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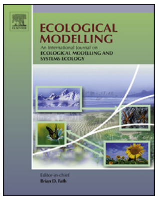

Climate change effects on red spruce decline mitigated by reduction in air pollution within its shrinking habitat range

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ABSTRACT

We investigated the potential effects of projected climate change on red spruce (*Picea rubens* Sarg.) growth in the Great Smoky Mountains of Southeastern USA. A model called Annual Radial Increment Model (ARIM) was used to capture ecosystem complexity manifested as direct and indirect effects in multi-factorial within- and across-scale interactions. The model was run under different scenarios, including projected climate change under reduced, no change, and increased atmospheric pollution. Modeled red spruce growth at end of 21st century (2080–2099) was compared to modeled growth at end of the 20th century (1980–1999). Red spruce growth at high elevations ($\geq$1700 m) declined by 10.8% when climate change interacted with a 10% increase in air pollution, but red spruce growth increased by 8.4% when air pollution decreased by 10%. In contrast, red spruce growth at low elevations (<1700 m) declined by 11.2% with a 10% increase in air pollution, 8.9% with no change, and 6.4% with a 10% decrease in air pollution. Our results suggest that red spruce populations at high-elevation may grow more rapidly under climate change if air pollution decreases, but populations at low-elevation may decline irrespective of air pollution changes as habitats shrink.

1. Introduction

There are conflicting predictions on the effects of climate change on forest systems. Some research has reported that it could shift phenological events (Chmielewski and Rötzer, 2001; Cornelius et al., 2013), shift the ranges of organisms (Colwell et al., 2008; Doak and Morris, 2010), and shrink the habitats of alpine species (Lenoir et al., 2008). In particular, most alpine and subalpine tree species are generally more vulnerable to climate warming than other tree species because they are adapted to lower optimal temperatures and have low genetic diversity (Hörsch, 2003; Larigauderie and Körner, 1995). However, field experimental research (Ainsworth and Long, 2005; Norby and Luo, 2004) and ecosystem modeling research (Schimel et al., 2000) suggest that elevated CO_2 and temperature levels will have positive growth effects on most plant species. Understanding ecosystem complexity may clarify the effects of climate change on forest systems.

Krivtsov (2004) defines ecosystem complexity as being manifested in indirect effects, rather than direct effects, that result from the modification of direct interactions between two ecosystem factors by separate factors. Indirect effects have powerful influences on ecosystems' functioning (Higashi and Patten, 1989; Salas and Borrett, 2011). For example, indirect effects contribute to the maintenance of diverse species composition through species interactions such as trophic chains and cascade (Bever, 2002, 2003) and habitat developments by interactions among species and environmental factors (Diekötter et al., 2007; Hunt et al., 1991). Such indirect effects are difficult to capture in either broad-scaled descriptive or fine-scaled experimental studies. Therefore, systems modeling, which integrates multifactorial direct and indirect interactions within ecosystems, is appropriate to study indirect effects.

Indirect effects operate both within scales (local or regional or global) and across scales (local to regional to global). Within-scale effects are processes that occur at one spatial scale. Across-scale interactions are processes at one spatial scale that interact with processes at another scale (Peters et al., 2007). For example, indirect effects contribute to species-specific habitat development (Diekötter et al., 2007). Indirect effects caused from across-scale

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interactions among soil (local scale), temperature (regional scale), precipitation (regional scale), and soil biota (local scale) and within-scale interactions between soil and soil biota produced a nitrogen-enriched patch favorable to a grassland species in a temperate grassland (Hunt et al., 1991). Much research in landscape ecology and related fields has focused on within-scale interactions, often at multiple independent scales (Cowen et al., 2006; Kent et al., 2006; King et al., 2004; Wheatley and Johnson, 2009), and do not account for interactions across scales (Breckling et al., 2005; Kerr et al., 2007; Nash et al., 2014; Peters et al., 2007; Schneider, 2001). For this reason, fine-scaled studies have limited power to understand issues at regional and global scales, and global-scaled studies are also not able to predict the impacts of global environmental changes on local scales (Carpenter et al., 2006; Diffenbaugh et al., 2005; Kerr et al., 2007; Nash et al., 2014). Across-scale interactions may lead to nonlinear behavior with thresholds that cannot be predicted by observations at independent single or multiple scales (Gunderson, 2008; Peters et al., 2007; Peterson, 2000; Schneider, 2001). Failing to understand across-scale interactions has caused poor predictions of global change effects on organisms and led to ineffective management decisions (Soranno et al., 2014). Therefore, consideration of both within- and across-scale interactions is needed to improve prediction of global change effects on local species (Diffenbaugh et al., 2005; Nash et al., 2014; Peters et al., 2007; Peterson, 2000).

A challenge of revealing causation by combining direct/indirect effects and within-/across-scale interactions for many factors is that there are many incommensurable dimensions and units. Koo et al. (2011a, b) addressed this challenge by developing a model for predicting tree growth called the Annual Radial Increment Model (ARIM). ARIM is based on photosynthetic inputs, respiratory outputs and hierarchically organized environmental controls that are represented as direct and indirect interactions among biotic and abiotic factors to explain within- and across-scale interactions at global, regional and local scales. Quantifying parameters is difficult in ecosystem modeling because different methods, measurements and units are involved. To integrate different models and factors in the submodels, ARIM calculates non-dimensionalized index values for each dimensioned variable by dividing yearly average values by the corresponding long-term mean, with the non-dimensionalized index values (NIV) representing relative deviations from the long-term mean.

Red spruce is an ecologically and commercially important conifer species that is declining in eastern North America (Dumais and Prévost, 2007). In a previous study, Koo et al. (2011a) applied ARIM to assess potential causes of red spruce growth decline in the Great Smoky Mountains of the southern Appalachians in the US. Acidic rains and clouds caused by complex interactions among air pollutants, precipitation, cloud immersions and topographic factors were the dominant factors leading to red spruce decline at

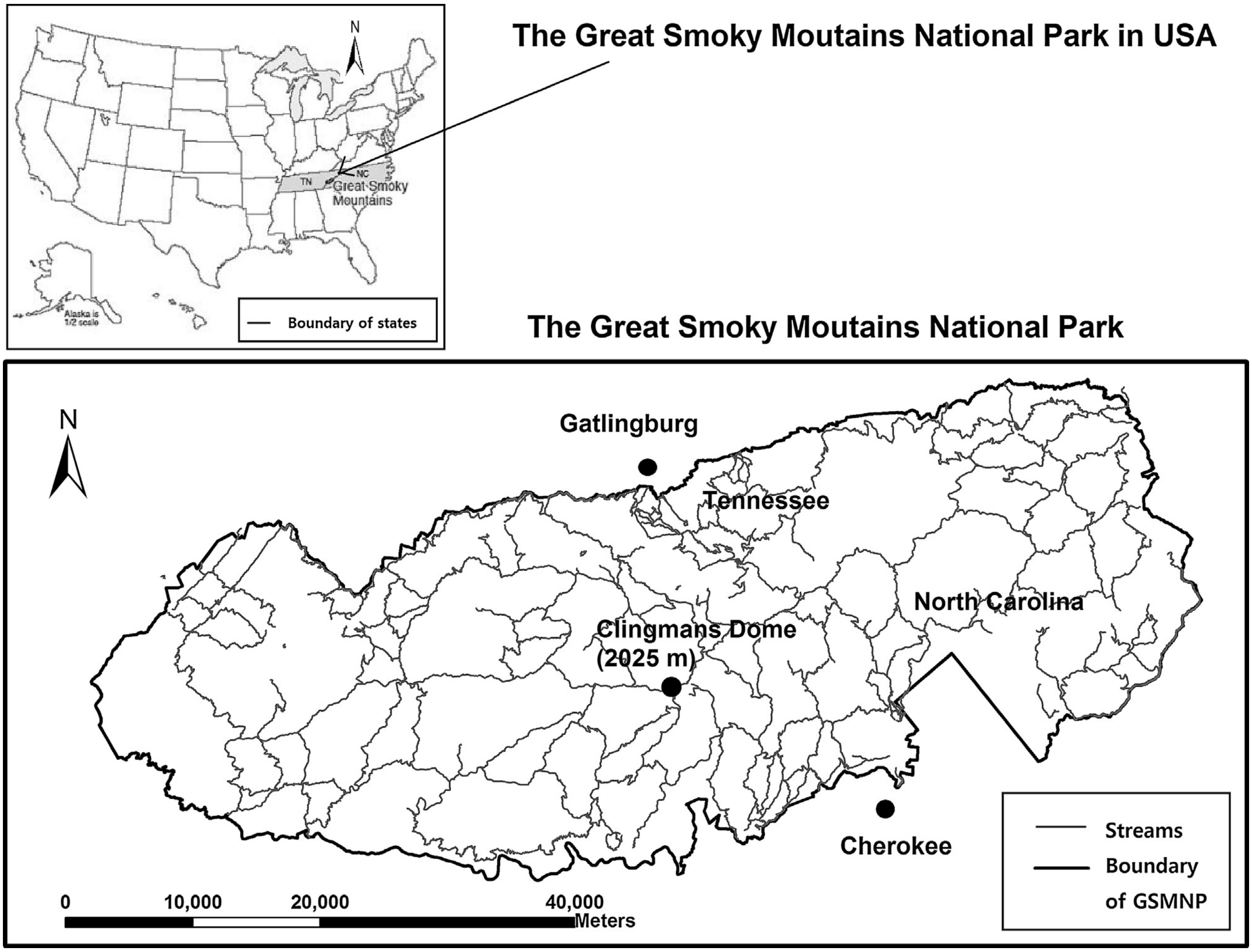

Fig. 1. The location of Great Smoky Mountains National Park (GSMNP) in the United States and the GSMNP with state boundary between Tennessee and North Carolina following a central high elevation ridge.