oak to replace the spruce-fir forest. This empirical knowledge agrees with our simulation results, which show that spruce and fir remain

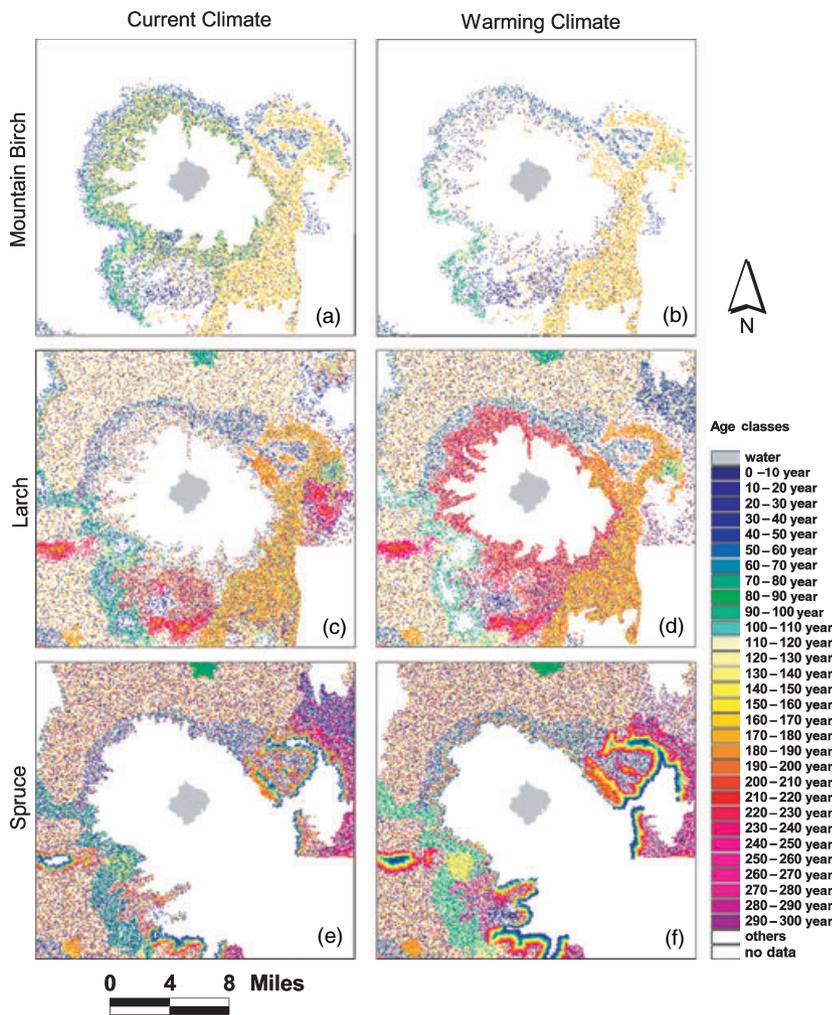


Figure 7 Comparison of simulated changes in the sub-alpine ecosystem for the year 2290 under the warming climate scenario from the Canadian Global Coupled Model (CGCM2) and the current climate scenario. The changes of species composition (mountain birch, larch, and spruce) under the warming climate scenario may transform the sub-alpine ecosystem into a spruce larch ecosystem. Refer to previous figures for species scientific names.

dominant in this forest ecosystem for at least 300 years of the model simulation period.

Effects of spatial configuration

Since our approach incorporated the spatial structure of the forest ecosystems in the simulation, the resilience of specific spatial structures to change can also be simulated. For example, after a large, mature forest (such as spruce-fir) is established, it resists the invading exotic seed from other ecosystems simply because its dimension (patch size) is greater than the seeding distance of the exotic seed (He & Mladenoff, 1999b; Lyford *et al.*, 2003). In addition, the established forest ecosystem uses the shade and other features to compete effectively against exotic species (Xu, 1992). Thus, significant changes usually occur near the edge of the ecosystem (e.g. northern and southern edges) at the beginning and gradually move into the interior areas. Our simulation results reflect this general pattern by showing that the strongest response to climate warming occurred first at both low and high elevation areas.

Our simulation results are comparable to those of another study of tree species migration rates in the eastern United

States (Iverson *et al.*, 2004, 2005). Iverson *et al.* (2004) modelled five species currently confined to the eastern half of the U.S. They found that migration for all five species was generally limited. There is a relatively high probability of colonization within a zone of 10–20 km from the current ecosystem boundaries, but a small probability of colonization where the distance from the current boundary exceeds *c.* 20 km. Their results reinforce our findings that the strongest response of tree species to climate warming occurs at the northern and the southern edges of forest ecosystem.

Effects of fire disturbance

Our approach incorporates fire disturbance in the simulation process, which is not simulated in gap models. The simulated effects of fire disturbance can be confirmed with the aid of empirical knowledge of the region. For example, larch (Fig. 5c) and a small amount birch (result not shown due to low percentage cover) in spruce-fir ecosystem were predicted to occur following fire disturbance. They are two early successional, shade intolerant species that usually occur after fire disturbance (Liu *et al.*, 1992; Shao *et al.*, 2001).

Comparison with current climate predictions

The predicted gradual transformation of forest ecosystems under the warming climate scenario is comparable to our results under the current climate. Under the current climate scenario, the simulation results showed that over 300 years, Korean pine only recovered in one third of the hardwood forest ecosystems where it previously was dominant (He *et al.*, 2002). We estimated that a full recovery would take another 200–300 years without human interference (e.g. seeding). Results from the current climate scenario indicate that landscape-scale recovery of Korean pine is often limited by the available seed sources (He *et al.*, 2002), and this would be particularly true for new species encroaching into existing forest ecosystems under warmer climates (Iverson *et al.*, 2004).

Comparison with the gap model predictions

Our results agree with the general trends predicted using gap models but are different in specific aspects. In the hardwood forest at low elevations (< 750 m), our coupled modelling approach does not predict the extinction of Korean pine. Instead, our results suggest that the Korean pine hardwood ecosystem could persist for at least 300 years under the warming climate. However, the abundance of Korean pine under such a scenario is much lower than it would be under the current climate scenario. This result is similar to predictions made using LINKAGES, except that LINKAGES predicted that Korean pine would disappear and broadleaf species would rapidly become dominant within 80 years. In the sub-alpine forest ecosystem at high elevations (1700–2000 m), a decline of mountain birch and an increase of larch and spruce moving into this ecosystem from lower elevations suggest that the sub-alpine ecosystem could be transformed into a spruce-larch forest ecosystem in *c.* 150 years. In the mid-elevation areas, environmental controls such as temperature, precipitation, and soils in The Changbai Natural Reserve have been found to exert a dominant influence on the dynamics of forest ecosystems (Miles *et al.*, 1983; Zheng *et al.*, 1997; He *et al.*, 2002), whereas the 4.6 °C annual temperature increase is secondary to the environmental controls. Spruce-fir forest distributed at mid elevation areas shows resilience to climate warming as reflected in the fact that the fluctuations of species trajectories of these forest ecosystems under the warming scenario follow those under the current climate scenario.

Comparison with palaeoecological studies

Maps of pollen data have long been unavailable for continental Asia despite their importance for palaeoecological and palaeoclimatic studies (Shi & Song, 2003). Ren & Zhang (1998) used pollen data from 65 Holocene sites and mapped eight pollen taxa and seven time periods for north-east China. These pollen maps show significant vegetation changes during the last

10,000 years in the current forest regions of north-east China. Their results showed that dominant forests follow the climate dynamics, with the early, warming Holocene characterized by widely distributed *Betula* trees, the mid, warmer Holocene by the *Quercus* and *Ulmus* trees, and cooler, late Holocene by the marked increase of *Pinus* and temperate mixed conifer and deciduous forest.

Similar results were also found in a study focusing on eastern North America during the last glacial maximum (Jackson *et al.*, 2000). Jackson *et al.* (2000) assembled pollen and plant macrofossil data in eastern North America and found that *Pinus*-dominated vegetation occurred extensively to 34° N and *Picea*-dominated forest grew in the colder continental interior, with temperate hardwoods growing in the warmer, Lower Mississippi Valley. Lyford *et al.* (2003) studied the fossil record in western North America and found that landscape structure and climate variability had strongly influenced on late Holocene plant migration. They found that the unsuitable habitat and fragmentation caused delay of plant migration, especially under the changing climate.

Studies of palaeoecology with respect to vegetation do not exist for our study area. Using similar studies conducted elsewhere presents some difficulties due to the differences in vegetation, environment, and the very large temporal scales in these studies. Nevertheless, qualitative comparisons such as those discussed above show that the trends and direction of forest responses to climate warming simulated in this study generally agree with results from those palaeoecological and palaeoclimatic studies.

CONCLUSIONS

We presented an alternative approach to gap models in predicting the response of forests to climate warming in The Changbai Natural Reserve. Our results suggest that climate warming will exert its dominant effects on forest ecosystems in the low and high elevation areas in contrast to the mid-elevation areas. This concurrently implies that the forest ecosystems near the southern and northern ranges of their distribution will have the strongest response to climate warming. Forest ecosystems (e.g. spruce-fir) distributed at mid elevation areas show resilience to climate warming. This also implies that large forest ecosystems that are distributed within the core geographic areas are unlikely to be transformed into other forest vegetation types within a short period of time (e.g. 80–100 years) as predicted by gap models (Deng *et al.*, 2000; Hao *et al.*, 2001).

Our results suggest that the disappearance of tree species in this region due to climate warming would not be expected within the 300-year period covered by the simulation. Neither Korean pine nor spruce-fir was completely replaced by broadleaf species during the simulation period. Even for the sub-alpine forest, mountain birch did not become extinct under the warming climate scenario, although its occurrence was greatly reduced. However, the

decreasing trends characteristic of Korean pine, spruce, and fir indicate that in simulations beyond 300 years these species could eventually be replaced by broadleaf tree species. A complete forest transition would take much longer than time periods predicted by gap models.

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