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Vulnerability of boreal indicators (ground-dwelling beetles, understory plants and ectomycorrhizal fungi) to severe forest soil disturbance

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ABSTRACT

Forest ecosystems can be greatly affected by multiple interacting disturbances, with outcomes that may range from degraded and poorly-functioning to novel but productive ecosystems. We assessed the vulnerability of boreal biotic indicators (epigeic beetles, understory plants, ectomycorrhizal fungi) to compound soil disturbances at 20 years post-logging in northcentral British Columbia (Canada) to examine these issues of ecological integrity. The study was a full factorial experiment with 3 levels of organic matter removal (tree boles only; tree boles + logging slash; tree boles + logging slash + forest floors) and 3 levels of soil compaction (0, 2, 4 cm impression), with a tree species split-plot of lodgepole pine (*Pinus contorta*) and hybrid white spruce (*Picea glauca* × *engelmannii*). There was little effect of soil disturbance on ground-dwelling beetles, particularly beneath pine. Removal of forest floors and, to a lesser degree, compaction significantly altered plant and fungal communities. There was no effect of retaining logging slash but a consistent influence of tree species on biotic communities likely due to initial differences in conifer growth rates. Average community dissimilarity of the 3 guilds from a least disturbed baseline (tree bole removal, no compaction) increased linearly by a small amount (4–6%) with each level of disturbance severity. Some degree of soil disturbance across landscapes can be acceptable in creating regeneration niches for rare and functionally important pioneer species, but we also see losses in ecological integrity, such as the spread of invasive plants, that merit concern in managing these ecosystems.

1. Introduction

Terrestrial ecosystems can exhibit consistent successional pathways after periodic, single disturbance events, especially with a surviving legacy of residual vegetation (Turner et al., 1998; White and Jentsch, 2001). More unpredictable species responses can arise when disturbance regimes are more frequent and severe than the recent past, or under compound disturbances, where multiple perturbations interact over a short period of time (Turner, 2010; Buma and Wessman, 2011). The impact of increased site disturbances on species composition and abundance may also be exacerbated by pervasive anthropogenic stresses such as atmospheric N deposition and invasive species (White and Jentsch, 2001). Biotic communities adapted to historical disturbance regimes might be ill equipped to cope with these new, multiple stresses that can overwhelm a system's inherent resilience (defined here as the magnitude of disturbance from which a system is able to recover to its original state; Myers-Smith et al., 2012) (Seidl et al., 2016). Successional trajectories are then potentially altered, sometimes in a non-linear fashion, with outcomes that can vary widely, ranging from degraded, poorly-functioning communities to highly novel but functionally stable and productive ecosystems (Schroder et al., 2005; Radeloff et al., 2015). For this reason there is a need for a better understanding of how these increasingly common, interacting anthropogenic disturbances can ultimately affect biotic communities and ecosystem services.

Much of the research into compound disturbance effects on forests (typically fire, insect, blowdown, and salvage logging interactions) has focused on tree species composition, an especially important indicator given the foundational role of trees in terrestrial ecosystems (Buma and Wessman, 2012; D'Amato et al., 2011; Kulakowski et al., 2013). But other site biota also make important contributions to nutrient cycling, water quality, food webs, and carbon sequestration (Huhta, 2007; Bormann et al., 2015; Azul et al., 2014). Harvest-related disturbance effects on soils were the impetus for the Long-term Soil Productivity Study (LTSP) (Powers, 2006), in which investigators physically altered

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forest soils through site organic matter (OM) removal and compaction in a full factorial design replicated throughout North America. Each treatment type (OM removal/compaction) has a distinct and potentially detrimental effect on site quality, either as losses of nutrients, propagules and habitat with logging slash/forest floor removal versus decreases in soil drainage and aeration with compaction (Thiffault et al., 2011; Ampoorter et al., 2011). Direct measures of tree response (e.g., bole volume, foliar nutrients) have been a primary metric of treatment effects for the LTSP in the initial decades of the study (Ponder et al., 2012), but as forest stands develop there is now an opportunity to examine the ecological integrity of these disturbed sites in more detail.

A comprehensive assessment of disturbance impacts on forest biotic communities should include multiple guilds or indicators because species responses do not always correlate well among different organism groups (Jonsson and Jonsell, 1999). We chose to monitor three common guilds of boreal forests: ground-dwelling ('epigeic') beetles (Carabidae and Staphylinidae), understory plants (vascular, bryophytes, and lichens), and ectomycorrhizal fungi (EMF) as a collective measure of biotic vulnerability (the degree to which a system is susceptible to, and unable to cope with, injury, damage or harm; De Lange et al., 2010) to soil disturbance. These three guilds are well recognized as responsive to tree mortality (harvest) as a primary disturbance event (Halpern, 1988; Haeussler et al., 2002; Pohl et al., 2007; Paquin, 2008; Simard, 2008), and furthermore demonstrate sensitivity in community composition to logging impacts on soils. For example, Rydgren et al. (2004), Berger et al. (2004) and Haeussler and Kabzems (2005) all reported that soil disturbances had a profound influence on early regenerating vegetation primarily because of the gains in ruderal over bud-banking species. Amaranthus et al. (1996) and Hartmann et al. (2012) found evidence of compaction effects on EMF species richness and community composition, while Lazaruk et al. (2008) noted that forest floor removal altered early-seral EMF communities. Walker et al. (2012) found altered species composition of EMF with coarse woody debris removal, in contrast to the limited effect noted by Mahmood et al. (1999). Beaudry et al. (1997) and Gandhi et al. (2008) reported clear-cutting or salvage harvesting followed by burning induced larger changes in carabid species composition and abundance than harvesting alone. Nitterus et al. (2007) and Work et al. (2014) also detected shifts in beetle community composition with slash removal. Much of the literature has reported the early (<5 yrs) effects of forest disturbances, which represents an important reorganizational phase of succession, but longer-term studies are needed to fully test the resilience of site biota (Bengtsson, 2002).

In this study we present community composition of three biotic guilds 20 years after exposure to compound soil disturbances created by site OM removal and compaction in the Sub-Boreal Spruce zone of central British Columbia. Our objectives were to document differences in species composition and abundance of the three biotic communities due to soil disturbance, and to quantify shifts (particularly non-linear) in community dissimilarity from the least disturbed treatment baseline (a bole-only removal, no compaction treatment). We use these findings to discuss four possible scenarios for the successional trajectories of biotic communities with increasing vulnerability to soil disturbance, including: (1) species composition is temporarily altered by tree harvest but unaffected by soil disturbance (null hypothesis), (2) the succession of biota is delayed by soil disturbance, but not ultimately changed, because of time lags in species recruitment with the recovery of habitat; (3) soil disturbance favours a new composition of species compared to less disturbed soils, pushing the system onto an alternative but equally functional trajectory; and (4) changes in soil properties and loss of suitable habitat persist during stand development, and subsequently diminish the community through reductions in species richness and increased dominance by generalist or invasive species (Clavel et al., 2011).

2. Methods

2.1. Site descriptions

The LTSP installations in central British Columbia are located in the Sub-boreal Spruce biogeoclimatic zone (SBS), characterized by cold, snowy winters and relatively warm, moist and short summers (Meidinger and Pojar, 1991). Three subzones were selected as sites (blocks) to replicate the LTSP experiment across a relative range of climatic conditions encompassed by SBS forests. Climate variables of mean annual temperature (MAT), precipitation (MAP) and heat:moisture index (AH:M = [MAT + 10]/[MAP/1000]; Tuhkanen, 1980) were obtained for the 2001–2010 decade at each study site by querying ClimateWNA (Wang et al., 2006) with latitude, longitude and elevation. The three test sites include the warm, dry SBSdw subzone near Williams Lake, BC (52°18′54″N, 121°54′51″W, elev. 1050 m a.s.l., MAT 3.8 °C, MAP 559 mm, AH:M 24.7), the moist, cold SBSmc near Topley, BC (54°36′43″N, 126°18′25″W, elev. 1100 m a.s.l., MAT 1.7 °C, MAP 614 mm, AH:M 18.2), the wet, cool SBSwk near Prince George, BC (54°21′57″N, 122°36′48″W, elev. 785 m a.s.l., MAT 3.3 °C, MAP 897 mm, AH:M 14.8). The sites are located within an approx. 200 km radius. Each site has deep, moderately well-drained to well-drained soils derived from ablation till, with textures ranging from sandy loam to loam (SBSdw 56% sand, 35% silt, 9% clay; SBSmc 52% sand, 27% silt, 21% clay; SBSwk 44% sand, 40% silt, 16% clay), up to 40% coarse fragments, and mor humus forms approximately 7 cm thick. Sites were level (SBSdw), or had slopes ranging from 2 to 12%. Preharvest stands were 112–140 years old and comprised predominantly of subalpine fir (*Abies lasiocarpa*), hybrid white spruce and lodgepole pine. Site indices, based on preharvest stands, averaged 17.5 m at 50 yrs.

2.2. Experimental design

Each LTSP site has nine plots (40 × 70 m each), arranged in a factorial combination of three organic matter removal treatments:

OM1 - Bole (stems) only removed, logging slash retained;
OM2 - Boles and crowns removed (whole-tree harvesting),
OM3 - Whole-tree and forest floor removed (mineral soil left intact),

And three soil compaction treatments:

C0 - No compaction;
C1 - Light compaction (2 cm impression into mineral soil),
C2 - Heavy compaction (4 cm impression).

Each site was hand-felled in the winter to minimize soil disturbance. Logging slash was removed by hand, and forest floors were extracted with an excavator and bucket attachment, with as little mineral soil removal as possible. Soil compaction to the required depths was done with an excavator-mounted hydraulic tamping plate. On the bole-only removal treatment, the logging slash was piled into rows to allow compaction without impressing the slash into the soil and then redistributed. The treatment plots were split (40 × 35 m) and planted with copper-treated 1 + 0 211 PSB (plug styroblocks) lodgepole pine or untreated 2 + 0 415 PSB hybrid white spruce seedlings. Local provenances were used for planting stock, and seedlings were planted at 2.5 × 2.5 m spacing in the spring following treatment installation. In the centre portion of