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RESEARCH ARTICLE

Coupling ecosystem and landscape models to study the effects of plot number and location on prediction of forest landscape change

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Abstract A fundamental but unsolved dilemma is that observation and prediction scales are often mismatched. Reconciling this mismatch largely depends on how to design samples on a heterogeneous landscape. In this study, we used a coupled modeling approach to investigate the effects of plot number and location on predicting tree species distribution at the landscape scale. We used an ecosystem process model (LINKAGES) to generate tree species response to the environment (a land type) at the plot scale. To explore realistic parameterization scenarios we used results from LINKAGES simulations on species establishment probabilities under the current and warming climate. This allowed us to design a series of plot number and location scenarios at the landscape scale. Species establishment probabilities for different land types were then used as input for the forest landscape model (LANDIS) that simulated tree species distribution at the landscape scale. To investigate the effects of plot number and location on forest landscape predictions, LANDIS considered effects of climate warming only for the land types in which experimental plots were placed; otherwise inputs for the current climate were used. We then statistically examined the relationships of response variables (species percent area) among these scenarios and the reference scenario in which plots were placed on all land types of the study area. Our results showed that for species highly or moderately sensitive to environmental heterogeneity, increasing plot numbers to cover as many land types as possible is the strategy to accurately predict species distribution at the landscape scale. In contrast, for species insensitive to environmental heterogeneity, plot location was more important than plot number. In this case, placing plots in land types with large area of species distribution is warranted. For some moderately sensitive species that experienced intense disturbance, results were different in different simulation periods. Results from this study may provide insights into sample design for forest landscape predictions.

Keyword Plot number · Plot location · Landscape prediction · Ecosystem and landscape modeling · Environmental heterogeneity · LANDIS · Changbai mountains

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Introduction

Climate warming, habitat fragmentation, and biodiversity loss occur at large spatial extents and over long temporal spans. Due to resource constraints, however, the available data to study these broad-scale phenomena are collected at relatively fine scales (Miller et al. 2004; Underwood et al. 2005). For example, most predictions of forest response to climate warming at landscape scales are based on data (e.g., growth rate and species composition change) collected from experimental or observational plots (Jansen and Bredemeier 2004; Liang et al. 2011a). Reconciling this mismatch between observation and prediction scales depends largely on how to place plots (plot number and location) in a heterogeneous landscape and how to extrapolate these results to broad spatial scales (Miller et al. 2004).

Generally, a plot-level experiment is local in nature and only represents the homogeneous environment in which the plot resides (Schmitz 2005). Extrapolating plot-level results to broad spatial scales requires a large number of plots and assumes that they cover variations of the environmental heterogeneity. These conditions are not always met, however, because plot-level data are often unavailable or inadequate in many regions. Under these circumstances, how to place plots in a heterogeneous landscape for broader scale predictions becomes critical. Inappropriate sample design, such as too few plots with limited locations may hamper the ability for landscape predictions (Abrahamson et al. 2011).

Species suitability to the environment varies spatially in a heterogeneous landscape, and the degree of variation indicates sensitivity of species to environmental heterogeneity. Setting plots on a heterogeneous landscape to make reliable landscape predictions is often contingent on the sensitivity of species to environmental heterogeneity (Hewitt et al. 2007). Species sensitive to a heterogeneous landscape require more plots than species that are insensitive to environmental heterogeneity (Peignéa et al. 2009). In addition, habitat or microhabitat preferences may affect how species respond to environmental heterogeneity (Underwood et al. 2005), and consequently affect the choice of plot location. Despite many attempts, the individual and combined effects of number of plots and their locations on landscape predictions have not been fully investigated.

Much attention has been paid to how to extrapolate plot-level results to broad spatial scales in forest change assessment (Jenkins et al. 2001; Aber et al. 2002; Jansen and Bredemeier 2004; Chiesi et al. 2011). There are two representative approaches: direct extrapolation and ecosystem modeling. The direct extrapolation approach often includes averaging plot-level data (e.g., ton/hectare for biomass) within a forest type and extrapolating to the area of each forest type. For example, Jenkins et al. (2001) developed estimates of forest biomass and NPP at the plot level using Forest Inventory and Analysis (FIA) data, which are spatially explicit plots containing tree-level measurements across most of the United States (Bechtold and Patterson 2005). These estimates were then aggregated by forest types to represent land area of various forest types. Fang et al. (1998, 2001) estimated forest biomass and carbon change of China for the past 50 years using direct field measurements and a national forest resource inventory database. They first estimated biomass of each forest type using total area of the forest type and the timber volume and biomass expansion factor (BEF, the ratio of all stand biomass to growing stock volume) and then extrapolated to provincial and national levels by forest types. The direct extrapolation approach does not typically predict future landscape dynamics.

The ecosystem modeling approach involves building mathematical relationships between the response variables (e.g., NPP and biomass) and the environmental factors in an ecosystem process model. In this approach, a study area is often divided into grids, and the response variables in each grid cell are simulated by the ecosystem process model. The simulated result for each grid cell is then aggregated to the entire study area. Many ecosystem process models (e.g., PnET-II and FOREST-BGC) are parameterized using gridded input data to account for variation of physical environments (Aber et al. 2002; Rastetter et al. 2003; Meigs et al. 2011). Ollinger et al. (1998) used PnET-II to estimate regional forest productivity and runoff in conjunction with a GIS dataset for the northeastern United States. FOREST-BGC and its derivatives, Biome-BGC and BEPS, were used to estimate nitrogen deposition (Eastaugh et al. 2011) and carbon stock (Chiesi et al. 2011) at the regional scale. Compared to the direct extrapolation approach, ecosystem modeling approach is capable of simulating future landscape dynamics.

Both direct extrapolation and ecosystem modeling approaches assume that plot-level data can be directly extrapolated to the landscape scale and ignore landscape processes such as seed dispersal (He et al. 2008). In fact, landscape processes, which are influenced by environmental heterogeneity, affect vegetation dynamics and interactions at individual sites or plots (He et al. 2008). Without accounting for landscape processes, extrapolation from plot-level data to the landscape scale may underestimate or overestimate the landscape-scale response (He and Mladenoff 1999). Thus, the objective of this study is to introduce a coupled modeling approach that links ecosystem processes at the plot scale and landscape processes at the landscape scale. In this approach, an ecosystem process model is used to simulate plot processes and a forest landscape model, which uses the results of the ecosystem process model as input, is used to simulate landscape processes (He et al. 2005).

In this study, we used this coupled ecosystem and landscape modeling approach to study the effects of plot number and location on predictions of tree species distribution at landscape scales. Specifically, we (a) evaluated the relative importance of plot number, plot location, and their interaction in predicting species distribution and (b) investigated how plot number and (c) plot location influenced forest landscape predictions. We designed a series of sample design scenarios with different plot numbers and locations combinations. The forest landscape model uses only for land types covered by plots the "correct" input values that correspond to climate warming, otherwise that of the current climate are used. We then statistically examined the relationships of response variables (species percent area) among these scenarios and the reference scenario in which plots were placed on all land types of the study area. We chose the Changbai mountains Natural Reserve in Northeast China as the study area because (a) the vegetation has an obvious vertical distribution corresponding to elevation changes, and thus the relationships between species and environmental heterogeneity is strong; (b) forests in this area are sensitive to climate warming (Hao et al. 2001), and thus species response to the warming climate is strong; and (c) prior studies have developed datasets (e.g., model parameterization and the reference scenario) from which this study can be built upon (He et al. 2005).

Approach and methods

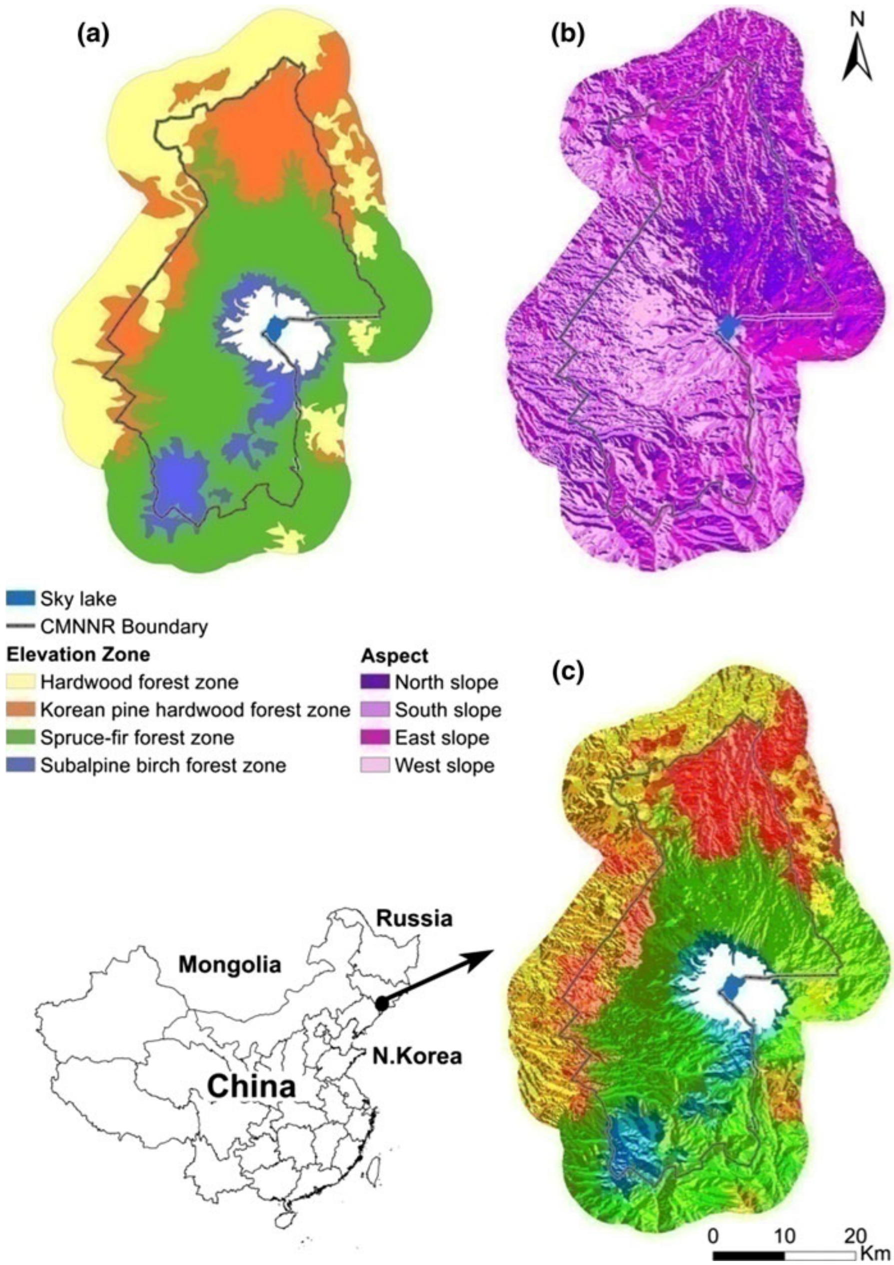
Study area

Our study area (4.1×10^5 ha) consisted of the Changbai mountain National Natural Reserve (CMNNR) and the 8 km surrounding area at 41°62′–42°49′N, 127°59′–128°38′E. CMNNR, a dormant volcano site located on the border of China and North Korea (Fig. 1), protects one of the largest natural temperate forests in the world (Shao et al. 1994; Stone 2006) and has been spared from logging and other severe human disturbances since it was established in 1960. The area has a temperate, continental climate, with long, cold winters and warm summers. Average annual precipitation and temperature are 1,012 mm and −3.2 °C, respectively (Chi et al. 1981). The growing season is ~150 days. Topographic features differ on the four sides of the mountain, with the north side having a relatively gentle slope (average slope <3 %) and the other sides having greater slopes (average 10 %) (Liu 1997; He et al. 2002).

There are four main vertical vegetation zones corresponding to an elevation change from 613 m at roughly the southern-most boundary to 2,691 m at the summit of Changbai mountain (Wang et al. 1980; Yang and Li 1985; Zhao et al. 2004) (Fig. 1a). The hardwood forest zone extends 8 km outside CMNNR (lower than 750 m elevation) where human activities have transformed the pine–hardwood forests into those mainly composed of hardwoods (Shao et al. 1996). Within CMNNR, from about 750 to 1,100 m, is the mixed Korean pine hardwood forest zone that includes Korean pine (*Pinus koraiensis*), aspen (*Poplus davidiana* Dode), birch (*Betula platyphylla* Suk), basswood (*Tilia amuresis* Rupr), ash (*Fraxinus mandshurica*), oak (*Quercus Mongolica*), maple (*Acer mono* Maxim), and elm (*Ulmus propingua*). The spruce–fir forest zone (1,000–1,700 m) is dominated by spruce (*Picea jezoensis*) and fir (*Abies nephrolepis* [Trautv.] Maxim), with characteristics of typical of boreal forests. The subalpine forest zone (1,700–2,000 m) is dominated by mountain birch (*Betula ermanii* Cham) and larch (*Larix olgensis*). No research was conducted for areas above 2,000 m due to the absence of tree species.

Elevation is a physical factor governing broad-scale forest distribution patterns (Han and Wang 2002) and affecting land use, which is reflected by distinct vegetation types along elevation zones in our study

Fig. 1 Geographic site of the study area that includes four elevation zones (**a**) and four aspect classes (**b**). Land types (**c**) are derived by overlaying elevation zones and aspects. Each land type unit is considered a homogeneous environment



area (Fig. 1a). Aspect and slope are physical factors governing fine-scale species composition by redistributing humidity and temperature in the environment. However, slope has only moderate effects in our study area because the local topography of most of the Changbai mountains area is relatively gentle. Thus, elevation and aspect are the most important factors that cause environmental heterogeneity in the Changbai mountains. In this study, the aspect of CMNNR and the 8 km surrounding area were divided into four classes: north, south, west, and east (Fig. 1b).

Approach overview

We used land types (Fig. 1c) derived from spatial overlay of environmental factors (four elevation zones and four aspect classes, total of 16 land types) to represent environmental heterogeneity. We simulated individual species biomass under both current and warming climate for each land type using an ecosystem process model (LINKAGES). The simulated biomass represented species suitability to the land type and was quantified by species establishment probability (SEP) under current and warming climate (He et al. 1999). Thus, SEPs encapsulated the effects of environmental factors (e.g., weather and soil) at the plot scale. SEPs were used as input parameters for a spatially explicit forest landscape model (LANDIS) that predicted species distributions at the landscape scale (Fig. 2).

To investigate the effects of plot number and location on forest landscape predictions, we assumed that effects of climate warming were observed only for the land types in which experimental plots were placed (SEPs under warming climate were used as LANDIS inputs), whereas no climate effects were monitored on the land types (SEPs under current climate were used as LANDIS inputs) in which no plots were placed. These treatments allowed us to design various sample design scenarios in this study, including a series of plot number and location scenarios (Fig. 2). We also had a reference scenario from a previous study in which plots were placed on all land types of the study area, and forest landscape predictions were made for climate warming (He et al. 2005).

We designed a set of plot number scenarios with increasing plot numbers to investigate how plot numbers influenced the forest landscape predictions. No significant difference in species percent area between a plot number scenario and the reference scenario indicated that predictions based on limited plots were similar to the prediction using a full number of plots; a significant difference indicated that the examined plot numbers were not sufficient to make the forest landscape predictions. We also designed a set of plot location scenarios with different locations but the same numbers of plots to investigate how plot location influenced the forest landscape predictions. The higher the correlation was between the plot location scenario and the reference scenario, the greater the contribution of the location to the forest landscape predictions.

Coupling ecosystem and landscape models

The ecosystem process model LINKAGES (Post and Pastor 1996), a derivative of the JABOWA/FORET class of gap models, was used to simulate the physiological response of each species to both current and warming climate within each land type (plot scale) (Hao et al. 2001; He et al. 2005). Individual species biomass (output of LINKAGES) was determined by simulating the interactions of climate (monthly

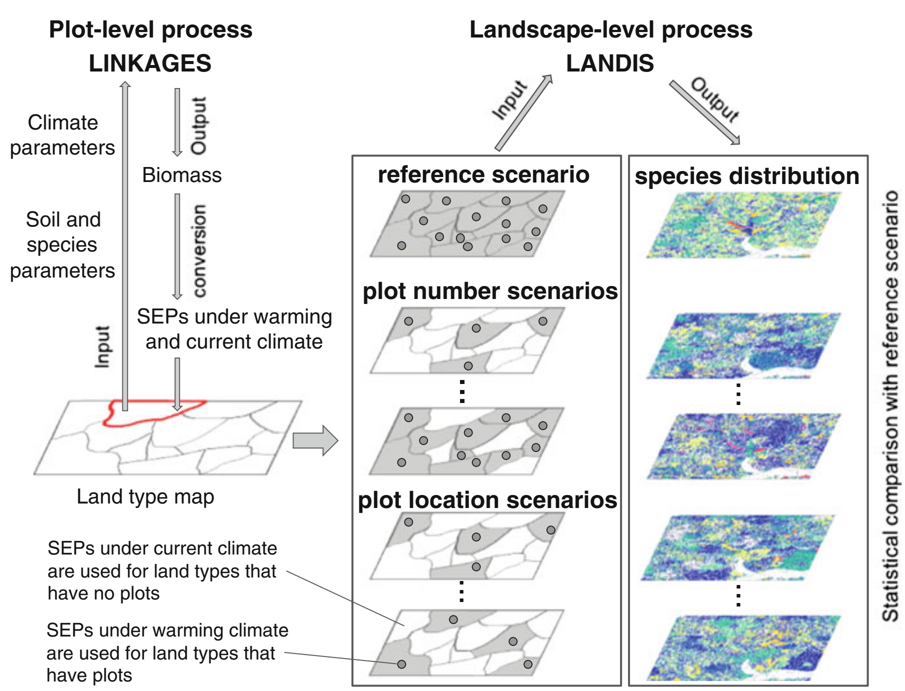


Fig. 2 The flowchart of approach overview. Species establishment probabilities (SEPs) under warming and current climate by land type are derived from LINKAGES, and then are used in LANDIS to predict species distribution at the landscape scale. Species distributions under different sample design scenarios (including a series of plot number scenarios and plot location scenarios) are compared with that under the reference scenario

temperature and precipitation), soil (e.g., soil water capacity, wilt point, total nitrogen, and total carbon derived from soil survey data in CMNNR) with ecological processes (e.g., competition, succession, and water and nutrient cycling), and species biological traits. These biological traits (e.g., longevity, maturity, shade and drought tolerance, and seeding capability) were compiled based on previous studies in this area or derived from forest inventory data (Wang et al. 1980; Yan and Zhao 1996; Hao et al. 2001). Compiling the current and warming climate data is described in Section A.1 in Appendix. Because a larger biomass represented greater species suitability to the land type, biomass was used to quantify species suitability to the land type in the form of SEP. Biomass for all land types under both current and warming climate was converted to two sets of SEPs using an empirical method (He et al. 1999, Section A.2 in Appendix). SEP values range from 0 to 1, with higher values having higher suitability to a land type (Mladenoff and He 1999). The SEP for a given species was coincident with a homogeneous environment (a land type) and might vary from one land type to another. SEPs encapsulate the effects of climate and environment on individual tree species at the experimental plot scale (land type) (Liang et al. 2011b).

Landscape-scale species distributions (quantified by species percent area, which is a percentage that the number of pixels in which a species occurs divided by the total number of pixels of the study area) under current and warming climate were predicted using a coupled modeling approach that links LINKAGES with a spatially explicit forest landscape model (LANDIS) (Fig. 2). The core of the coupled modeling approach was that LANDIS simulated forest succession and landscape processes (e.g., dispersal) using SEPs derived from LINKAGES as one of the input parameters (the other input parameters were described in detail in He et al. 2002, 2005). In LANDIS, according to environmental heterogeneity, a heterogeneous landscape can be delineated into various land types, and each land type has two sets of SEPs of both current and warming climate for each species (Table 1). Species percent area at the landscape scale under current climate was derived from the simulation results of LANDIS under the scenario that every land type in the study area used SEPs under the current climate. Likewise, species percent area under warming climate at the landscape scale was derived from the simulation results of LANDIS under the scenario of forest landscape predictions under warming climate that every land type used SEPs under warming climate.

Sample design scenarios

To investigate how plot numbers influenced the forest landscape predictions, we designed a set of plot number scenarios with different plot numbers. The design of the plot number scenarios was to increase plot numbers from four (S4) to eight (S8) to 12 (S12), with random locations for the plots (Fig. 3). We began with four plots because there are four elevation zones in the study area, and a plot in a specific elevation zone generally cannot represent the characteristics of the other elevation zones (Liang et al. 2011a). The S4 scenario was composed of four plots, one in each elevation zone in a randomly chosen land type. The S8 scenario was composed of eight plots with one additional plot randomly chosen in each of the four elevation zones based on S4. The S12 scenario was composed of 12 plots representing three plots chosen randomly in each of four elevation zones based on S8.

To investigate how plot location influenced forest landscape predictions, we emphasized the effects of plot location by keeping the same numbers of plots. The plot location scenario placed all plots on one of four slopes (north, south, east, and west slopes, denoted as SN, SS, SE, and SW) (Fig. 3). There are four elevation zones, and therefore each plot location had four plots. For example, SN was a scenario with four plots placed on the north slope of the four elevation zones. Each plot number and location scenario had five replicates in which plots were randomly chosen five times (scenario replications).

Model simulation

We used LANDIS 6.0 (www.missouri.edu/~landis.htm), an expanded version of LANDIS 4.0 (He et al. 2005), to simulate 12 of the most common tree species within our study area: Korean pine, spruce, fir, mountain birch, birch, larch, oak, ash, maple, aspen, bass, and elm. We simulated our study area from 1990 to 2190 at 5-year time steps. All spatial data were presented at the resolution of 100 × 100 m, compatible with previous simulation studies, which yielded 960 rows and 647 columns. Disturbance such as forest harvesting, fire, and wind were not simulated because

Table 1 Species-specific establishment probabilities for 16 land types under the current and warming climate

Land type			Current climate					Warming climate				
	Elevation	Aspect	Spruce	Birch	Korean pine	Fir	Larch	Spruce	Birch	Korean pine	Fir	Larch
1	The hardwood	North	0.000	0.865	0.612	0.000	0.418	0.294	0.000	0.000	0.298	0.282
2	forest zone	South	0.000	0.865	0.506	0.000	0.418	0.254	0.000	0.000	0.234	0.255
3		East	0.000	0.784	0.480	0.000	0.397	0.241	0.000	0.000	0.222	0.230
4		West	0.000	0.825	0.558	0.000	0.419	0.295	0.000	0.000	0.272	0.269
5	The mixed	North	0.471	0.408	0.586	0.438	0.658	0.882	0.089	0.171	0.828	0.420
6	Korean pine	South	0.351	0.367	0.436	0.326	0.592	0.656	0.072	0.127	0.616	0.378
7	hardwood	East	0.390	0.390	0.484	0.362	0.628	0.693	0.077	0.134	0.650	0.381
8	forest zone	West	0.430	0.390	0.534	0.399	0.659	0.842	0.089	0.163	0.791	0.441
9	The spruce–fir	North	0.702	0.078	0.108	0.660	0.322	0.016	0.479	0.669	0.012	0.212
10	forest zone	South	0.522	0.064	0.080	0.491	0.290	0.012	0.431	0.498	0.009	0.191
11		East	0.551	0.067	0.085	0.518	0.292	0.013	0.457	0.553	0.010	0.202
12		West	0.670	0.078	0.103	0.630	0.339	0.015	0.457	0.610	0.011	0.212
13	The subalpine	North	0.038	0.002	0.000	0.056	0.130	0.000	0.684	0.556	0.000	0.000
14	forest zone	South	0.033	0.001	0.000	0.044	0.118	0.000	0.684	0.459	0.000	0.000
15		East	0.031	0.001	0.000	0.042	0.107	0.000	0.620	0.436	0.000	0.000
16		West	0.038	0.001	0.000	0.051	0.124	0.000	0.653	0.506	0.000	0.000

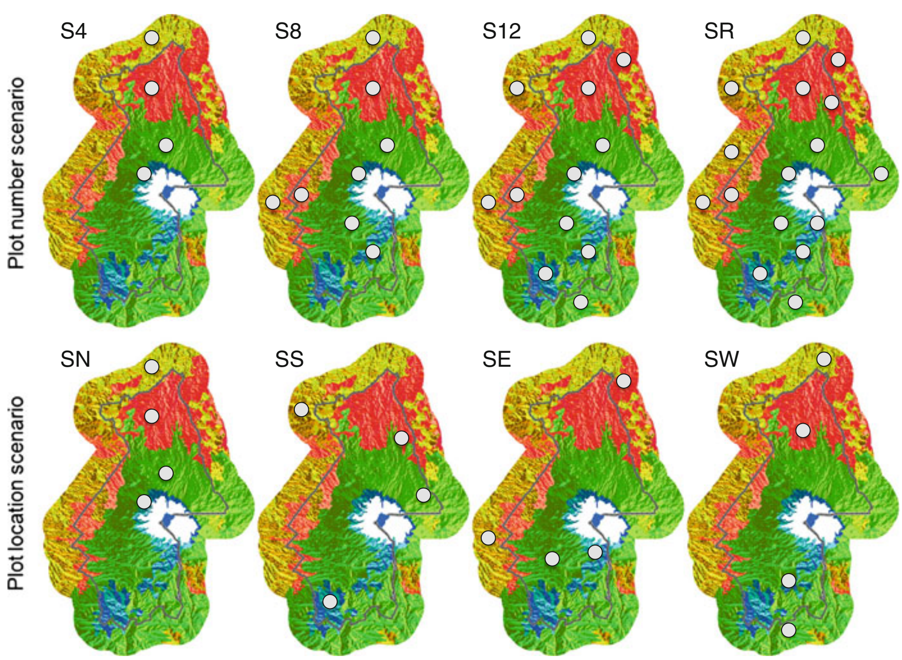


Fig. 3 Schematic maps of plot number scenarios (S4, S8, S12), plot location scenarios (SN, SS, SE, and SW) and the reference scenario (SR). The base map is land type map. *Circle* represents plot

our objective was to examine the natural successional trajectories of the main dominant species. The model replications (five times) started with the same input parameters with the exception of random seed numbers used to account for the effects of stochastic components, such as seed dispersal and seedling establishment. LANDIS 6.0 statistics were used to process the simulation results. These statistical results were summarized as percent area. Simulation results were analyzed by short term (0–50 years), middle term (50–100 years), and long term (100–200 years) separately.

Quantify the relative importance of plot number, location, and their interaction

Initially we conducted a two-factor univariate analysis in General Linear Model (SPSS 16.0) between the different plot number scenarios (S4, S8, and S12) and the reference scenario for the short, middle, and long terms, respectively. The dependent variables (species percent areas of simulated species under the S4, S8, S12 scenarios, each with five replicated scenarios and the reference scenario) were tested for normality and homogeneity of variances in the residuals. Two-factor independent variables (plot number and location) were both fixed factors. Type III sums of squares derived from the univariate analysis were used to quantify the relative importance of plot number, location, and their interaction to species distribution prediction at the landscape scale. Higher type III sums of square values indicated stronger contributions to forest landscape predictions. The actual type III sums of square values of plot number, location, and their interaction were comparable within one statistical model (analyzing one species in a certain simulation period, e.g., oak in the short term) but not necessarily between two or more statistical models. Therefore, we transformed the actual type III sums of square values into proportions for comparing the differences of the relative importance of plot number, location, and their interaction among short, middle, and long terms, as well as among simulated species.

Based on our initial analysis, we conducted ANCOVA's (SPSS 16.0) to test for differences between the simulated results derived from different plot number scenarios (S4, S8, and S12) and the simulated results of the reference scenario in the short, middle, and long terms, respectively. The dependent variables were species percent areas of simulated species under S4, S8, S12 (averaging five paralleled scenarios of S4, S8, S12), and the reference scenario. Plot number was the fixed factor (main effect), whereas plot location was the covariable. Least Significant Difference was used for multiple comparisons on the statistical significance of the coefficients. The within-group variance (five model replicates) was completely caused by the stochastic components, and the between-group variance was derived from different plot number scenarios. This allowed us to analyze the differences between the plot number scenario and the reference scenario after controlling for the effects of plot location. No significant difference between S4, S8, S12, and the reference scenario indicated that the predictions based on these plots were similar to the prediction that has the full number of plots, whereas a significant difference suggested that these plots were not sufficient to make the forest landscape prediction.

For our final analysis, we conducted partial correlation analysis between different plot locations scenarios (SN, SS, SE, and SW) and the reference scenario. This allowed us to analyze the correlations of one location and the reference scenario after controlling for the effects of other locations. The partial correlation coefficient (r) was used to characterize the relative contribution of plot locations (different aspects) to the forest landscape prediction. The larger the partial correlation coefficient was between plot location scenario and the reference scenario, the greater the contribution of this location to the forest landscape prediction. The differences of partial correlation coefficient under different plot location scenarios indicated different predictive potentials of the four slopes. We also transformed partial correlation coefficients of different locations into proportions for comparing the differences of the relative contributions of plot location among simulated species.

Results

Relative importance of plot number, location, and their interaction

For spruce and birch, the proportions of type III sums of square values for plot number were larger than those for plot location and their interaction (Fig. 4), indicating that the relative importance of plot number effects on the forest landscape prediction was larger. In addition,

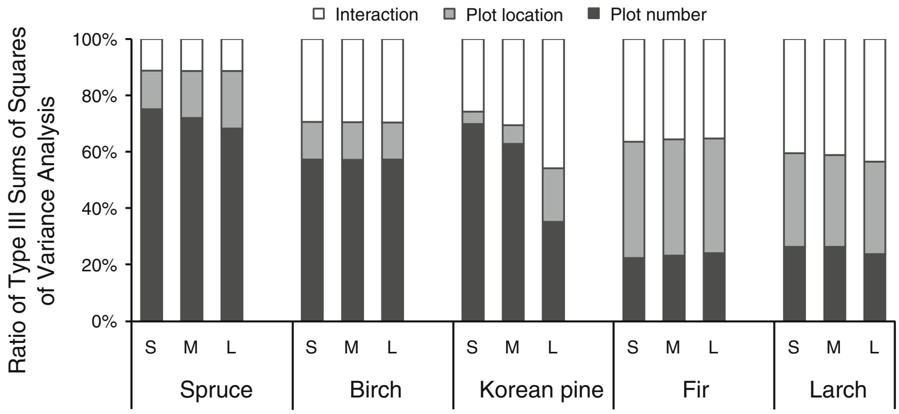


Fig. 4 Ratio of the type III sums of square values of a fixed model (both plot number and location are fixed factors) corresponding with the relative importance of plot number, location, and their interaction to species distribution prediction at the landscape scale in the short (S), middle (M) and long terms (L)

there was no obvious variation for the two species among three simulation periods on the ratios of type III sums of square values for plot number, location, and their interaction. This also indicated that the relative importance of the effects of plot number, location, and their interaction on forest landscape predictions had little change in the short, middle, and long terms. However, for Korean pine, the relative importance in the three time frames had variations (Fig. 4). The relative importance of plot number effects on forest landscape predictions was larger in the short and middle terms than in the long term, whereas in the long term the interaction of plot number and location accounted for increasing variations in the relationships between sample design scenarios and the reference scenario.

In contrast, for fir and larch, these relationships between sample design scenarios and the reference scenario were otherwise quite robust to variations in plot location and the interaction of plot number and location. For fir, type III sums of square values of plot number, location, and interaction accounted for 23, 41, and 36 %, respectively, in the entire simulation period, and for larch accounted for 26, 33, and 41 %, respectively (Fig. 4). For the two species in the entire simulation period, the effects of both plot location and interaction on forest landscape predictions were larger than plot number effects, indicating that landscape-scale distribution predictions of these species depend mostly on proper location.

The effects of plot number scenarios on landscape predictions

Spruce tests showed significant differences between the reference scenario and S4, S8, S12 in the short, middle, and long terms, respectively ($p < 0.05$, Fig. 5), indicating that predictions under these three plot number scenarios were not sufficient to predict landscape-scale change. For fir and larch, no significant difference was found between the reference scenario and S4, S8, and S12 in the three simulated periods ($p > 0.05$, Fig. 5), suggesting that predictions based on four, eight and 12 plots were similar to the prediction that has the full number of plots. The differences between the reference scenario and the three plot number scenarios of spruce were all significant, and the differences for fir and larch were all not significant, indicating that the quality of predictions did not change with increasing plot number. That is to say, the predictive potentials of plots for these three species were not sensitive to plot numbers.

However, not all species follow these patterns. For example, for birch, prediction based on four plots was not similar to the prediction with full number of plots, whereas that based on eight plots was similar, showing increasing plot number effects. Korean pine experienced a more complicated situation. The predictions based on 12 plots were similar to the prediction that has the full number plots in the short and middle terms, whereas in the long term eight plots were enough. The effects of plot number not only vary with increasing plot number, but also differ among the short, middle, and long terms.

The effects of plot location scenarios on landscape predictions

The partial correlation coefficients among the four location scenarios (SN, SS, SE, and SW) and the reference scenario in the short, middle, and long terms

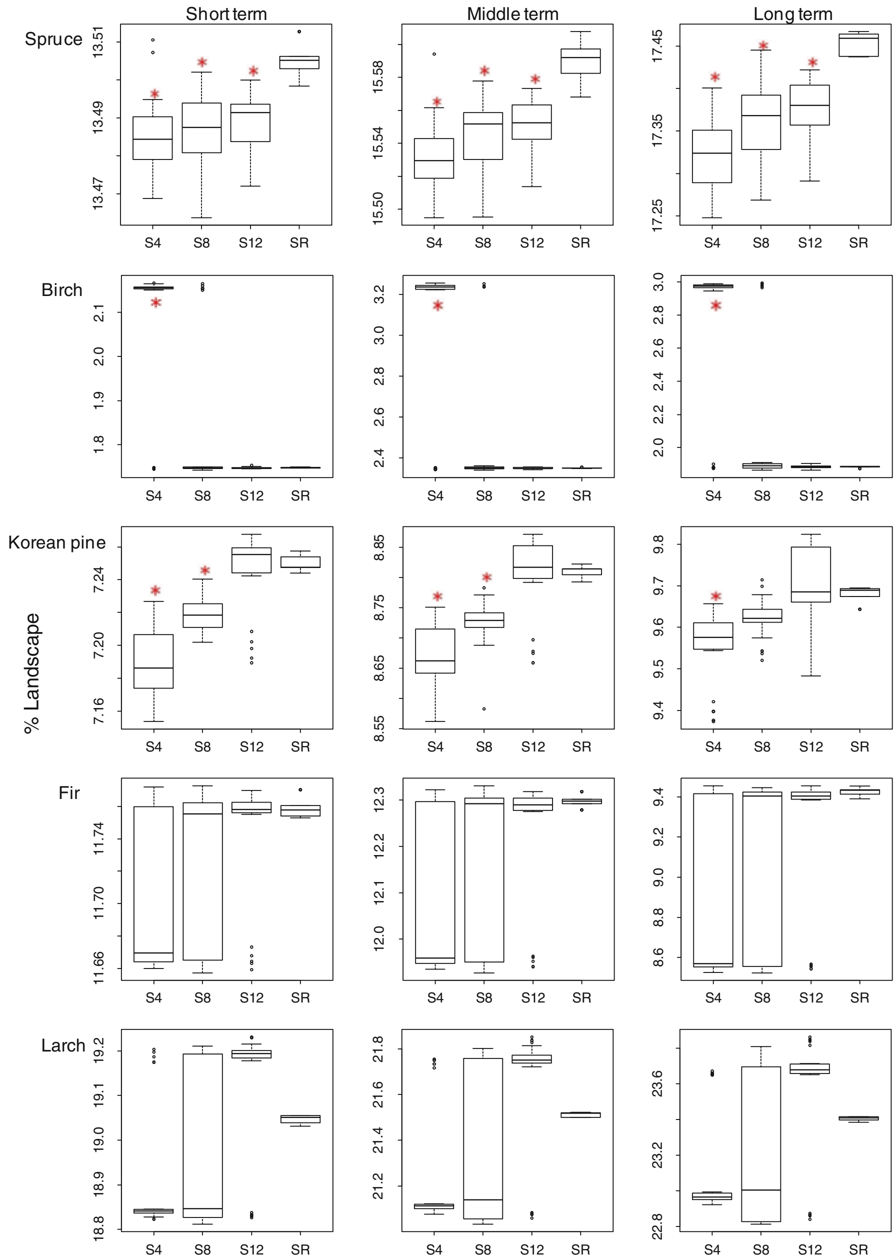


Fig. 5 Differences in species percent area between different plot numbers scenarios (S4, S8, and S12) and the reference scenario (SR) in the short, middle, and long terms. * indicates a significant difference ($p < 0.05$)

were consistent with those throughout the entire simulation period (Fig. 6). For most of the species, one or two aspects performed best in predicting forest landscape change under climate warming.

For spruce, the reference scenario was more highly correlated with SN and SE than with SS and SW, indicating that plots on the north and east slopes made larger contributions to landscape change predictions (43 and 32 %, respectively) than plots on the south and west slopes (11 and 14 %, respectively). For birch and fir, plots on the north and south slopes made larger contributions to landscape change predictions than plots on the east and west slope. Moreover, distribution areas of these two species on the north and south slope are larger than those on the other slopes. For Korean pine, plots on both the south and east slopes made larger contributions, whereas for larch plots on the north and west slope made larger contributions.

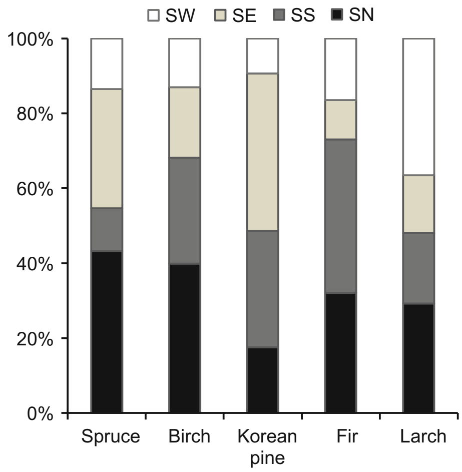


Fig. 6 Ratio of partial correlation coefficients between different plot locations scenarios (SN, SS, SE, and SW) and the reference scenario during the entire simulation period

Discussion

Sample size and sampling design is an important issue in many disciplines. For example, in a remote sensing classification, rules and formulas exist to determine the actual number of ground reference samples for assessing the accuracy of individual categories (Stehman et al. 2003; Wickham et al. 2010). The number of samples can be adjusted based on the relative importance of a particular category or by the inherent variability within each category. The general consensus from sampling theory is that categories that have low variability require fewer samples and categories that have high variability require more samples (Congalton 1991). In ecological studies, however, it is often unfeasible to have a large number of plots because of relatively high human and financial costs associated with experimental plots (Jansen and Bredemeier 2004). Ecological studies require considering plot number, location, and their interaction using a balanced approach between predictability and practicality. Thus, studying sample design (plot number and location) on a heterogeneity landscape is essential in predictions of landscape-scale responses.

We introduced a coupled ecosystem and landscape modeling approach to study the effects of plot number and location on prediction of tree species distribution at landscape scales. We designed a set of plot number and location scenarios with increasing plot numbers randomly placed on various land types. We set different parameters to differentiate land types having plots from land types having no plots. We then used the coupled model to simulate the effects of plot number, plot location, and their interaction on forest landscape predictions. Our approach revealed the sensitivity of species to environmental heterogeneity and based on which sample design may be considered for predicting landscape-scale responses.

Our results show that for some species highly sensitive to environmental heterogeneity, the contributions of plot number are generally larger than the contributions of plot location. This suggests that the high sensitivity species have different responses on different land types. Consequently, most or all land types need to have a plot to fully capture the species suitability to environment. Such a finding is reinforced by tree species in our study area. For example, spruce is a dominant species in spruce–fir forests and has a wider distribution than fir in the study area (He et al. 2002). Community structure of spruce–fir forest is strongly affected by elevation and aspect (Chen and Bradshaw 1999), resulting in varying suitability of spruce to environment among different land types. Under a warming climate, spruce migrates upward as the whole system; however, during this migration, spruce remains highly sensitive to environmental heterogeneity (He et al. 2005). Thus, for spruce, relatively more plots are needed to accurately predict species distribution.

Our results also show that for species that are moderately sensitive to environmental heterogeneity, plot number makes a relatively large contribution to forest landscape predictions, as do plot location and interaction. Suitability of these species to environment has a moderate spatial variation, which is weaker than the variation of species with high sensitivity. Thus, moderate number of plots is sufficient to cover all variations of species suitability to environment. The prediction of some plots with appropriate locations can approximate the predictions based on the full number of plots. This result is also reflected in tree species simulated in our study. For example, birch is moderately sensitive to environmental heterogeneity. The suitability of birch to environment is different on some but not all land types. The effects of plot number on forest landscape predictions illustrate that the predictions require having plots on some (e.g., land types with large area of species distribution) but not on all land types to cover the variations of species suitability.

Our results show that for species insensitive to environmental heterogeneity, the contributions of plot location and interaction to predict species distribution at the landscape scale are significantly larger than the contributions of plot number. Suitability of these species to environment has a weak spatial variation, and thus a few plots are able to cover all variations; however, these plots should be placed on the locations with high contributions for prediction quality (such as land types with large area of species distribution). Such a finding is supported by larch, an azonal species that is wide-spread in the Changbai mountains (Yan and Zhao 1996; Zhao et al. 1998). Larch also adapts to diverse environmental conditions and spans almost all elevation zones (Leng et al. 2007). Prediction based on four appropriate plots in the four elevation zones is similar to the prediction based on the full number of plots in the entire simulation period. The quality of prediction would not vary with increasing plot number, demonstrating the weak sensitivity of larch to the environment heterogeneity (Leng et al. 2007, 2008). By analyzing the relative contributions of different plot locations to forest landscape predictions, we also found that plots on the west slope made the largest contributions. Thus, for larch, plot location or interaction of number and location are important in forest landscape predictions.

The most complicated situation that we observed was the possible variation in relative contributions of plot number, location, and their interaction to forest landscape predictions in different simulation periods. For example, for Korean pine, a dominant species in Korean pine hardwood forests, plot number accounted for most of the effects on predicting species distribution at the landscape scale in the short and middle terms, whereas the long-term landscape prediction was mainly influenced by plot location and interaction. Our results indicate that accurate landscape prediction requires more plots in the short and middle terms, whereas in the long term relatively fewer plots are sufficient. This demonstrates that Korean pine is moderately sensitive to environmental heterogeneity but varies in different simulation periods. There are several reasons for this complexity. First, Korean pine experienced intense historical harvest and showed a strong post-harvest recovery during short- and middle-term simulations (Zheng et al. 1997; He et al. 2002). Predicting a dramatic increase in total area resulting from a strong recovery would require more plots. Although under warming climate Korean pine can compete with spruce and fir at their lower elevation zone, the limited seeds and dispersal of Korean pine due to historical harvest decreased the likelihood of a large-scale landscape change from spruce–fir to mixed Korean pine forest (He et al. 2005; Liang et al. 2011a). Thus, the increase in total area of Korean pine under climate warming in the long term was mostly within the current elevation zone. Different ratios of the contributions of plot number and location in the short, middle, and long terms govern different sample designs for forest landscape predictions.

This study used standard statistic tests to determine whether differences exist between a plot number or location scenario with the reference scenario. Statistical significance may not translate to an ecological significance. For example, while mean values under predictions with four plots and a full number of plots may be statistically different, their ecological differences may be acceptable. This study did not aim to study whether a significant statistical difference warrants a significant ecological difference. However, results from this study reveal such differences and provide a basis for studying this issue in the future.

Conclusions

We investigated the effects of plot number and location on predicting tree species distribution at the landscape scale. Our results indicated that for species highly or moderately sensitive to environmental heterogeneity (e.g., spruce and birch), increasing plot numbers to cover as many land types as possible is the strategy to accurately predict species distribution at the landscape scale. In contrast, for species insensitive to environmental heterogeneity (e.g., larch and fir), plot location was more important than plot number in predicting forest landscape change. In this case, placing plots in land types with large area of species distribution is warranted. The most complicated situation was observed for some moderately sensitive species (e.g., Korean pine). Plot number made a larger contribution than plot location to forest landscape predictions in the short and middle terms, whereas location made a larger contribution in the long term. Such complexity may be due to limited dispersal capability and past human harvest that affected seed sources and subsequently delayed recovery.

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References

Aber JD, Ollinger SV, Driscoll CT, Likens GE, Holmes RT, Freuder RJ, Goodale CL (2002) Inorganic N losses from a forested ecosystem in response to physical, chemical, biotic and climatic perturbations. Ecosystems 5:648–658

Abrahamson IL, Nelson CR, Affleck DLR (2011) Assessing the performance of sampling designs for measuring the abundance of understory plants. Ecol Appl 21(2):452–464

Bechtold WA, Patterson PL (2005) The enhanced forest inventory and analysis program—national sampling design and estimation procedures. Gen Tech Rep SRS-80. Asheville: U.S. Department of Agriculture, Forest Service, Southern Research Station p 85

Chen JQ, Bradshaw AG (1999) Forest structure in space: a case study of an old growth spruce-fir forest in Changbaishan Natural Reserve, PR China. For Ecol Manage 120:219–233

Chi ZW, Zhang FS, Li XY (1981) Preliminary analysis on the climate of the Changbai mountain area. Res For Ecosyst 2:179–186

Chiesi M, Chirici G, Barbati A, Salvati R, Maselli F (2011) Use of BIOME-BGG to simulate Mediterranean forest carbon stocks. Forest 4:121–127

Congalton RG (1991) A review of assessing the accuracy of classifications of remotely sensed data. Remote Sens Environ 37:35–46

Eastaugh CS, Pötzelsberger E, Hasenauer H, Abrams M (2011) Assessing the impacts of climate change and nitrogen deposition on Norway spruce (Picea abies L. Karst) growth in Austria with BIOME-BGC. Tree Physiol 31(3):262–274

Fang JY, Wang GG, Liu GH, Xu SL (1998) Forest biomass of China: an estimation based on the biomass-volume relationship. Ecol Appl 8:1084–1091

Fang JY, Chen AP, Peng CH, Zhao SQ, Ci LJ (2001) Changes in forest biomass carbon storage in China between 1949 and 1998. Science 292:2320–2322

Han YZ, Wang ZQ (2002) Spatial heterogeneity and forest regeneration. J Appl Ecol 13(5):615–619

Hao ZQ, Dai LM, He HS, Mladenoff DJ, Shao GF (2001) Potential response of major tree species to climate warming in Chingbai mountain. Chin J Appl Ecol 12:653–658

He HS, Mladenoff DJ (1999) Effects of seed dispersal in the simulation of long-term forest landscape change. Ecosystems 2:308–319

He HS, Mladenoff DJ, Crow TR (1999) Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecol Model 112:213–233

He HS, Hao ZQ, Larsen DR, Dai LM, Hu YM, Chang Y (2002) A simulation study of landscape scale forest succession in northeastern China. Ecol Model 156:153–166

He HS, Hao ZQ, Mladenoff DJ, Shao GF, Hu YM, Chang Y (2005) Simulating forest ecosystem response to climate warming incorporating spatial effects in north-eastern China. J Biogeogr 32:2043–2056

He HS, Keane RE, Iverson LR (2008) Forest landscape models, a tool for understanding the effect of the large-scale and long-term landscape processes. For Ecol Manage 254:371–374

Hewitt JE, Thrush SF, Dayton PK, Bonsdorff E (2007) The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. Am Nat 3(169):398–407

Jansen M, Bredemeier M (2004) Interdisciplinary forest ecosystem experiments at Solling, Germany—from plot scale to landscape level integration. For Snow Landsc Res 78(78):33–52

Jenkins JC, Birdsey RA, Pan Y (2001) Biomass and NPP estimation for the mid-atlantic region (USA) using plot-level forest inventory data. Ecol Appl 11(4):1174–1193

Leng WF, He HS, Bu RC, Hu YM (2007) Sensitivity analysis of the impacts of climate change on potential distribution of three larch(larix) species in northeastern China. J Plant Ecol 31(5):825–833

Leng WF, He HS, Bu RC, Dai LM, Hu YM, Wang XG (2008) Predicting the distributions of suitable habitat for three larch species under climate warming in Northeastern China. For Ecol Manage 254:420–428

Liang Y, He HS, Bu RC, Hu YM, Shao GF (2011a) Are plot data effective for landscape prediction: a simulation study of tree species response to climate warming under varying environmental heterogeneity. Ann For Sci 68:899–909

Liang Y, He HS, Lewis BL (2011b) Responses of tree species to climate warming at different spatial scales. Chin Geogr Sci 21(4):427–436

Liu QJ (1997) Structure and dynamics of the subalpine coniferous forest on Changbai mountain, China. Plant Ecol 132:97–105

Meigs GW, Turner DP, Ritts WD, Yang ZQ, Law BE (2011) Landscape-scale simulation of heterogeneous fire effects on pyrogenic carbon emissions, tree mortality, and net ecosystem production. Ecosystems 14(5):758–775

Miller JR, Turner MG, Smithwick EAH, Dent CL, Stanley EH (2004) Spatial extrapolation: the science of predicting ecological patterns and processes. Bioscience 54(4):310–320

Mladenoff DJ, He HS (1999) Design and behaviour of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff DJ, Baker WL (eds) Advances in spatial modeling of forest landscape change: approaches and applications. Cambridge University Press, Cambridge, pp 125–162

Ollinger SV, Aber JA, Federer CA (1998) Estimating regional forest productivity and water yield using an ecosystem model linked to a GIS. Landscape Ecol 13:323–334

Peignéa J, Vian JF, Cannavacciuolo M, Bottollier B, Chaussod R (2009) Soil sampling based on field spatial variability of soil microbial indicators. Eur J Soil Biol 45(5–6):488–495

Post WM, Pastor J (1996) Linkages–an individual-based forest ecosystem model. Clim Change 34:253–261

Rastetter EB, Aber JD, Peters DPC, Ojima DS, Burke I (2003) Using mechanistic models to scale ecological processes across space and time. Bioscience 53(1):68–76

Schmitz OJ (2005) Scaling from plot experiments to landscapes: studying grasshoppers to inform forest ecosystem management. Oecologia 145:225–234

Shao GF, Schall P, Wishampel JF (1994) Dynamic simulations of mixed boradleaved-Pinus koriensis forests in the Changbaishan biosphere reserve of China. For Ecol Manage 70:169–181

Shao GF, Zhao G, Shugart HH, Wang S, Schaller J (1996) Forest cover types derived from landsat thematic mapper imagery for the Changbai mountain area of China. Can J For Res 26:206–216

Stehman SV, Wickham JD, Smith JH, Yang L (2003) Thematic accuracy of the 1992 National Land-Cover data for the eastern United States: statistical methodology and regional results. Remote Sens Environ 86:500–516

Stone R (2006) A threatened nature reserve breaks down Asian borders. Science 313(5792):1379–1380

Underwood N, Hamback P, Inouye BD (2005) Large-scale questions and small-scale data: empirical and theoretical methods for scaling up in ecology. Oecologia 145:177–178

Wang Z, Xu Z, Tan Z, Dai H, Li X (1980) The main forest types and their features of community structure in northern slope of Changbai mountain. For Eco Res 1:25–42

Wickham JD, Stehman SV, Fry JA, Smith JH, Homer CG (2010) Thematic accuracy of the NLCD 2001 land cover for the conterminous United States. Remote Sens Environ 114:1286–1296

Yan XD, Zhao SD (1996) Simulating the response of Changbai Mt. forests to potential climate change. J Environ Sci 8:354–366

Yang H, Li D (1985) Distribution patterns of dominant tree species on northern slope of Changbai mountain. Res For Ecosyst 5:1–14

Zhao SD, Yan XD, Yang SH, Tao DL, Dai LM (1998) Simulating responses of northeastern China forests to potential climate change. J For Res 9(3):166–172

Zhao SQ, Fang JY, Zong ZJ, Zhu B, Shen HH (2004) Composition, structure and species diversity of plant communities along an altitudinal gradient on the northern slope of Mt. Changbai, Northeast China. Chin Biodivers 12(1):164–173

Zheng DL, Wallin DO, Hao ZQ (1997) Rates and patterns of landscape change between 1972 and 1988 in the Changbai mountain area of China and North Korea. Landscape Ecol 12(4):241–254