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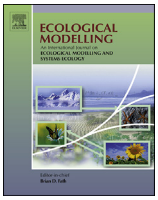

Past-century decline in forest regeneration potential across a latitudinal and elevational gradient in Canada

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ABSTRACT

The regeneration niche of trees greatly narrows the fundamental niche and is sensitive to climatic change. Development from seed and phenology are regulated by biological and environmental controls, shaping forest successional pathways. We hypothesized that recent climate change is reducing regeneration suitability in northern forests. We used a process-based ecophysiological model to examine changes in forest regeneration conditions across an elevational and latitudinal gradient in Alberta, Canada from 1923 to 2012. We compared these results to a recent empirical study in the region to infer the recent drivers of regeneration change in northern forests. Our results suggest that these forests are experiencing climatically driven declines in conditions suitable for regeneration. Contrary to previous findings indicating poorer current conditions in low elevation forests, we found more stable regeneration potential there, attributable to a relative abundance of soil moisture. Rocky soils resulted in modeled losses of soil moisture at higher elevations, potentially preventing upslope migrations of species despite warming. We identify potential mechanisms driving unexpected tree regeneration patterns described in previous studies. Our simulations suggest a delayed response of forest regeneration to warming throughout the past 90 years.

1. Introduction

Tree development and phenology are related to climate through evolutionary controls, influencing the early niche space of trees, with plasticity potentially providing a buffer to maintain fitness (Aitken et al., 2008; Vitasse et al., 2013). Important tree development and phenology events include germination, establishment, bud burst, growth, bud set, leaf senescence, seed fall, and dormancy, among others (Richardson et al., 2013; Walck et al., 2011). Climatic change can uncouple the phasing of fine-scale seasonal weather variations with developmental processes and phenology beyond the range of plasticity, reducing regeneration rates (Fridley, 2012; Richardson et al., 2013). This phase uncoupling can alter the duration of important phenological processes and timing of phenological events.

The widespread adaptation of trees to local climatic conditions (Alberto et al., 2013) indicates that tree phenology is intricately tuned to optimize fitness for local environmental conditions through gene expression, posttranslational modification, and, genetic and epigenetic inheritance (Cooke et al., 2012; Liu et al., 2010; Matzke and Mosher, 2014). Environmental effects are estimated to exert greater influence on plasticity than genetics in northern forests (Vitasse et al., 2013), while phenotypic variation reflecting phylogeographic origins (Alberto et al., 2013) is not necessarily adaptive (Duputié et al., 2015). Extreme weather events, such as frost or drought, occurring at critical times during tree development can have strong demographic effects on forests. Given the importance of fine-scale climatic and phylogenetic variability, high temporal resolution climate data (Cook et al., 2010) along with a range of aggregate species tolerances can aid in the modeling of these dynamics at the landscape scale, where individual- or population-level data is seldom attainable.

We hypothesized that warmer conditions combined with changes in soil water balance (Dobrowski et al., 2013; Piedallu

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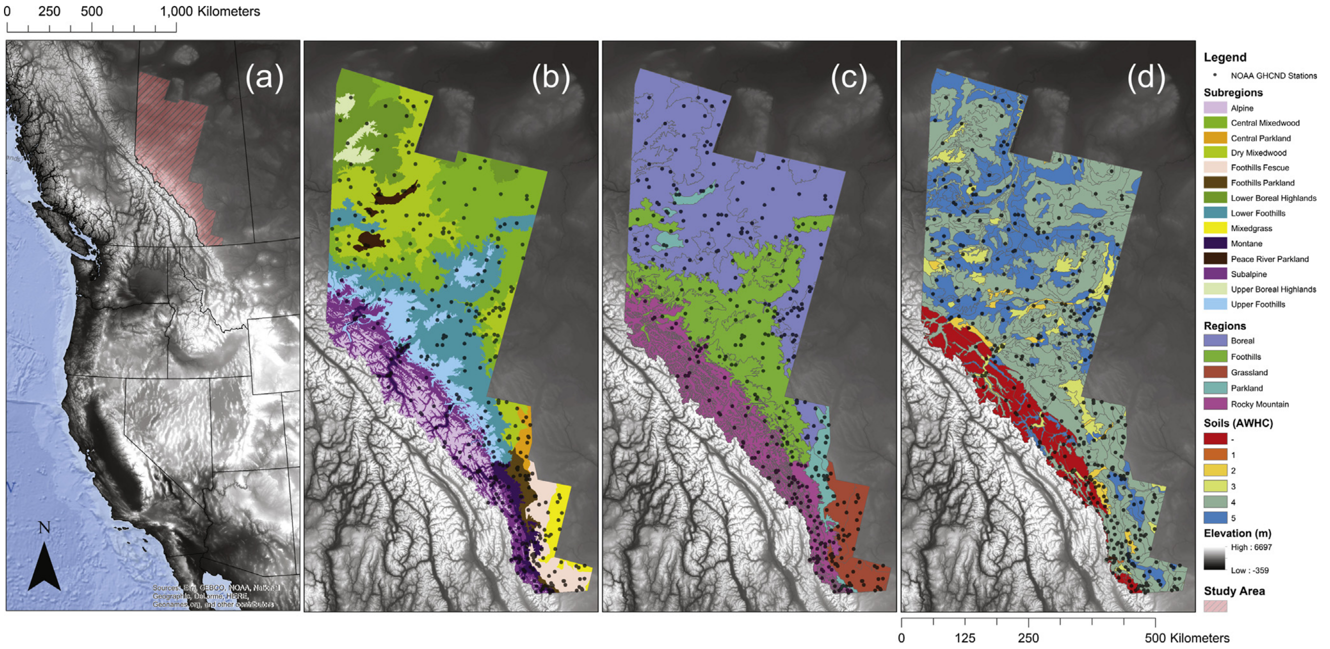

Fig. 1. Study area overlaid on 90-m resolution NASA SRTM topography: (a) study area geographic context within North America; (b) biogeoclimatic subregions and weather stations; (c) biogeoclimatic regions with subregion outlines and weather stations; (d) Soil regions with outlines and weather stations; available water holding capacity (AWHC) classes are shown, the most sensitive edaphic model parameter, with red representing bare rock or effectively zero. (For interpretation of the references to color in the figure legend, the reader is referred to the web version of this article.)

et al., 2013) and more rapid and severe extreme weather events (Allen et al., 2010; Kamae et al., 2014; Trenberth et al., 2014) are altering regeneration patterns in northern forests. Recent empirical evidence suggests that this shift is already occurring (Boisvert-Marsh et al., 2014; Lenoir et al., 2009; Urbieta et al., 2011; Zhang et al., 2015). However, direct measurement remains confounded by forest turnover, which can increase the amount of space available for recruitment (Carvalhais et al., 2014; Park Williams et al., 2013; Woodall et al., 2013; Zhu et al., 2014, 2012). Additional confounding factors include patterns of fine-scale climate (Dobrowski et al., 2013) and ontogenetic niche variation, whereby the niches of species can change throughout development (Bertrand et al., 2011a; Cavender-Bares and Bazzaz, 2000; Donohue et al., 2010; Eriksson, 2002; Niinemets, 2010; Urbieta et al., 2011).

We suggest that changes to tree regeneration throughout northern forests in recent decades have been driven by interactions between climatic change and local soil patterns. To test this hypothesis, we used a species-specific ecophysiological model that explicitly represents major tree regeneration processes, based on forest gap models. We parameterized the model for tree species and soil textural classes across a 25.2 million hectare study area in Alberta, Canada, encapsulating an important elevational and latitudinal gradient. We used daily resolution historical weather station data for three decadal periods over the last century, and for the most recent decade, to model the effects of climatic change on forest regeneration throughout the past 90 years.

2. Materials and methods

2.1. Study area

We applied the Tree And Climate Assessment Germination and Establishment Model (TACA-GEM) across fourteen biogeoclimatic regions of western Alberta, Canada (Natural Regions Committee, 2006) (Fig. 1), coextensive with ecoregions in the United States (Ricketts, 1999). The study area comprises a transition zone from boreal forest at lower elevations to higher elevation Cordilleran foothills and montane forests in the southern Canadian Rocky Mountains. We derived soil and climate parameters for thirteen natural subregions, excluding the treeless alpine subregion. Regional soil properties reflect a recent glacial history, primarily consisting of morainal and glacio-lacustrine parent materials, with gray luvisols and black chernozems representing the dominant soil types (Natural Regions Committee, 2006). Luvisols are periodically saturated and depleted of oxygen, whereas Chernozems occurs in semiarid and subhumid climates, representing the dominant soil of the Canadian southern interior plains (Soil Classification Working Group, 1998). The region consists primarily of well-drained upland soils.

Elevational and latitudinal gradients segment the study area biogeoclimatically, with mean elevations ranging from 525 meters in the boreal to 2350 meters in the alpine. The study area covers a latitudinal gradient from 49° at the U.S. border to 58° at the northernmost point (NAD83 datum). The heavily forested foothills region experiences higher levels of precipitation than surrounding areas, supporting productive lodgepole pine (*Pinus contorta* var. *latifolia*) forests and an active timber industry. While most Canadian provincial harvest levels remained stable over the past four decades, harvest increased approximately four-fold in Alberta (National Forestry Database, 2013), alongside a rise in oil, gas, and mineral extraction activities. Regionally abundant species include lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and black spruce (*Picea mariana*) (Natural Regions Committee, 2006; Zhang et al., 2015). Previous studies show that this region became warmer and drier throughout the 20th century (Luo and Chen, 2013; Peng et al., 2011).

2.2. TACA-GEM model design

The latest version of the Tree And Climate Assessment Germination and Establishment Model (TACA-GEM) presented herein (Fig. 2) builds on establishment-only TACA-EM (Nitschke and Innes, 2008) and extends previous TACA-GEM versions (Nitschke et al.,