Forest Ecology and Management 381 (2016) 93–105

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Relative influence of climate, soils, and disturbance on plant species richness in northern temperate and boreal forests

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A R T I C L E I N F O

Article history:
Received 18 March 2016
Received in revised form 11 July 2016
Accepted 12 July 2016
Available online 22 September 2016

Keywords:
Biodiversity
Emulating natural disturbance
Ecosystem complexity
Disturbance intensity
Silviculture
Forest ecology
Forest management

A B S T R A C T

In this study we sought answers to two questions (i) What is the relative influence of silvicultural disturbances on species richness in northern temperate and boreal forests? and (ii) In a scenario where emulating natural disturbances is applied, do collinearity and hierarchical structure exist among climate, soils, disturbance of the forest canopy and forest floor, exotic species, and species richness? By capitalizing on the NEBIE plot network, a large-plot experimental study designed to evaluate the effects of intensification of silviculture on fiber production and biodiversity. We demonstrate that silvicultural disturbances act with contemporary climate, soils, and historic fire regimes to influence plant species richness in northern temperate and boreal forests in Ontario, Canada. Relationships between various factors and plant species richness (total and for each life form: woody, herbaceous, bryophyte, and lichen) were analyzed using general linear (GLM) and structural equation modelling (SEM). Results of GLM indicate that climate accounted for the overwhelming percentage of variation in species richness of each of the plant life form groupings (>50% and often >70%), while soil properties, canopy structure, silvicultural practices, and degree of natural disturbance each accounted for on the order of 10% or less of variation in species richness. Results of fitted SEM suggested strong collinearity and hierarchy among climate, soils, historic fire regimes, and silviculture systems; however, the effect of silvicultural intensity on plant species richness was independent of climate, soils, and historic fire regimes.

Abbreviations	
NEBIE	The NEBIE acronym refers to the intensity of the silvicultural treatments, natural (unharvested), [and in order of increasing stocking levels from 40% to 80%]: extensive, basic, intensive, and elite (for treatment details, see Bell et al., 2008). Natural disturbance: Forest ecosystem responds (e.g., to fire, insects, and/or disease) without human inputs; Extensive: Stocking is >40% and desired tree species are free of major insect pests; Basic: Stocking is >60% and desired tree species are free of interspecific competition and major insect pests; Intensive: Stocking is >80% and desired tree species are free from inter- and intraspecific competition and major insect pests; Elite: Stocking is >80% and desired tree species are free from inter- and intraspecific competition, nutrient deficiencies, and major insect pests
GLM	General linear model
SEM	Structural equation modelling

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http://dx.doi.org/10.1016/j.foreco.2016.07.016
0378-1127/© 2016 Published by Elsevier B.V.

1. Introduction

Global threats to biodiversity require conservation measures that extend beyond parks and protected areas. These measures now apply to the conservation of biodiversity in managed forests (Lindenmayer et al., 2006; Wintle and Lindenmayer, 2008). Unfortunately, forest management and, more specifically, the intensification of silviculture, is commonly considered a threat to biodiversity (e.g., Kimball and Hunter, 1990; Lieffers et al., 2003; also see review by Puettmann et al., 2009). Recent research indicates that plant species richness in northern temperate and boreal forests of North America is influenced by intensification of silviculture (Wang and Chen, 2010; Pidgen and Mallik, 2013; Bell et al., 2014), but the influence of silviculture relative to other factors is not fully understood.

Disturbances are often viewed as essential for maintaining biodiversity (e.g., Petraitis et al., 1989; Hobbs and Huenneke, 1992); however, in a review of 130 ecological studies relating disturbance and plant species richness, Mackey and Currie (2000) concluded that "disturbance is unlikely to account for more than small amounts of variance" in the differences in species richness in nature. Results from observational forestry studies conducted at regional scales (e.g., de Vries et al., 2003; Graae et al., 2004; Werth et al., 2005; Martín-Queller et al., 2013) also suggest that, relative to the effect of climate, the influence of anthropogenic disturbances on forest species richness is negligible.

Compared to climate, the relative influence of disturbance may be scale dependent. For example, focusing on studies extending over 800 km, Hawkins et al. (2003) observed that in 82 of 85 cases measures of energy, water, or the water–energy balance explained more of the spatial variation in richness than other variables. Results from the nine cases cited in their review involving field sampling of woody and/or herbaceous species indicated that water combined with energy accounted for 50–86% of the variation in species richness.

Nichols et al. (1998) put forward several additional explanations to account for the relatively weak relationship between disturbance and species richness at regional scales. First, the effects of disturbances may (i) offset one another, (ii) be relatively weak when climate and soils vary widely, and/or (iii) be represented by nonlinear relationships, all of which may reduce the probability of identifying a relationship between diversity and disturbance. However, other factors such as the implementation of *emulating natural disturbances* in forest management (Perera and Buse, 2004) may be as or more important. At present, knowledge of the interrelationships among disturbances and their effects on biodiversity, and more specifically the use of intensive silviculture in conjunction with emulating natural disturbances, is limited. In this study, we presumed that disturbance (i.e., harvesting and silviculture), when applied in a manner that emulates natural disturbances, would act with contemporary climate, soils, and historic disturbance regimes to influence species richness. Collinearity and hierarchies among explanatory variables have been observed in several forest studies (see Graae et al., 2004; Caplat et al., 2008; Wang et al., 2008; Leithead et al., 2012).

In this paper we address two questions: (i) What is the relative influence of harvesting and silvicultural disturbances on species richness in northern temperate and boreal forests? and (ii) In a scenario where emulating natural disturbance guidelines are applied, do collinearity and hierarchical structure exist among climate, soils, disturbance of the forest canopy and forest floor, exotic species, and species richness?

2. Materials and methods

We sought answers to our questions about species richness using fifth-year post-harvesting plant diversity data collected from the NEBIE plot network in Ontario, Canada. NEBIE is a stand-level experiment initiated in 2001 to study the effects of intensification of silviculture on northern temperate and boreal forest ecosystems. The NEBIE acronym refers to the intensity of the silvicultural treatments, i.e., natural (unharvested), extensive, basic, intensive, and elite (for treatment details, see Bell et al., 2008).

2.1. Experimental and treatment designs

NEBIE includes six independent randomized complete block experiments (sites), each designed to test a range of silvicultural intensities. NEBIE sites are located across a broad climatic gradient in several forest types: boreal conifer (Sioux Lookout), boreal mixedwood (Dryden, Kapuskasing, Timmins), northern temperate mixedwood (Petawawa), and northern temperate hardwood (North Bay). NEBIE spans 45°58′N to 50°0′N, and 77°26′W to 92°46′W within a geographic area measuring 300 km north–south and 1100 km east–west. Across the area, average daily temperatures range from 0.7 to 4.3 °C, extreme annual minimum temperatures range from −40.0 to −46.7 °C, growing degree days >5 °C vary from 1370 to 1779, annual rainfall is 517.2–774.6 mm, and total precipitation ranges between 705 to 1008 mm (Appendix A). Soils vary among sites with soil depths ranging from 40 to >120 cm, organic matter depth from 1.8 to 7.4 cm, and soil moisture from 0 (xeric) to 6 (hydric). Dominant soil textures are sandy at the Sioux Lookout site, coarse loamy at the Dryden, Petawawa, and North Bay sites, clayey at the Kapuskasing site, and silty at the Timmins site.

Plots, or experimental units (EUs), were approximately 100 × 200 m (2 ha) in size, ensuring that treatments could be applied in a semi-operational manner. Treatments were initially replicated four times within each site; however, one of the four temperate hardwood blocks was not harvested as planned, resulting in only three replications in this forest type. The design resulted in 115 experimental units (6 sites × 5 treatments × 4 blocks; except North Bay which has 3 blocks).

For each site, silvicultural strategies thought to have a high probability of leading to economically viable management outcomes were designed keeping forest composition and soils in mind and randomly assigned to plots within that site. Guidelines for emulating natural disturbance patterns (OMNR, 2001), i.e., a minimum of 25 stems ha^{-1} left unharvested, were applied at all but the boreal conifer site. The clear cut and seed tree systems were applied to boreal conifer and boreal mixedwoods, respectively. The shelterwood system (see Smith et al., 1997) was applied to northern temperate hardwood and northern temperate mixedwood forests. Plots of unharvested mature forest, which represent the pre-harvest stands, were randomly selected to act as untreated controls.

2.2. Sampling methods

Species richness was assessed for four groups of plant life forms: woody plants (i.e., trees and shrubs), herbaceous plants (i.e., forbs, grasses, sedges, and ferns and ferns allies), and bryophytes and lichens. Species richness, as used here, is the number of plant species observed in each of the 115 permanent EUs. Within each EU, woody plants were assessed in two categories: tree species >10 m using four 20 m × 20 m sub-plots, and tree and shrub species ⩽10 m using forty 2 m × 2 m subplots. Herbaceous plants and bryophytes and lichens were assessed using 2.83 m radius plots. See Bell et al. (2014) for further details.

Explanatory variables included indicators of abiotic and biotic conditions. In all, 42 explanatory variables were available to assess their relationship with species richness (see Appendix).