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Decline of ectomycorrhizal fungi following a mountain pine beetle epidemic

Roland Treu,[1] Justine Karst,[2,3,5] Morgan Randall,[2] Gregory J. Pec,[2] Paul W. Cigan,[3] Suzanne W. Simard,[4] Janice E. K. Cooke,[2] Nadir Erbilgin,[3] and James F. Cahill, Jr.[2]

[1]*Centre for Science, Athabasca University, 1 University Drive, Athabasca, Alberta T9S 3A3 Canada*
[2]*Department of Biological Sciences, Biological Sciences Building, University of Alberta, Edmonton, Alberta T6G 2E9 Canada*
[3]*Department of Renewable Resources, 442 Earth Sciences Building, University of Alberta, Edmonton, Alberta T6G 2E3 Canada*
[4]*Department of Forest and Conservation Sciences, Forest Sciences Centre, 2424 Main Mall, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada*

Abstract. Forest die-off caused by mountain pine beetle (MPB; *Dendroctonus ponderosa*) is rapidly transforming western North American landscapes. The rapid and widespread death of lodgepole pine (*Pinus contorta*) will likely have cascading effects on biodiversity. One group particularly prone to such declines associated with MPB are ectomycorrhizal fungi, symbiotic organisms that can depend on pine for their survival, and are critical for stand regeneration. We evaluated the indirect effects of MPB on above- (community composition of epigeous sporocarps) and belowground (hyphal abundance) occurrences of ectomycorrhizal fungi across 11 forest stands. Along a gradient of mortality (0–82% pine killed), macromycete community composition changed; this shift was driven by a decrease in the species richness of ectomycorrhizal fungi. Both the proportion of species that were ectomycorrhizal and hyphal length in the soil declined with increased MPB-caused pine mortality; <10% of sporocarp species were ectomycorrhizal in stands with high pine mortality compared with >70% in stands without MPB attacks. The rapid range expansion of a native insect results not only in the widespread mortality of an ecologically and economically important pine species, but the effect of MPB may also be exacerbated by the concomitant decline of fungi crucial for recovery of these forests.

Key words: extraradical hyphae; forest die-off; lodgepole pine, Pinus contorta; *macromycetes; mountain pine beetle,* Dendroctonus ponderosa; *mycorrhizal symbionts; northwestern Alberta, Canada.*

Introduction

Recent, large-scale outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) have killed ~28 million ha of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in western North America (Alberta Sustainable Resource Development 2012 [*available online*],[6] British Columbia Ministry of Forests, Lands and Natural Resource Operations 2012 [*available online*],[7] Man 2012), an area equivalent to the entire forested area of Sweden. Cascading effects of this disturbance include alterations to carbon storage (Kurz et al. 2008), hydrology (Rhoades et al. 2013), nutrient cycling (Griffin et al. 2011), and regeneration of the forests (Astrup et al. 2008). In addition to changes in the functioning of these forests, MPB may also cause a cascading loss in biodiversity. In particular, pine species such as lodgepole pine form symbiotic associations with ectomycorrhizal (EM) fungi (Trappe 1962, Harley and Harley 1987), which facilitate water and nutrient uptake of their hosts (Smith and Read 2008). Species of EM fungi differentially acquire resources from soils in exchange for sugars (carbohydrates) synthesized by their host trees, and, for the most part, these sugars are the sole energy source for these fungi (Smith and Read 2008). Ectomycorrhizal fungi form extremely diverse, spatially variable communities sensitive to the presence, health, and identity of hosts and to soil conditions (Dahlberg 2001, Izzo et al. 2005, Tedersoo et al. 2006). These symbiotic organisms directly depend on tree hosts for their survival, and are critical for forest

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[5] Corresponding author. E-mail: justine@karst.ca

[6] http://mpb.alberta.ca/Resources/documents/MPB-WhyAreTheyHere.pdf

[7] http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/Updated-Beetle-Facts_May2012.pdf

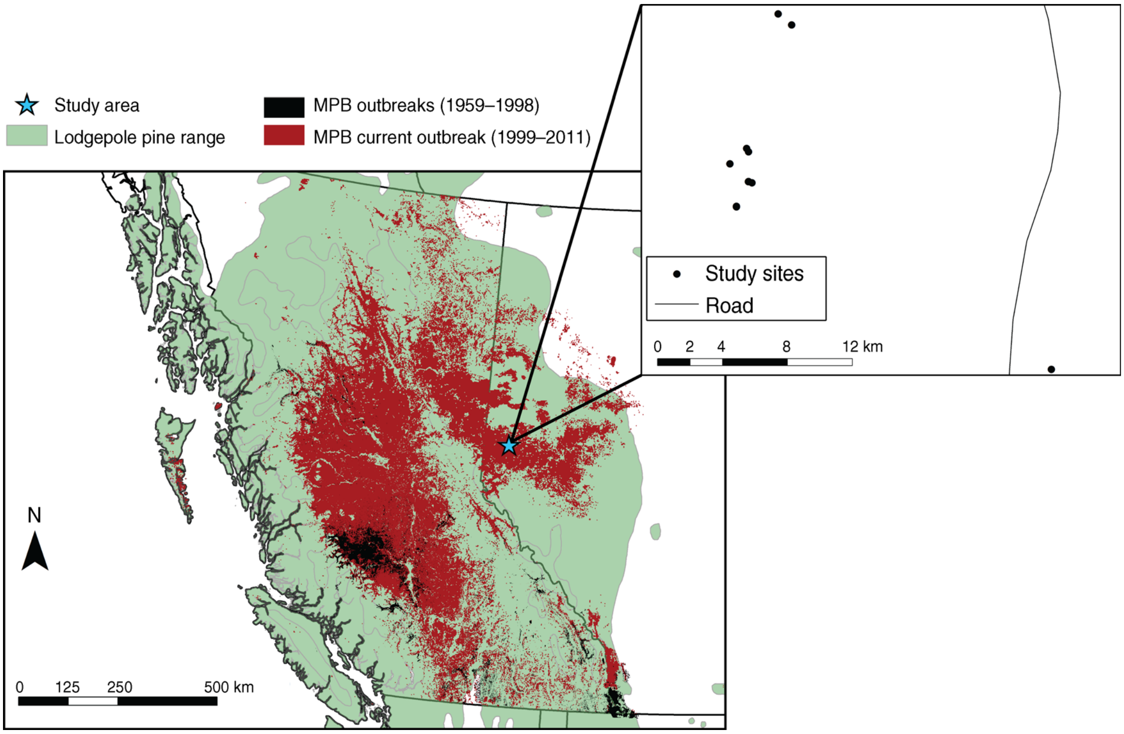

FIG. 1. Map showing historic (1959–1998) and current (1999–2011) range of mountain pine beetle (*Dendroctonus ponderosae*) in relation to study area. The inset shows locations of field sites. Mountain pine beetle (MPB) attack data were obtained from G. Thandi and S. W. Taylor (*unpublished data*), Alberta Environment and Sustainable Resource Development (footnote 1), and British Columbia Ministry of Forests, Lands, and Natural Resources (footnote 2). Lodgepole pine (*Pinus contorta* var. *latifolia*) range distribution is a digital representation of Little (1971). The map was created by C. Cullingham.

regeneration and succession (Perry et al. 1989, Jones et al. 2003).

Widespread, synchronous mortality of mature trees following MPB infestation may alter EM communities, with subsequent feedbacks on seedling regeneration. Following beetle-induced tree mortality, inputs of photosynthetically derived sugars—the single most important resource driving EM fruiting (Last et al. 1979)—decrease, and abiotic soil conditions change (Clow et al. 2011, Griffin et al. 2011). When host trees die or are removed, the abundance of ectomycorrhizas in soils declines rapidly (Jones et al. 2003); however, patterns in the diversity of sporocarps, the fruiting structure of EM fungi, may differ from fungal patterns belowground (Gardes and Bruns 1996, Dahlberg et al. 1997). We predicted that both sporocarp and hyphal production of EM fungi decrease following infestation by MPB. To test this prediction, we measured the aboveground fungal community (EM and saprotrophic fungi) along a natural gradient of tree mortality caused by MPB attack. Within each of 11 stands we also quantified the abundance of fungal hyphae in soils along this same gradient. Here, we report that the rapid range expansion of MPB indirectly causes declines in aboveground EM fungal richness and belowground hyphal abundance.

METHODS

Study site and tree surveys

The study was conducted in northwestern Alberta, Canada (54°39′ N, 118°59′ W; elevation, 1027 m) within the Lower Foothills natural subregion (Beckingham et al. 1996). Soils are Orthic Gray Luvisols and support stands of pure lodgepole pine or pine mixed with other conifer and hardwood species. We used a GIS layer of recent mountain pine beetle (MPB) activity (within the last four years, i.e., 2009 and 2010) provided by Alberta Environment and Sustainable Resource Development (Edmonton, Alberta, Canada) to locate 11 sites within a 50-km region (Fig. 1; see Plate 1) bordering provincial permanent sampling plots with overstories dominated ($\geq$80%) by even-aged (120 ± 0.4 years old [mean ± SE]) lodgepole pine. At each site, we installed a 900-m^2 plot (30 × 30 m), within which four subplots (36 m^2) were positioned at each corner to sample tree attack. In June 2011 we sampled all trees within each subplot and noted species, diameter at breast height, health status, and cause and year of death when applicable. Attacks by MPB were confirmed using bole examination to note the presence of pitch tubes, subcortical galleries, exit holes, and MPB life stages. In June 2012 we revisited all previously sampled trees to document current-year MPB-induced mortality. We averaged the subplot values to generate estimates of basal area of pine, and MPB-induced mortality for each plot.

Aboveground sporocarp survey

In June, July, and September of 2012 we surveyed all sites for epigeous fungal sporocarps. In this region the MPB epidemic has progressed relatively quickly since the initial attacks recorded in the area in 2006, leading to widespread pine mortality during the timeframe of the study. Tree death following attack by the beetle also occurs quickly, much faster than the years it would take to comprehensively sample both above- and belowground fungal communities and resolve differences in diversity. Thus, we deemed multiple samplings within a single year to be a conservative measurement of immediate changes in the fungal community. In each plot a systematic grid was established to locate 10 reference points to collect fungal fruiting bodies. Using standard mycological field procedures described in Mueller et al. (2004), and ensuring a minimum of site disturbance, all sporocarps were collected in each plot during each visit and a preliminary field identification was obtained for all specimens. Subsequently, fruiting bodies were taken to the laboratory for further microscopical examination and closer identification to the species or at least genus level. Representative collections of some less common species were dried and preserved, and are stored in the T.S. Bakshi Herbarium (Athabasca University, Athabasca, Alberta, Canada). The categorization of species as EM or non-EM was according to Trappe (1962) and Harley and Harley (1987).

Measuring belowground hyphal abundance

To investigate the consistency between above- and belowground patterns of fungi, we used mesh bags to sample extraradical hyphae in soils. These bags (Mikro-Tek, Timmins, Ontario, Canada) contained 6 g of biochar pellets soaked in distilled water for 24 h and were installed in each plot at the same 10 reference points used to sample fungal sporocarps. Biochar is a common substrate in soils of boreal forests (Zackrisson et al. 1996, Ohlson et al. 2009), potentially occupied by EM fungi and predicted to be avoided by saprotrophic fungi as they decompose organic matter in the soil for energy. Bags were made of landscape fabric, which allowed entry of fungal hyphae but excluded roots (mesh size, 67.2 ± 11.76 μm [mean ± SE]). On 30–31 May 2012 bags were installed horizontally between mineral soil and the organic layer where EM fungi are known to be active (Wallander et al. 2001). Between 31 July and 3 August the bags were harvested and stored at 4°C for 72 h prior to long-term storage at −20°C. The timing of burial coincides with the two wettest months of the growing season for this region (Environment Canada 2007**)**. Methods of hyphal extraction followed standard techniques (Appendix A) and a modified line-intersect method was used to calculate hyphal length (Tennant 1975). Data were pooled within each site to obtain a plot-level estimate of the abundance of fungal hyphae in soils.

Statistical analyses

To identify differences in the sporocarp community composition across the gradient of mortality, nonmetric multidimensional scaling (NMS) ordination was performed on presence/absence species data averaged for the June, August, and September 2012 sampling periods. Separate analyses were conducted on three types of data: (1) for all sporocarps (mycorrhizal and non-mycorrhizal), (2) for EM sporocarps alone, and (3) for non-mycorrhizal sporocarps alone. All ordinations were conducted in PC-ORD version 6.0 (McCune and Mefford 2011) using the “slow and thorough procedures” with Sorensen distances and random starting configurations (McCune et al. 2002). Each of the resulting NMS ordination scores from Axis 1 were regressed against the gradient of pine mortality.

RESULTS

Tree survey

Sites were dominated by lodgepole pine, which comprised between 66% and 99% of tree basal area (m^2/ha). In sites with <90% lodgepole pine basal area, quaking aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* Mill. BSP), and paper birch (*Betula papyrifera* Marshall) ranked as the three next most common tree species (Appendix B). Mountain pine beetle (MPB)-induced mortality in the study area was first reported in 2006 and peaked in 2010, with localized outbreaks spreading through several sites as recently as July 2012, by which time a wide gradient of lodgepole pine mortality (0–82% basal area killed) had formed.

Aboveground sporocarp survey

A total of 207 fungal species (ectomycorrhizal [EM] and non-mycorrhizal) were identified across all stands, comprising 124 non-mycorrhizal and 83 EM fungal species, respectively (Appendix C). Plots (900 m^2) had an average of 30 fungal species each; sporocarp richness (EM and non-mycorrhizal sporocarps combined) did not differ across the gradient of tree mortality (P = 0.684). Increased sampling would be required to exhaustively survey these stands, but this was not possible due to the short time frame over which pine mortality occurred and because of the limited size of the

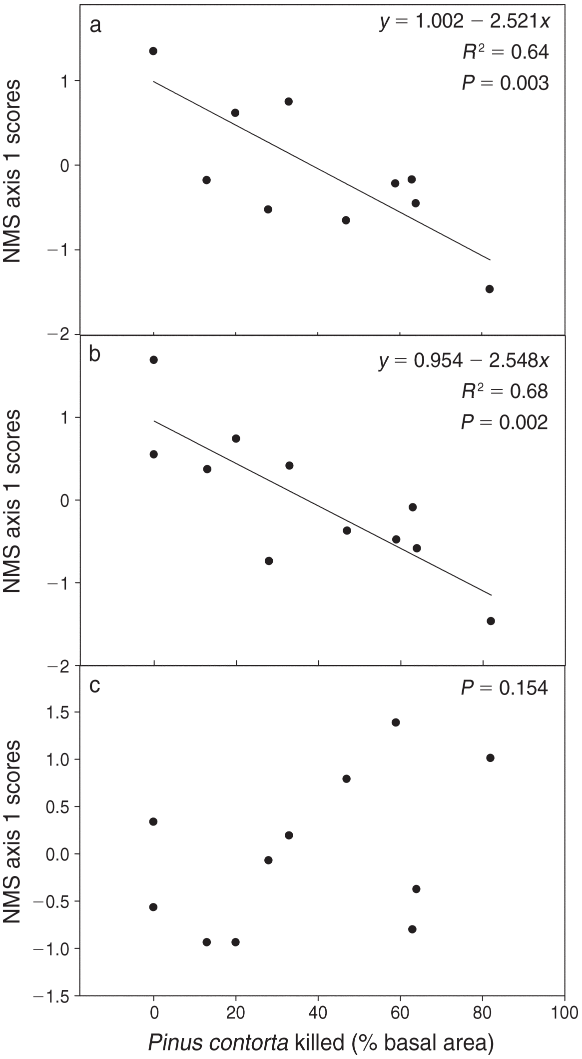

FIG. 2. Nonmetric multidimensional scaling (NMS) ordination axis 1 scores of sporocarp community composition as a function of lodgepole pine (*Pinus contorta* var. *latifolia*) basal area killed by mountain pine beetle (*Dendroctonus ponderosae*). (a) Total sporocarp community composition; NMS axis 1 scores explain 35% of the variance. (b) Ectomycorrhizal sporocarp community composition; NMS axis 1 scores explain 52% of the variance. (c) Non-mycorrhizal sporocarp community composition; NMS axis 1 scores explain 20% of the variance.

sites (Appendix D). Changes in the sporocarp community composition across the gradient of mortality were driven primarily by shifts in EM species (Fig. 2a–c). Community shifts in non-mycorrhizal sporocarps were not pronounced (Fig. 2c), although *Entoloma* sp. and *Galerina* sp. were mostly found in stands with high pine mortality. Among the non-mycorrhizal fungal species, *Galerina marginata*, *Lichenomphalia umbellifera*, and *Marasmius androsaceus* were found across the gradient of pine mortality. *Xeromphalina cauticinalis* was the only saprotrophic fungal species found in all stands.

The proportion of species that were EM declined with increasing pine mortality (Fig. 3) and as a necessary consequence, species richness also declined. Ectomycorrhizal species richness decreased from ~20 to 3 species across the gradient of tree mortality. In the most severely attacked stand, *Lactarius affinis*, *L. rufus*, and *Russula* sp. 11 comprised the sporocarp community while the remainder (~80%) of fungal species was saprotrophic. In contrast, up to 90% of the fungal species found in stands without MPB attacks were EM. Among the EM fungi some species of *Cortinarius*, *Russula*, *Inocybe*, and *Lactarius* occurred in stands without attacks, while *Chroogomphus ochraceus*, *Hydnum repandum*, *Laccaria laccata*, *Leccinum fibrillosum*, and *Suillus flavidus* were found across stands without MPB attacks to intermediate levels of pine mortality. *Hygrophorus piceae* was found in all but the most severely attacked stand, while *Lactarius rufus* was the most generalist EM species found across the entire gradient of beetle-killed stands. Mortality due to MPB rather than initial pine productivity is likely driving these relationships; both total overstory and lodgepole pine basal area were not significantly correlated with pine mortality (Appendix E).

Belowground hyphal abundance

Hyphal abundance in soils decreased with increased pine mortality ($y = 7.237 - 2.336\,x$; $R^2 = 0.62$; $P = 0.002$) (Appendix F). Mean hyphal length across all sites was 0.62 ± 0.09 m hyphae/g biochar (mean ± SE). Sites with no pine mortality due to MPB had an average of 1.50 ± 0.1 m hyphae/g biochar, ~3.5 times more than the most severely attacked sites.

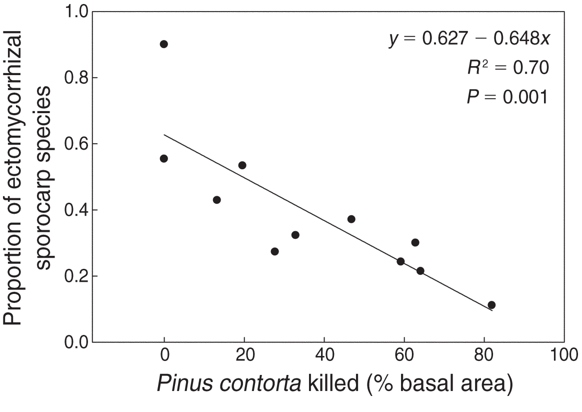

FIG. 3. Shift in proportion of sporocarp species that are ectomycorrhizal along a gradient of percentage of lodgepole pine (*Pinus contorta* var. *latifolia*) basal area (m^2/ha) killed by mountain pine beetle (*Dendroctonus ponderosae*).

PLATE 1. (Top left) One of the 11 sites surveyed in northwestern Alberta, Canada, for (lower left) sporocarp composition (a species of *Russula* is in the foreground), and (right) mountain pine beetle (*Dendroctonus ponderosa*) activitiy (e.g., the presence of subcortical galleries). Photo credits: top left, Lyle Dechief; lower left, M. Randall; right, P. Cigan.

DISCUSSION

We observed cascading effects of mountain pine beetle (MPB; *Dendroctonus ponderosae*) on both above- and belowground occurrences of ectomycorrhizal (EM) fungi, namely sporocarps and hyphal abundance. Though MPB is a species native to western North America, the northward, eastward, and high-elevation range expansion during the course of the current outbreak has resulted in spread of this insect into novel pine habitats (Cullingham et al. 2011, de la Giroday et al. 2012). From this expansion has emerged the decline of EM fungi indirectly caused by MPB. Ectomycorrhizal fungi can decrease in abundance and richness following fire (Cairney and Bastias 2007) and harvesting (Jones et al. 2003), disturbances both common to western pine forests. Whether the consequences of the decline of EM fungi on seedling regeneration will be similar following fire and harvesting to those following MPB infestation are unknown. Several key differences between beetle infestation and fire/harvesting exist. Specifically, there is a longer phase of tree mortality following beetle attack than that which occurs following harvesting, and the understory remains intact in beetle-killed stands in contrast with pine forests disturbed by fire or harvesting (Edburg et al. 2012). The vast spatial extent of tree mortality following MPB is also greater than that resulting from fire or harvesting; the distance seeds and spores must travel to regenerate a forest is much larger than for most harvested or burned areas. Recruitment of EM hosts has also been limited in areas that have experienced extensive mortality of *Pinus contorta* (Astrup et al. 2008). From these differences, the decline of EM fungi may interact with the remaining forest in a way that is unpredictable because no natural analogue exists for this particular disturbance.

Some EM species (e.g., *Suillus flavidus*, *S. tomentosus*, and *Chroogomphus ochraceus*) found in our survey form mycorrhizal associations exclusively with *Pinus* (Miller 1964, Smith and Thiers 1964). In stands dominated by pine, abundance of these fungi with narrow host ranges may be reduced as a result of epidemic-level beetle attacks of the mature trees that contribute most of the roots colonized by these fungi. In the absence of compatible EM fungi, pine species may suffer significant growth reductions (Nuñez et al. 2009), resulting in a negative feedback between beetle attack and pine regeneration. Other species found in our survey have low (e.g., *Laccaria laccata*) or intermediate (e.g., *Leccinum fibrillosum*) host specificity and may be able to switch hosts following severe MPB attack in mixed stands. Several EM hosts unsusceptible to MPB (*Abies balsamea*, *Betula papyrifera*, *Picea glauca*, *Picea mariana*, *Populus tremuloides*) present in these stands may sustain those EM fungi not specific to pine. This may also be the case for *Lactarius rufus* and *L. affinis*, both of which occurred in severely attacked sites and are known to be associated with several conifer and broadleaved species (Trappe 1962, Hesler et al. 1979). Several EM genera commonly found belowground in lodgepole pine stands (e.g., *Amphinema*, *Phialocephala*, *Piloderma*, and *Tomentella*) in similar ecoregions as our study location were not detected in our aboveground surveys, likely because they form no or indistinct fruit bodies (Bradbury et al. 1998, Teste et al. 2012).

The formation of EM fruit bodies depends on a sufficient supply of carbohydrates from the tree host (Last and Fleming 1985, Lamhamedi et al. 1994, Yarwood et al. 2009). When recent photosynthates are decreased through tree girdling or defoliation, a shift in the community composition of belowground EM fungi to taxa requiring less carbon is often observed (Saikkonen et al. 1999, Saravesi et al. 2008, Pena et al. 2010). Aboveground responses of EM fungi to defoliation, however, are variable. Manual defoliation of *Pinus sylvestris* caused a threefold reduction in ectomycorrhizal sporocarp production with a concomitant decrease in sporocarp diversity (Kuikka et al. 2003). This finding contrasts with results of manual defoliation of *Pinus pinaster*, where sporocarp abundance, richness, and diversity were unaffected by foliage loss; however, EM species richness declined and community composition shifted (Pestaña and Santolamazza-Carbone 2011). The presence of substitute EM hosts, identity of host species, and the degree of photosynthate reduction may all affect the response of above- and belowground EM fungi. Unlike EM fungi, saprotrophic fungi acquire carbon exclusively through decomposition of organic materials and thus are less likely to be immediately responsive to tree mortality, as shown in our study. Saprotrophic fungi may have a particular preference for litter type (Dix and Webster 1995) or be influenced more by soil texture than by overstory composition (Santos-Silva et al. 2011).

We found that hyphal abundance decreased with increasing pine mortality. Mycorrhizal hyphae increase absorption surface area of colonized roots and directly influence nutrient cycling through excretion of a variety of organic acids and enzymes important in mineral weathering and breakdown of organic matter (Landeweert et al. 2001, Högberg and Högberg 2002). A reduction in mycorrhizal hyphae in soils may impact nutrient acquisition for remaining or establishing hosts, and reduce carbon storage in soils (Orwin et al. 2011). Our measures of hyphal abundance are lower than those collected from bags filled with sand or soil buried in conifer forests (Pampolina et al. 2002, Johnson et al. 2003, Van Hees et al. 2003). The majority of studies report increases in root colonization and hyphal production by EM fungi in response to biochar addition (Warnock et al. 2007). The discrepancy in hyphal lengths could be due to a difference in EM species present—hyphal abundance varies with specific mycorrhizal exploration types (Agerer 2001).

The extent of the current MPB epidemic in North America is unprecedented in recorded history, making it one of the few clear examples of a "native invader" (Simberloff 2011). Here, we provide evidence that the consequences of MPB have far-reaching multi-trophic effects. In addition to the loss of a dominant overstory tree species, mycorrhizal fungi critical to forest health and regeneration also appear to decline. How the decline of EM fungi affects the successional trajectory of stands disturbed by this novel agent of mortality is unknown.

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Supplemental Material

Appendix A

Methods to quantify abundance of mycorrhizal hyphae (*Ecological Archives* E095-093-A1).

Appendix B

Composition and abundance of secondary tree species (*Ecological Archives* E095-093-A2).

Appendix C

A table presenting sporocarp species recovered in 2012 survey (*Ecological Archives* E095-093-A3).

Appendix D

Species accumulation curves for sporocarp surveys (*Ecological Archives* E095-093-A4).

Appendix E

Initial stand productivity of study sites (*Ecological Archives* E095-093-A5).

Appendix F

Linear regression of relationship between hyphal length and lodgepole pine killed by mountain pine beetle (*Ecological Archives* E095-093-A6).