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ORIGINAL PAPER

Inoculation of ophiostomatoid fungi in loblolly pine trees increases the presence of subterranean termites in fungal lesions

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Abstract Many bluestain (ophiostomatoid) fungi are inoculated into trees via bark beetle activity, but their ecological roles are not fully understood, particularly for interactions with invertebrates outside bark beetle and phoretic mite associations. Recently, correlational field studies and small-scale laboratory feeding trials have demonstrated subterranean termites have increased presence on and preferential feeding of bluestain-infected wood, but experimental field evidence is lacking. To test the hypothesis that bluestain fungi increase termite presence in infected trees, we inoculated 72 loblolly pine trees in the southeastern USA with one of four bluestain fungi (*Ophiostoma minus*, *O. ips*, *Leptographium terebrantis*, *L. procerum*), a combination (*O. minus* + *L. terebrantis*), or H_2O as a control. Over four years, all fungi-inoculated trees formed lesions around injection sites, while control trees formed no lesions except for two contaminated control trees that were excluded from analyses. Bluestain-inoculated trees had increased termite presence in and around fungal lesions, whereas control trees had no termites present. Specifically, termites were present on 35 % of fungi-inoculated trees, presence was consistent over time, and there was no difference among fungal species. This study experimentally demonstrates a link between bluestain fungi and subterranean termites in forests, which could impact tree dynamics post-bluestain infection.

Keywords Bark beetles · Bluestain fungi · Forest ecology · *Pinus taeda* · *Reticulitermes* · Southeastern USA

Introduction

Bark beetles and subterranean termites are keystone species that have wide-ranging impacts on many forest ecosystems by mediating nutrient flow between above- and below-ground systems (Mller et al. 2008; Coulson and Klepzig 2011; Jouquet et al. 2011). Globally, many forests are experiencing increased frequency and severity of bark beetle outbreaks (Kurz et al. 2008; Meddens et al. 2012; Sambaraju et al. 2012). Even in the southeastern USA where management practices have minimized southern pine beetle (*Dendroctonus frontalis* Zimmermann) outbreaks in the last 1015 years (Clarke et al. 2016), hundreds of thousands of trees are still annually attacked by southern pine beetle (Coulson and Klepzig 2011; Nowak et al. 2015). At epidemic population levels, southern pine beetle-attacked trees often die within 23 weeks of infestation (Coulson and Klepzig 2011).

Microbially mediated ecological interactions between bark beetles and living host trees are fairly well studied. Indeed, associated fungi have been hypothesized to be mutualists (e.g., mycangial fungi), commensalists, and

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antagonists (e.g., fungi introduced via phoretic mites) with bark beetles during their attack of living host trees (Klepzig et al. 1991, 2001; Coulson and Klepzig 2011; Six and Wingfield 2011). For instance, bark beetles, root-feeding weevils, and their phoretic mites vector bluestain (ophiostomatoid) fungi to trees during attacks (Klepzig et al. 2001). In the pine forests of the southeastern USA, some of the more common bluestain fungi associated with bark beetles (e.g., *Dendroctonus* and *Ips* spp.) and root-feeding weevils (e.g., *Hylastes, Hylobius,* etc.) are *Ophiostoma minus* (Hedgc.) H. and P. Sydow, *O. ips* (Rumb.) Nannf., *Leptographium procerum* (W.B. Kendr.) M.J. Wingf, and *L. terebrantis* (Wingfield et al. 1993), and they are commonly associated with senescing pines (Klepzig et al. 1991; Otrosina et al. 1999; Eckhardt et al. 2007). Bluestain fungi do not decompose the structural components of wood (cellulose, hemicellulose, and lignin), but some species may accelerate or facilitate pine tree death when present by reducing resin flow (Wingfield et al. 1993; Eckhardt et al. 2007; Coyle et al. 2015; Six and Wingfield 2011). Despite the large body of knowledge about fungus-mediated interactions between bark beetles and their living hosts, almost nothing is known about how the presence of bluestain fungi influences subsequent invertebrate communities as they utilize bark beetle-attacked trees.

Recently, Little and colleagues (Little et al. 2012a, b, 2013a) demonstrated a novel link between bluestain fungi and subterranean termites. Specifically, in laboratory choice feeding assays, *Reticulitermes flavipes* Kollar and *Coptotermes formosanus* Shiraki both consumed >3 and 2 times more wood inoculated with *O. minus* than controls, respectively (Little et al. 2012a, b). Moreover, in field stake trials, subterranean termites located and degraded wooden stakes inoculated with *O. minus* more than untreated stakes (Little et al. 2013a). Although these studies provide evidence that subterranean termites are able to identify and preferentially consume small pieces of dead wood inoculated with certain bluestain fungi, there are no experimental studies demonstrating whether these same patterns occur at the scale of whole trees in natural settings. However, Riggins et al. (2014) found a correlation between the presence of *L. procerum*, and *L. terebrantis* and subterranean termites in the roots of loblolly pine trees in the southeastern USA. Although the latter study is only correlational, together these studies suggest there may be a direct link between the presence of certain bluestain fungi and increased subterranean termite presence and activity. If bluestain fungi alter the succession of invertebrates and microbes in bark beetle-attacked trees, this could have significant effects on decomposition rates of bark beetle-attacked trees once they die.

Dead wood constitutes a significant proportion of carbon storage in forest ecosystems, serves as habitat for both invertebrates and vertebrates, and can be a long-term sink and source for nutrients (McMinn and Crossley 1993; Pan et al. 2011). Bark beetle outbreaks can generate millions of dead trees and therefore are major contributors to dead wood stock in forests (Kurz et al. 2008; Meddens et al. 2012; Maynard et al. 2015). Termites can substantially increase decomposition rates of dead wood (Bradford et al. 2014). If termites recruit to trees recently attacked by bark beetles and preferentially feed on them, this could have previously unacknowledged impacts on pine forest ecosystem structure and function. For example, enhanced termite activity can accelerate tree death, decay, and fall rate (Osbrink et al. 1999), and if this occurs in natural forests (e.g., Grace 1987), it could alter forest ecosystem dynamics such as nutrient cycling and succession through gap creation, changes in hydrology, coarse woody debris input, and biogeochemistry (Schowalter 1981). Moreover, this would definitively link a keystone forest herbivore with perhaps the most ecologically important invertebrate detritivore in many pine forest ecosystems.

Here we investigate whether previous laboratory and correlational field examples of a positive association between bluestain fungi and subterranean termites can be experimentally replicated in apparently healthy trees in existing forests. In this study, we inoculated healthy loblolly pine trees in the southeastern USA with four common bluestain fungi to test the hypothesis that subterranean termites would preferentially locate and inhabit trees inoculated with bluestain fungi.

Methods

We selected 72 healthy loblolly pine trees from a 16 ha stand in the John Starr Experimental Forest in Mississippi (33°20′7.03″N, −88°52′39.73″W). Trees were designated healthy if they were asymptomatic (no signs of insects or disease), with normal needle color, and no cankers or deformities. Soils in the study area are primarily Falkner and Longview silt loam with 0–2 % slope, and site index (base age 25) for the stand is 58. The experimental stand was planted with Weyerhaeuser™ second-generation loblolly pine seedlings in 1983 at an 8 × 10 spacing density (1344 trees per ha) and is scheduled for final harvest in 2021. The stand underwent a first commercial thinning in 2006 at age 23, and pine basal area was reduced from approximately 2660 to 505 m^2 ha^{-1}. During the most recent inventory in 2009, pine and hardwood basal areas were 611 m^2 ha^{-1} (with 171 trees per ha) and 106 m^2 ha^{-1} (with 27 trees ha^{-1}), respectively. The stand had been managed with prescribed burns every 3 years and was last burned April 2011, ca. 3 months before the initiation of this study, but not since. At study inception, the stand was 32 years old, with an overstory of loblolly pine.

Focal trees that were at least 50 m apart from each other were arbitrarily selected. These trees had a mean DBH and height of 26.4 ± 3.8 cm and 19.4 ± 1.9 m., respectively. On July 6 and 7, 2011, we inoculated trees with one of six treatments: *O. minus*, *O. ips*, *L. terebrantis*, *L. procerum*, *O. minus* + *L. terebrantis* (combo), or sterilized, distilled H_2O as a control. These species are closely related bluestain fungi that were chosen because of their prevalence throughout the southeastern USA (Wingfield et al. 1993), their association with the southern pine bark beetle guild or common root-feeding weevils, their previous implications for stimulating termite feeding in laboratory and field studies (*Ophiostoma* spp.: Little et al. 2012a, b, 2013a), and their correlation with subterranean termite presence in the field (*Leptographium* spp.: Riggins et al. 2014). Cell stock of previously identified cultures of *L. terebrantis, L. procerum, O. minus,* and *O. ips* was available from prior studies (see Little et al. 2012a, b, 2013a) for use in this study, and reference cell stock is stored in the Forest Entomology Laboratory at Mississippi State University. Methods used in Little et al. (2013a) were used to produce mycelia and prepare fungal slurries for tree injections. Trees were inoculated with one of the aforementioned six treatments using six separate Direct-Inject® systems (1 for each treatment) from ArborSystems™, Inc. (Omaha, NE) using 3.8 cm Portle® needles. Fungal slurries contained 5 grams of hyphae macerated in 100 mL of sterilized DI water. Injections were made ca. 16 cm above the soil line in four locations for each tree: one at each cardinal direction (N, S, E, and W). Injections were made 3.8 cm into each tree, and care was taken to ensure penetration through the cambium layer. We marked near each injection site with spray paint to facilitate their location upon harvest. All four injection sites on a given tree received 2 mL treatment solution (H_2O or fungal slurry dependent on treatment). Injection needles were flushed with 95 % ETOH, and flame sterilized between each injection and tree to minimize cross-contamination. Although this method of inoculation does not mimic how bark beetles and their phoretic mites normally inoculate trees with bluestain fungi, it allows us to isolate the effects of focal bluestain fungi treatments on termite presence from the myriad of other variables associated with bark beetle colonization of a host tree. Additionally, the inoculum load used here is far more concentrated than natural exposure from bark beetle activity, which should maximize the chances of observing termite recruitment to infected trees given injections sites were localized rather than dispersed across tree trunks.

Trees were harvested at six sampling times that spanned 4 years on a pseudo-log time scale: 1, 2, 7, 12, 14, and 43 months. Sampling dates were August 10, 2011, October 19, 2011, May 15, 2012, August 7, 2012, October 31, 2012, and March 25, 2015. Two trees from each treatment (12 total) were selected for harvest using a random number generator during each sampling period. At each harvest time, focal trees were marked as alive (green needles: evidence of new growth like tree rings) or dead (brown needles: lack of tree growth). Prior to felling, the area around each injection site (and down to and ca. 5 cm below the soil surface) was exposed by removing the bark and some of the sapwood using a hatchet. Presence or absence of subterranean termites was noted, and if present, their distance from the nearest fungal lesion was measured. The bluestain fungal infection of wood occurs at different rates along the 3 primary planes (Little et al. 2013b). Subsequently, we measured length (max), and width (max) of lesions to the nearest cm, and overall surface area of each lesion was also estimated to the nearest cm^2 using a 1 1 cm gridded transparency. Focal trees were felled ca. 1.3 m above the ground, and a second level cross-sectional cut at the injection point was made using a chainsaw to expose the four injection sites and fungal lesions. At this time, the depth (max) of fungal lesions at each injection point was recorded by measuring the distance from injection point toward the pith. At the final harvest date (March 2015), DBH was again measured to determine whether tree growth differed among treatments.

*Statistical analysis*We tested the null hypothesis that presence of bluestain fungi in loblolly pine trees would not lead to higher instances of subterranean termites in and near fungal injection sites. We used a binomial logistic regression with presence or absence of termites as the binary response variable, and bluestain fungus or control as the categorical predictor variable. We then tested whether and which specific fungal species were associated with presence of termites using binomial logistic regression. Presence or absence of termites again was the binary response variable, with treatment (*L. terebrantis*, *L. procerum*, *O. minus*, *O. ips*, Combo, and Control) as the categorical predictor variable. We also tested the effect of time on presence or absence of termites by treating time (levels = 6) as a categorical predictor variable. Two control trees (one sampled on May 15, 2012 and August 7, 2012) had lesions present at injection sites, which indicated that these trees were contaminated during or after setup. All other controls had no measureable lesions other than injection needle puncture wound. These two contaminated controls were excluded from the analysis.

To quantify potential impacts of bluestain fungi on host trees, we first determined whether differences in tree growth were evident among treatments. This allowed us to determine whether differences in the presence of termites resulted from reductions in tree health or just from the presence of the fungi itself. The difference in diameter at breast height between time 0 (July 2011) and the final harvest ca. 4 years after (March 2015; $DBH_{final}DBH_{initial}$)

was used as the dependent variable in an ANOVA. We then tested for a difference in lesion size among fungal treatments. Lesion size measurements were $\log_{10}$ (x + 1) transformed to meet test assumptions. We tested for differences in lesion surface area, width, length, and depth among treatments using ANCOVA, with time as a covariate. All analyses were performed in SPSS v22 (IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp) with = 0.05.

Results

All trees were alive and apparently healthy at the time of harvest regardless of treatment. Trees responded to experimental bluestain injections by forming lesions around fungal injection sites, which prevented further fungal spread. All trees had growth rings beyond lesion point. After 4 years, DBH increased an average of 3.76 1.91 cm, with no differences among treatments (ANOVA: $F_{5,6} = 1.288$, $p = 0.378$)

Lesion size: surface area, depth (radial), and width (tangential) generally increased with time (p 0.001) except for lesion length (longitudinal), which showed no relationship with time ($p = 0.943$; Fig. 1). Treatment also impacted lesion dimensions; specifically, controls, as expected, had essentially no lesions except for the actual injection wound site (Fig. 1). Unlike controls, injection with bluestain fungi produced lesions ($p < 0.001$), but in general, there was little difference in lesion dimensions among bluestain treatments (Fig. 1). At the final harvest (ca. 4 years), average lesion sizes for all bluestain treatments were 39.5 23.35 cm^2, 15.27 5.24, 2.85 1.77, and 7.09 1.99 cm for surface area, length (longitudinal), width (tangential), and depth (radial), respectively.

The presence of bluestain fungi increased the presence of subterranean termites in and around injection sites on trees (logistic regression: *d.f.* = 1, $\chi^2 = 7.827$, $p = 0.005$, Fig. 2). Specifically, termites were found either on lesions or on average within 10.1 9.8 cm from lesions on the tree under the bark. Termites were mostly found in the cambium layer (between the bark and the xylem). Only worker termites were encountered, and there always multiple individuals (generally >10) present; however, only presence or absence, not quantity, was recorded, which is common in termite surveys due to their eusocial colony structure (Grace 1987; Osbrink et al. 1999). Often termites were found in subcortical access tunnels between the lesion and ca. 5 cm below the soil line. In many cases, we observed mud tubes, but did not quantify their presence. Because only workers were present, we were not able to identify termite species. However, there are only three subterranean termite species reported from this region of Mississippi (*R. flavipes*, *R. virginicus* (Banks), and *R. hageni* (Banks)), and *R. flavipes* and *R. virginicus* are the two most common subterranean termites in the region, with *R. flavipes* being by far the dominant species (Wang and Powell 2001). On average, termites were present on 35 % of all bluestain fungi-inoculated trees, and there was only a trend for termite presence to differ among bluestain

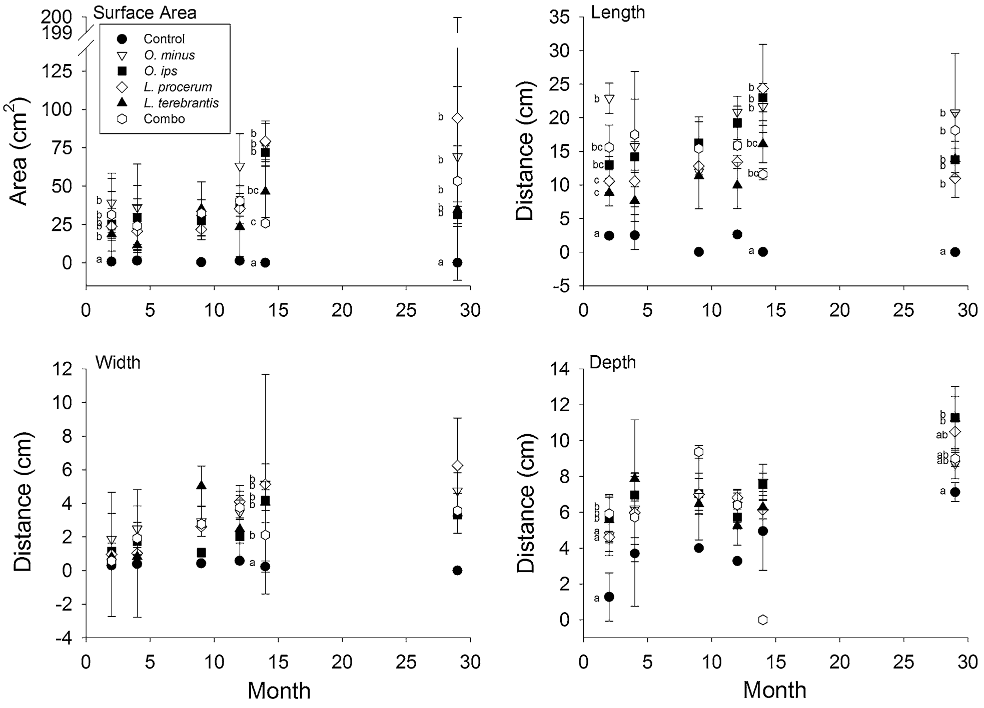

Fig. 1 Lesion dimensions over time across treatments. *Letters* indicate differences among treatments within that month

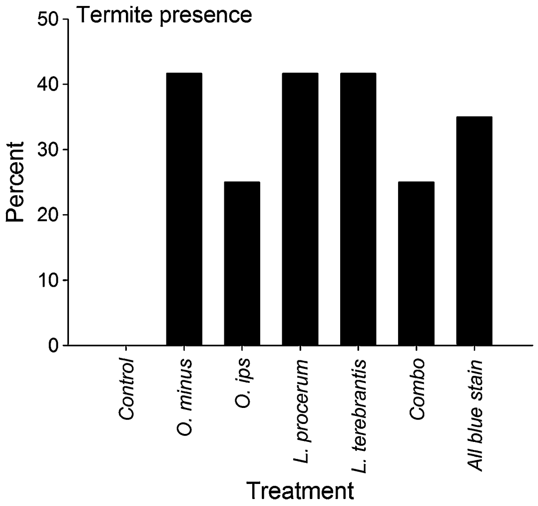

Fig. 2 Percent of trees with termites across treatments. All dates are combined for each treatment as time had no effect on termite presence. The All bluestain *bar* represents the average percentage of all trees with termites for *O. minus, O. ips, L. procerum, L. terebrantis* and Combo treatments combined. Controls had 0 trees with termites present

treatments (logistic regression: *d.f.* = 5, $\chi^2 = 9.627$, $p = 0.087$; Fig. 2). There was no relationship with sampling date and presence or absence of termites (logistic regression $\chi^2 = 8.448$, *d.f.* = 5, $p = 0.133$).

Discussion

The presence of bluestain fungi following bark beetle and root-feeding weevil herbivory has long been recognized, but fungal impact on subsequent invertebrate colonization of host trees has received little attention. Bluestain fungi have only recently been linked to preferential termite feeding, and natural experiments at the scale of whole trees were lacking. Here we experimentally demonstrated for the first time that inoculation of healthy trees with four common bluestain fungi, *O. minus, O. ips, L. procerum,* and *L. terebrantis* increases the presence of subterranean termites on trees at or near inoculation sites. The overall percentage of termites on living trees we inoculated with bluestain fungi was 35 %, which is >2 times the incidence of termites found in a general survey of coarse woody debris in a nearby forest (Wang and Powell 2001). Trees inoculated with *O. minus, L. procerum*, and *L. terebrantis* had the greatest proportion of termites present (41.7 % of trees for each fungal treatment; Fig. 2). Moreover, termite presence on bluestain-inoculated trees remained consistent over time (time: $p = 0.133$). This indicates that bark beetle-attacked trees could undergo accelerated decomposition because termite occurrence on bluestained wood is relatively long term, begins while trees are still standing, and at incidence rates >2 times greater than natural coarse woody debris levels (e.g., Wang and Powell 2001).

The mechanisms underlying termite detection of wood containing certain bluestain fungi remain unknown. Termite detection could be opportunistic or termites may be attracted to one or more cues emitted by bluestain-infected trees. In the former, random foraging could result in a chance discovery of bluestain-infected trees followed by increased worker termite recruitment, which would lead to increased termite presence. In the latter, stressed, dying, or dead trees can produce a myriad of biochemical cues (e.g., root exudates, terpenoids, alcohols, phenolics, etc.) that heterotrophs like termites could use to identify trees with compromised or depleted defenses (Tingey et al. 1980; Grayston and Jones 1996; Bais et al. 2006). Accordingly, tree death, bark beetle presence, and associated physiological stress cues may be necessary to elicit a stronger termite response. Future experiments where trees are either just inoculated or inoculated and girdled (i.e., killed) would test this hypothesis.

The ecological drivers of termite preferential feeding on wood containing bluestain fungi are also unknown. Bluestain fungi may be an abundant source of scarce essential nutrients like N, P, and Na, all of which stimulate termite wood consumption (Prestwich et al. 1980; Botch et al. 2010; Clay et al. 2015). Alternatively, the presence of bluestain fungi may act as a cue for a high-quality resource such as a long-term and relatively early decay habitat for colonization. Trees naturally infected with bluestain fungi have likely been attacked by bark beetles, which often kills the host tree. After attack, trees can start falling as early as 3 years after death, or stand for as long as 20 years (Lewis and Hartley 2006). Even at an earlier rate of tree fall, these trees potentially constitute a long-term resource as shelter and food for subterranean termites, particularly since once a tree falls, decay rate and competition from other decay organisms can substantially increase (Vanderwel et al. 2006). Bluestain fungi as nutrient sources or as indicators of long-term resources are not mutually exclusive hypotheses, and additional experimentation is needed to determine the mechanisms driving termite detection of and preferential feeding on bluestain-infected wood.

Simply wounding trees via injection did not increase termite presence on trees. Uninfected control trees did not have termites present at any point during the experiment, despite receiving control injections of sterile water (and minor needle wounds). We could not verify successful bluestain infection in the interim between inoculation and destructive sampling without damaging trees and confounding the experiment. However, all experimentally inoculated trees formed canker-like lesions and callus tissue formation, compartmentalizing characteristic dark blue-black stained sapwood indicating successful inoculation. Only two control trees formed lesions, which we believe were caused by accidental contamination because lesion formation and bluestain coloration were present and consistent with the experimental fungal treatments. These two contaminated controls had termites present upon harvest. We did not quantify fungal communities upon harvest; however, future experiments will investigate the potential interactions in fungal heterotroph communities subsequent to bluestain fungi establishment in fallen bark beetle-killed trees and their potential impacts on termites.

Over the long term, termite utilization of recently bark beetle-attacked trees could undermine the structural integrity of the trees via hollowing trunks and deterioration of the root system (e.g., Osbrink et al. 1999). Although *C. formosanus* were numerically dominate, Osbrink et al. (1999) found 4.1 % of live loblolly pines in New Orleans, LA, USA; trees were infested with *Reticulitermes* sp. and termite damage both from *C. formosanus* and *Reticulitermes* sp. likely contributed to weakening tree structural integrity. Additionally, Grace (1987) also found *Reticulitermes* spp. associated with living trees in Canada. In these instances, trees could become increasingly susceptible to storm damage (e.g., snapping or uprooting; e.g., Osbrink et al. 1999). Gap formation from downed trees can have widespread impacts on forest ecosystems, including enhancing biodiversity and altering nutrient cycling dynamics (Schowalter 1981; Mller et al. 2008). The biological interaction between subterranean termites, and bluestain fungi in bark beetle trees could influence forest structure, hydrology, and biochemistry through gap creation, and accelerate coarse woody debris input to soil ecosystems. Given that termites are typically the primary wood decomposers other than microbes in forest ecosystems where termites occur (Bradford et al. 2014), termite preference for bluestained wood could also have significant impacts on its decomposition processes. Bark beetle-produced coarse woody debris decomposition is thus likely to be substantially accelerated when termites are present. However, the ecosystem impacts are unexplored, and termite feeding preference data only exist for a handful of bluestain and termite species, and only in the southeastern USA (Little et al. 2012a, b, 2013a; Riggins et al. 2014).

Although we found no direct mortality consequences of stem inoculation with *O. minus, O. ips, L. procerum, and L. terebrantis*, their presence could have indirect implications on tree health via recruitment of termites. This is a novel hypothesis, and although not tested here, tree surveys in Louisiana have demonstrated the detrimental impacts of Formosan, and to a lesser extent, native *Reticulitermes* sp. subterranean termites can have on live trees (Osbrink et al. 1999). Ecologically, the link between bark beetles, termites, and bluestain fungi is likely to be important given the landscape scale impacts of bark beetles and the wide overlapping ranges of bark beetles, root-feeding weevils and termites (Eggleton and Tayasu 2001; Kurz et al. 2008; Coulson and Klepzig 2011). A positive feedback loop such as this between bark beetles, root-feeding weevils and subterranean termites could substantially accelerate the rates of tree death, fall, and decay, which could impact forest nutrient cycles, biogeochemistry, hydrology, and succession. Future studies that examine impacts of termites on bluestained standing and felled trees and their associated detritivores are needed to understand these potential impacts on forest ecosystem dynamics.

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Compliance with ethical standards

Conflict of interest NL and JR are coinventors on a pending patent application involving bluestain fungi in baiting methods for termites. Authors and their institutions may financially benefit from this patent.

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