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Structural Complexity Enhancement increases fungal species richness in northern hardwood forests

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ABSTRACT

Forest management practices directly influence microhabitat characteristics important to the survival of fungi. Because fungal populations perform key ecological processes, there is interest in forestry practices that minimize deleterious effects on their habitats. We investigated the effects on fungal sporocarp diversity of modified uneven-aged forest management practices in northern hardwood ecosystems, including a technique called Structural Complexity Enhancement (SCE). SCE is designed to accelerate late-successional stand development; it was compared against two conventional selection systems (single tree and group) and unmanipulated controls. These were applied in a randomized block design to a mature, multi-aged forest in Vermont, USA. Eight years after treatment, fungal species richness was significantly greater in SCE plots compared to conventional selection harvests and controls ($p < 0.001$). Seven forest structure variables were tested for their influence on fungal species richness using a Classification and Regression Tree. The results suggested that dead tree and downed log recruitment, as well as maintenance of high levels of aboveground biomass, under SCE had a particularly strong effect on fungal diversity. Our findings show it is possible to increase fungal diversity using forestry practices that enhance stand structural complexity and late-successional forest characteristics.

Introduction

Forest management practices directly influence microhabitat characteristics important to the survival of fungi (Bader et al., 1995; Heilmann-Clausen and Christensen, 2003; Jones et al., 2003; Martius et al., 2004; Kranabetter et al., 2005). Characteristics important for fungal survival include soil compaction (Ballard, 2000; Pilz and Molina, 2002), litter and downed coarse woody debris (DCWD) accumulation (Siitonen, 2001; Nordén et al., 2004; Lindner et al., 2006; Lonsdale et al., 2008; Müller and Bütler, 2010), changes in soil chemistry (Keizer and Arnolds, 1994; Durall et al., 2006), and canopy closure, which affects soil temperature, moisture, and DCWD respiration (Ballard, 2000; Straatsma et al.,

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2001; Jones et al., 2003; Martius et al., 2004; Forrester et al., 2012; Walker et al., 2012). Fungi provide a variety of ecological functions, and thus an understanding of how forest management practices affect fungal populations and community composition, through the manipulation of microhabitat characteristics, is important for sustainable forestry intended to maintain these functions.

Fungi participate in numerous ecological processes important for forest ecosystem health and productivity. Saprobic fungi affect the decomposition of organic matter, making nutrients available for uptake by plants (Ingham et al., 1985; Kernaghan, 2005; van der Wal et al., 2013). Mycorrhizal fungi form a mutualistic symbiosis with plants, thereby enhancing uptake of nutrients and water by extending the effective area of root systems in exchange for photosynthates (Govindarajulu et al., 2005). Through the growth of mycorrhizal hyphae, fungi also improve soil aeration and porosity (Miransari et al., 2008). Ectomycorrhizal fungi can improve resistance to root pathogens, for instance through physical shielding of root tips by fungal mantles and, in some cases, release of anti-pathogenic chemicals (Duchesne et al., 1989). Fungi contribute to the cycling of organic compounds through the mineralization of nitrogen and phosphorus (Ingham et al., 1985; Govindarajulu et al., 2005). Furthermore, fungal diversity is a major driver of plant diversity. For example, artificially increased fungal diversity increased plant diversity in grassland ecosystems (van der Heijden et al., 1998), and artificially reduced fungal diversity decreased plant diversity in British meadows (Gange et al., 1993). Fungi also provide harvestable mushrooms for human consumption (Pilz and Molina, 2002), representing a culturally and economically high value non-timber forest product in the northeastern U.S. (Robbins et al., 2008) and other temperate regions globally (Pilz and Molina, 2002; Christensen et al., 2008; Cai et al., 2011). We propose that silvicultural practice targeted at maintaining and promoting fungal diversity, perhaps even enhancing populations of beneficial (i.e. mycorrhizal) or harvestable fungi, could be an important element of sustainable forest management.

Researchers in the Vermont Forest Ecosystem Management Demonstration Project (FEMDP) are studying a variety of silvicultural treatments relating to sustainable forest management within the northeastern United States (McKenny et al., 2006; Smith et al., 2008). They are testing an uneven-aged harvest treatment that utilizes disturbance-based (see Seymour et al., 2002; North and Keeton, 2008) forestry principles to accelerate the development of late-successional structural characteristics, termed Structural Complexity Enhancement (SCE) (Keeton, 2006).

Forest management practices that promote late-successional structures are of particular interest because northern hardwood forests have shifted from a historic predominance of late-successional forests to the currently predominant second growth, young to mature (40–80-year old) forests (Lorimer and White, 2003). Riparian functions (Keeton et al., 2007), habitat values (Keddy and Drummond, 1996; McGee et al., 1999), and carbon storage (Harmon et al., 1990; Houghton et al., 1999; Rhemtulla et al., 2009; Keeton et al., 2011) associated with late-successional forests have declined as a result. In the context of global climatic change, the question of whether promoting late-successional structural conditions might also contribute to ecosystem resilience has taken on new significance.

As an experimental approach, SCE uses disturbance-based practices, such as small group selection with structural retention and variably-sized gaps (Franklin et al., 2007; Kern et al., 2013), to accelerate development of structural heterogeneity and late-successional forest characteristics. Disturbances decrease canopy closure, increase microtopographic features, such as downed wood, and affect soil conditions (e.g. compaction, temperature and moisture) that collectively influence microhabitats for fungal species (Ballard, 2000; Straatsma et al., 2001; Jones et al., 2003; Martius et al., 2004; Walker et al., 2012). The central idea behind disturbance-based forestry methods is that emulation of natural processes, such as local disturbance regimes, is more likely to perpetuate the evolutionary environment to which organisms are adapted (North and Keeton, 2008), although global change may shift these boundary conditions over time. In the U.S. Northeast this would entail harvesting practices, like those employed by SCE, that mimic the single-tree to partial canopy mortality associated with low to intermediate intensity disturbances (Seymour et al., 2002; Hanson and Lorimer, 2007). Retention of legacy structures, such as residual live and dead trees, also helps approximate disturbance effects while promoting late-successional structure (Choi et al., 2007; Bauhus et al., 2009; Gustafsson et al., 2012). By providing suitable substrata, such as standing live/dead trees, downed logs, and cycling organic matter to the soil system, they may help “lifeboat” fungi through the post-harvest recovery period (Franklin et al., 2000; Outerbridge and Trofymow, 2009).

SCE promotes the development of vertically differentiated canopies, variable horizontal density (i.e. gappiness), reallocation of basal area to large diameter classes, and elevated downed log and large snag densities. These characteristics are often poorly represented after conventional harvesting techniques (Gore and Patterson 1986; McGee et al., 1999). This has important implications for forest floor microhabitats, such as spatial variations in moisture, temperature, and substratum within the treatment (McKenny et al., 2006; Smith et al., 2008). We studied fungal sporocarp diversity as an indicator for forest ecosystem response to silvicultural treatment. We predicted that practices, like SCE, which maintain canopy cover and promote late-successional structure, will sustain and possibly improve fungal diversity (species richness).

In the FEMPD, in which this fungal response study is nested, the SCE treatment is compared against two conventional uneven-aged harvest treatments, “Single Tree Selection” (STS) and “Group Selection” (GS), modified to enhance post-harvest structural retention and an untreated control (see Keeton, 2006). SCE has been shown to increase herbaceous species richness post-harvest due to effects on forest structural heterogeneity (Smith et al., 2008), and it has been shown to increase terrestrial salamander populations through an increase in habitat availability, particularly enhanced large log densities (McKenny et al., 2006). This study adds a third taxonomic group as a potential indicator of biodiversity response.

Our first hypothesis was that fungal sporocarp diversity would be greater in the SCE treatment than in the conventional