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Importance of colonization and competition in forest landscape response to global climatic change

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Abstract The tree species composition of a forested landscape may respond to climate change through two primary successional mechanisms: (1) colonization of suitable habitats and (2) competitive dynamics of established species. In this study, we assessed the relative importance of competition and colonization in forest landscape response (as measured by the forest type composition change) to global climatic change. Specifically, we simulated shifts in forest composition within the Boundary Waters Canoe Area of northern Minnesota during the period 2000–2400 AD. We coupled a forest ecosystem process model, PnET-II, and a spatially dynamic forest landscape model, LANDIS-II, to simulate landscape change. The relative ability of 13 tree species to colonize suitable habitat was represented by the probability of establishment or recruitment. The relative competitive ability was represented by the aboveground net primary production. Both competitive and colonization abilities changed over time in response to climatic change. Our results showed that, given only moderate-frequent windthrow (rotation period = 500 years) and fire disturbances (rotation period = 300 years), competition is relatively more important for the short-term (<100 years) compositional response to climatic change. For longer-term forest landscape response (>100 years), colonization became relatively more important. However, if more frequent fire disturbances were simulated, then colonization is the dominant process from the beginning of the simulations. Our results suggest that

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the disturbance regime will affect the relative strengths of successional drivers, the understanding of which is critical for future prediction of forest landscape response to global climatic change.

1 Introduction

The current global climatic changes in temperature, CO_2, precipitation and radiation can have substantial effects on forest landscape compositions and patterns (Hansen et al. 2001). The tree species composition of a forested landscape may respond to climate change through two primary succession mechanisms: (1) colonization of suitable habitats and (2) competitive dynamics of established species. Colonization of suitable habitats is mainly determined by tree species' relative colonization ability, while the competitive dynamics are mainly determined by species' relative competitive ability. A species' colonization ability can be determined by its fecundity, the spatial distribution of seeds (Higgins et al. 2003), and seedling establishment. Climatic change could affect species fecundity through the process of flowering and seed production (LaDeau and Clark 2001; Memmott et al. 2007), and affect seedling establishment through the modification of environmental factors (e.g., temperature and moisture) (He et al. 1999; Price et al. 2001). The competitive ability of established plants is determined by the growth rate; height, leaf and root longevity; life history attributes; and many other characteristics (Grime 2001; Roberts 1996). However, growth rate is assumed to be a major determinant of transient dynamics of competition (Tilman 1988). Projected climate changes could affect growth rates through the modification of photosynthesis due to changes in temperature, water availability, CO_2 concentration and photosynthetically active radiation [PAR] (Long et al. 2004).

There have been several simulation studies assessing the effects of modified competitive and colonization abilities on forest landscape composition and pattern responses to projected global climatic change. He et al. (1999) assessed the forest landscape change due to the modification of species colonization ability as determined by a seedling establishment probability. Scheller and Mladenoff (2005, 2008) assessed the forest landscape composition and biomass change by the joint modification of colonization ability (determined by the response of seedling establishment probability) and competitive ability (determined by the response of aboveground net primary production). However, there have been no studies quantifying the relative importance of these two succession drivers (i.e., the colonization driver as determined by the response of colonization ability to climatic changes, and the competition driver as determined by the response of competitive ability to climatic changes). Assessing the relative contributions of competition and colonization could be important for our understanding and prediction of forest landscape response to global climatic change. If the colonization driver is more important, then future research and modeling efforts should focus more on species' colonization ability in order to precisely predict forest landscape response. In another way, if the competition driver is more important, then research and modeling efforts should focus more on inter-species competition dynamics.

The forest landscape response to climatic change is composed of responses of different processes at different scales. In this study, we coupled a forest ecosystem process model (PnET-II) and a forest landscape model (LANDIS-II) to study how colonization of suitable habitats and competition among species at the forest succession level can affect forest compositions at the landscape level. Specifically, we assessed the relative importance of colonization as determined by seedling establishment probability and competition as determined by aboveground net primary production in the response of a transitional forest landscape (the Boundary Waters Canoe Area) to global climatic change. Since disturbances are important factors shaping forest succession and landscape dynamics (Frelich 2002) and fire disturbances may increase due to climatic change, we also assessed the effects of different fire-disturbance regimes on the importance of colonization and competition in forest landscape response.

2 Study area

Our study area (about 195,000 ha) is part of the Boundary Waters Canoe Area (BWCA) in northern Minnesota, USA (Fig. 1). BWCA has a cold temperate continental climate (Heinselman 1973). BWCA forests are transitional between boreal forests and Great Lakes north temperate forests. Almost all of the presettlement flora and fauna native to the area are currently present in the BWCA forests (Heinselman 1973; Scheller et al. 2005). The main tree species include red pine (*Pinus resinosa*), jack pine (*Pinus banksiana*), white pine (*Pinus strobus*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*) and quaking aspen (*Populus tremuloides*) (Baker 1989; Heinselman 1973). Other species including red maple (*Acer rubrum*), black ash (*Fraxinus nigra*), sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*) and balsam poplar *Populus balsamifera*) are also present (Heinselman 1973; Scheller et al. 2005). The life history attributes of tree species present in our study area are shown in Table 1.

Due to high fire frequency, the BWCA forests were historically dominated by even-aged stands of two fire-adaptive species: jack pine and quaking aspen (Heinselman 1973; Scheller et al. 2005). Because of fire suppression since the 1910s

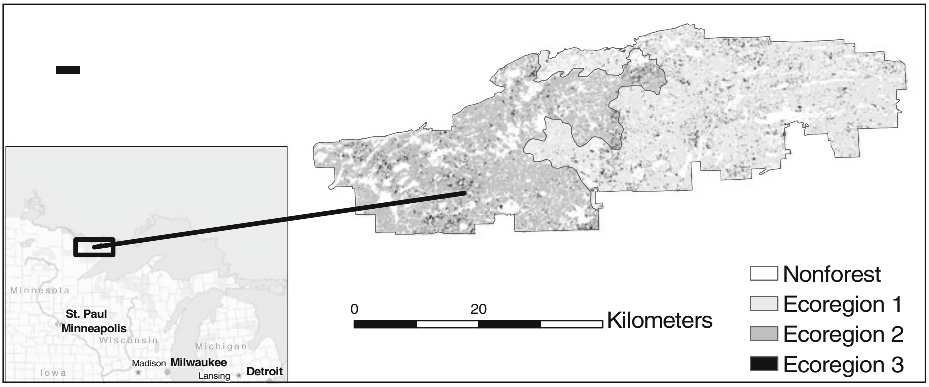

Fig. 1 Study area within the Boundary Waters Canoe Area Wilderness, Minnesota, USA

Table 1 Species life-history attributes

Species	LNG	MTR	ST	FT	ED	MD	VP	MAXVP	GGDMin	GDDMax	POT	FNC	MLMA	LRY
Aspen	160	25	1	2	200	5000	0.9	90	743	2900	20.0	2.5	83	1.0
Paper birch	230	30	2	2	200	5000	0.5	70	484	2036	18.8	2.3	100	1.0
Balsam poplar	150	25	1	2	200	5000	0.4	150	555	2491	17.7	2.5	80	1.0
Red maple	150	10	3	3	100	200	0.5	150	1260	6600	25.1	2.4	75	1.0
Sugar maple	300	40	5	3	100	200	0.1	240	1222	3100	25.0	2.5	85	1.0
Black ash	300	30	2	2	70	140	0.1	200	1000	2261	21.8	2.1	76	1.0
Red pine	300	40	2	3	12	275	0	0	1100	2035	21.5	1.5	250	2.3
White pine	350	40	3	4	100	250	0	0	1100	3165	22.5	2.2	175	3.0
Jack pine	200	15	1	3	20	40	0	0	830	2216	19.9	2.3	244	1.6
White spruce	250	40	4	1	30	200	0	0	280	1911	17.8	1.5	286	4.0
Black spruce	200	20	3	1	80	300	0	0	247	1911	17.7	1.5	286	4.0
Balsam fir	150	25	5	1	30	160	0	0	560	2386	19.6	1.6	204	4.0
White cedar	300	35	4	1	45	60	0	0	1000	2188	21.0	1.3	222	2.0

Data for POT are from Xu et al. (2007). Data for GGDMin and GDDMax are from Pastor and Post (1985). Other data are from Scheller et al. (2005)

LNG longevity (year), *MTR* age of maturity (year), *ST* shade tolerance (1 least tolerant and 5 most tolerant), *FT* fire tolerance (1 least tolerant and 5 most tolerant), *ED* effective seeding distance (meter), *MD* maximum seeding distance (meter), *VP* vegetative reproduction probability, *MAXVP* maximum age of vegetative reproduction (year), *GGDMin* minimum growing degree days, *GDDMax* maximum grow degree days, *POT* optimum temperature for photosynthesis (°C), *FNC* foliage nitrogen content (%), *MLMA* maximum leaf mass area (g m^{-2}), *LRY* leaf retention years (years)

(Baker 1992; Frelich and Reich 1995), the shade-intolerant and early-to-middle succession species are being replaced by shade-tolerant species including white spruce, black spruce, balsam fir and white cedar (Scheller et al. 2005). The current level of fire suppression caused fire frequency during the last century to be much lower than for the presettlement period.

Windthrow is another common disturbance in BWCA (Rich et al. 2007). The blowdown in 1999 affected about 30% of the all BWCA and about 5% in our study area (Scheller et al. 2005). The windthrow-caused mortality depends on age, species and diameter at breast height (DBH) (Rich et al. 2007). Species most susceptible to windthrow are early successional and shade intolerant (e.g., aspen, jack pine and red pine), while shade tolerant species, such as, white cedar and red maple, are least susceptible. The mortality generally increases with DBH. The wind-induced thinning of the forest favors white cedar, paper birch and red maple. There was also clear-cut logging until late the 1970s (Scheller et al. 2005).

The current species age cohort information in our study area are based on the TM imageries interpretation and forest stand age maps (Scheller et al. 2005). Within our study area, about 48% of the forestland is occupied by aspen-birch forest (forest dominated by aspen or birch), about 32% by spruce-fir forest (forest dominated by spruce or fir), about 18% by pine forest (forest dominated by jack pine, red pine or white pine), and less than 1% by maple-ash forest (forest dominated by maple or ash) and white cedar forest. Our study area is divided into three forested ecoregions (Fig. 1). Ecoregions 1 and 2 are based on State Soil Geographic (STATSGO) Data Base (Scheller et al. 2005; STATSGO 1994) with different soil water holding capacity. Ecoregion 3 is the lowland where only black spruce and black ash can establish.

3 Methods

In order to assess the relative importance of competition and colonization in forest landscape response to climatic change, a forest landscape model incorporating both colonization and competition processes was necessary. In this study, we used a spatially dynamic forest landscape model, LANDIS-II (Scheller et al. 2007; see Section A.1 in Appendix for details), to simulate the forest landscape response (measured by the forest type composition change) due to future climatic changes. The colonization process in the LANDIS-II model is simulated through seed dispersal (Ward et al. 2004), light condition assessment (Scheller and Mladenoff 2004), and seedling establishment based on a seedling establishment probability (SEP) (He and Mladenoff 1999a; Mladenoff and He 1999). The LANDIS-II model simulates competition as a function of available growing space and the growth rate specific to each tree species as determined by the potential or maximum aboveground net primary production ($\mathrm{ANPP}_{\mathrm{potential}}$, i.e., the production capacity) (Scheller and Mladenoff 2004). The actual ANPP for any species-age cohort will be dependent upon $\mathrm{ANPP}_{\mathrm{potential}}$, cohort age (younger cohorts grow slower), and overstory competition.

We assume that the response of species' colonization ability to climatic change was governed by the modification of seedling establishment probability, and the response of species' competitive ability was determined by the modification of potential aboveground growth rate. In order to simulate large-scale landscape change, forest landscape models generally do not simulate complex ecosystem processes (e.g., the water and carbon cycles). However, the estimation of seedling establishment probability and aboveground net primary production under climatic change requires detailed small-scale ecosystem processes (e.g. water and carbon fluxes). In this study, we used a forest ecosystem process model, PnET-II (see Section A.2 in Appendix for details), to estimate SEP (which determines the colonization ability response to climatic change) and $\text{ANPP}_{\text{potential}}$ (which determines the competitive ability response to climatic change) for the LANDIS-II model (See Fig. 2 for a better understanding of model coupling and Section A.3 in Appendix for details). The PnET-II model is a process-based model of carbon and water cycles in forest ecosystems (Aber and Federer 1992; Aber et al. 1995; Ollinger et al. 2002). It simulates the effect of climatic change on forest photosynthesis by applying adjusting factors for light (dependent on input of PAR), temperature (dependent on the deviance of current temperature to the optimum photosynthetic temperature for specific species), water availability (dependent on input of precipitation and soil water holding capacity), water vapor deficit, and ambient CO_2 concentration.

Since disturbances are important factors shaping forest succession and landscape dynamics (Frelich 2002), in this study, we simulated a current level moderate-frequent windthrow disturbances with a rotation period of 500 years (the rotation period refers to the average interval between two successive disturbances for all sites in the study area) (Scheller et al. 2005). The probability of fire may also increase under future climatic change due to the reduction of snow cover period and fuel moisture (Westerling et al. 2006). It is possible that contemporary fire suppression activities may not be sustainable. Therefore, we simulated forest landscape change under three potential disturbance scenarios: (1) with moderate-frequent windthrow disturbances and no fire disturbances (assuming successful fire suppression); (2) with moderate-frequent windthrow disturbances and a moderate-frequent fire regime (rotation period = 300 years); and (3) with moderate-frequent windthrow disturbances and a very frequent fire regime (rotation period = 65 years). The fire regime with a 300-year rotation period represents a management policy of moderate fire reintroduction based on Scheller et al. (2005). The fire disturbances regime with a 65 year rotation

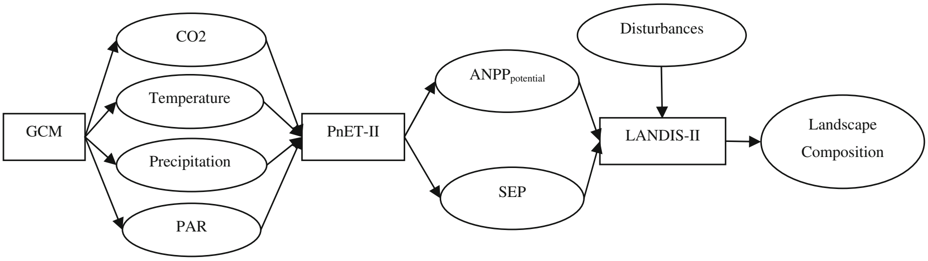

Fig. 2 Flow diagram of model coupling. The *ovals* represent input/output variables for a certain model. The *rectangles* represent models. *$ANPP_{\text{potential}}$* Potential/Maximum aboveground primary production; *SEP* species establishment probability. $\text{ANPP}_{\text{potential}}$ and SEP may be modified by climatic change and is estimated by the PnET-II model. The modification of $\text{ANPP}_{\text{potential}}$ is used to represent species' colonization ability response to climatic change. The modification of SEP is used to represent species' competitive ability response to climatic change. *PAR* photosynthetic active radiation; *GCM* global circulation model

Table 2 Global climate model predictions used in the two-way ANOVA

Emission scenarios	Model	Institute	Project
A1B	AGCM + OGCM	Center for Climate System Research, National Institute for Environmental Studies, Japan	IPCC TAR
	Mk2.0	Australia's Commonwealth Scientific and Industrial Research Organization, Australia	IPCC TAR
	AOM	Goddard Institute for Space Studies, USA	IPCC FAR
	CM3.0	Institute for Numerical Mathematics, Russia	IPCC FAR
	NCAR-PCM	National Centre for Atmospheric Research, USA	IPCC TAR
A1FI	AGCM + OGCM	Center for Climate System Research, National Institute for Environmental Studies, Japan	IPCC TAR
A1T	AGCM + OGCM	Center for Climate System Research, National Institute for Environmental Studies, Japan	IPCC TAR
A2	CGCM2	Canadian Center for Climate Modelling and Analysis, Canada	IPCC TAR
	AGCM + OGCM	Center for Climate System Research, National Institute for Environmental Studies, Japan	IPCC TAR
	Mk2.0	Australia's Commonwealth Scientific and Industrial Research Organization, Australia	IPCC TAR
	Mk3.0	Australia's Commonwealth Scientific and Industrial Research Organization, Australia	IPCC FAR
	HADCM3	Hadley Centre for Climate Prediction and Research, UK	IPCC TAR
	NCAR-PCM	National Centre for Atmospheric Research, USA	IPCC TAR
B1	AGCM + OGCM	Center for Climate System Research, National Institute for Environmental Studies, Japan	IPCC TAR
	Mk2.0	Australia's Commonwealth Scientific and Industrial Research Organization, Australia	IPCC TAR
	Mk3.0	Australia's Commonwealth Scientific and Industrial Research Organization, Australia	IPCC FAR
	AOM	Goddard Institute for Space Studies, USA	IPCC FAR
	CM3.0	Institute for Numerical Mathematics, Russia	IPCC FAR

Table 2 (continued)

Emission scenarios	Model	Institute	Project
B2	CGCM2	Canadian Center for Climate Modeling and Analysis, Canada	IPCC TAR
	AGCM + OGCM	Center for Climate System Research, National Institute for Environmental Studies, Japan	IPCC TAR
	Mk2.0	Australia's Commonwealth Scientific and Industrial Research Organization, Australia	IPCC TAR
	HADCM3	Hadley Centre for Climate Prediction and Research, UK	IPCC TAR
	NCAR-PCM	National Centre for Atmospheric Research, USA	IPCC TAR
IS92a	CGCM2	Canadian Center for Climate Modelling and Analysis, Canada	VEMAP
	HADCM3	Hadley Centre for Climate Prediction and Research, UK	VEMAP

There were three runs for HADCM3 under A2 emission scenario in TAR
IPCC TAR IPCC Third Assessment Report; *IPCC FAR* IPCC Fourth Assessment Report; *VEMAP* Vegetation-Ecosystem Modeling and Analysis Project

period represents the presettlement disturbances regime (Heinselman 1973). Fire size is simulated based on a lognormal distribution (He and Mladenoff 1999b) with a mean fire size of 7,500 ha (Heinselman 1973).

3.1 Analysis of variance

A two-way analysis of variance (ANOVA) design is used to assess the relative importance of colonization and competition in forest-type composition response to climatic change (see Section A.4 in Appendix for details). Since there are uncertainties in the climatic change predictions (Kerr 2001; Mahlman 1997; Schwartz et al. 2002; Weaver and Zwiers 2000), the importance of colonization and competition was assessed under a potential climate change range as determined by an ensemble of 27 selected climate projections based on major global climate models under seven major greenhouse gas emission scenarios defined by IPCC Special Report on Emission Scenario (SRES 2000) (Table 2 and Fig. 3). Using this climate projection ensemble and a hierarchical clustering approach (Hastie et al. 2001), we define five levels of seedling establishment probabilities and five levels of aboveground primary production capacities (Fig. 4, see Section A.5 in Appendix for a more detailed explanation).

Using two-way ANOVA, we decompose the variance of output into partial variances contributed by colonization, competition, interaction between competition and colonization, and random variability. The ratios of partial variances to total variances are used to measure the importance of different successional drivers. In order to capture the climatic change through time, SEP and $\mathrm{ANPP}_{\mathrm{potential}}$ between year 2000 and 2090 AD were linearly interpolated based on the values under the 1990–2000 AD mean climate and the values for a specific combination under the

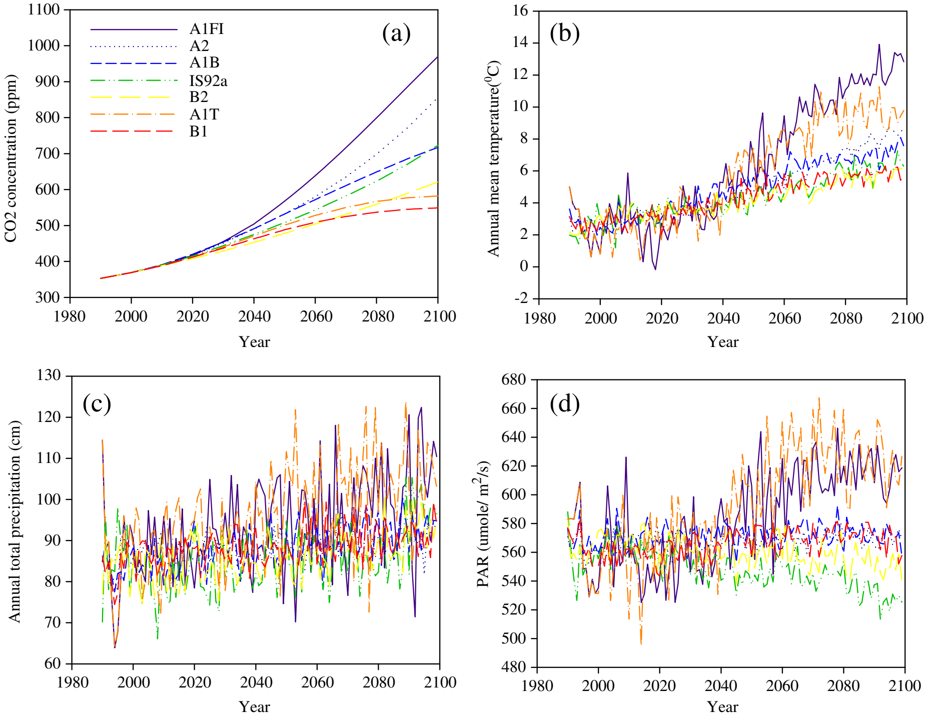

Fig. 3 Annual mean climate variable for 27 predictions in seven CO_2 emission scenarios: **a** annual mean CO_2 concentration (ppm); **b** annual mean temperatures (°C); **c** annual precipitation (cm); **d** annual mean PAR (μmol s^{-1} m^{-2})

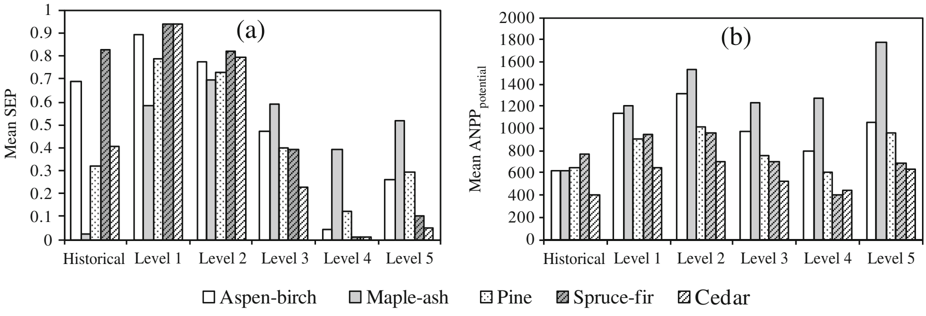

Fig. 4 Mean values of seedling establishment probability (SEP) (**a**) and potential aboveground net primary production (ANPP$_{potential}$) (**b**) for each forest type under historical climate during 1990–2000 AD and different SEP and ANPP levels under projected mean climate of the period 2090–2099 AD. The SEP and ANPP levels are defined based on a cluster analysis using an ensemble of 27 climate predictions from major global climate models under seven major greenhouse gas emission scenarios defined by IPCC. Based on SEP of spruce-fir forest, SEP levels 1–2 represents seedling establishment probabilities under mild climatic change and SEP levels 4–5 represents seedling establishment probabilities under more dramatic climatic change. See Fig. 9 in Appendix for a complete list of SEP and ANPP$_{potential}$ for individual species

2090–2099 AD mean climate. After 2099, we used SEP and $\text{ANPP}_{\text{potential}}$ based on those estimated for the 2090–2099 AD mean climate, assuming the climate stabilizes after year 2099 AD. Because most greenhouse gas emission scenarios predict that CO_2 will continue to rise after 2099 AD (IPCC 2001), our predictions after 2099 AD are conservative.

3.2 Model output

To examine the potential response of forest-type compositions, we classified the simulated forests into five forest types: aspen-birch (aspen, paper birch and balsam poplar), maple-ash (red maple, sugar maple and black ash), pine (red pine, white pine and jack pine), spruce-fir (white spruce, black spruce and balsam fir) and cedar (white cedar). For a particular landscape cell, assignment of forest type was based on the cumulative biomass for the five forest types. We used the landscape metric analysis software, APACK (Mladenoff and DeZonia 2000), to calculate the percentage area of different forest types in the forested ecoregions.

4 Results

The potential mean values of SEP and $\text{ANPP}_{\text{potential}}$ under projected future climatic change are shown in Fig. 4. Our results show that there are more dramatic changes in SEP than that in $\text{ANPP}_{\text{potential}}$. The SEP of spruce-fir under predicted future climatic change is substantially reduced compared to that during 1990–2000 AD (Fig. 4a). The coupled models realistically simulates the forest dynamics in our study area. Previous studies have already suggested that, with global warming, white pine would be favored, while spruce-fir would be reduced (Iverson and Prasad 1998, 2001; Jacobson and Dieffenbacher-Krall 1995; Shafer et al. 2001; Xu et al. 2009). These observations are in agreement of our simulation that pine forest will be favored with moderate disturbances under more dramatic climatic change (Fig. 4a, SEP levels 4–5 in Figs. 10c and 11c in Appendix). Our results shows that fire disturbances can play an important role in the simulated forest dynamics. Under scenarios with moderate-frequent and very-frequent fire disturbances, there is a high percentage area of aspen-birch or pine forest (Figs. 11a, c and 12a, c in Appendix), mainly because fire disturbances can create burned areas where the aspen-birch can opportunistically establish with their long dispersal distances and the pine species can compete against spruce-fir with their relatively higher fire tolerance (Table 1). This is in agreement with the observations that BWCA is historically dominated by pioneer forests of jack pine and aspen as a result of high severity crown fires (Aaseng et al. 2003; Heinselman 1973). Base on our simulations, under mild climatic change (i.e., SEP level 1 and 2, see Fig. 4a) with no fire disturbances, the study area is predicted to be dominated mainly by spruce-fir, pine, or cedar forest (SEP level 1 and 2 in Fig. 10c–e in Appendix). This is in agreement with the observation that the shade-intolerant and early-to-middle succession species are being replaced by shade-tolerant species including white spruce, black spruce, balsam fir and white cedar as a result of fire suppression since the 1910s (Baker 1992; Frelich and Reich 1995).

Using a two-way ANOVA for each year, we calculated the relative importance of colonization as determined by SEP and competition as determined by $\text{ANPP}_{\text{potential}}$

in forest landscape response to climatic change. Under both scenarios with no fire disturbances and moderate-frequent fire disturbances, competition was relatively more important at the beginning of the simulation when there were few opportunities

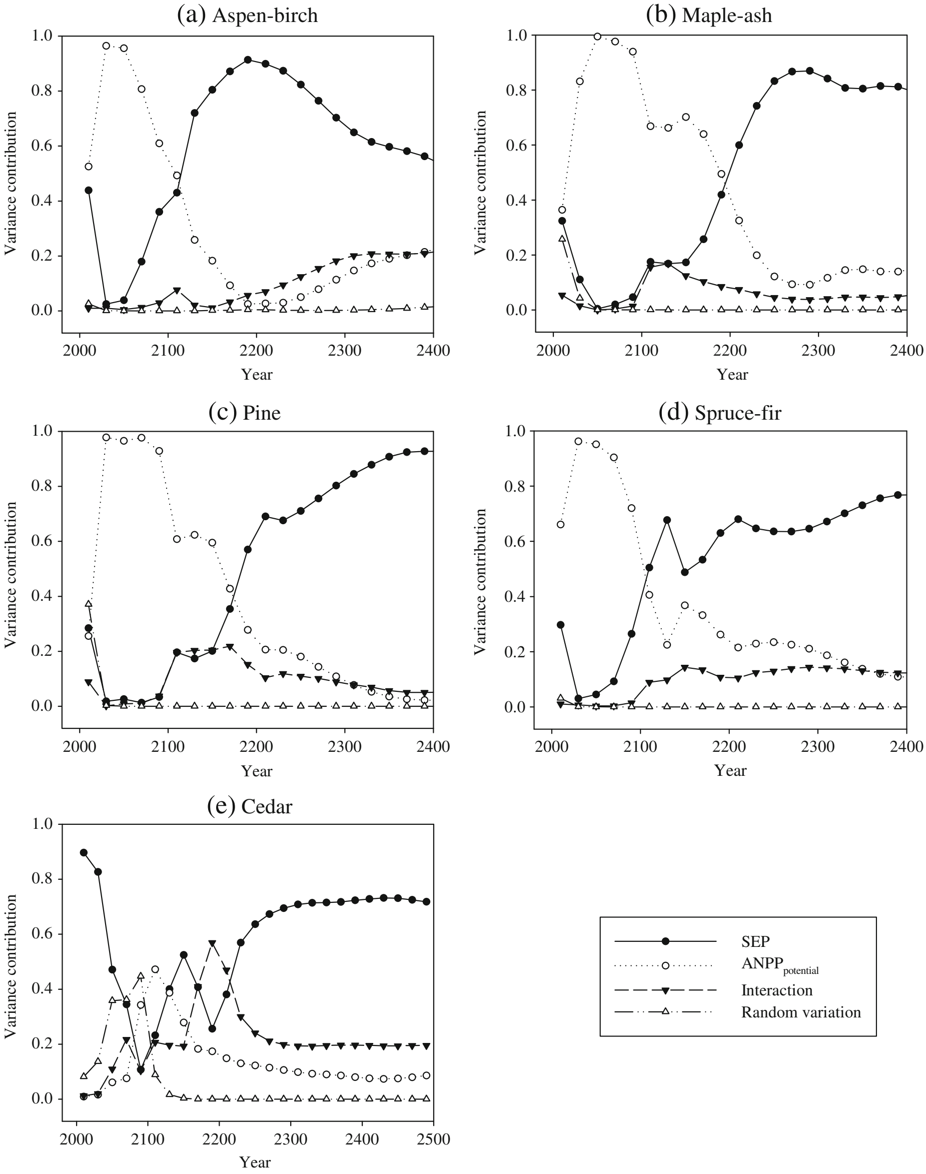

Fig. 5 a–e Variance contributions by colonization as determined by seedling establishment probability (SEP), competition as determined by potential aboveground net primary production (ANNP$_{\text{potential}}$) and their interactions under the scenario with mild windthrow (rotation period = 500 years) and no fire disturbances for colonization (Fig. 5, we did not plot the scenario with moderate-frequent fire disturbances which has a similar pattern as the scenario with no fire disturbances). Specifically, competition was relatively more important before year 2100 AD for

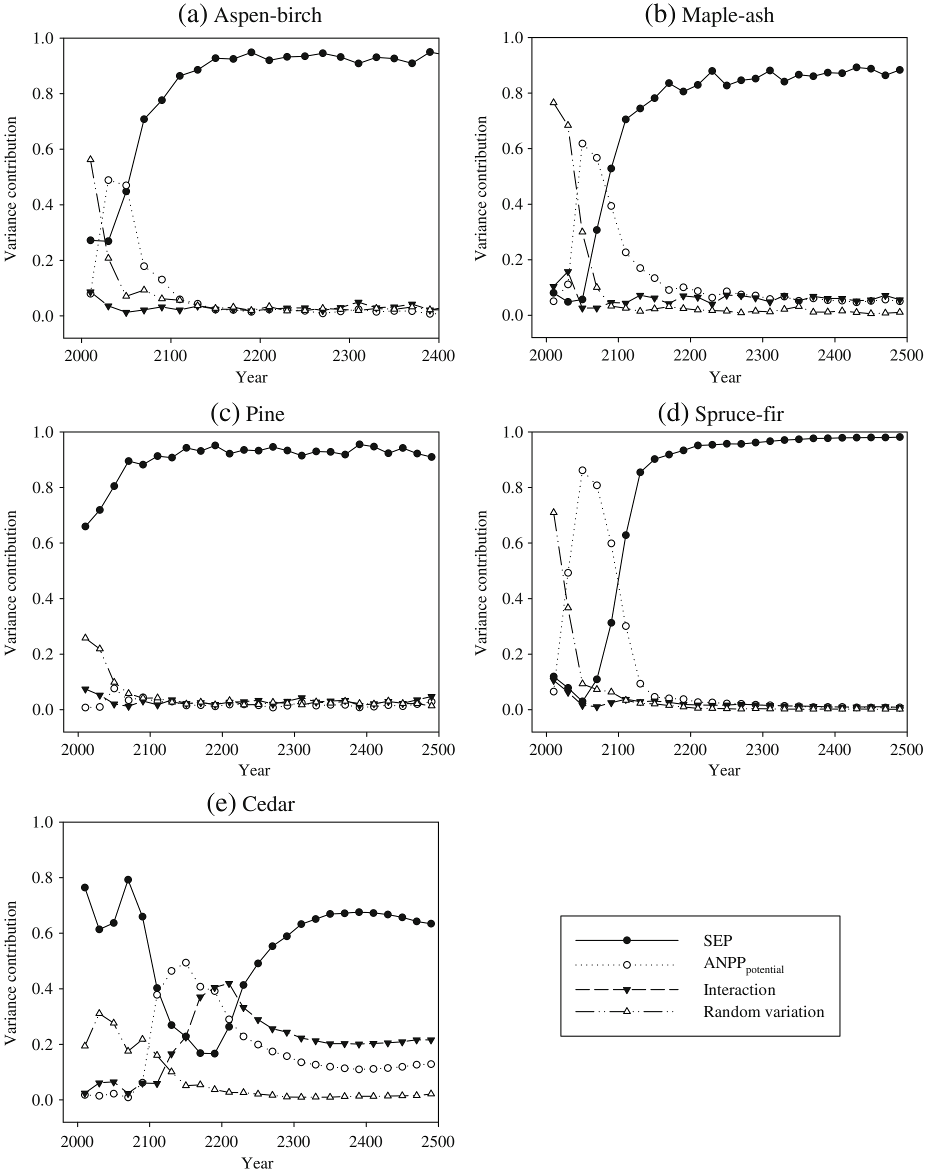

Fig. 6 **a–e** Variance contributions by colonization as determined by seedling establishment probability, competition as determined by potential aboveground net primary production capacity and their interactions under the scenario with moderate-frequent windthrow disturbances (rotation period = 500 years) and very frequent fire disturbances (rotation period = 65 years)

aspen-birch and spruce-fir (Fig. 5a, d), and before 2200 AD for maple-ash and pine (Fig. 5b, c). Note that due to a relatively small changes in species competition and colonization ability at the very beginning of the simulation, the random variation due to environmental stochasticity had a relatively high contribution and the relative importance for competition and colonization was highly uncertain (before 2100 for cedar and before 2020 AD for all other forest types). When there were more opportunities for colonization due to windthrow and fire disturbances, colonization became more important, particularly after 2100 AD for aspen-birch and spruce-fir (Fig. 5a, d); after 2200 AD for maple-ash and pine (Fig. 5b, c); and after 2240 AD for cedar (Fig. 5e).

For scenarios with more frequent fire disturbances, since there are more opportunities for colonization and shorter period of time for interspecies competition after seedling establishment, our simulation shows that colonization can be the dominant driver of succession from the beginning of the simulation for aspen-birch and pine forests (Fig. 6). For all forest types except for cedar, the results also show that the dominance of colonization is much higher than that for scenarios with mild disturbances (Fig. 6).

5 Discussion

Given moderate-frequent disturbances, our results suggest that competition is more important in the short-term (<100 years) landscape response to climate change because there are fewer opportunities for colonization. However, under scenarios with more frequent fires, colonization was the dominant cause for the short-term landscape response since there is a very short period of time for competition after seedling establishment. Our simulation results suggest that disturbance intensity could affect the relative importance of the primary drivers of succession. This highlights the importance of incorporation of disturbances into future prediction of forest landscape response to global climatic change, in view that there may be more intense and more frequent disturbance under global climatic change, including fire (Westerling et al. 2006), windthrow (Peltola et al. 1999) and insect outbreaks (Fleming and Candau 1998; Gustafson et al. 2010).

Our analysis highlights where efforts should be focused to reduce the uncertainty associated with climate change projections (Chen et al. 2000; Higgins et al. 2003; Stainforth et al. 2005). If the goal of a landscape study is to determine short-term dynamics, more attention should be paid to reducing the uncertainty in growth rates. In contrast, heavily disturbed landscapes or longer duration projections should focus on reducing the uncertainty associated with colonization, including seed production, dispersal and the probability of establishment. Although we did not consider the effects of migration, our results can inform users when and where immigration from neighboring biomes will become a significant driver of landscape change (Dyer 1995; Higgins et al. 2003; Iverson et al. 2004; Malcolm et al. 2002; Scheller and Mladenoff 2008).

Our analysis can also have important implications for carbon management. During potentially more dramatic disturbances under future climates, it is possible that the current forest species can retreat from their native ranges but without enough colonization from suitable replacement species. This can reduce the overall forest carbon storage, which can have substantial positive feedback to the global climate system. Therefore, in future forest management, we should be prepared for such a dramatic change and increase the forest diversity in their ability of adaptation to climatic change by means of fire control or forest plantation establishment.

Forest landscape response to climatic change is a multiscale complex process. There are many possible drivers including seed production (Greenwood et al. 2002; LaDeau and Clark 2001); seed dispersal (Higgins et al. 2003); seedling establishment (He et al. 1999); competition for nutrients; water and light (Gleeson and Tilman 1990); forest diebacks (Auclair 1993; Cox et al. 2004); herbivores (Howlett and Davidson 2003); pathogens and parasites (Moorcroft et al. 2006); and genetic adaptation (Bradshaw and Holzapfel 2006). In our study, response of species' colonization ability to climatic change was governed by the modification of seedling establishment probability. Colonization also depends on fecundity, which may increase under global climatic change (LaDeau and Clark 2001). However, the LANDIS-II model simulates species colonization at the site-level and does not incorporate the fecundity of individual trees. Since we simulated to a large extent at a spatial resolution of 85 meters, the exclusion of fecundity should not substantially affect the importance of colonization. Herbivores may also reduce the seedling survival (Howlett and Davidson 2003) and alter the importance of colonization in the forest landscape response. We did not incorporate this into our study due to the lack of available data. The migration of tree species from the south was not incorporated since the species of boreal forest and temperate forest tree species are both present in this area. The immigration of distant tree species from the south will be limited by sparse abundance (Iverson et al. 2004) and dispersal barriers (Scheller and Mladenoff 2008) and they may take many centuries to arrive in the BWCA.

In our study, response of species' competitive ability to climatic change was assumed to be determined by the modification of potential aboveground growth rate. Potential growth rate reflects differential abilities to acquire light, water, and nutrients (Aber and Federer 1992). Root production may also be important for forest succession and landscape change (Gleeson and Tilman 1990). However, this will be reflected in $ANPP_{\mathrm{potential}}$ representing differential ability to acquire light, water, and/or nutrients. Climatic change may also affect competitive ability by increasing mortality through drought and high temperature, which may result in forest dieback (Auclair 1993; Cox et al. 2004; Mantgem and Stephenson 2007). Forest dieback will affect the importance of colonization since it will create opportunities for colonization. We did not incorporate this process due to the limited availability of appropriate mechanistic models. Finally, because our simulations were based on 10-year time steps, we did not simulate competition at the seedling stage, which may have substantial effects on competition among saplings and trees (Meiners and Handel 2000).

In the future, more processes should be incorporated and tested to determine their importance in forest landscape response to global climatic change. For example, the same framework could be deployed to determine the relative contribution of varying maximum seed dispersal distances (Clark et al. 1998) to landscape composition if migration is assumed to be a significant factor. We should also consider the effects of different social-economic factors. In our study, the social-economic factors are only implicitly considered through the incorporation of different green-house emission scenarios, which depends on future population growth and economic development

(SRES 2000). However, the energy requirements by human society can have a substantial effect on forest landscape in the future with forest biomass as a potential source of renewable energy (Marland and Schlamadinger 1995). To comprehensively assess the future of forest ecosystems and their feedbacks to the global climate system, forest landscape models should be coupled with social-economic models to incorporate energy needs as determined by local population size, economy development, and energy cost associated with harvest and transportation.

Our study demonstrates the potential of coupling different models, originally developed for different scales, to measure ecosystem response to climatic change. The forest growth and succession models are commonly based on empirical growth curves of individual trees. However, climatic change may modify the growth curves to an extent that has not been observed in the past and the empirical relationship between environmental factors and species growth may not hold (King 1993). An important advantage of coupling a landscape model with an ecosystem process model is that we are able to partially account for the physiological acclimation under the climatic change. For example, in our study, we incorporated the process of stomata conductance reduction (which will ameliorate the effect of water stress) and CO_2 fertilization effect on photosynthesis (which will ameliorate the effect of high temperature) using the PnET-II model. There is also a need to couple individual tree processes into landscape models, to provide the flexibility to incorporate additional ecological processes (Purves et al. 2008). However, model coupling should consider model complexity (i.e., the number of parameters required), data availability, and relative knowledge gained. Under circumstances when a single process explains most variation, the addition of further model detail to explain the residual variation is not warranted.

For forest landscape models, it is always difficult to validate the simulation results due to the lack of detailed forest data at large spatial and long time scales (He 2008). However, since the model parameters and structures in both models are estimated based on historical forest inventory data and widely tested phenomenological functions that have strong basis in fundamental plot-scale physiology, their validity is consistent with the established theory and observed data (Rastetter et al. 2003). The LANDIS model is developed from the simplification of GAP models, a type of model to simulate the forest growth and succession dynamics at plot level using observed long term forest inventory data (Bugmann 2001). The validity of the LANDIS model assumptions is illustrated in many simulation studies from different forest types including various temperate deciduous forest systems of the Midwestern United States (Gustafson et al. 2000, 2004; He and Mladenoff 1999b; Scheller and Mladenoff 2005; Sturtevant et al. 2004a, b) and China (He et al. 2002); boreal forest ecosystems of North America (Mehta et al. 2004; Pennanen et al. 2004), Finland (Pennanen and Kuuluvainen 2002), Russian (Gustafson et al. 2010), and China (Wang et al. 2006; Xu et al. 2004); coastal chaparral of Southern California, USA (Franklin et al. 2001), transitional areas between boreal forest and temperate forest (Scheller et al. 2005) and high elevation coniferous forests of Switzerland (Schumacher et al. 2004). Furthermore, the PnET-II model has been developed from long-term, high-resolution gross and net carbon balance data measured at the Harvard Forest by eddy covariance towers and water and nutrient-balance data sets at Hubbard Brook (Aber and Federer 1992; Ollinger et al. 2002; Rastetter et al. 2003). Its validity has been illustrated in many applications in Northeastern US forests (Aber et al. 1995;

Jennifer 1999). The validity of both PnET and LANDIS model can strongly support our results in this paper, although they are still subjective to different sources of uncertainties as was discussed earlier.

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Appendix

A.1 LANDIS-II model

LANDIS models are spatially dynamic forest landscape models of disturbance, succession and management (Mladenoff and He 1999; Mladenoff et al. 1996; Scheller et al. 2007). The LANDIS models simulate forest dynamics by tracking species age cohorts (cohort of trees with the same age range). Many extensions have been developed for the LANDIS models including a fire disturbances extension (He and Mladenoff 1999b), a harvesting extension (Gustafson et al. 2000), a biological disturbances extension (Sturtevant et al. 2004a, b), a windthrow extension (Mladenoff and He 1999), and a succession extension with biomass accumulation (Scheller and Mladenoff 2004). In this study, we selected the LANDIS-II model (Scheller et al. 2007) which includes the biomass accumulation succession extension. With the biomass succession extension and disturbance extensions, simulated forest landscape change is driven by species life history attributes, competition and colonization abilities of multiple species, within-population variability due to age and aboveground biomass, natural variability due to different disturbance processes (e.g., fire and windthrow), and spatial heterogeneity due to variation of edaphic properties.

The LANDIS-II model simulates inter-specific competition based on the growth rate specific to each tree species as determined by potential aboveground net primary production capacity (Scheller and Mladenoff 2004). The potential aboveground net primary production capacity should be estimated for a specific climate and soil condition using ecosystem process models (in this study, the PnET-II model, for details see Section A.2 in this Appendix). Also dependent upon climate and soils, each cell (or site) has an available growing space (kg biomass/cell). The oldest cohorts appropriate growing space first, but are also subject to greater mortality. For younger cohorts, the species with the fastest growth rate (i.e., the largest aboveground net primary production capacity) will be allocated relatively more growing space, than those with lower growth rates, and will therefore achieve a greater actual aboveground net primary productivity. Actual aboveground net primary productivity is balanced by biomass loss for each cohort. Biomass loss is determined by a cohort biomass and age and represents both whole-tree mortality (e.g., stand thinning, not including disturbance induced mortality) and the loss of limbs and branches.

Tree species colonization in the LANDIS-II model is simulated through seed dispersal (Ward et al. 2004), light condition assessment (Scheller and Mladenoff 2004), and seedling establishment (He and Mladenoff 1999a; Mladenoff and He 1999). Seed dispersal is primarily determined by a species' potential seed dispersal distances as a function of a double exponential distribution (Ward et al. 2004). The light condition assessment is determined by species shade tolerance and available light. Species with shade tolerance classes 1 to 4 (higher value indicates higher tolerance ability of species) can only be establish when the available relative living biomass (ratio of available living biomass to maximum living biomass) are less than 0.247, 0.326, 0.428 and 0.588, respectively (Scheller and Mladenoff 2004). For a species with shade class 5, it can establish under any amount of aboveground biomass. Seedling establishment is determined by the seedling establishment probability, which quantifies the probability of seedling establishment under specific climate and soil conditions and will be modified by future climatic change. The current version of the LANDIS-II model does not incorporate an extension to calculate seedling establishment probabilities for different species. Thus they need to be estimated under specific climatic and edaphic conditions outside the LANDIS-II model.

The inputs for the LANDIS-II model include spatial inputs (an initial species and age cohort map and an ecoregions map) and non-spatial inputs (species life history attributes, aboveground net primary production capacities, seedling establishment probabilities, and disturbances regimes). The initial species and age cohort maps are derived from thematic image interpretation and forest stand age maps (Scheller et al. 2005). The study area was divided into three ecoregions (Fig. 1). Ecoregions 1 and 2 were derived from the Soil Geographic Data Base (Scheller et al. 2005; STATSGO 1994) and have differences in soil water holding capacities. The average soil water holding capacities are 6.67 and 10.02 cm for Ecoregions 1 and 2, respectively. Ecoregion 3 was limited to areas designated as lowlands for spruce and black ash forests. Species life history attributes are based on Scheller et al. (2005) (Table 1). The aboveground net primary production capacity and seedling establishment probability inputs were derived based on PnET-II model simulations

A.1.1 Fire disturbance

The base fire extension in LANDIS-II uses stochastic simulation approaches to simulate the fire disturbance (He and Mladenoff 1999b; Yang et al. 2004). The fire probability (P) of each cell is determined by the mean rotation period (RP) and time since last fire (T),

$$P = B \times T \times RP^{-(e+2)} \tag{1}$$

where B is the fire probability coefficient designed for model calibration. In order to simulate the fire disturbance, the model first locates the candidate ignition point on each ecoregion randomly. The number of the candidate ignition points (N_{ip}) is determined from the ignition coefficient, which is user-defined (N_{ip} = ignition coefficient × total cell number of each ecoregion). LANDIS calculates the fire probability (P) of the candidate ignition point by Eq. 1 and a random number (P_r) is generated to check if this cell will be ignited. If the cell were ignited, LANDIS simulates the fire spread. The fire probabilities of all the four adjacent cells are calculated using Eq. 1 and a random number is generated to check if the fire will be spread to the adjacent cell. Fire spreads until either the desired fire size is reached, or the surrounding cells cannot burn, or non-forest surrounds the cell. The desired fire size is drawn from a lognormal distribution based on a user-defined mean fire size and maximum fire size.

The actual fire severity is divided into 5 classes. Class 1 fire is the least severe fire while class 5 fire is the most severe fire. The severity classes are determined by the fuel accumulation since last fire. The mortality of species age cohort is determined by the fire severity class, cohort ages (young cohorts are most vulnerable to fire), and species susceptibility determined by fire tolerances class (class 1–5 with class 1 of least tolerant of fire and class 5 of most tolerant of fire). Within the burned area, all cohorts of the species will be killed if a species tolerance class is less than the fire severity class. Otherwise, only the younger age cohorts will be removed by fire while the older cohorts can partially survive.

A.1.2 Wind throw disturbances

The windthrow disturbance extension simulated in LANDIS-II is similar in design to the fire disturbance extension (Mladenoff and He 1999). Species life-span is divided into five classes (0–20%, 21–50%, 51–70%, 71–85%, and 86–100% of the entire life span) with each class corresponding to the five susceptibility classes. Susceptibility class 1 corresponds to the youngest age class and is least susceptible, while susceptibility class 5 corresponds to the oldest class and is the most susceptible. The wind tolerance for each species and differential susceptibility by ecoregion is not currently incorporated in the model. Each wind event has an intensity which is currently drawn from a uniform random distribution, scaled from 0 to 1.0.

A.2 PnET-II model

Under global climatic change, a temperature increase in the Northern Hemisphere could benefit southern species by providing their optimal growing temperatures and could be detrimental to northern species by putting them in a state of supra-optimal growing temperatures and high environmental stresses (e.g. draught) (Davis and Zabinski 1992; Xu et al. 2007). The precipitation change may affect soil water availability and thus alter species' competition or colonization ability under future climatic conditions (Koerner et al. 2005; Pastor and Post 1988; Suttle et al. 2007). Photosynthetic active radiation (PAR) is the energy source for photosynthesis and will vary under global climatic change depending on predicted cloud cover and albedo. The CO_2 enrichment could stimulate the photosynthesis of tree species, restrict photorespiration (Drake et al. 1997; Korner 2006; Long et al. 2004), and reduce the stomata conductance which can increase the water use efficiency (Medlyn et al. 2001; Saxe et al. 1998).

The PnET-II model is a process based model for carbon and water dynamics in forest ecosystems (Aber and Federer 1992; Aber et al. 1995; Ollinger et al. 2002). The model version 5.1 takes into consideration the effect of temperature, precipitation, CO_2 and PAR. The PnET-II model simulates the temperature effect on forest photosynthesis by applying a temperature adjusting factor ($DTemp$) based on the deviance of current temperature from an optimum temperature,

$$DTemp = \frac{4(Tday - PsnT_{\min})(PsnT_{\max} - T_{day})}{(PsnT_{\max} - PsnT_{\min})^2} \tag{2}$$

where $PsnT_{\min}$ and $PsnT_{\max}$ are the minimum and maximum photosynthetic temperatures for a species, respectively, and T_{day} is the mean daytime temperature. PnET-II simulates the CO_2 effect on forest photosynthesis using the equation as follows (Ollinger et al. 2002),

$$R_{ca} = 1.22(C_i - 68)/(C_i + 136) \tag{3}$$

where R_{ca} is the rate of photosynthesis at a given atmospheric CO_2 concentration (C_a) relative to that which occurs at CO_2 saturation. C_i is the internal leaf CO_2 concentration that occurs at the ambient CO_2 concentration, which varies over time. The adjusting factor of CO_2 (DCO_2) enrichment effect on the photosynthesis is calculated by

$$DCO_2 = 1 + (R_{ca1} - R_{ca0})/R_{ca0} \tag{4}$$

where R_{ca1} and R_{ca0} are the rate of photosynthesis at elevated and current CO_2 concentration. The PnET-II model simulates the effect of precipitation on photosynthesis by applying a water availability adjusting factor ($DWater$),

$$DWater = \frac{Trans_i}{PotTrans_d} \tag{5}$$

where $Trans_i$ is actual transpiration (cm/day) and $PotTrans_d$ is the prorated unstressed transpirational demand (cm/day). The PnET-II model simulates the PAR effect on photosynthesis via the light effect adjusting factor ($LightEff$),

$$LightEff = 1.0 - e^{-I \cdot \ln(2)/HalfSat} \tag{6}$$

where I represents the light intensity (J.m $^{-2}$. sec $^{-1}$) determined by the PAR, and *HalfSat* is the half saturation light level (J. m^{-2}. sec). In the PnET-II model, the CO_2 effect on conductance change is related to the ratio of CO_2 flux across the leaf surface and the absolute CO_2 concentration gradient from ambient air to the leaf interior (Ollinger et al. 2002). Because the stomata conductance response to increased [CO_2] enrichment is much stronger in deciduous trees than coniferous trees (Medlyn et al. 2001), we only simulated the CO_2 effect on the water use efficiency for deciduous trees.

A.3 Estimation ANPP and SEP

Potential aboveground net primary production inputs were calculated from estimates of wood and foliage production in the model. The PnET-II model does not specifically calculate seedling establishment probability. The seedling establishment is related to the seed germination, seedling growth and mortality, which may depend on the light levels, temperature and soil moisture (Castro et al. 2004; He et al. 1999). Since the CO_2 enrichment can stimulate seedling growth, it may increase the probability of seedling establishment even if water and nutrient availabilities are limited (Samuelson and Seiler 1993). Polley et al. (1999) reported that atmospheric CO_2 enrichment can more than double seedling survivorship of honey mesquite (*Prosopis glandulosa*) under drought conditions after an 82 day experiment. Darbah et al. (2007) reported that elevated CO_2 increased germination rate of birch by 110% compared to ambient CO_2 concentrations and decreased seedling mortality by 73%.

In this study, we calculated the seedling establishment probability by the product of the environmental adjusting factors of light effectiveness, water availability and CO_2 for photosynthesis (calculated in PnET-II), and another adjusting factor for growing degree days ($DGDD$), which are commonly used to represent the overall effect of temperature on tree growth (Botkin et al. 1972; Pastor and Post 1985),

$$DGDD = \frac{4(GDD - GDD_{\text{min}})(GDD_{\text{max}} - GDD)}{(GDD_{\text{max}} - GDD_{\text{min}})^2} \tag{7}$$

where GDD_{min} and GDD_{max} are the minimum and maximum growing degree days for a species, respectively, and GDD is the current growing degree days. We did not use the optimal temperature function in Eq. 2 to assess the temperature effect on species establishment, since the seedling establishment may be influenced by the growing season length (Galen and Stanton 1999).

A.4 ANOVA analysis

Since the colonization response to climatic change is assumed to be mainly determined by SEP and the competition response is assumed to be mainly determined by $\text{ANNP}_{\text{potential}}$, assessing the importance of colonization and competition is equivalent to assessing the importance of SEP and $\text{ANNP}_{\text{potential}}$. Using the PnET-II model and ensemble of 27 climate projections (Table 2), we can calculate 27 sets of SEP and 27 sets of $\text{ANNP}_{\text{potential}}$ under the predicted 2090–2099 AD mean climate. Each set of SEP or $\text{ANNP}_{\text{potential}}$ includes all the values of 13 tree species (Table 1) in the three ecoregions. One set of values defines a pattern of SEP or $\text{ANNP}_{\text{potential}}$, which determines the relative difference in SEP or $\text{ANNP}_{\text{potential}}$ among different species (see Fig. 4 for a better understanding). The patterns of SEP or $\text{ANNP}_{\text{potential}}$ among different species are important for colonization or competition processes at the forest succession level. For example, a pattern of SEP with higher values for pine species compared to spruce-fir species under climatic change will cause the forest landscape to favor the pine species in the colonization process.

For the ANOVA, we need to define potential patterns (or levels) of SEP and $\text{ANNP}_{\text{potential}}$ under future climatic change. An intuitive definition of the potential levels of SEP or $\text{ANNP}_{\text{potential}}$ is to directly use the 27 sets of SEP or $\text{ANNP}_{\text{potential}}$ calculated by the PnET-II model under the ensemble of 27 climate predictions. Namely, one set of SEP or $\text{ANNP}_{\text{potential}}$ values are used to define one potential level of SEP or $\text{ANNP}_{\text{potential}}$, respectively. In this way, there will be 27 levels for both SEP and $\text{ANNP}_{\text{potential}}$. If four replicates for each two-factor combinations are used to account for environmental stochasticity in the simulation, we need at least 2916 simulations ($27 \times 27 \times 4$). However, since it takes about one hour to generate a single simulation with the LANDIS-II model for our study area, that would be too computational expensive. Furthermore, the levels defined in this way may not be efficient since some sets of values may be very similar while others are much different. For efficiency, we may need to group the similar sets together and define fewer levels. In this study, we used a hierarchical clustering approach (Hastie et al. 2001) to obtain five clusters of seedling establishment probabilities (See Section A.5 and Fig. 7 in the Appendix) and five clusters of aboveground primary production capacities (See Section A.5 and Fig. 8 in this Appendix). Then we defined the ANOVA levels using the mean values for each cluster. So defined,

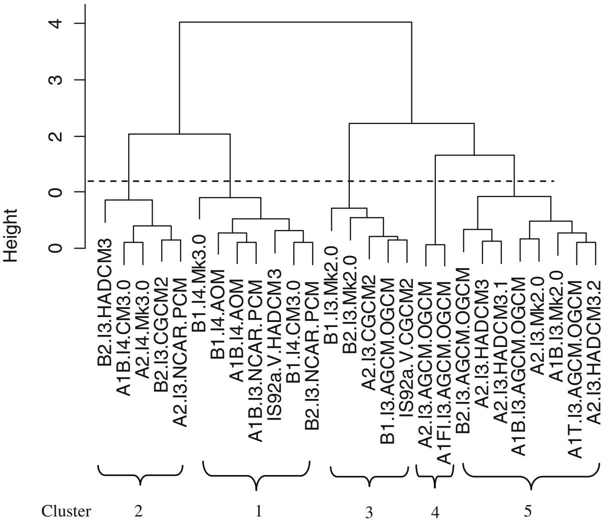

Fig. 7 Hierarchical clustering dendrogram based on seedling establishment probabilities under the 2090–2099 predicted climates. The *dashed line* to cut the cluster trees into five clusters. The clustering is applied on the seedling establishment probabilities for the 13 tree species in three ecoregions, calculated by the PnET-II model under the predicted climates for the period 2090–2099 AD from the ensemble of 27 climate predictions. The *vertical axe* indicates the maximum difference between the two sets of seedling establishment probabilities. The *nodes* are the global climate predictions profiles formatted as "Emission Scenario.Project.Global Climate Model". Project "*I*3", "*I*4" and "*V*" represent IPCC Third Assessment Report, IPCC Fourth Assessment Report, and Vegetation-Ecosystem Modeling and Analysis Project, respectively

the ANOVA levels are computational more feasible for the LANDIS-II simulation and can capture the range of competitive abilities and colonization abilities under future climate change. There are a total of 25 combinations of SEP levels (five levels) and $\mathrm{ANNP}_{\mathrm{potential}}$ levels (five levels). For each combination, we incorporated stochastic variations due to fire, dispersal, and establishment (which can affect both competition and colonization processes) by replicating each simulation four times.

In the two-way ANOVA, for a model output Y (e.g., the percentage area of the pine forest), the sum of square of Y can be divided as follows (Rice 1995),

$$\begin{aligned}\sum_{i=1}^{I}\sum_{j=1}^{J}\sum_{k=1}^{K}\left(Y_{ijk}-\bar{Y}_{...}\right)^2 &= JK\sum_{i=1}^{I}\left(\bar{Y}_{i..}-\bar{Y}_{...}\right)^2+IK\sum_{j=1}^{J}\left(\bar{Y}_{.j.}-\bar{Y}_{...}\right)^2\\ &\quad+K\sum_{i=1}^{I}\sum_{j=1}^{J}\left(\bar{Y}_{ij.}-\bar{Y}_{i..}-\bar{Y}_{.j.}+\bar{Y}_{...}\right)^2\\ &\quad+\sum_{i=1}^{I}\sum_{j=1}^{J}\sum_{k=1}^{K}\left(Y_{ijk}-\bar{Y}_{ij.}\right)^2 \qquad (8)\end{aligned}$$

where I and J, respectively, are the number of levels for seedling establishment probabilities and aboveground primary productions; and K is the number of replicates

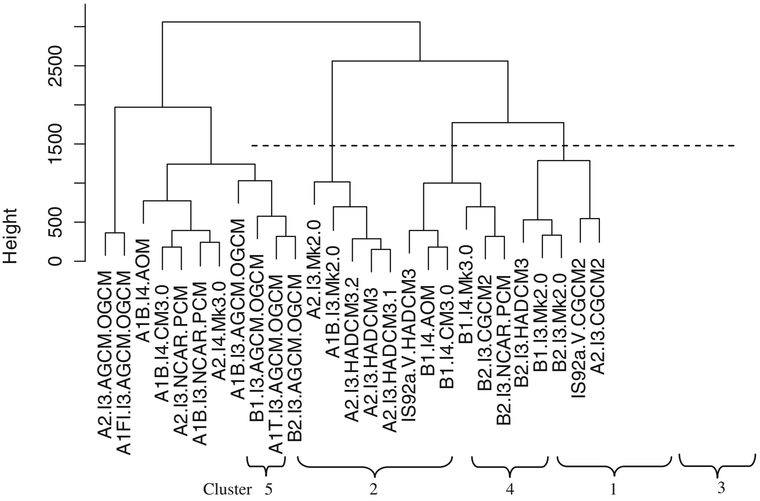

Fig. 8 Hierarchical clustering dendrogram based on potential aboveground net primary production capacity under the 2090–2099 predicted climates. The *dashed line* to cut the cluster trees into five clusters. The clustering is applied to the aboveground net primary production capacities for the 13 tree species in three ecoregions, calculated by the PnET-II model under the predicted climates for the period 2090–2099 AD from the ensemble of 27 climate projections. The *vertical axe* indicates the maximum difference between the two sets of aboveground net primary production capacities. The *nodes* are the global climate predictions profiles formatted as "Emission Scenario.Project.Global Climate Model". Project "*I*3", "*I*4" and "*V*" represent IPCC Third Assessment Report, IPCC Fourth Assessment Report, and Vegetation-Ecosystem Modeling and Analysis Project, respectively

for each combination of seedling establishment probability level and aboveground primary production level. Y_{ijk} represents the *k*th replicate of the model output with seedling establishment probability level *i* and aboveground primary production level *j*. $\bar{Y}_{...}$ is the overall mean of the model output calculated by

$$\bar{Y}_{...} = \frac{1}{IJK} \sum_{i=1}^{I} \sum_{j=1}^{J} \sum_{k=1}^{K} Y_{ijk}. \tag{9}$$

$\bar{Y}_{i..}$ is the mean value of model output given seedling establishment probability level is *i*,

$$\bar{Y}_{i..} = \frac{1}{JK} \sum_{j=1}^{J} \sum_{k=1}^{K} Y_{ijk}. \tag{10}$$

Similarly, $\bar{Y}_{.j.}$ is the mean value of model output given aboveground primary production level *j*,

$$\bar{Y}_{.j.} = \frac{1}{IK} \sum_{i=1}^{I} \sum_{k=1}^{K} Y_{ijk}. \tag{11}$$

If we divided Eq. 8 with the total number of model runs (i.e., $I \times J \times K$), then

$$\begin{aligned}\frac{1}{IJK}\sum_{i=1}^{I}\sum_{j=1}^{J}\sum_{k=1}^{K}\left(Y_{ijk}-\bar{Y}_{...}\right)^2 &= \frac{1}{I}\sum_{i=1}^{I}\left(\bar{Y}_{i..}-\bar{Y}_{...}\right)^2+\frac{1}{J}\sum_{j=1}^{J}\left(\bar{Y}_{.j.}-\bar{Y}_{...}\right)^2\\ &\quad+\frac{1}{IJ}\sum_{i=1}^{I}\sum_{j=1}^{J}\left(\bar{Y}_{ij.}-\bar{Y}_{i..}-\bar{Y}_{.j.}+\bar{Y}_{...}\right)^2\\ &\quad+\frac{1}{IJK}\sum_{i=1}^{I}\sum_{j=1}^{J}\sum_{k=1}^{K}\left(Y_{ijk}-\bar{Y}_{ij.}\right)^2 \qquad (12)\end{aligned}$$

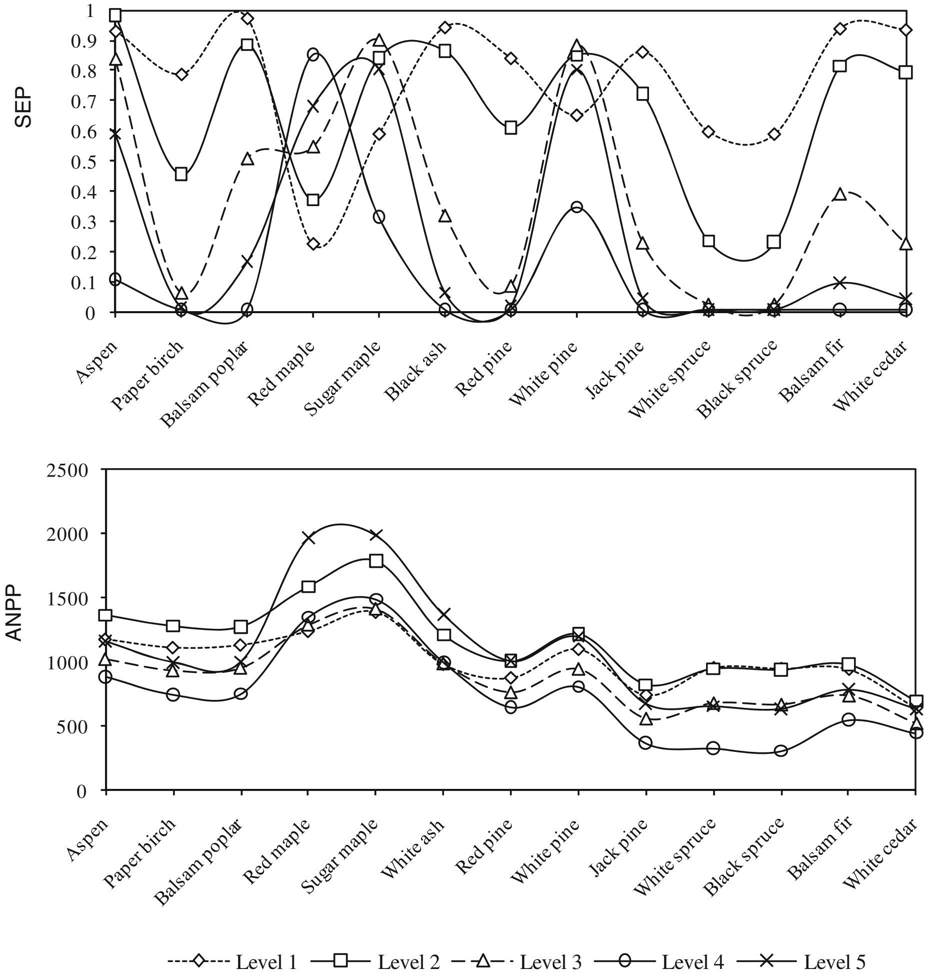

Fig. 9 Levels of seedling establishment probability [SEP (**a**)] and potential aboveground net primary production [$\text{ANPP}_{\text{potential}}$ ($\text{g m}^{-2}\ \text{year}^{-1}$) (**b**)] under the projected mean climate of period 2090–2099 AD. Plotted are the means values across ecoregion 1 and 2 under different levels

which can be shown to be

$$\begin{aligned}\hat{Var}(Y) &= \hat{Var}(E(Y|X_1)) + \hat{Var}(E(Y|X_2)) \\ &\quad + \left[\hat{Var}(E(Y|X_1,\ X_2)) - \hat{Var}(E(Y|X_1)) - \hat{Var}(E(Y|X_2))\right] \\ &\quad + \hat{Var}(Y|X_1,\ X_2) \end{aligned} \tag{13}$$

where X_1 represents the succession driver for colonization determined by seedling establishment probability and X_2 represents the succession driver for competition determined by aboveground net primary production capacity. $\hat{Var}(.)$ represents the estimated variance (i.e. the sample variance) of a variable. $E(\cdot)$ represents the expected value of a variable. If Eq. 13 is divided by $\hat{Var}(Y)$ on both sides, we get

$$S_1 + S_2 + S_{12} + S_E = 1 \tag{14}$$

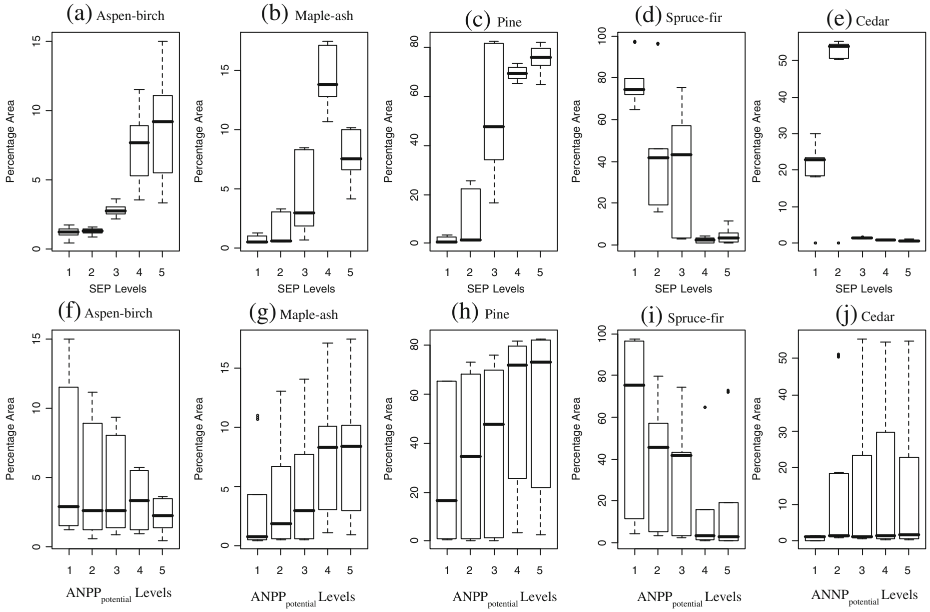

Fig. 10 Boxplots of the mean percentage area during 2290–2390 AD for different forest types at different seedling establishment probability (SEP) levels (**a**–**e**) and different potential aboveground net primary production (ANNP$_{\text{potential}}$) levels (**f**–**j**) under the scenario of moderate-frequent windthrow disturbances (rotation period = 500 years) and no fire disturbances. The SEP and ANNP$_{\text{potential}}$ levels are defined based on an ensemble of 27 climate predictions made by major global circulations models under seven green-house emission scenarios

where

$$S_1 = \frac{V\hat{a}r\,(E\,(Y|X_1))}{V\hat{a}r\,(Y)}$$

$$S_2 = \frac{V\hat{a}r\,(E\,(Y|X_2))}{V\hat{a}r\,(Y)}$$

$$S_{12} = \frac{\left[V\hat{a}r\,(E\,(Y|X_1,\ X_2)) - V\hat{a}r\,(E\,(Y|X_1)) - V\hat{a}r\,(E\,(Y|X_2))\right]}{V\hat{a}r\,(Y)}$$

$$S_E = \frac{V\hat{a}r\,(Y|X_1,\ X_2)}{V\hat{a}r\,(Y)} \tag{15}$$

Based on Saltelli and Tarantola (2002), the variance contribution S_1, S_2 and S_{12} can be used to assess the importance of X_1 and X_2 and their interaction, respectively. Specifically, in response to climate change, S_1, S_2, S_{12} and S_E were used to measure the importance of colonization as determined by seedling establishment probability, competition as determined by aboveground net primary production capacity, the interaction between the colonization and competition, and random variability, respectively.

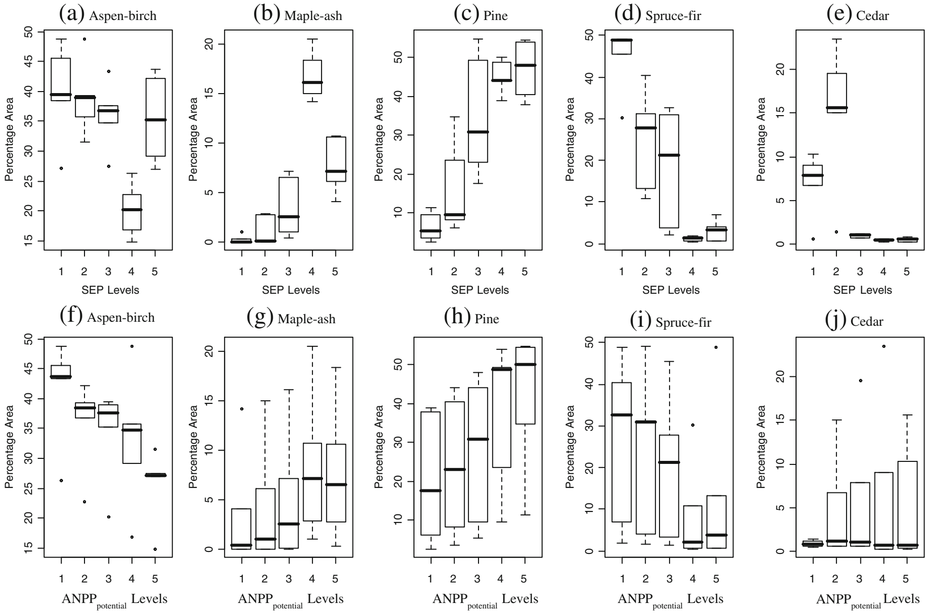

Fig. 11 Boxplots of the mean percentage area during 2290–2390 AD for different forest types at different seedling establishment probability (SEP) levels (**a**–**e**) and potential aboveground net primary production (ANNP$_{\text{potential}}$) levels (**f**–**j**) under the scenario of moderate-frequent windthrow disturbances (rotation period = 500 years) and fire disturbances (rotation period = 300 years). The SEP and ANNP$_{\text{potential}}$ levels are defined based on an ensemble of 27 climate predictions made by major global circulations models under seven green-house emission scenarios

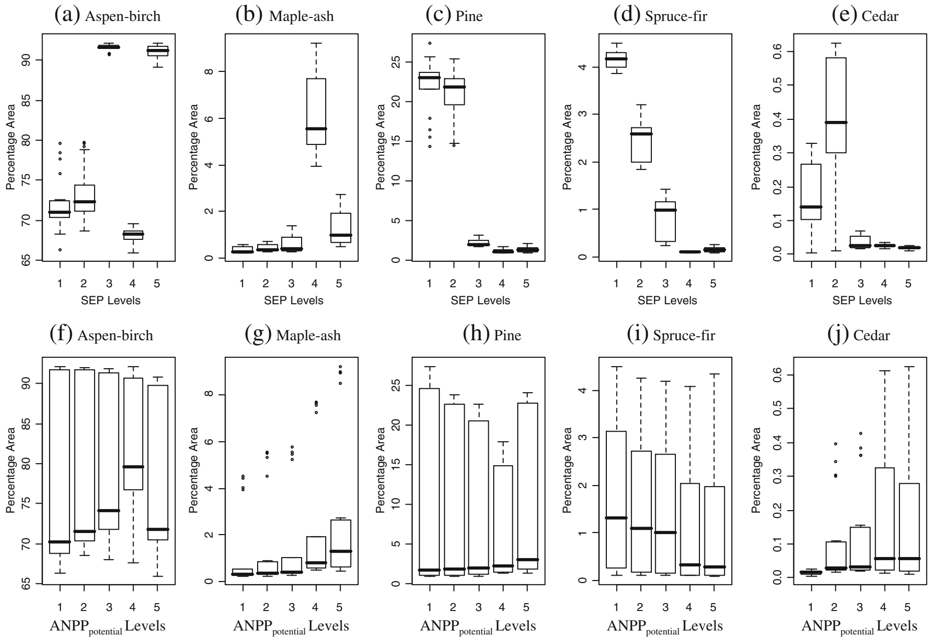

Fig. 12 Boxplots of the mean percentage area during 2290–2390 AD for different forest types at different seedling establishment probability (SEP) levels (**a**–**e**) and potential aboveground net primary production (ANNP$_{\text{potential}}$) levels (**f**–**j**) under the scenario of moderate-frequent windthrow disturbances (rotation period = 500 years) and very frequent fire disturbances (rotation period = 65 years). The SEP and ANNP$_{\text{potential}}$ levels are defined based on an ensemble of 27 climate predictions made by major global circulations models under seven green-house emission scenarios

A.5 Hierarchical clustering

Hierarchical clustering is a successive clustering technique, which builds a clustering tree (called a dendrogram) based on the difference between different objects. The clustering tree then can be divided into clusters of different objects based on a specified maximum difference between clusters.

In this study, the hierarchical clustering was used to classify the seedling establishment probabilities (Fig. 7) and potential aboveground net primary production capacities (Fig. 8) for all 13 tree species in three ecoregions into five clusters. The clustering is based on the maximum differences between the two sets of seedling primary production capacities. See Fig. 9 for the defined levels or clusters of seedling establishment probabilities and potential net primary production. See Figs. 10, 11, and 12 for simulated forest type percentage areas at the defined levels.

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