RESEARCH ARTICLE

Elasticity and loop analyses: tools for understanding forest landscape response to climatic change in spatial dynamic models

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Abstract Spatially explicit dynamic forest landscape models have been important tools to study large-scale forest landscape response under global climatic change. However, the quantification of relative importance of different transition pathways among different forest types to forest landscape dynamics stands as a significant challenge. In this study, we propose a novel approach of elasticity and loop analyses to identify important transition pathways contributing to forest landscape dynamics. The elasticity analysis calculates the elasticity to measure the importance of one-directional transitions (transition from one forest type directly to another forest type); while the loop analysis is employed to measure the importance of different circular transition pathways (transition from one forest type through other forest types back to itself). We apply the proposed approach to a spatially explicit dynamic model, LANDIS-II, in a study of forest landscape response to climatic change in the Boundary Waters Canoe Area (BWCA) incorporating the uncertainties in climatic change predictions. Our results not only corroborate the findings of the previous studies on the most likely future forest compositions under simulated climatic variability, but also, through the novel application of the elasticity and loop analyses concepts, provide a quantitative assessment of the specific mechanisms leading to particular forest compositions, some of which might remain undetected with conventional model evaluation methods. By quantifying the importance of specific processes (transitions among forest types) to forest composition dynamics, the proposed approach can be a valuable tool for a more quantitative understanding of the relationship between processes and landscape composition/patterns.

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Introduction

We are in a time of climatic warmth unprecedented over the past 1200 years (Osborn and Briffa 2006).

According to the Intergovernmental Panel on Climate Change (IPCC), the global mean surface temperature will continue to increase by 1.1 to 6.4°C over the next 100 years mainly due to the CO_2 enrichment by fossil fuel use (IPCC 2007). The corresponding precipitation and photosynthetic active radiation (PAR) may also increase or decrease depending on the specific spatial location (IPCC 2007).

Forest ecosystems are one of the world's most important ecosystems that may be substantially affected by this global climatic change at different scales (Dale et al. 2001). Climatic change may affect tree species abundance, distribution, forest community characteristics (e.g., species richness and diversity) and biome distributions (Long 1991; Neilson and Drapek 1998; Bachelet et al. 2001; Hansen et al. 2001; Iverson and Prasad 2002). At the individual tree level and small plot level, field experiment studies using Free-Air CO_2 Enrichment (FACE) have shown that the CO_2 enrichment may increase light use efficiency, water use efficiency and nitrogen use efficiency; with possible long-term down-regulation and acclimation (Drake et al. 1997; Long et al. 2004). However, the traditional field experiment research would be difficult to capture the long-term forest landscape response at large spatial scales. Thus, forest landscape simulation models based on our prior knowledge for the individual species response have been important tools to study the large-scale forest landscape change under global climatic change (Baker et al. 1991; Gustafson et al. In Review; Miller and Urban 1999; He et al. 2002; Lenihan et al. 2003; Schumacher and Bugmann 2006; Lenihan et al. 2008).

There may be complex interactions among different species in the forest landscape response, due to the differential response of individual species to different climate variables, such as temperature, CO_2, PAR, and precipitation. Therefore, it is a challenging task to accurately identify important transition pathways among different forest types responsible for a certain forest landscape change, especially if there are many different species. Although one can visually (i.e., qualitatively) assess the importance of different transition pathways by examining a series of simulated forest-type maps of a forested landscape, there is not a formal quantitative method to consistently evaluate the relative importance of various transition pathways in forest landscape change. The problem of

relying on informal qualitative assessment is confounded, when one needs to evaluate hundreds of simulations to account for the uncertainty in the global climatic change predictions (Xu et al. 2009).

The elasticity and loop analyses are prevalent approaches in demographic studies of individual species in ecology, where they are employed to understand the underlying mechanism of simulated dynamics in matrix population models (van Groenendael et al. 1994; Caswell 2001). In this study, we propose a novel application of these approaches as a formal method to quantitatively measure the importance of different transition pathways in the forest landscape response to climatic change. In general, given that the landscape dynamics can be represented in the form of transition matrices, such a formal method allows for more informed assessments of the differential responses within that landscape to external perturbation, such as climatic change, particularly in the presence of disturbances, such as fire. The ability to evaluate landscape responses in a quantitative and consistent manner is especially noteworthy when uncertainty in these responses is likely to be high.

Methodology

For a forest landscape model, we can represent the model output for different forest types (e.g., the area of different forest types):

$$\vec{n}(t+1) = A(t)\,\vec{n}(t) \tag{1}$$

where $\vec{n}(t)$ is the state vector for areas of different forest types at time t and $A(t)$ is the estimated transition probability matrix,

$$A(t) = \begin{bmatrix} p_{11}(t) & p_{21}(t) & \cdots & p_{m1}(t) \\ p_{12}(t) & p_{22}(t) & \cdots & p_{m2}(t) \\ \vdots & \vdots & \ddots & \vdots \\ p_{1m}(t) & p_{2m}(t) & \cdots & p_{mm}(t) \end{bmatrix} \tag{2}$$

with $p_{ij}(t)$ denoting the transition probability from forest type j to forest type i. The transition matrix $A(t)$ can be estimated by overlapping two forest type maps simulated in the forest landscape model at time t and time $t + 1$.

In the study of forest landscape response to climatic change, we are concerned with the

importance of different transition pathways in a specified time period (e.g., from time t_1 to time t_2) to the forest dynamics (e.g., an increase of a certain forest type). Mathematically, we need to calculate the sensitivity of a specific forest type state at time t_2 $[n_k(t_2)]$ to the transition probability in $A(t)$ $[t = t_1, \ldots, t_2]$. The sensitivity is measured by the ratio of the forest type change to a small change in the transition probability (see Appendix A in Supplementary material for details). For example, the sensitivity $S_{ij}^{(k)} = dn_k(t_2)/dp_{ij}$ [p_{ij} represents the random variable for the transition probability during the period from time t_1 to time t_2, which can take value $\{p_{ij}(t_1), p_{ij}(t_1 + 1),\ldots, p_{ij}(t_2)\}$] measures the importance of transition pathway from forest type j to forest type i during the period from time t_1 to time t_2 to the state of forest type k at time t_2. Since $n_k(t_2)$ is an outcome of the dynamic change of forest type k within the specified time range, and $dn_k(t_2)/dp_{ij}$ is calculated based on an iterative approach accounting for its areal changes during the same range (see Eq. A2 in Appendix A in Supplementary material), it is equivalent to say that $S_{ij}^{(k)}$ indicates the importance of transition pathway from forest type j to forest type i to the dynamics of forest type k within the specified time range.

For parameters with very different magnitudes, it would be misleading to use the sensitivity to measure the importance of different parameters. In order to overcome this potential problem, the sensitivity indices are generally normalized to measure the importance of different parameters. The normalized sensitivity is termed the elasticity, which measures the proportion change of forest type due to the proportion change of transition probability. For the sensitivity $S_{ij}^{(k)} = dn_k(t_2)/dp_{ij}$, we can obtain the elasticity by the following equation,

$$e_{ij}^{(k)} = \frac{\bar{p}_{ij}}{n_k(t_2)} \frac{dn_k(t_2)}{dp_{ij}} \tag{3}$$

where $e_{ij}^{(k)}$ is the elasticity of transition pathway from forest type j to forest type i for the kth forest type in the model output during time period from time t_1 to time t_2, $\bar{p}_{ij}$ is the average of the transition probabilities $\{p_{ij}(t_1), p_{ij}(t_1 + 1),\ldots, p_{ij}(t_2)\}$. The elasticity measures the relative importance of different transition pathways to the forest landscape change during the specified time range. For example, a high value of

$e_{23}^{(3)}$ during year 2000–2100 AD indicates that the one-directional transition from forest type 2 to forest type 3 is important for the forest type 3 during the specified time period. Based on the additive properties for derivatives, elasticity for the combination of different forest types can also be easily calculated (see Appendix B in Supplementary material for details). It is notable that, in the matrix population model long-term dynamics, the sum of the elasticity values is one (van Groenendael et al. 1994). For the forest landscape model, the sum of the elasticity values for all transition pathways is not necessarily equal to one due to the transient dynamics (e.g., the ratio of proportion change in model output to the proportion change in parameter could be larger than one).

A major disadvantage of the elasticity analysis is that it only gives an indication of the contribution of each individual transition between any two forest types constituting the particular forested landscape (this is equivalent to transition between any two stages of a single species in demographic analysis) per se, without taking into account the succession of transition pathways a site may undergo (equivalent to an individual of a species passing through different stages in its life-cycle in demographic analysis). Loop analysis overcomes this limitation by distributing elasticities of all elements in the transition matrix to the transition cycles or 'loops' (van Groenendael et al. 1994). As applied to forest landscape dynamics, then each transition loop represents a distinct pathway cycle in the forest landscape. For example, a transition loop can be composed of one-directional transition from landscapes dominated by aspen to landscapes dominated by white spruce due to natural succession, and transition from landscapes dominated by white spruce back to landscapes dominated by aspen due to fire disturbances. Furthermore, the elasticity of every loop represents the contribution of that transition cycle to the variable of interest, such as relative abundances of different tree species. In this way, comparisons can be made between transitions involving different species.

Since the introduction of the loop analysis to population ecology by van Groenendael et al. (1994), it has been further formalized by several researchers (Wardle 1998; Güneralp 2007; Sun and Wang 2007;

Adams 2008) based on graph-theoretical concepts. The loops identified by these formal approaches, however, are, in general, not unique. Different sets of loops may be identified with different preference criteria which should be selected for the specific research questions at hand. In this study, we adopted the decomposition algorithm proposed by Güneralp (2007), as it rests on a clear and ecologically relevant logic that is simple to apply: the algorithm preferentially selects shorter loops (i.e., cycles involving smaller number of transitions), as such loops seem ecologically and demographically more relevant (Charlesworth 1994; de Kroon et al. 2000). The decomposition algorithm first represents the elasticity matrix by a directed graph (Fig. 1a). Then the algorithm first identifies the shortest loops (self-loops) (Fig. 1b), followed by the two-transition loops (Fig. 1c), and so on (Fig. 1d). As each loop is identified, its characteristic elasticity is subtracted from the elasticity values of the corresponding transitions in the directed graph. Thus, the directed graph is updated every time a loop is identified. The algorithm proceeds as such, until the updated directed graph does not contain any more loops. The loop elasticity is the product of the number of transitions forming the loop and the characteristic elasticity (the smallest of the elasticity values of those transitions). To check for potential bias due to the preferential selection of shorter loops that might result in overestimating the elasticity from shorter loops, we also used a modified version of Güneralp's algorithm, which gives preference to the longer loops (i.e. transition cycles involving larger number of tree species). The program codes and further details on the algorithms are presented elsewhere (Güneralp 2007; Zuidema et al. 2009).

Finally, the loop analysis will decompose the elasticity matrix into the elasticity incorporated into loops and the remaining elasticity assigned to transition pathways (one-directional transitions), not incorporated into any of the loops (Fig. 1e). Based on the loop analysis, we can measure the importance of specific transition loops and of those one-directional transitions not incorporated into specific loops (left-out transitions) to forest dynamics based on their elasticity values. For the forest landscape model simulation, we focus on transition loops which may be driving change. Thus, we exclude self-loops (the loops that keep the forest type as it is to the next time step). For a better comparison of the importance of transition loops and left-out one-directional transitions, we also calculate the percentage of total elasticity (excluding the self-loop elasticity) explained by each pathway (Fig. 1e).

In steady-state applications of demographic loop analysis, it is expected that the total elasticity will be distributed completely among the identified loops (van Groenendael et al. 1994; Güneralp 2007). This is because each loop represents a possible life-cycle that a representative individual may follow in its life-span. Over the long-term, as the population asymptotically approaches its steady-state, and since the driving force behind the population's dynamics are these cyclic transitions (i.e., life-cycles) composed of individual one-directional transitions, these loops completely account for the observed characteristics of that population which influence its asymptotic growth rate. For forest landscape models, the landscape dynamics is, by definition, a continuous process of change and the influence of many transitions are spread over time. If the forest landscape is in an equilibrium state over a relatively long time during the period of interest, the analysis approaches increasingly to that of the asymptotic dynamics during which the influence of individual transitions are more or less balanced. So the landscape change dynamics would be entirely influenced by the cyclic transitions represented by the identified loops. However, in the presence of strong non-equilibrium forest landscape changes, the influences of individual transitions are not balanced. Namely, forest dynamics are mainly dominated by non-cyclic transitions (transitions causing forest dynamics to move away from its current state and not be compensated by other transitions) and with few transition cycles. Thus, there may be very few individual one-directional transitions that can be incorporated into transition cycles in the loop analysis. Consequently, the influence of shorter transition chains, particularly those that appear as left-out transitions in the loop analysis, becomes more pronounced. This suggests that, the elasticity of transition loops can be used to measure the importance of pathways contributing to equilibrium forest dynamics dominated by transition cycles, while the elasticity of left-out transitions can be used to measure the importance of pathways contributing to the non-equilibrium forest dynamics dominated by non-cyclic transitions.

Fig. 1 Illustration of loop decomposition based on Güneralp (2007). *1–5* represents forest type *1–5*. **a–e** represent different loop decomposition steps. The percentage in **e** are the percentage of loop/link elasticity among the sum of elasticity matrix in **a** excluding diagonal values for self-loops. See text for details
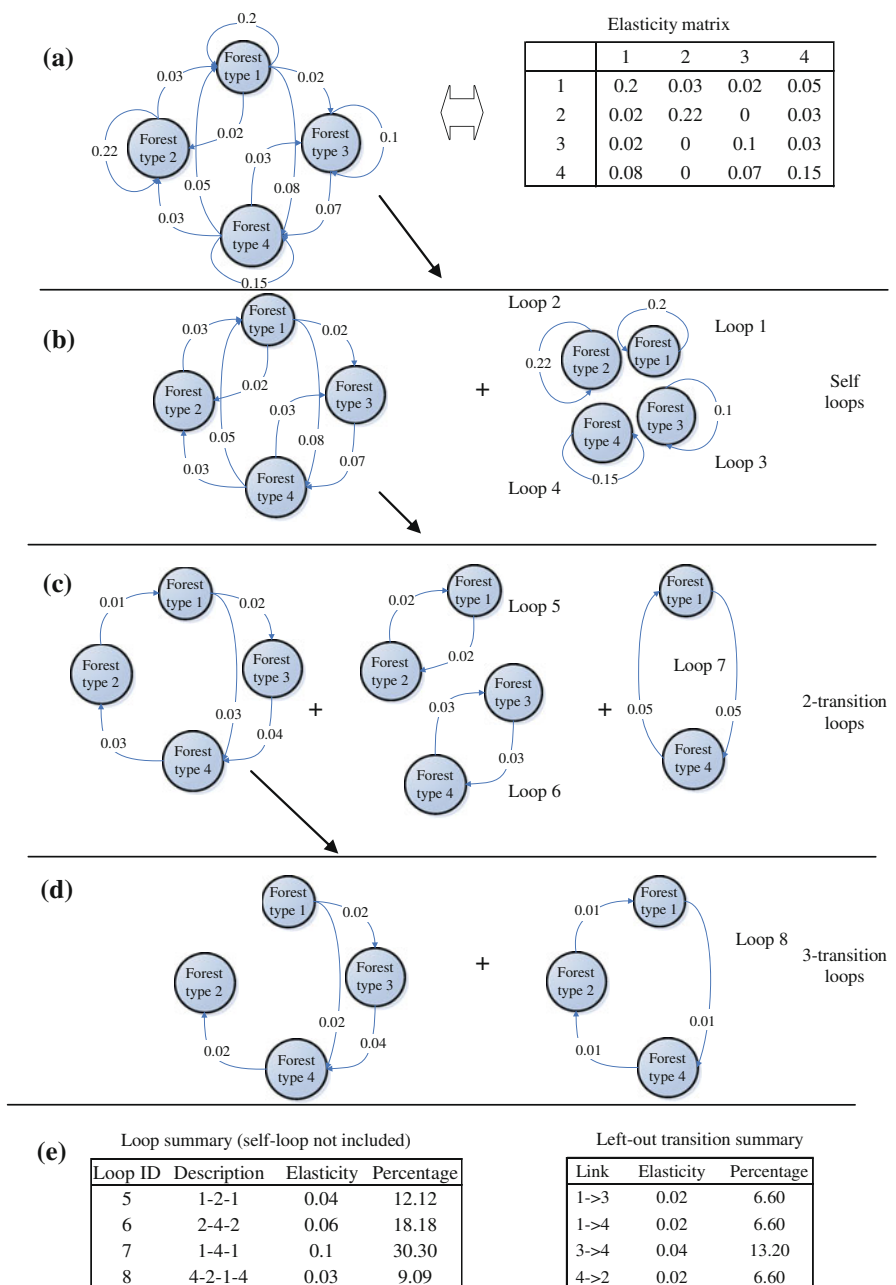
Application

In this study, we apply the proposed elasticity and loop analyses to study the importance of different transition pathways in forest landscape response to climatic change in the Boundary Waters Canoe Area (BWCA). We couple a spatially explicit dynamic forest landscape model, LANDIS-II (Scheller et al. 2007), with a forest ecosystem process model, PnET-II (Aber et al. 1995; Ollinger et al. 2002), to simulate the forest landscape response (measured by the forest type composition) to future climatic change (Fig. 2). The LANDIS-II model simulates the forest-type composition response to future climatic change by modifying the species' competitive and colonization ability. In the LANDIS-II model, the species'
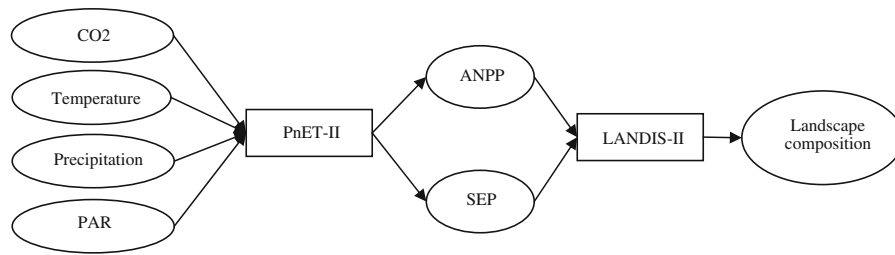
Fig. 2 Flow diagram of model coupling. The *ovals* represent input/output variables for a certain model. The *rectangles* represent models. *ANPP* abound ground primary production, *SEP* species establishment probability

competitive ability under future climate may change through the modification of the growth rate determined by the aboveground net primary production (ANPP). The colonization ability may change through the modification of the species establishment probability (SEP), which defines the probability of seedling establishment (assumes no competition from other species) under a specific climate and soil conditions. The forest landscape change in the LANDIS-II model is jointly determined by species life history attributes (e.g., longevity, dispersal distance, shade and fire tolerance, see Table 1), ANPP, SEP and disturbances (Scheller and Mladenoff 2004).

The PnET-II model is used to provide the estimate of ANPP and SEP under future climates (Scheller and Mladenoff 2005; Xu et al. 2009), which are driven by climate variables including temperature, precipitation, CO_2 and PAR.

Study area description

Our study area (about 195,000 ha) is part of the Boundary Waters Canoe Area (BWCA) in northern Minnesota, USA (Fig. 3). BWCA has a cold temperate continental climate (Heinselman 1973). The area

Table 1 Main species attribute parameters

Species	LNG	MTR	ST	FT	ED	MD	VP	MAXVP	GGDMin	GGDMax	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
White ash	200	30	4	2	70	140	0.1	70	1298	5993	25.5	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

Note: Data for POT are from Xu et al. (2007). Data for GGDMin and GGDMax are from Pastor and Post (1985). Fir tolerance are based on Starker (1934). 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, *GGDMax* 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
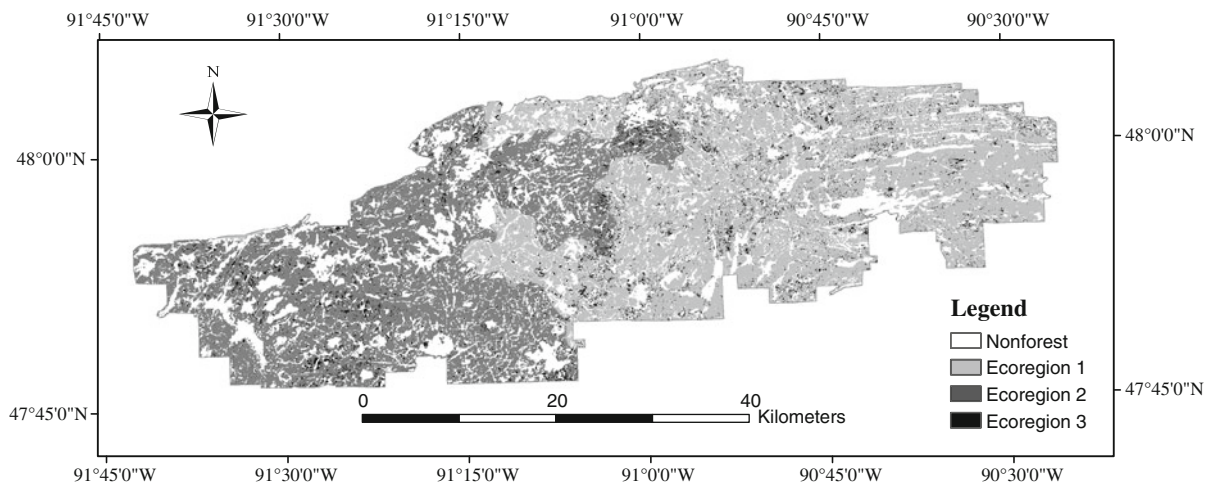
Fig. 3 Study area within the Boundary Waters Canoe Area Wilderness, Minnesota, USA

is dominated with numerous lakes of different sizes, accounting for about 17% of the study area. Soils are generally thin due to glacial scouring, although some till, outwash, and lacustrine deposits exist. The main soils are inceptisols, entisols and histosols (Moser et al. 2007). Soil type and depth to bedrock are highly heterogeneous at fine spatial scales (Heinselman 1973). Topography in the study area is a relatively homogenous with local difference in elevation ranging from 30 to 150 m (Heinselman 1973; Baker 1989).

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*) (Heinselman 1973; Baker 1989). 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 (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 is close to total suppression (>1000 year rotation 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 (e.g., 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 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. 3). Ecoregions 1 and 2 are based on State Soil Geographic (STATSGO) Data Base (STATSGO 1994; Scheller et al. 2005) with different soil water holding capacity. Ecoregion 3 is the lowland where only black spruce can establish.

Scenario analysis

Since there is a large amount of uncertainty in the climatic change prediction, we use a global climatic change ensemble (27 predictions from different global climatic change models under different greenhouse gas emission scenarios) to assess the possible uncertainty in the future forest landscape response prediction (Table 2). For the 27 selected climate prediction profiles, the mean CO_2 concentration ranged from 546.80 ppm (scenario: B1) to 923.25 ppm (scenario: A1FI) in 2099 AD (Fig. 4a). There is roughly 2–8°C annual mean temperature increase during the period 2000–2099 AD (Fig. 4b) and a relatively slight increase in the annual precipitation as compared to the inter-annual variability within the predictions (Fig. 4c). The climate models indicate a slight decrease in mean PAR during the period 2000–2099 AD, except for emission scenarios A1FI and A1T (Fig. 4d).

It is worth noting that it would be misleading to directly use the 27 predictions to represent the uncertainty in the climatic change prediction, since they do not constitute a true sample for the future. Therefore, in order to better capture the uncertainty in the climatic change prediction, we sample 209 monthly profiles (monthly time-series values) from the 27 climatic change prediction ensembles. We use a profile-based interpolation method to sample from the ensemble, the details of which is presented elsewhere (Xu et al. 2009). Specifically, we first generate a random sample for the mean values of the temperature, precipitation, CO_2 and PAR during the period 2090–2099 AD based on their correlation structure, and the lower and upper boundaries. In order to obtain the values of monthly climatic variables which are required as inputs for the PnET-II model, for each sampled mean value, we

first locate two neighborhood profiles within the ensemble. Then monthly climate variable values are then interpolated based on the inverse distance weighed average of the monthly values from the two neighborhood prediction profiles.

We simulate the PnET-II and LANDIS-II models based on these 209 sampled monthly climate profiles. The climatic change may increase the fire probability (Westerling et al. 2006), so that the current near total fire suppression activities in BWCA may not be sustainable. Thus, in this study, we run the coupled models under the scenario with moderate fire disturbances (with a rotation period of 300 years) after the year 2100; and before 2100, we assume relatively successful fire suppression (see Fig. 5). We also simulate the windthrow disturbances with a rotation period of 500 years.

We transform the LANDIS-II output into the form of Eq. 1 by overlapping two forest type maps at two consecutive time steps (time step = 20 years for our study). Finally, we apply the elasticity and loop analyses on the resulting time-series transition matrices to identify the important transition pathways (transition loops and left-out one-directional transitions) contributing to the forest dynamics under the influence of simulated future climatic change, disturbances (fire and windthrow), and natural succession.

Results

Our results show that there is a large amount of uncertainty in the forest landscape response prediction (Fig. 6). The uncertainty is relatively high for pine, spruce–fir and aspen–birch forests. Although we may have prior knowledge about the potential transition pathway in the forest landscape response (e.g., potential increase of pine forest under climatic change), it is important that we can quantitatively identify the transition pathways contributing to both equilibrium and non-equilibrium forest dynamics. Based on the dominance of forest types determined by the mean percentage area during the period from year 2300 to year 2400, we divided the 209 simulations into three groups: (1) simulations where pine forest is predicted to be the dominant forest (127 simulations); (2) simulations where spruce–fir is predicted to be the dominant forest (34 simulations);

Table 2 Global climate model predictions used in the uncertainty and sensitivity analyses

Emission scenarios	Model	Institute	Project
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
A1T	AGCM + OGCM	Center for Climate System Research, National Institute for Environmental Studies, Japan	IPCC TAR
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
A1	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
A1B	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
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
A1FI	AGCM + OGCM	Center for Climate System Research, National Institute for Environmental Studies, Japan	IPCC TAR

Note: There were three runs for the HADCM3 model 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

and (3) simulations where aspen–birch is predicted to be the dominant forest (48 simulations).

For a better understanding of the pathways responsible for the dominance of a specific forest type, we apply the elasticity and loop analyses for each individual simulation within each group. Within each group, we identify the most important transition pathways based on two subjective criteria: (1) the average elasticity value is larger than 0.05; and (2) the transition pathway appears in at least 40% of the
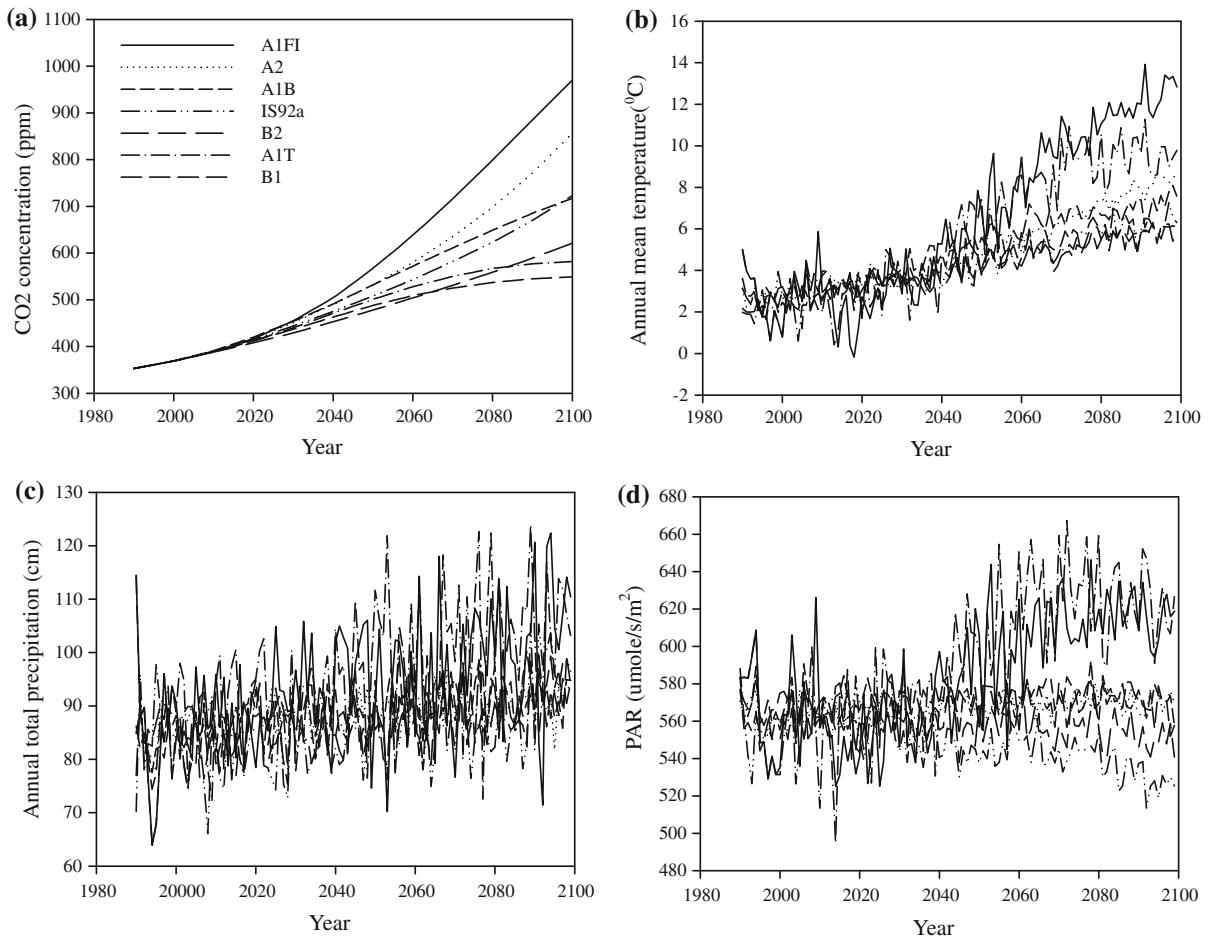
Fig. 4 Mean climate variable change in BWCA for 27 predictions with seven CO_2 emission scenarios. **a** Annual mean CO_2 concentration (ppm), **b** annual mean temperatures (°C), **c** annual precipitation (cm), and **d** annual mean PAR (μmol s^{-1} m^{-2})

Fig. 5 The burned area simulated by LANDIS-II with a mean fire return interval of 300 years assuming a relatively successful fire suppression until year 2100 AD
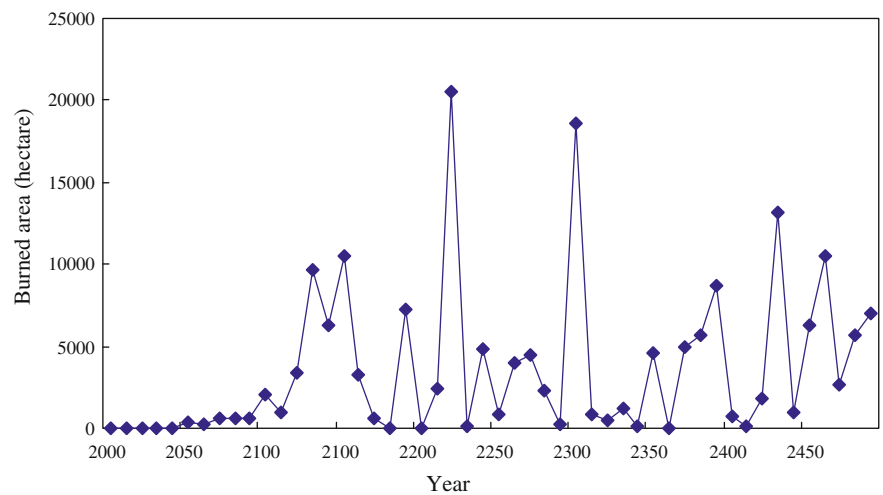
Fig. 6 Uncertainty in forest type percentages of **a** aspen–birch (aspen, paper birch and balsam poplar); **b** maple–ash (red maple, sugar maple and white ash); **c** pine (red pine, white pine and jack pine); **d** spruce–fir (white spruce, black spruce and balsam fir); and **e** cedar (white cedar). For a particular landscape cell, the assignment of forest type is based on the cumulative biomass of the five forest types. The uncertainty is resulted from a 209 samples from an ensemble of 27 climatic predictions by major global circulation models under different greenhouse emission scenarios
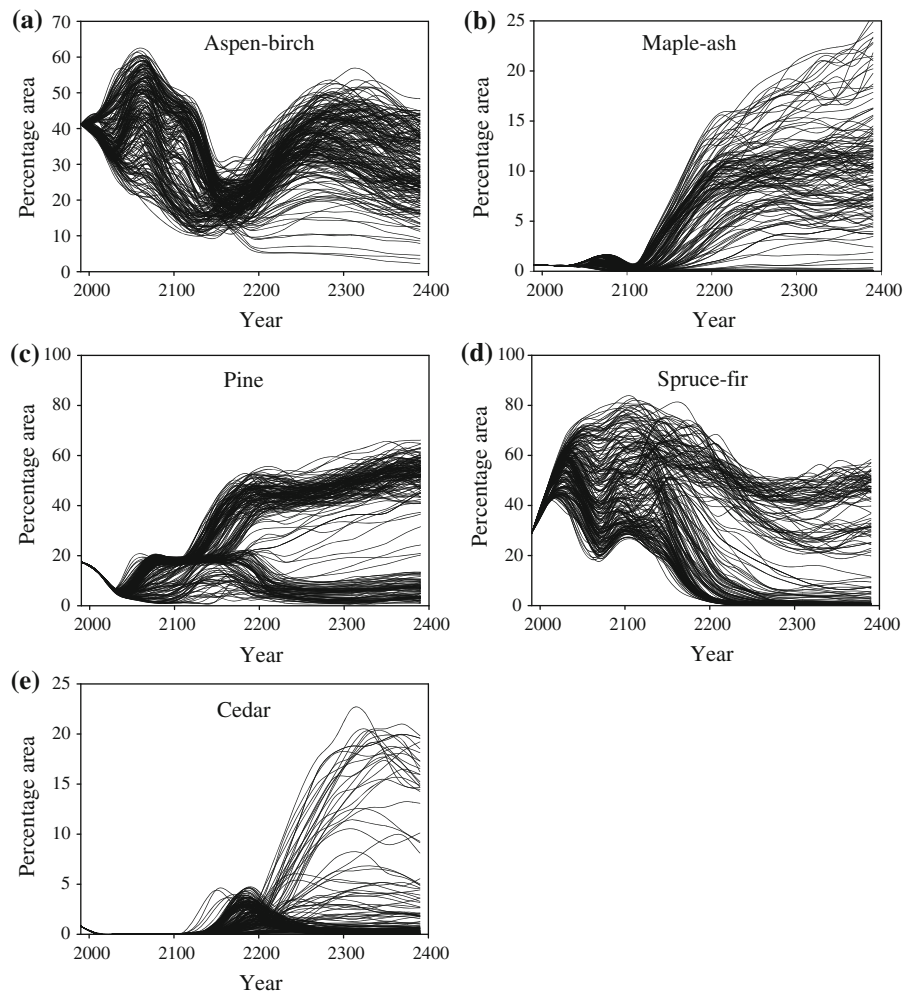
simulations. Based on these criteria, we select roughly 10 influential loops and 10 influential left-out transitions out of the total number of pathways identified for each group of simulations (the totals range from 141 to 227 across all the simulations and include both the transitions forming the loops and left-out transitions). The overall forest landscape dynamics shown in Fig. 6 indicate that the areal cover of the maple–ash forest shows a strong tendency to increase over time. Thus, we also conduct the elasticity and loop analyses to identify the important transition pathways contributing to the maple–ash forest dynamics in the simulations where the maple–ash accounts for more than five percent of our study area during the period from year 2300 to year 2400 (a total of 122 simulations). The application of the adapted version of Güneralp's (2007)

algorithm, in which preference is given to longer loops, revealed that the results in our study were relatively insensitive to the particular loop selection algorithms used.

Our results show that, for the dominance of pine forest, the influential left-out transition pathways include not only direct transitions from a variety of forest types (fir, birch, aspen, jack pine and red maple) to white pine forest, but also indirect transition from fir to aspen, fir to red maple, and jack pine to aspen (Table 3). The importance of indirect transitions is linked to the important transition loops (e.g., loop between aspen and birch, loop between aspen and white pine, loop between red maple and white pine, see Table 4) and important direct left-out transitions related to white pine (e.g., birch to white pine and red maple to white pine). Our results show

Table 3 The most influential left-out transition pathways contributing to dynamics of pine forest

Left-out transition	Frequency[a]	Average percent of elasticity explained	Average of transition elasticity
Fir → White pine	127	15.74	0.55
Birch → White pine	127	12.03	0.42
Fir → Aspen	115	6.79	0.24
Fir → Red maple	127	4.43	0.15
Aspen → White pine	127	3.66	0.13
Birch → Fir	68	3.13	0.11
Jack pine → Aspen	127	2.85	0.10
Jack pine → White pine	126	1.35	0.05
Red maple → White pine	127	1.33	0.05

[a] Indicates the number of times the transition being identified by elasticity and loop analyses

Table 4 The most influential transition loops contributing to dynamics of pine forest

Loop	Frequency[a]	Average percent of elasticity explained	Average of loop elasticity
Aspen → Birch → Aspen	127	8.38	0.30
Aspen → Birch → Fir → Aspen	111	5.52	0.19
Aspen → White pine → Aspen	127	4.48	0.16
Birch → Fir → Birch	127	4.45	0.16
Aspen → Fir → Aspen	127	3.47	0.12
Birch → Red maple → Birch	127	2.48	0.09
Aspen → Black spruce → Aspen	127	1.77	0.06
Red maple → White pine → Red maple	127	1.42	0.05

[a] Indicates the number of times the transition loop being identified by elasticity and loop analyses

that most of the important transition loops contributing to the equilibrium dynamics of pine forest do not contain white pine, except for the transition loop between aspen and white pine and the transition loop between red maple and white pine (Table 4). The main reason is that most of the transition loops are related to aspen, birch and fir, from which there are important left-out transition pathways to white pine. The results also show that the elasticity for left-out transitions is relatively higher than that for transition loops (Tables 3, 4). This suggests that the pine forest dynamics are mainly controlled by non-equilibrium disturbances which push the pine forest away from its initial state (potentially due to climatic change, since it has a higher growing temperature (Table 1)).

For the dominance of spruce–fir forest, the influential left-out transition pathways include transition from jack pine to aspen, jack pine to birch, aspen to birch, birch to fir, and aspen to black spruce (Table 5). The transitions from jack pine to aspen and birch may result from fire disturbances, while the transitions from birch and aspen to fir or black spruce

Table 5 The most influential left-out transition pathways contributing to the dynamics of spruce–fir forest

Left-out transition	Frequency[a]	Average percent of elasticity explained	Average of transition elasticity
Birch → Fir	34	17.76	0.54
Aspen → Birch	34	6.42	0.19
Jack pine → Birch	34	2.95	0.09
Jack pine → Aspen	34	2.56	0.08
Aspen → Black spruce	34	1.90	0.06

[a] Indicates the number of times the transition being identified by elasticity and loop analyses

may result from natural succession since fir and black spruce are late-succession species with high shade tolerance and longevity. The equilibrium dynamics of spruce–fir forest are mainly controlled by transition loops between birch and fir, white pine and fir, aspen and fir, and fir and black spruce (Table 6). The transition loop between aspen and fir may result from

Table 6 The most influential transition loops contributing to the dynamics of spruce–fir forest

Loop	Frequency[a]	Average percent of elasticity explained	Average of loop elasticity
Birch → Fir → Birch	34	16.85	0.51
White pine → Fir → White pine	34	9.94	0.30
Aspen–Fir → Aspen	34	7.62	0.22
Fir → Black spruce–Fir	34	4.66	0.14
Aspen → Birch → Aspen	34	2.85	0.09
Jack pine → Fir–Jack pine	34	2.80	0.08
White cedar → Fir → White cedar	34	2.03	0.07
Aspen → Birch → Fir–Aspen	14	2.02	0.07
Birch → Fir → → Black spruce	12	1.96	0.06
Fir → White spruce–Fir	34	1.63	0.05
Birch → Black spruce → Birch	34	1.69	0.05

[a] Indicates the number of times the transition loop being identified by elasticity and loop analyses

the natural succession (from aspen to fir) and fire disturbances (from fir to aspen). The transition loop between white pine and fir may result from both natural succession (from white pine to fir) and climatic change (from fir to white pine). Our results also show that there are more influential transition loops than left-out transition pathways, suggesting that the spruce–fir forest dynamics are mainly controlled by equilibrium dynamics resulted from natural succession and fire disturbances.

For the dominance of aspen–birch forest, the influential left-out transition pathways include transition from white cedar, fir, jack pine and black spruce to aspen or birch (Table 7). The transitions from fir to white cedar and from fir to white pine are also important due to the transitions from white cedar and fir to aspen–birch (Table 7) and transition loops between fir and white pine (Table 8). The transition from aspen to birch occurs because birch has a relatively old maximum age compared to aspen

(Table 1). The importance of white cedar and fir transition to aspen–birch is because they have a very low fire tolerance (Table 1). This suggests that the potential dominance of aspen–birch in the future mainly depends on the succession niches created by fire disturbances and the dominance of fir and white cedar, which is not favored by the climatic change, due to their relatively low growing temperature (Table 1). The transition pathways controlling the equilibrium dynamics for aspen–birch forest include transition loop between birch/aspen and fir, transition loop among aspen, birch and fir, transition loop between aspen and birch, and transition loop between white pine and fir (Table 8). Most of the loops that include aspen/birch are related to the natural succession and fire disturbances, while the loop between white pine and fir may result from both the natural succession (from white pine to fir) and the climatic change (from fir to white pine). The transition loop between white pine and fir may indirectly affect

Table 7 The most influential left-out transition pathways contributing to the dynamics of aspen–birch forest

Left-out transition	Frequency[a]	Average percent of elasticity explained	Average of transition elasticity
White cedar → Aspen	48	7.68	0.37
White cedar → Birch	45	5.98	0.28
Fir → Aspen	48	5.92	0.24
Aspen → Birch	43	5.02	0.21
Jack pine → Aspen	48	4.33	0.19
Fir → White cedar	48	3.49	0.16
Fir → White pine	45	2.00	0.09
Jack pine → Birch	48	1.80	0.07
Black spruce → Birch	48	1.35	0.06

[a] Indicates the number of times the transition being identified by elasticity and loop analyses

Table 8 The most influential transition loops contributing to the dynamics of aspen–birch forest

Loop	Frequency[a]	Average percent of elasticity explained	Average of loop elasticity
Birch → Fir → Birch	48	18.48	0.78
Aspen → Birch → Fir → Aspen	40	8.72	0.39
Aspen → Birch → Aspen	48	6.80	0.29
White pine → Fir → White pine	48	4.91	0.20
Aspen → Fir → Aspen	48	4.13	0.17
Aspen → Birch → White pine → Aspen	41	2.56	0.11
Jack pine → Fir → Jack pine	48	1.97	0.08
Fir → White cedar → Fir	48	1.39	0.06
Birch → Jack pine → Birch	48	1.44	0.06
Birch → White pine → Birch	48	1.16	0.05

[a] Indicates the number of times the transition loop being identified by elasticity and loop analyses

aspen–birch since the left-out transition from fir to aspen is an important transition pathway.

For the increase of maple–ash forest during our simulation period, the influential left-out transition pathways include direct transitions from fir, white pine, aspen and birch to red maple and indirect transitions from birch and fir to white pine, from fir and jack pine to aspen, and from birch to fir (Table 9). The transitions from aspen and birch to red maple may result from natural succession since red maple is a late-successional species. The transitions from fir and white pine to red maple may result from the relatively higher above ground net primary production for red maple (Xu et al. 2007), which provides an advantage for light competition. The equilibrium dynamics of maple–ash forest are mainly controlled by the transition loops related to aspen, birch and fir (Table 10), which are important components in the left-out transition pathways as well (Table 9).

Discussion

One key topic in landscape ecology is to understand the relationship between landscape pattern (e.g., fragmentation) and ecological process (e.g., fire and climatic change) at large scales (Turner et al. 2001). There is a long history of using different landscape metrics (e.g., the fragmentation index) to describe landscape use and land cover changes resulted from natural and anthropogenic disturbances (O'Neill et al. 1987; Turner 1990; Gustafson 1998). However, there are very few quantitative approaches available to quantify the processes contributing to the landscape composition and pattern change. Our proposed elasticity and loop analysis can help us quantify the importance of specific processes (transitions among forest types) contributing to the forest composition dynamics, which could be valuable toward a more quantitative understanding of the relationship between

Table 9 The most influential left-out transition pathways contributing to maple–ash forest dynamics

Left-out transition	Frequency[a]	Average percent of elasticity explained	Average of transition elasticity
Fir → Red maple	122	11.57	0.48
Fir → White pine	122	7.51	0.31
Birch → White pine	122	6.10	0.25
White pine → Red maple	122	5.95	0.24
Fir → Aspen	114	5.61	0.24
Aspen → Red maple	122	3.68	0.15
Birch → Red maple	122	3.57	0.14
Birch → Fir	57	2.51	0.11
Jack pine → Aspen	122	2.59	0.11
Aspen → Birch	65	1.30	0.05

[a] Indicates the number of times the transition loop being identified by elasticity and loop analyses

Table 10 The most influential transition loops contributing to the maple–ash forest dynamics

Loop	Frequency[a]	Average percent of elasticity explained	Average of loop elasticity
Aspen → Birch → Aspen	122	8.18	0.34
Aspen → Fir → Aspen	122	5.12	0.22
Aspen → Birch → Fir → Aspen	110	5.14	0.21
Birch → Fir → Birch	122	4.06	0.17
Aspen → White pine → Aspen	122	3.64	0.15
Birch → Red maple → Birch	122	2.96	0.12
Aspen → Birch → White pine → Aspen	62	2.25	0.10
Red maple → Fir → Aspen	122	1.94	0.08
Aspen → Black spruce → Aspen	122	1.72	0.07
Aspen → Birch → White cedar → Aspen	72	1.16	0.05
Red maple → White Pine → Red maple	122	1.11	0.05

[a] Indicates the number of times the transition loop being identified by elasticity and loop analyses

ecological processes and landscape composition/patterns.

In this study, we more or less listed 10 influential left-out transition links and 10 influential transition loops (Tables 3, 4, 5, 6, 7, 8, 9 and 10) out of 141–227 pathways for the forest dynamics identified by elasticity and loop analyses. Visual assessment with simulated maps may be able to identify a few of the most important pathways, but it would be very challenging for visual assessment to identify such a large number of pathways and compare their relative importance. Previous studies have already suggested that white pine would be favored, while spruce–fir would be reduced under climatic change (Jacobson and Dieffenbacher-Krall 1995; Iverson and Prasad 1998, 2001; Shafer et al. 2001; Xu et al. 2009). By using elasticity and loop analyses, we can identify not only important direct transition pathways (pathways related to white pine), but also indirect transition pathways (e.g., transition from fir to aspen, fir to red maple and jack pine to aspen) contributing to the pine forest dynamics. The elasticity and loop analyses also show that the transition loop between birch and fir is important for pine forest dynamics, due to its link to white pine via the left-out transitions from both species. Since this loop does not include pine, it could be very difficult to be identified by visual checking simulated maps. Clearly, the elasticity and loops analyses is a powerful tool which can help us gain more insights from different spatial models (e.g., land use and cover change model), especially in the case of complex dynamics and incorporating uncertainties based on Monte-Carlo simulations.

Loop analysis may yield different loop sets depending on the selection criteria (Wardle 1998). Loop analysis, therefore, calls for giving preference to loops with a certain characteristic, for example, short loops (Güneralp 2007). Such selection may unduly influence the distribution of elasticity values over loops (Adams 2008). Hence, setting preferences should be guided by the research questions at hand and, where possible, robustness checks should be performed as we did here with Güneralp's (2007) method. The recent resurgence of interest in the topic promises further methodological advances on loop analysis procedures (Güneralp 2007; Sun and Wang 2007; Adams 2008).

Notwithstanding the potential of the elasticity and loop analyses for studying the spatial dynamics in forest landscape models, their utility is ultimately limited by the models that are used to simulate landscape changes. As far as we know, the current forest landscape models are mainly empirical models. For example, in our analysis, most of the transition pathways that are identified are the succession pathways common to our study area, because our model is based on the previous knowledge of life history attributes and assumptions of climatic change effect on seedling establishment and NPP. The strength of the proposed method is to measure the importance of different transition pathways. However, it is possible that the climatic change could potentially modify the succession pathways. For example, the CO_2 enrichment can increase the light compensation point for photosynthesis and thus increase the establishment probability for less

shade-tolerant species under shaded understory (Mohan et al. 2007). To incorporate that, we need to have models that adequately represent the actual mechanisms through which CO_2, temperature and precipitation interact with the species. However, that requires an improved theoretical understanding of species strategy for survival and growth, and new lab and field experimental validation.

Conclusions

In this study, we propose a novel application of elasticity and loop analyses in the study of forest landscape change in response to future climatic variability. The proposed method can help us identify and quantify the important pathways contributing to both equilibrium and non-equilibrium forest dynamics, which allows for a more reliable and consistent evaluation of forest landscape change compared to the predominantly qualitative assessment based on visual examination. Although we applied this method to study forest landscape response to a climatic change study, it can potentially be applied to study the dynamics of any landscape or ecosystem. The ability to evaluate landscape responses in a quantitative and consistent manner is especially noteworthy when uncertainty in these responses is likely to be high as in the case of projected climatic variability.

Our results for BWCA forest landscape response to climatic change not only corroborate the findings of the previous studies on the most likely future forest compositions under simulated climatic variability, but also points to certain processes that may remain unnoticed in the landscape that provides clues to the specific mechanisms leading to particular forest compositions under the influence of simulated climatic change, fire, and windthrow disturbances.

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