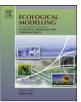
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## Plant toxins and trophic cascades alter fire regime and succession on a boreal forest landscape

Zhilan Feng<sup>a</sup>, Jorge A. Alfaro-Murillo<sup>a</sup>, Donald L. DeAngelis<sup>b,\*</sup>, Jennifer Schmidt<sup>c</sup>, Matthew Barga<sup>d</sup>, Yiqiang Zheng<sup>a</sup>, Muhammad Hanis B. Ahmad Tamrin<sup>a</sup>, Mark Olson<sup>c</sup>, Tim Glaser<sup>c</sup>, Knut Kielland<sup>c</sup>, F. Stuart Chapin III<sup>c</sup>, John Bryant<sup>c</sup>

<sup>a</sup> Department of Mathematics, Purdue University, West Lafayette 47907, IN, USA

<sup>b</sup> U.S. Geological Survey and Department of Biology, University of Miami, P.O. Box 249118, Coral Gables 33124, FL, USA

<sup>c</sup> Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks 99775, AK, USA

<sup>d</sup> School of Computer Engineering, Purdue University, West Lafayette 47907, IN, USA

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## ABSTRACT

Two models were integrated in order to study the effect of plant toxicity and a trophic cascade on forest succession and fire patterns across a boreal landscape in central Alaska. One of the models, ALFRESCO, is a cellular automata model that stochastically simulates transitions from spruce dominated 1 km<sup>2</sup> spatial cells to deciduous woody vegetation based on stochastic fires, and from deciduous woody vegetation to spruce based on age of the cell with some stochastic variation. The other model, the 'toxin-dependent functional response' model (TDFRM) simulates woody vegetation types with different levels of toxicity, an herbivore browser (moose) that can forage selectively on these types, and a carnivore (wolf) that preys on the herbivore. Here we replace the simple succession rules in each ALFRESCO cell by plant-herbivore-carnivore dynamics from TDFRM. The central hypothesis tested in the integrated model is that the herbivore, by feeding selectively on low-toxicity deciduous woody vegetation, speeds succession towards high-toxicity evergreens, like spruce. Wolves, by keeping moose populations down, can help slow the succession. Our results confirmed this hypothesis for the model calibrated to the Tanana floodplain of Alaska. We used the model to estimate the effects of different levels of wolf control. Simulations indicated that management reductions in wolf densities could reduce the mean time to transition from deciduous to spruce by more than 15 years, thereby increasing landscape flammability. The integrated model can be useful in estimating ecosystem impacts of wolf control and moose harvesting in central Alaska.

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## 1. Introduction

Field studies and theoretical modeling studies both strongly suggest that in the boreal forest of North America the chemical defenses of woody plants, via their effect on the preferences of moose (*Alces alces*) for the twigs of winter-dormant woody plants (browse), can cause spatial variation in vegetation dynamics, nutrient cycling and biogeochemistry across landscapes (Bryant and Chapin, 1986; Pastor et al., 1988, 1999; Bryant et al., 1991; Irons et al., 1991; McInnes et al., 1992; Kielland et al., 1997, 2006; Moen et al., 1997, 1998; Kielland and Bryant, 1998; Oswood et al., 2006; Butler and Kielland, 2008; Feng et al., 2009). Furthermore, in this biome, predators such as wolves can also influencevegetation

\* Corresponding author at: Department of Biology, University of Miami, Coral Gables, FL 33124-0421, USA. Tel.: +1 305 284 1690; fax: +1 305 284 3039. *E-mail address:* ddeangelis@bio.miami.edu (D.L. DeAngelis).

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dynamics through their effect on moose density. When moose are abundant their browsing can suppress the growth of edible browse species, but when wolf predation reduces moose density, the amount of biomass of edible browse can increase because of the reduced herbivory (Vucetich and Peterson, 2004). Thus, in boreal North America, the combined effect of chemical defenses of winter-dormant woody plants and predation may reduce moose browsing and, as a consequence, may significantly affect the functioning of the ecosystem. However, to the best of our knowledge, these interactions across three trophic levels have never been quantitatively integrated with landscape processes at large temporal and spatial scales. Bridging this gap would provide opportunities for wildlife biologists, plant community ecologists, and ecosystem and regional modelers working in boreal forests to develop a common conceptual framework that allows complex interactions between trophic and successional dynamics to make informed suggestions about the management of wildlife, ecosystems, landscapes, and land-atmosphere feedbacks. Without