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The site-scale processes affect species distribution predictions of forest landscape models

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ABSTRACT

Forest landscape models (FLMs) are important tools for testing basic ecological theory and for exploring forest changes at landscape and regional scales. However, the ability of these models to accurately predict changes in tree species' distributions and their spatial pattern may be significantly affected by the formulation of site-scale processes that simulate gap-level succession including seedling establishment, tree growth, competition, and mortality. Thus, the objective of this study is to evaluate the effects of site-scale processes on landscape-scale predictions of tree species' distributions and spatial patterns.

We compared the deviations and similarity in species distribution (quantified by species' percent cover) as well as its spatial pattern derived from two FLMs: (1) an age cohort model with simplified site-scale processes based on the presence or absence of age cohorts (a representative version: LANDIS 6.0), and (2) a stand density model with detailed site-scale processes based on stand density (a representative version: LANDIS PRO 7.0), which have the same framework but different site-scale process formulations.

We found that site-scale processes affected the simulated species' percent cover and spatial pattern. The importance of site-scale processes to individual species' predictions depended on species' ecological traits such as shade tolerance, growth rate, seed dispersal, and other factors. For early-successional species, simulated distributions were insensitive to the formulation of site-scale processes. Conversely, for shade-tolerant, middle-to late-successional species simulated distributions were highly sensitive to the formulation of site-scale processes. Species' shade tolerance may accentuate this simulation sensitivity. In addition, because the stand density model incorporated additional quantitative information, their simulation results had a higher year-to-year variation than those from the age cohort model. The degree of spatial aggregation of species' distributions was insensitive to the formulation of site-scale processes, whereas patch size and arrangement (landscape composition) for the species distribution were sensitive. Results from this study revealed the differences in simulation results between these two models with different site-scale process formulations, which may help narrow down prediction uncertainties and point to areas where representations of site-scale processes need to be enhanced in the future.

1. Introduction

Forest landscape models (FLMs) are important tools for testing basic ecological theory and for exploring forest changes at landscape and regional scales. They simulate forest change including site-scale and forest landscape-scale processes (He, 2008; Keane et al., 2004; Perry and Enright, 2006; Scheller and Mladenoff, 2007; Taylor et al., 2009). Site-scale processes include growth, mortality, and competition, which are represented in FLMs to be non-spatial and occur at each individual site (cell), whereas forest landscape-scale processes include seed dispersal and forest disturbance, which are spatial and stochastic (He, 2008). Both types of processes affect forest change at landscape to regional scales (Araújo and Luoto, 2007; Dawson et al., 2011; Gustafson et al., 2010).

Because of their spatially explicit and interactive nature, computational loads for FLMs may be intractable when the site-scale processes simulated become too complex. Thus, FLMs typically simplify these processes in order to simulate relatively large landscapes (Mladenoff, 2004). Information tracked at each site in early FLMs is either aggregated as the presence or absence of species' age cohorts (e.g., in LANDIS) (Mladenoff and He, 1999) or forest

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type (e.g., in LANDSUM and SIMMPPLE) (Chew et al., 2004; Keane et al., 2002). Consequently, tree growth in these FLMs is simplified as age increment (Li and Barclay, 2001; Mladenoff and He, 1999) rather than DBH and crown increment as simulated in forest stand models (e.g., Pacala et al., 1996). Resource competition at site scales is either simplified by comparing species shade tolerance classes so that shade-tolerant species successionally replace shade intolerant species (e.g. in LANDIS) or simplified by using successional pathways so that late-successional forest types replace early- and middle- successional types determined by predefined transition probabilities (Chew et al., 2004; Keane et al., 2004; Roberts, 1996). Stand structure in these FLMs is also greatly simplified as the presence or absence of defined age cohorts or simply forest types (He, 2008). The simplified formulations of vegetation dynamics in early FLMs may be sufficient for landscapes where forest landscape-scale processes such as fire or harvest can override site-scale processes (Schumacher et al., 2004; Turner, 2010). However, the FLMs with simplified site-scale processes omit tree density and size metrics that are key mechanisms determining site-scale resource competition (Bohlman and Pacala, 2012; Moorcroft et al., 2001; Wang et al., 2013). Thus, the FLMs with simplified site-scale processes may not produce realistic predictions for forest landscapes where effects of disturbance do not predominate and where site-scale processes largely drive forest landscape change (Schumacher et al., 2004; Wang et al., 2013).

Recent FLMs have improved the formulation of site-scale processes by adding quantitative information (e.g. tree numbers and biomass) at each site. For example, LANDIS II adds biomass to each species' age cohort and uses a ratio of actual biomass to potential biomass to quantify resource availability at each site, assuming age-cohort biomass by species implicitly incorporates tree density information (Scheller et al., 2007, 2011). LANDCLIM also replaces the presence/absence of species' cohorts in the LANDIS model with species' biomass dynamics, which tracks numbers of trees and biomass by species' age cohort. Site-scale resource competition is determined by growth- and density-dependent mortality driven by maximum stand biomass (Schumacher et al., 2004). In TreeMig, reproduction is modeled in a detailed way, including seed production by adult trees, seed dispersal, seed bank dynamics, germination, and sapling development. Moreover, TreeMig accounts for within-cell structure in terms of horizontal and vertical heterogeneity within the forest stand (Lischke et al., 2006). In addition, LANDMOD is scaled up from a gap model to accelerate the computation efficiency (Garman, 2004), where growth and mortality functions and bioclimatic values are fitted by meta-modeling to model gap simulations (Urban et al., 1999).

Studies have shown that simulated forest change is highly sensitive to the formulation of site-scale processes (Araújo and Luoto, 2007; Dawson et al., 2011; Elkin et al., 2012; McMahon et al., 2011; Purves and Pacala, 2008; Tylianakis et al., 2008). For example, different formulations of tree growth rates at the site-scale lead to different FLMs simulation results when more detailed response variables are considered, such as species compositional changes associated with elevation. In contrast, such effects are not accounted for when results are assessed at larger spatial (landscape) scales and when coarse-scale response variables (e.g., total forest biomass) are considered (Elkin et al., 2012; Liang et al., 2013). Other studies also have shown that different formulations of site-scale processes in FLMs affect the mechanisms used to simulate inter-specific competition, which consequently can lead to conflicting simulation results (Kellomäki et al., 2008; Spittlehouse and Stewart, 2004). For example, LANDCLIM includes only the presence or absence of seeds and does not link seed numbers to adult tree density and maturity. Applying LANDCLIM thus may result in the domination of long lived, shade tolerant species in the long run (Schumacher et al., 2004). In addition, some FLMs limit seed numbers of shade intolerant species (Pennanen and Kuuluvainen, 2002). This limitation is modeled by rules that force these species to establish only in open gaps (Pennanen et al., 2004), leading to biased estimation of the distribution of shade-intolerant species.

Despite many attempts, it remains a challenge to determine the effects of site-scale processes on predicting forest landscape change. This is because differences in FLMs design and formulation make it difficult to identify and separate the effects of site-level processes. Comparing models with the same framework but different site-scale process formulations thus might overcome some of these problems.

In our study, we chose two FLMs, variants from the LANDIS model family: (1) a model with simplified site-scale processes based on the presence or absence of age cohorts (the age cohort model) (He et al., 2005; Mladenoff and He, 1999; Yang et al., 2011), and (2) a model with detailed site-scale processes based on stand density (the stand density model) that includes consideration of gap level succession (Wang et al., 2013) for evaluating effects of site-scale processes on landscape-scale predictions of tree species distribution and spatial pattern. Specifically, we examined (1) the deviations in species distribution (quantified by species relative abundance) as well as spatial pattern derived from the two models; (2) the similarity of overall and year-to-year variation in species distribution and pattern derived from the two models; and (3) whether the response of spatial pattern predictions to site-scale processes was similar to predictions of species distribution. Our study also examined how the drivers of site-scale dynamics, species' ecological traits such as shade tolerance, growth rate, and seed dispersal, influenced individual species' predictions.

2. Methods

2.1. Case study landscape

Our study area (4.1×10^5 ha) was located in the Changbai Mountain National Natural Reserve (CMNNR) and the 8 km surrounding area at 41°62′–42°49′N, 127°59′–128°38′E. CMNNR lies within the highest mountain range in northeastern China and protects one of the largest natural temperate forests in the world (Shao, 1996; Stone, 2006). There are four vertical vegetation/elevation zones ranging from 740 m at the lowest elevation to 2691 m at the summit of the Changbai Mountains. Elevations from 740 to 1100 m are predominantly a mixed Korean pine-hardwood forest zone, including Korean pine (*Pinus koraiensis* Siebold & Zucc.), basswood (*Tilia amuresis* Rupr), Asian white birch (*Betula platyphylla* Suk), aspen (*Poplus davidiana* Dode), ash (*Fraxinus mandshurica*), Mongolian oak (*Quercus mongolica* [Fisch] Ledeb.), maple (*Acer mono* Maxim) and elm (*Ulmus propingua*). From 1100 to 1700 m lies the evergreen coniferous forest zone dominated by jezo spruce (*Picea jezoensis* Siebold & Zucc.) and Manchurian fir (*Abies nephrolepis* [Trautv.] Maxim), with characteristics typical of boreal forests. From 1700 to 2000 m lies the subalpine forest zone dominated by mountain birch (*Betula ermanii Cham*) and Olga Bay larch (*Larix olgensis* A. Henry). Elevations above 2000 m include tundra, bare rock and a volcanic lake (Shao, 1996). Hardwood forests extend 8 km outside the nature reserve (lower than 750 m elevation) where human activities have transformed the pine–hardwood forests into those mainly comprising hardwoods. The Changbai Mountains is also comprised of azonal vegetation types and other types such as larch forests, aspen-birch forests, alpine meadows, sparse forests, windthrow areas, abandoned forests, as well as cut-over sites and other areas subject to human use. Along with the zonal vegetation types, there are 20 land cover types distributed mainly along elevational gradients.