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# The effect of species diversity on tree growth varies during forest succession in the boreal forest of central Canada

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ABSTRACT

Although major advances have demonstrated that species diversity has a general positive effect on forest ecosystem productivity, some studies report negligible or even negative effects, highlighting remaining uncertainty in our knowledge of the ecological mechanisms that influence diversity–productivity relationships. In particular, ecological succession is postulated to drive temporal shifts in the strength and direction of diversity–productivity relationships, but few studies have explicitly tested this hypothesis because long-term succession data (from forest initiation to eventual climax) are rare.

Using a detailed, replicated chronosequence (space-for-time substitution) study design of 53 natural forest stands (ages 8 to 210 years) in the boreal forests of central Canada, we investigated the relationship between neighbourhood species diversity and tree growth of five dominant boreal tree species, covering entire, long-term secondary successional sequences following stand-replacing wildfire.

We found compelling evidence that the strength of the relationship between species diversity and tree growth changes over the course of secondary succession, following a general "hump-shaped" pattern, with mid-succession stages of higher functional diversity exhibiting the strongest growth–diversity relationships. However, tree species exhibited individualistic responses to succession-driven changes in species diversity, with broadleaf species (e.g., *Populus tremuloides*) generally showing negative responses, whereas conifers (e.g., *Pinus banksiana*) responded more favorably to higher neighbourhood diversity. Furthermore, our results show the effect of individual tree size on the relationship between species diversity and tree growth to be highly variable, contradicting the hypothesis that larger trees benefit more from complementarity due to size-asymmetric competitive ability. These results contribute to disentangling the mechanisms that link species diversity to forest growth and function, which is important to sustainable forest management planning and for predicting the consequences of global biodiversity loss, especially for the boreal forest, which plays a critical role in controlling global carbon flux and climate.

## 1. Introduction

The past several decades have seen a sharp increase in the number of studies investigating the relationship between species diversity and forest ecosystem productivity (Hooper et al., 2005; Zhang et al., 2012). Although major advances have demonstrated that species diversity generally, positively affects forest ecosystem productivity (Duffy et al., 2017), some studies report negligible or even negative effects (e.g., Edgar & Burk, 2001; Vilà et al., 2003; Laganière et al., 2015). A number of possible explanations for these divergent responses have been postulated, including the potential role of ecological succession in driving temporal shifts in the strength and direction of diversity–productivity relationships (Paquette & Messier, 2011; Barrufol et al., 2013; Lasky et al., 2014); and recognition that at finer biotic scales, individual species may exhibit differential responses to local, neighbourhood diversity depending on site conditions, distance between trees, and relative tree position within the forest canopy (Chamagne et al., 2017; Fichtner et al., 2017; Williams et al., 2017). Accordingly, closer examination of fine-scale processes from which ecosystem-level responses emerge is critical to disentangling the mechanisms that link species diversity to forest ecosystem productivity for predicting the consequences of global biodiversity loss (Hooper et al., 2012).

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The positive effect of species diversity on forest ecosystem productivity is thought to be primarily driven by complementarity, which encompasses the more specific mechanisms of niche (resource) partitioning and interspecific facilitation (Hooper et al., 2005; Williams et al., 2017; Mina et al., 2018). Therefore, it is not unreasonable to expect that the nature of the relationship between species diversity and individual tree species growth will vary as forests undergo secondary succession because community structure and site conditions are known to vary as forests age (Whittaker, 1970; White, 1979; Fridley, 2001; Forrester, 2014). Following severe disturbance, resources such as light and soil nutrients are often plentiful, and the establishment and abundance of species exhibiting overlapping functional traits is high (e.g., photophilia), reducing the effectiveness of niche partitioning (Pacala & Rees, 1998). However, as communities develop, competition intensifies, and site resources become increasingly limited (Odum, 1969; Huston & Smith, 1987; Glenn-Lewin et al., 1992). This can potentially amplify the effectiveness of complementarity (e.g., facilitation), as positive biotic interactions are expected to increase under harsher, resource-limited conditions (Bertness & Callaway, 1994; Maestre et al., 2009). Furthermore, as communities transition from fast-growing, early succession colonizers to slower-growing, shade-tolerant species, overlapping mixtures of early and late-succession species may promote stronger niche partitioning due to greater diversity of contrasting functional traits (Huston & Smith, 1987; Forrester, 2014; Reich, 2014). However, in the long-term absence of severe disturbance, forests may become dominated by climax communities of late-succession species, exhibiting high functional redundancy, e.g., high abundance of shade-tolerant species (White, 1979; Chen & Popadiouk, 2002). Concurrent increases in the availability of site resources, related to senescence of overstorey trees, reduces competition and may diminish the benefits of complementarity (see Fig. 1, conceptual diagram). Despite previous efforts to investigate the relationship between species diversity and tree species growth (e.g., Cavard et al., 2010; Chamagne et al., 2017; Fichtner et al., 2017), few studies have explicitly tested how diversity–productivity relationships vary with secondary forest succession over the long-term because this has been constrained by the availability of succession sequences (e.g., Guo, 2003; Barrufol et al., 2013; Lasky et al., 2014).

The relationship between species diversity and tree species growth may also be influenced by individual tree size as this strongly affects the ability of individuals to compete for site resources (Coomes et al., 2011). For example, competition for light among trees is size asymmetric, in that larger trees capture disproportionally greater amounts of light when interacting with smaller ones. As a result, the effect of complementarity on growth may be stronger for trees of relatively larger size. This is indirectly supported by Zhang et al. (2016), who showed that overstorey tree species diversity had a positive effect on upper canopy trees but its influence on smaller, understorey trees was negligible. Other studies report conflicting results, showing stronger complementarity benefits among smaller, rather than larger trees, depending on regional climate (Madrigal-González et al., 2016), or no size-dependent effect at all (Báez & Homeier, 2018). Such differences in results may be because past studies have not included a wide enough range of tree sizes, with most focusing on trees greater than 10 cm in diameter at breast height (DBH). Moreover, directly using DBH to represent tree size neglects the important influence of forest age on tree size, as trees of the same size may constitute different forest strata (e.g., understorey versus overstorey) depending on stage of succession.

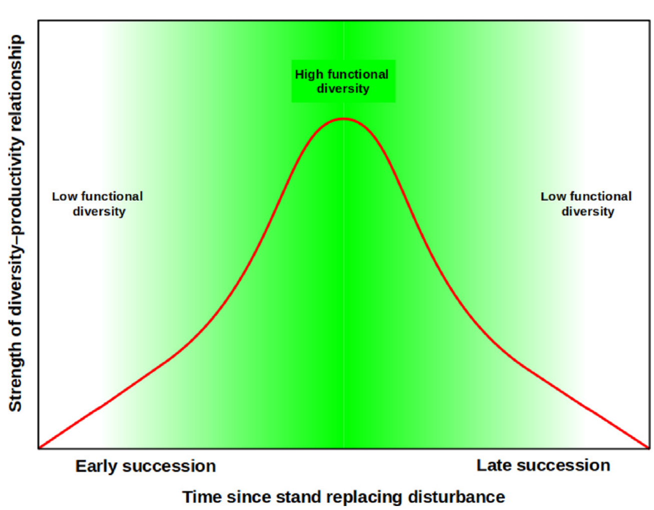


**Fig. 1.** Conceptual diagram of hypothetical change in strength of the diversity–productivity relationship following post-fire boreal forest succession with changes in functional diversity.

The circumpolar boreal forest is the largest intact terrestrial biome in the world. It is critical to regulating global carbon flux, but its productivity is considered sensitive to changes in species diversity (Paquette & Messier, 2011; Jucker et al. 2016; Liang et al., 2016). A deeper understanding of the mechanisms that drive boreal productivity is critical to addressing global climate change. In this study, we used a detailed chronosequence (space-for-time substitution) design to investigate the relationship between neighbourhood species diversity and tree growth of five dominant tree species across 53 natural stands in the boreal forests of central Canada, covering a wide range of forest stand ages (from 8 to 210 years old) and species compositions following stand-replacing wildfire. These forests provide a unique and novel opportunity to study diversity–productivity relationships across entire, long-term succession sequences (from forest initiation to climax) as their dynamics are largely driven by wildfire and dominant post-fire succession pathways are well documented (e.g., Carleton & Maycock, 1978; Bergeron and Dubue, 1988; Taylor & Chen, 2011). Furthermore, relative to temperate and tropical forests, the boreal contains fewer tree species, which potentially simplifies disentangling individual species contributions to diversity effects. We hypothesized that (1) the effect of neighbourhood species diversity on tree species growth would change as forests underwent secondary succession and become stronger when competition for resources intensifies and as functional diversity increases when early and late-succession species codominate (Fig. 1); and (2) the effect of species diversity would increase with relative tree size because trees have size-asymmetric competitive ability for resources.

## 2. Methods

### 2.1. Study area

Our study was conducted in the boreal forest, approximately 150 km north of Thunder Bay, Ontario, Canada (49°40′ N and 89°50′ W, Fig. 2). This area is characterized by warm summers and cold, snowy winters. Mean annual temperature is 1.9 °C and mean annual precipitation is 824.8 mm (582.7 mm as rainfall and 238.2 cm as snowfall) as measured by the closest meteorological station in Cameron Falls, Ontario, Canada (Environment Canada, 2019). Soils in our study area were largely deposited by the Wisconsinan glaciation, which ended approximately 9500 years ago in this region. Stand-replacing wildfire is the most common natural disturbance in the study area, with an average fire-return interval of approximately 100 years during the past century, resulting in a mosaic of stand ages across the landscape (Senici et al., 2010). Dominant tree species in our study area, in order from least to most shade tolerant, include jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea* mariana Mill. BSP), and balsam fir (*Abies balsamea* [L.] Mill.).