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Abiotic and Biotic Factors Affecting Loblolly Pine Health in the Southeastern United States

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Southern pine forests are important fiber and wood sources, and critical to local, regional, and national economies in the United States. Recently, certain areas of southern pine forests, especially those dominated by loblolly pine (*Pinus taeda*), have been reported to exhibit abnormally high levels of tree dieback and mortality. However, causal agents either have not been well defined or are controversial in their impacts on tree health. We assessed various abiotic (e.g., slope, aspect, soil characteristics) and biotic (e.g., tree species, stand characteristics, presence of root fungi) factors in 37 healthy (asymptomatic) and unhealthy (symptomatic) sites to elucidate specific factors affecting loblolly pine health in Alabama and Georgia. Soil nutrient content did not differ statistically between healthy and unhealthy sites, but manganese contents were slightly greater, and nitrogen and carbon contents were slightly lower in healthy sites. Unhealthy sites did have a higher silt content than did healthy sites. Pine stems and basal area were greater on unhealthy than on healthy sites, whereas opposite trends were observed for the incidence of stem cankers and mechanical damage. An increased incidence of the root fungal pathogen *Heterobasidion irregulare*, the causal agent of Heterobasidion root disease, was found on unhealthy sites, but incidence of *Leptographium* spp. did not differ between the two site types. Thus, soil attributes, stand structure, and management history seem to be the most critical factors affecting loblolly pine health, at least at the local level. Further, some of these factors may be improved through appropriate silvicultural techniques, emphasizing the importance of silviculture in maintaining pine health throughout the southern region.

Keywords: decline, *Heterobasidion*, *Leptographium*, *Pinus taeda*, soils

Why do trees die? This is one of the most common and important questions asked by tree biologists, foresters, and forest health specialists worldwide (Franklin et al. 1987, Cailleret et al. 2017). Although it is universally agreed that stress factors—abiotic or biotic—can initiate a cascading series of events that eventually lead to tree mortality (Sinclair 1966, Manion 1981, Waring 1987), these factors often interact, and it may be difficult to identify the principal cause of tree death. Certainly, there are cases where the primary cause can be identified relatively easily (e.g., non-native insects and/or fungi known to be aggressive invaders, or high-impact weather events such as ice storms or hurricanes). However, trees generally die from a combination of predisposing (e.g., poor nutrition or advanced age), inciting (e.g., drought), and contributing (e.g., bark beetles and associated fungi) factors (Sinclair 1966). These factors (abiotic and biotic, natural and human-induced) make up the "decline-and-death spiral" (Manion 1991). Sinclair (1964) was among the first to describe a decline syndrome as "premature progressive loss of vigor and health." The word

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decline has been attributed to unhealthy forest conditions in many different ways; however, decline symptomology has been somewhat consistent across studies (e.g., Adams et al. 1985, Hinrichsen, 1987, Sonesson and Drobyshev 2010, Chen et al. 2017, Wong and Daniels 2017). For example, several progressive stages of decline have been described: (1) reductions in radial increment and terminal twig growth; (2) tufting, dwarfing, or chlorosis of foliage; (3) crown thinning; (4) branch and root death; (5) production of sprouts and/or increased seed production; and (6) eventual death of the entire crown (Sinclair 1964).

North America has experienced several large-scale forest health issues (termed "declines") in recent decades, including red pine (Klepzig et al. 1991, Erbilgin and Raffa 2003, Aukema et al. 2010), aspen (Worrell et al. 2010, 2013, Anderegg et al. 2012), sugar maple (Bauce and Allen 1992, Kolb and McCormick 1993, Horsley et al. 2002), and yellow cedar (D'Amore and Hennon 2006, Hennon et al. 2012) declines. These forest health issues are a manifestation of many stress factors; for example, climatic change over decades and interactions with native bark beetles and a non-native fungus contributed to growth reductions and mortality of whitebark pine, *Pinus albicaulis* Engelm., in the Canadian Rockies (Wong and Daniels 2017).

The concept of "pine decline" was first proposed in 1968 when mortality of loblolly pine, *P. taeda* L., was reported in parts of Alabama (Brown and McDowell 1968, Brown et al. 1969, Roth and Peacher 1971). This mortality continued over a period of several decades (Hess et al. 1999, 2002), and as reports spread to parts of Georgia and South Carolina (Eckhardt et al. 2010) this concept of "pine decline" became known as "southern pine decline" (SPD) based on the notion that the phenomenon is widespread in the southeastern United States (Eckhardt and Menard 2008, Eckhardt et al. 2010, Zeng et al. 2014). Although no specific cause of mortality was ever concretely identified, several factors were identified as possible contributors to the issue. These factors included the pathogens *Heterobasidion irregulare* Garbelotto and Otrosina, *Leptographium* spp. fungi, *Phytophthora cinnamomi* Rands, and *Pythium* spp. fungi; several species of lower stem and root infesting beetles; and various land and soil characteristics (Brown and McDowell 1968, Hess et al. 1999, 2005).

There is little scientific consensus on the extent or cause of SPD or even agreement on use of the term SPD to describe mortality that might be more directly attributed to known disease and insect pests. Root-feeding beetles and *Leptographium* spp. fungi are often associated with unhealthy pines purported to have SPD (Eckhardt et al. 2007, 2010, Eckhardt and Menard 2009). These root feeding beetles are generally thought of as secondary colonizers of trees that are stressed, dying, or dead (Matusick et al. 2013, Helbig et al. 2016). In addition, most *Leptographium* spp. fungi that occur in the southeastern United States are not considered primary pathogens (Eckhardt 2013). Although SPD has been suggested to occur over a large geographic area (Eckhardt et al. 2010), no such pattern was found using regional tree census data collected by the USDA Forest Service, Forest Inventory and Analysis (FIA); rather, data from this study (Coyle et al. 2015) suggest several abiotic and/or biotic factors interacting at the local level leading to mortality rather than a regional set of factors.

Forestry is a major economic force in the southeastern United States. (http://forestryimpacts.net/) contributing over US$230 billion to the economy and helping generate over 1 million jobs (Boby et al. 2014). Comprising only 2 percent of the world's total forested area, this region—of which 86 percent is privately owned (Butler and Wear 2013)—produces 18 percent of the world's pulpwood and 7 percent of its industrial roundwood (Hanson et al. 2010). Southern pine forests, which include loblolly, longleaf (*Pinus palustris* Mill.), slash (*Pinus elliotti* Engelm.), and shortleaf (*Pinus echinata* Mill.), grow on 70 million acres in the southeastern United States (Robertson et al. 2011) and are the primary forest product of the region. The loblolly/shortleaf species group accounts for 71 percent of softwood volume in the southeastern United States (Oswalt et al. 2014); loblolly pine is the most economically important tree species in the region. Thus, any uncertainty regarding factors that may negatively affect loblolly pine (or other southern pine) health has significant implications for forest management practices. Indeed, and despite the countervailing evidence, some forest landowners and managers remain concerned about SPD as a threat to pine growth and yield, sometimes to the point of wondering whether they should change their management practices to minimize its potential impact (Coyle et al. 2016).

Our research objective was to determine what, if any, specific stand or site factors were associated with low vigor and health of loblolly pine stands. During this 3-year study, we examined stands across a wide geographic area and assigned plots randomly within the stands, allowing us an unbiased evaluation of abiotic and biotic factors that have sometimes been implicated in SPD. We measured several stand-level variables, including tree size, age, density, and slope and aspect, as stands reported to be affected by SPD tended to be >35 years old (Brown and McDowell 1968, Eckhardt et al. 2007), on south-facing aspects and on steeper slopes (Eckhardt and Menard 2008). We evaluated soil texture and nutrient concentration in relation to tree health, as poor soil quality has been linked to poor pine health in the southeastern United States (Ryu et al. 2013). Root samples were taken to record the presence of root beetle transmitted fungi (*Grosmannia* and *Leptographium* spp.) and *H. irregulare*, all of which are common root pathogens in the southeastern United States, to determine their association with tree health. We hypothesized that we would find stand characteristics related to stressed trees (e.g., overstocked stands, older tree age, poor soils, etc.) as well as a greater prevalence of root infesting fungi, in trees with poorer health (i.e., areas purported to have SPD).

Management and Policy Implications

With the importance of forestry in an economic and ecological context in the southeastern United States, reports of forest die-off or decline need to be carefully considered. Because of the diverse landscape in the region, the health and vitality of many forest stands are impacted by fine-scale site characteristics. Any management recommendations pertaining to forest die-offs or declines are, therefore, dependent upon knowing exactly why forest health suffered. Our study shows the interconnectedness of forestry and forest health, and that forest health is often dictated by many variables. As such, blanket management recommendations are rarely useful; instead, management should be made on a site-by-site basis. This strategy will allow local site characteristics to play more prominently into management decisions.

Materials and Methods

Study Locations

Between 2012 and 2014, we sampled (typically during the summer months) 37 forested sites under federal, state, or private ownership in the Piedmont and Coastal Plain regions of Alabama (n = 15) and Georgia (n = 22), United States (Figure 1, Supplemental Table 1). This area has a humid subtropical climate, with average summer (July/August) and winter (December/January) temperatures of 27 and 8° C, respectively (www.ncdc.noaa.gov/). Rainfall averages 1,100 to 1,400 mm per year. Major soil orders in our study area included Ultisols, Entisols, and Inceptisols. Sites were dominated by *P. taeda*, with some sites containing *P. palustris* and *P. virginiana* Mill. Common hardwoods included *Acer rubrum* L., *Cornus florida* L., *Liriodendron tulipifera* L., *Liquidamber styracifula* L., and various *Quercus* spp. Understory flora generally included briars (e.g., *Ribes* and *Rubus* spp.), vines (e.g., *Parthenocissus quinquefolia* [L.] Planch., *Toxicodendron radicans* [L.] Kuntze, *Smilax* spp.), and various ferns, forbs, and grasses.

Experimental Design

Sampled pine sites were either symptomatic with tree dieback (n = 24) or healthy and asymptomatic (n = 13). Site selection was based on previously reported pine health issues (Eckhardt 2003) or by asking a local federal or state forester to indicate sites they would consider in "declining health" or in "good health." There was some inherent uncertainty in site selection, as SPD means different things to different managers (symptoms often occur on a spectrum, and may include loss of or yellowing foliage and declining tree canopies, all the way to tree mortality). Nine sites in Alabama were considered positive for SPD in a previous study (Eckhardt 2003). Those in Georgia were called unhealthy by the forest manager or landowner, and we acknowledge this may have meant different things to different people. However, this gets to the crux of the issue: are there any differences between healthy sites and those purported to have SPD? Those managers who believed they had SPD were more likely to make recommendations on how to manage SPD, and at this point there are no established recommendations. At each site, three plots were established every 250 m along a transect in similar soil series, modeled after the FIA plot sampling protocol (Bechtold and Patterson 2005). Plot coordinates were identified before visiting the sites to ensure random placement of the center plot points. Within each plot, we established four 10-m radius subplots—one at the plot center, and three others 50 m from the center subplot at 0°, 120°, and 240°. Hence, we sampled a total of 12 subplots per site for a total of 444 subplots for the study.

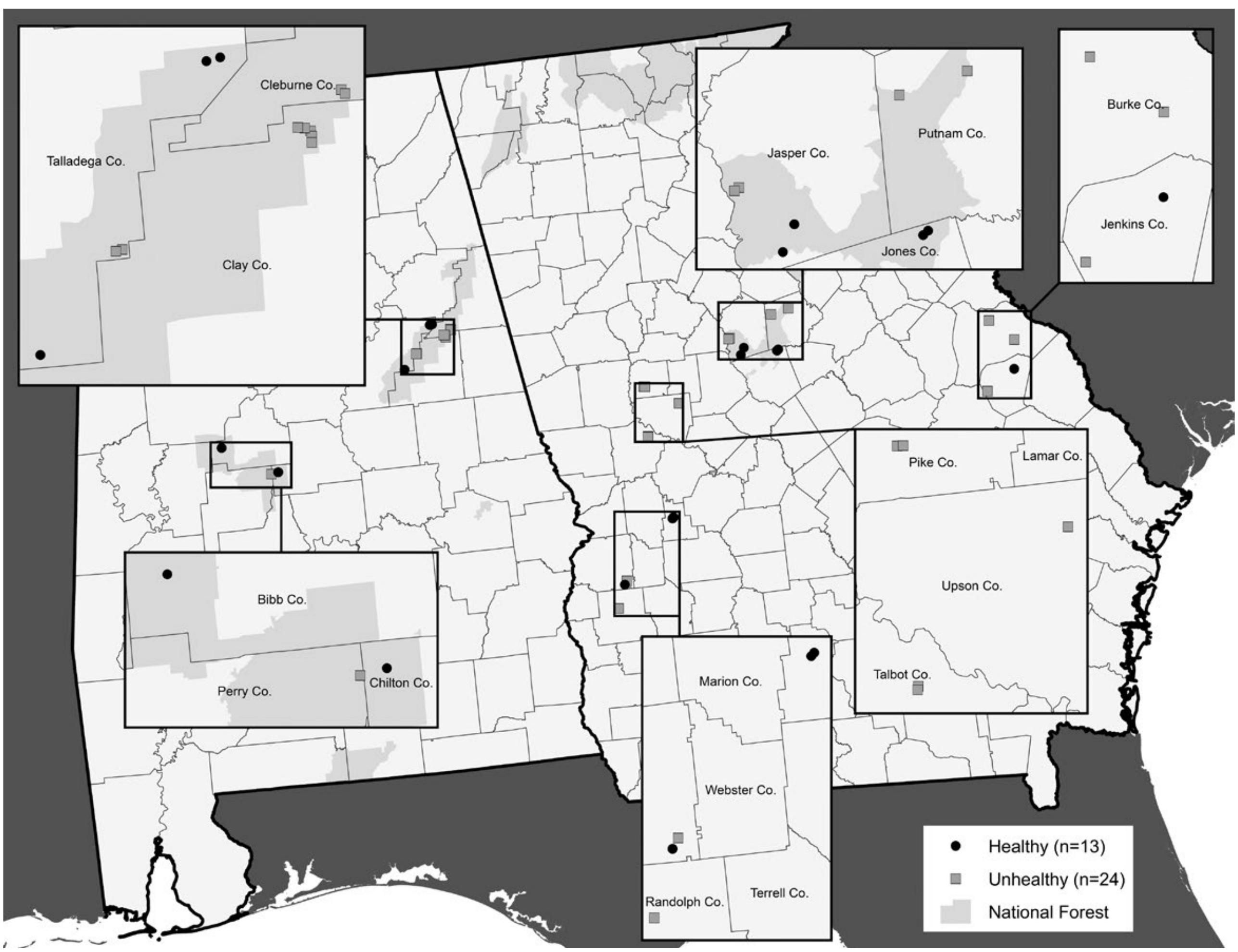

Figure 1. Sites sampled in Alabama (n = 15) and Georgia (n = 22), United States, from 2012 to 2014. Sites were classified as either asymptomatic (healthy) or symptomatic (showing decline symptoms, e.g., sparse, yellowing crowns, dieback, mortality, or previously reported as having pine decline).

Site-Level Sampling

Site-level variables, including stand age or age class (if available), area, and silvicultural and disturbance history (e.g., thinning, prescribed burns, harvests, and replanting), were obtained from the managing forester or landowner. Within each subplot, we recorded slope, azimuth, and other observations (e.g., proximity to a road or waterway, recent burn intensity, etc.). Species and diameter at breast height (dbh) were recorded from each live tree ≥2.5 cm. We also recorded dbh for all dead trees ≥2.5 cm, although these trees were classified only as pine or hardwood. From each subplot, up to three mature pine trees (if present) were randomly selected as sample trees (hereafter called "sample trees") from which we recorded the height to the nearest meter, crown condition on a 0–4 rating (0, completely healthy with no noticeable crown dieback/foliage discoloration/browning; 1, ≤25 percent crown dieback or browning; 2, 26–50 percent crown dieback or browning; 3, 51–75 percent crown dieback or browning; 4, ≥75 percent crown dieback or browning); all crown condition ratings were carried out by the same person. We noted if crown dieback occurred from needlecast disease (which can be caused by several fungal species and is common in some areas of the southeastern United States), but in no case was this apparent. We also collected a tree core at dbh for age determination.

Tree Damage Sampling

We inspected the entire bole of sample trees for signs of damage from several biotic and abiotic factors. Insect damage in the form of pitch tubes or visible sawdust from pine bark beetles (including *Dendroctonus* or *Ips* spp.) was recorded as present/absent (as were all tree damage metrics). Fire scars resulting from overly hot burns that led to tree damage and mechanical injury on tree trunks from machinery were recorded. Stem cankers from fusiform rust (*Cronartium quercuum* [Berk.] Miyabe ex. Shirai f. sp. *fusiforme*) were recorded. All tree-damage inspections were done by the same person to maintain consistency in data collection.

Soil Sampling

We collected seven soil samples from random locations within each subplot at 0–15 and 15–30 cm depths using a 2.5-cm-diameter corer. Soil samples within a subplot were composited and air-dried. Following air drying, samples were sieved through a 2 mm sieve. Soil pH and nutrient levels were determined at the Water and Soil Laboratory, University of Georgia, Athens. Soil samples were pulverized in a Spex 8200 ball mill grinder (Spex® SamplePrep LLC, Metuchen, NJ), and total C and N were determined using dry combustion on a CE Elantec Flash 2000 (CE Elantec, Inc., Lakewood, NJ) (Dumas method; Bremner 1996). The pH was measured using a 0.1 M $CaCl_2$ solution at a 1:1 soil/solution ratio in an AS-3000 Dual pH Analyser (LabFit, Burswood, Western Australia, Australia) (Liu et al. 2005, 2008, Thompson et al. 2010, Kissel et al. 2012, Sonon and Kellel 2012). Available soil macro- (P, K, Ca, Mg) and micronutrients (Mn, Zn) were measured following Mehlich 1 extraction (Melich 1953, 1978). Extracts were then analyzed in a Thermo Jarrell-Ash Enviro I ICAP Spectrometer (Thermo Jarrell-Ash Corp., Franklin, MA). Soil texture was determined using the method of Bouyoucos (1962). Soil samples were mixed with sodium hexametaphosphate (Calgon®, Baltimore, MD), and hydrometer measurements were recorded at three subsequent times to determine sand, silt, and clay content.

Root and Fungal Sampling

Three root samples were collected from each sample tree, one each from a small (<2 cm diameter), medium (2–6 cm diameter), and large (>6 cm diameter) root. Each sample was collected from a different root, which was excavated within 30 cm of the soil surface and inspected to confirm it was alive and connected to the sample tree. All root samples were immediately bagged, put into coolers within 12 hours of collection, refrigerated upon return to the laboratory, and held in this manner until processing, which was generally within 2 weeks of collection.

Roots and all equipment were surface-sterilized with 95 percent ethanol. Each root sample was separated into eight (1.3 × 1.3 cm) pieces and placed on a selective 2 percent malt extract agar (MEA) media with 200 mg of cycloheximide (Singleton et al. 1992) to isolate *Leptographium* fungal species. Two additional pieces of each root sample (2.5 × 2.5 × 3 cm) were placed into plastic bags with a paper towel saturated in deionized water. Petri dishes were sealed with Parafilm®, and both dishes and bags were left for 2 weeks at room temperature. All root pieces were visually examined for *H. irregulare* or *Leptographium* spp. fungal growth using morphological characteristics of the fungi (under the guidance of WJO, a forest pathologist).

Pure cultures of all *Leptographium* spp. were made using the single spore isolation method (Choi et al. 1999) from plates with *Leptographium* spp. and grown on 2 percent MEA media without cycloheximide. Pure cultures were left at room temperature, and a final check for the presence of *Leptographium* was recorded after 2 weeks. Samples of *Leptographium* spp. pure cultures were placed in two different slants using 2 percent MEA in 2 mL vials and stored at 4.4° C for permanent storage. One slant of each isolate was sent to the University of Pretoria, South Africa, for use in future taxonomic work with this group, whereas the remaining slants were stored at the University of Georgia.

Statistical Analyses

We translated subplot-level observations of insect damage, fire damage, mechanical damage, or stem cankers on sampled pine trees, as well as the presence of *H. irregulare* or *Leptographium* spp., into six corresponding variables: insect, fire, mechanical damage, stem cankers, Heterobasidion, and Leptographium. We computed values for each of these variables as subplot-level proportions, i.e., the number of sampled trees, out of a maximum of three trees, where the given condition was observed. Accordingly, we assumed that each variable followed a binomial distribution.

Topographic aspect can be a problematic variable in the sense that values far apart numerically can convey similar directional information. For example, aspect values of 2° and 358° both indicate northward-facing slopes. To facilitate analyses, we converted field measurements of aspect into two continuous variables, eastness and northness, where eastness = sin (aspect * π / 180) with a maximum value of 1, and northness = cos (aspect * π / 180) for a maximum value of –1. For field observations where no measurable aspect was reported, both variables were set to 0.

We performed analyses to identify significant differences between healthy (or asymptomatic) and unhealthy (or symptomatic) sites in terms of the measured variables. Because of our experimental design, our data had a hierarchical structure, with survey sites nested within states, plots nested within sites, and subplots nested within plots. Ignoring one or more levels of nesting in hierarchically structured data can impact both variance estimation and significance testing (Moerbeek 2004, Bell et al. 2013). Multilevel modeling provides a way to account for variability at each hierarchical level, as well as dependencies between levels (Singer 1998, Zhu 2014). Multilevel models, which are sometimes called hierarchical or hierarchical linear models, are considered mixed models because they incorporate both fixed (constant across all levels) and random (variation between levels) effects. They have been used most commonly in social science and medical research, although there are also examples from environmental science and ecology (McMahon and Diez 2007, Qian et al. 2010).

The GLIMMIX procedure in SAS v. 9.4 can be used to construct generalized linear mixed models (GLMMs) in cases where the response is not normally distributed (Zhu 2014). We used the GLIMMIX procedure to build multilevel logistic regression models that fit each continuous explanatory variable (Supplemental Table 2) to a dichotomous response (healthy or unhealthy). Notably, the designation as healthy or unhealthy was made at the site level, whereas the measurements for each explanatory variable were recorded at a lower level of observation (i.e., from subplots nested within plots on each site). This type of relation between response and explanatory variables in a multilevel model is sometimes called a *micro–macro relation* (Snijders and Bosker 2012, Bennink et al. 2013). In practice, micro–macro relations can be addressed by aggregating the lower-level values for the predictors to the level of the response variable (e.g., using group means) while also accounting for group heterogeneity (Bennink et al. 2013). To do this, we adopted the latent variable approach of Croon and van Veldhoven (2007). Briefly, we calculated adjusted site-level means for each explanatory variable that were weighted according to both the between-site and within-site variance, which we computed using nested analysis of variance (ANOVA) methods. Croon and van Veldhoven (2007) showed that linear regression applied to adjusted means acting as a latent variable yielded unbiased estimates given a continuous response variable. In the case of a dichomotous response, logistic (or in some cases probit) regression should be applied instead (Bennink et al. 2013).

For computational efficiency, multilevel logistic regression models and other GLMMs are often solved using pseudo- or quasi-likelihood methods for parameter estimation (Bolker et al. 2008). Because we had a dichotomous response and random effects, we used the Laplace approximation method to approximate the true model likelihoods, thereby minimizing bias in the variance components and enabling likelihood-based inference (Bolker et al. 2008). Additionally, we applied the Morel–Bokossa–Neerchal (MBN) empirical covariance estimator when computing the standard errors of the fixed effects (Morel et al. 2003). The MBN estimator, which incorporates small-sample bias correction, ensures that the fixed-effect standard errors are robust to misspecification of the covariance structure (Kiernan 2018). The fixed effects in this case refer to the individual explanatory variables (i.e., their site-level adjusted means), whereas each model also included up to two random effects, one for states and another for sites within states. We fit each model using a logit link function and tested the random effects (i.e., model covariance parameters) using Wald Z tests. If a random effect prevented convergence during likelihood estimation or caused the variance–covariance matrix to be not positive definite, we removed the effect and reran the model.

After evaluating the continuous explanatory variables individually, we tested a series of multivariate models. The largest of these models (Model 1) included 11 variables. We omitted variables for which we could not evaluate random effects during univariate testing because the model failed to converge or resulted in a nonpositive definite variance–covariance matrix. We also chose only a single representative from groups of highly correlated variables (i.e., where |Spearman's r| > .7). We then constructed a series of reduced models from Model 1, selecting the one that minimized the Akaike information criterion and Bayesian information criterion as our final reduced model (Model 2). We used the same model settings (e.g., Laplace approximation, MBN covariance estimator) that we adopted during univariate testing.

In separate analyses, we used the GLIMMIX procedure to analyze the six proportion variables described previously (insect, fire, mechanical damage, stem cankers, Heterobasidion, and Leptographium). For each of these variables, we tested whether the proportions observed on the subplots (as the response) were explained by the sites' designations as healthy or unhealthy. In addition to this fixed effect, we included up to four random effects in each model: for states, for sites within states, for plots within sites, and for subplots within plots. As with the logistic regression models for the continuous explanatory variables, we used the Laplace approximation to approximate the true model likelihoods. We fit each model using a logit link function and tested the random effects using Wald Z tests. As before, if a random effect prevented convergence or caused the variance–covariance matrix to be not positive definite, we re-ran the model after removing the effect.

Results

Site Characteristics

We measured a total of 11,716 trees in Alabama and Georgia during this study (Table 1). Trees in Alabama were 33 percent pines, whereas trees in Georgia were 45 percent pines. Most measured trees were alive (94 percent in Alabama, 87 percent in Georgia) (Table 1). We sampled a total of 997 and 3,531 live pine trees in Alabama and Georgia, respectively. Sampled pines were on average >10 years older in Alabama than those in Georgia, but the mean dbh of pines in each state was nearly identical (Table 1).

Landscape and Soil Characteristics

Healthy and unhealthy stand conditions did not differ significantly with respect to the derived measurements of slope, eastness, and northness (all $P > .412$). The silt content of soils was 71 percent greater at unhealthy sites at the 0–15 cm depth ($t = 2.36$; OR 4.0, 95 percent CI: 1.21–13.26; $P = .024$) and 49 percent greater at

Table 1. Stand characteristics of pine health study plots in Alabama and Georgia, US.

Stand Attributes	Alabama	Georgia
Total trees (live + dead) measured	3,265	8,451
Pine:hardwood ratio of total trees	0.50	0.83
Live trees measured	3,056	7,354
Pine:hardwood of live trees	0.47	0.88
Total live pine trees sampled	997	3531
Age range of pines (years)	10–120	6–78
Mean pine tree age (±SE)	36.1 ± 0.7	25.3 ± 0.3
dbh range of pines (cm)	2.3–71.0	2.5–144.8
Mean dbh (±SE) of pines (cm)	21.3 ± 0.4	21.2 ± 0.1

the 15–30 cm depth (t = 2.12; OR 2.8, 95 percent CI: 1.04–7.61; P = .041), but sand and clay content did not differ significantly between healthy and unhealthy stand conditions at either soil depth (all P > .382, Table 2). Soil pH did not differ between healthy and unhealthy sites in either soil depth (all P > .181) (Table 2).

Soil Nutrients

The overall range of soil nutrient values was similar in Alabama and Georgia, but values varied greatly, sometimes differing by almost 100-fold. Nitrogen amounts ranged from 0.01 to 0.25 percent in Alabama, and from 0.01 to 0.26 percent in Georgia, whereas carbon ranged from 0.30 to 7.98 percent in Alabama and from 0.12 to 7.31 percent in Georgia. Calcium concentrations were particularly wide-ranging (25 to 2,163 ppm in Alabama, 42 to 2,350 ppm in Georgia) as were manganese (1 to 159 ppm in Alabama, 1 to 259 ppm in Georgia) and magnesium (7 to 402 ppm in Alabama, 11 to 394 ppm in Georgia). Phosphorus and potassium values ranged from 1 to 75 and from 11 to 183 ppm, respectively, in Alabama, and from 1 to 27 and from 12 to 246 ppm, respectively, in Georgia. Zinc values in Alabama ranged from 1 to 23 ppm, whereas those in Georgia ranged from 1 to 8 ppm.

Soil nutrient concentrations did not differ between healthy and unhealthy stand conditions at either soil depth (all P > .063; Table 2). It is notable, however, that manganese concentrations were 67 percent greater at the 0–15 cm soil depth (t = –1.92; OR 0.47, 95 percent CI: 0.21–1.05; P = .064) and 74 percent greater at the 15–30 soil depth (t = –1.70; OR 0.53, 95 percent CI: 0.25–1.13; P = .099) of healthy stands. Also, at the 15–30 cm soil depth, nitrogen concentrations were 20 percent greater in unhealthy stands (t = 1.92; OR 3.2, 95 percent CI: 0.9–10.9; P = .063) and carbon concentrations were 30 percent greater (t = 2.97; OR 2.6, 95 percent CI: 0.8–7.9; P = .094) in unhealthy stands.

Forest Composition

The number of live pine, hardwood, other conifer, or total trees per acre did not differ significantly between healthy and unhealthy stand conditions (all P > .105, Table 3). Likewise, pine, hardwood, other conifer, and total tree basal area were not different between stand conditions (all P > .270, Table 3). Unhealthy stand conditions had 83 percent more dead pine trees per acre (t = 2.59; OR 4.0, 95 percent CI: 1.4–12.0; P = .014) and a 91 percent greater dead pine basal area (t = 2.29; OR 5.0, 95 percent CI: 1.2–20.8; P = .028) than healthy stand conditions. Trees per acre and basal area of dead hardwoods did not differ between healthy and unhealthy stand conditions (all P > .389, Table 3).

Tree Health

As expected, tree health ratings (measured by crown condition) were lower, i.e., trees were healthier, in healthy (mean ± SE, 0.97 ± 0.04) than in unhealthy (1.43 ± 0.04) stand conditions (t = 2.19; OR 6.9, 95 percent: CI 1.15–41.86; P = .036). Neither insect nor fire damage incidence differed between healthy and unhealthy stand conditions (insect damage, P = .279; fire damage, P = .469; Figure 2). Healthy sites had a higher incidence of stem cankers (t = 2.73; OR 5.4, 95 percent: CI 1.60–30; P = .007), which included nonfestering healed cankers, and mechanical damage (t = 3.51; OR 11.9, 95 percent: CI 2.97–47.44; P < .001) than unhealthy stand conditions (Figure 2). Incidence of *Leptographium* spp. in roots did not differ significantly between healthy and unhealthy stand conditions (P > .131), but *H. irregulare* was more

Table 2. Mean ± SE of soil variables.

Soil depth	Soil variable	Stand condition		Significance level
		Healthy	Unhealthy	
0–15 cm soil depth	pH, calcium chloride	4.35 ± 0.03	4.26 ± 0.02	
	pH, water	4.95 ± 0.03	4.86 ± 0.02	
	Calcium (ppm)	384 ± 24	312 ± 16	
	Potassium (ppm)	39 ± 4	48 ± 2	
	Magnesium (ppm)	73 ± 5	65 ± 3	
	Manganese (ppm)	60 ± 4	36 ± 2	*
	Phosphorus (ppm)	5.8 ± 0.5	6.4 ± 0.2	
	Zinc (ppm)	2.7 ± 0.2	2.5 ± 0.1	
	Nitrogen (percent)	0.09 ± 0.00	0.10 ± 0.00	
	Carbon (percent)	2.12 ± 0.10	2.14 ± 0.09	
	Sand (percent)	76.5 ± 1.2	72.1 ± 0.7	
	Clay (percent)	14.2 ± 1.0	12.0 ± 0.3	
	Silt (percent)	9.3 ± 0.5	15.9 ± 0.6	**
15–30 cm soil depth	pH, calcium chloride	4.52 ± 0.03	4.40 ± 0.02	
	pH, water	5.12 ± 0.03	5.00 ± 0.02	
	Calcium (ppm)	215 ± 12	172 ± 9	
	Potassium (ppm)	28 ± 3	34 ± 2	
	Magnesium (ppm)	69 ± 5	66 ± 4	
	Manganese (ppm)	33 ± 3	19 ± 1	*
	Phosphorus (ppm)	3.6 ± 0.2	4.0 ± 0.1	
	Zinc (ppm)	1.9 ± 0.2	1.7 ± 0.1	
	Nitrogen (percent)	0.04 ± 0.00	0.05 ± 0.00	*
	Carbon (percent)	0.69 ± 0.03	0.99 ± 0.05	*
	Sand (percent)	66.6 ± 1.6	61.7 ± 0.8	
	Clay (percent)	19.5 ± 1.2	17.6 ± 0.5	
	Silt (percent)	13.9 ± 0.7	20.7 ± 0.6	**

Note: *Variables that differed significantly at α = 0.10 between healthy and unhealthy stand conditions. **Variables that differed significantly at α = 0.05 between healthy and unhealthy stand conditions.

Table 3. Mean ± SE of stand variables.

Stand variable	Stand condition	
	Healthy	Unhealthy
Live pine trees/ha	263.4 ± 11.4	452.0 ± 24.0
Live pine basal area (m²/ha)	13.3 ± 0.5	17.3 ± 0.7
Dead pine trees/ha	**49.4 ± 05**	**90.4 ± 4.9**
Dead pine basal area (m²/ha)	**1.0 ± 0.1**	**2.0 ± 0.1**
Live hardwood trees/ha	375.1 ± 26.1	575.3 ± 31.9
Live hardwood basal area (m²/ha)	3.2 ± 0.5	4.4 ± 0.3
Dead hardwood trees/ha	109.0 ± 15.6	197.0 ± 11.6
Dead hardwood basal area (m²/ha)	0.6 ± 0.1	1.1 ± 0.1
Other live conifer trees/ha	31.9 ± 0.0	66.0 ± 3.0
Other live conifer basal area (m²/ha)	0.05 ± 0.00	0.44 ± 0.05
Live trees/ha	580.4 ± 29.7	908.4 ± 42.7
Live tree basal area (m²/ha)	15.9 ± 0.6	18.5 ± 0.8

Note: Variables that differed significantly between healthy and unhealthy stand conditions are shown in bold.

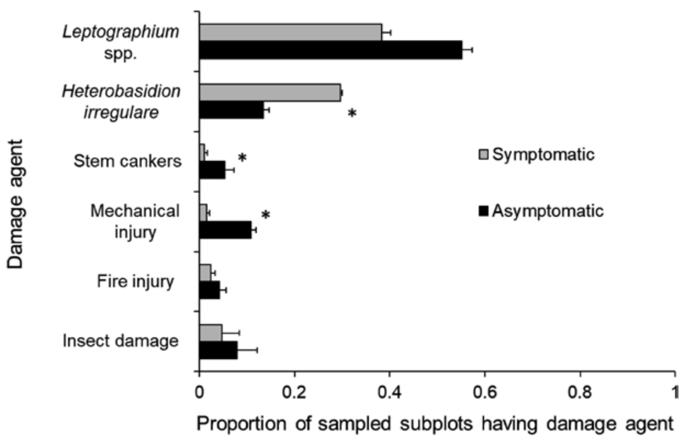

Figure 2. Presence of various damage agents in study subplots in Alabama and Georgia, United States, during sampling in 2012–2014. Variables that differed significantly at α = 0.05 between healthy and unhealthy stand conditions are denoted by an asterisk.

commonly found in pine roots in unhealthy stands ($t = -2.60$; OR 0.20, 95 percent CI: 0.06–0.67; $P = .010$; Figure 2).

Final Inferential Model to Identify a Suite of Associated Significant Factors

The final reduced model to predict unhealthy pine sites, based on all variables for which the random effect of sites within states was relevant, included five variables (Table 4). These variables included soil and tree components.

Discussion

This large-scale study on loblolly pine health in two southeastern states found only a few trends related to landscape and soil factors. The silt content of soils was greater in unhealthy stand conditions, a finding that is somewhat counterintuitive, as greater silt contents are typically associated with a high soil water holding capacity and decreased water stress during low rainfall periods. It appears that this relation was driven by a series of plots located in the Clay, Cleburne, and Talladega counties, Alabama. These unhealthy study sites had silt contents that ranged (all plots and soil depths combined) from 21 to 38 percent. Further, these plots contained some of the steepest slopes in the study, with several plots having an average slope of 12° (nearly twice the average for unhealthy stand condition plots). So, whereas the plots appeared to have favorable soils for loblolly pine development, many were also very steep for this region, which likely contributed to increased water stress and overall tree condition. Steep terrain has been associated with poor pine health in this region (Eckhard and Menard 2008). Nitrogen and carbon concentrations were slightly elevated in some soils in unhealthy, declining stands. Although on the low end of loblolly pine's preferred range, soil pH and nitrogen were still within the range of acceptable values for the southeastern United States (Subedi and Fox 2016). Rather than a causal mechanism, it seems likely that these small differences are the result of increased litter inputs from declining and dead trees on unhealthy sites.

The greatest difference in landscape or soil attributes observed between healthy and unhealthy stand conditions was for the micronutrient manganese, which was greater (albeit at the $\alpha = 0.10$ level) at both soil depths of healthy stands (Table 2). Several explanations for greater manganese concentrations in healthy stands are possible. First, manganese may be deficient in unhealthy stands. In a study of micronutrient fertilization of slash pine, Jokela et al. (1991) found Mn to be the only micronutrient to which there was a growth response, and they suggested that Mn deficiency may be common across pine-growing regions of the southeastern United States. Second, manganese may be involved in the chemistry of the stress response and greater production or concentration of terpenes that improves pest resistance. For example, studies on nonwoody and aromatic plants indicated that higher concentrations of Mn led to increased common pine terpenoids such as α-pinene and elevated expression of genes involved in terpenoid biosynthesis pathways (Ghannadnia et al. 2014, Nazari et al. 2017); however similar studies on pines are lacking. Finally, Mn occurs in greater concentrations in soils with greater concentrations of ferromagnesian minerals. The relation between stand health and manganese may reflect a relation between stand health and other profile characteristics. For instance, stands occurring on rhodic soils may be healthier, and this is reflected in Mn concentrations. Soil characteristics (e.g., compaction) are known to impact pine growth (Parker and Van Lear 1966, Foil and Ralston 1967, Hatchell et al. 1970), and anecdotally (as evidenced by the amount of effort required to obtain the soil sample) soils in unhealthy sites seemed much more compacted than did those from healthy sites. Future efforts to evaluate the effects of soil bulk density on pine health would be warranted.

Decades of research have led to a thorough understanding of southern pine silviculture (e.g., Rauscher and Johnsen 2004, Fox et al. 2007, Sharma et al. 2016, Zhao et al. 2016). Abiotic factors, such as soils and climate, contribute to the ability of southern pines to grow and thrive, but stand management activities such as thinning and prescribed burning also contribute substantially to a tree's potential success. Unhealthy sites had a higher pine basal area than healthy stands (Table 3), although the differences were not statistically significant. Although the basal area values encountered were not especially high, hardwood competition in conjunction with nutrient-poor soils (Table 2) may have caused enough stress on trees to cause them to be less healthy. For example, a higher hardwood basal area and the associated stress on pines likely contributed to increased stand susceptibility to southern pine beetle (*Dendroctonus fronatalis* Zimmermann) in

Table 4. Final model (df = 30, Akaike information criterion = 18.5; Bayesian information criterion = 29.6) to predict unhealthy pine sites based on data collected in this study.

Effect	Estimate	SE	*t*-value	*P*-value
Intercept	121.03	29.05	4.166	<.001
Manganese content in 0–15 cm depth	–166.14	39.25	–4.233	<.001
Silt content in 0–15 cm depth	116.51	35.90	3.245	.003
Nitrogen content in 15–30 cm depth	64.71	19.16	3.378	.002
Dead pine trees/ha	78.59	20.43	3.847	<.001
Tree health rating	65.69	14.68	4.475	<.001

Note: See Statistical Analyses subsection for a detailed description of model construction.

Mississippi, United States (Nowak et al. 2015). Further, bark beetle pheromones are more likely to linger in dense stands (Thistle et al. 2004), which can increase the chance of conspecifics detecting the pheromone and initiating additional attacks. Adequate light and soil moisture availability are critical factors for the development of southern pine stands (Kozlowski 1949, Daniels et al. 1986, Samuelson et al. 2014), both of which can be impacted by hardwood competition (Miller et al. 1991, 2003).

We expected to find an increased prevalence of stem damage via wounds and cankers in unhealthy stands, but the opposite occurred. Damage to the tree trunk, whether by insects, fungi, or management activities, can create wounds in the tree that may serve as infection points for micro-organisms (Vasiliauskas and Stenlid 1998). However, trees in healthy sites appeared better able to tolerate such damage, and their natural defensive capabilities likely helped maintain their overall apparent health. Greater mechanical damage in healthy stands likely stemmed from thinning operations (Han and Kellog 2000), whereas unhealthy stands did not appear to have been thinned. Even careful thinning operations are likely to leave some mechanical damage. Alternatively, thinning operations, while inevitably causing some damage, create less dense populations of trees, thereby reducing competition for resources and related sources of stress. The result is a smaller and more resilient population of trees that can tolerate such damage. Another possibility is that thinning operations removed unhealthy trees, leaving only the fittest remaining. Fusiform rust stem cankers were also more prevalent in healthy stand conditions. Fusiform rust is more common on healthy, fast-growing trees, and many *Quercus* spp. (the required secondary host for fusiform rust) were growing in or near our study plots.

We recovered *Leptographium* spp. from both unhealthy and healthy sites. *Leptographium* spp. are commonly recovered from bark beetles and unhealthy or dead trees (Wingfield and Marasas 1983, Barnard et al. 1985, 1991, Jacobs et al. 2000, Lee et al. 2005), so an association of *Leptographium* spp. with unhealthy southern pine sites (Otrosina et al. 1999, Eckhardt et al. 2004a, 2007) is not surprising. Further, the root-feeding insects that transmit these fungi also have a well-established ecological role as colonizers of dying or dead woody material (especially cut stumps) and are attracted to host trees whose defenses are compromised (Blackman 1941, Matusick et al. 2013, Helbig et al. 2016, Be et al. 2017). However, association of *Leptographium* spp. from a statistically similar proportion of healthy (than unhealthy) sites likely reflects natural root turnover and suggests a cosmopolitan distribution of these fungi at the genus level. Even healthy pine stands have some dying roots (Copeland 1952), which likely provide suitable host material for the root-feeding insect vectors.

In the southeastern United States, the role of *Leptographium* spp. as related to tree health has been as secondary colonizers of dying host material. In North America, *L. wageneri* [Kendr.] Wingf. varieties are the only *Leptographium* spp. with the ability to be primary tree-killing pathogens (by causing black stain root disease in Western conifers [Lockman and Kearns 2016]). Our work addressed *Leptographium* spp. identification at the genus level, and we acknowledge there may be differences in which species of this fungal group are found within a forest (the taxonomy of this group is in the process of revision, and new species are regularly being described [e.g., Huang and Chen 2014, Liu et al. 2017, Marincowitz et al. 2017]), and possibly even in their virulence to host trees. However, none of the species identified in the southeastern United States to date have been proven to be a primary tree-killing pathogen (Eckhardt et al. 2004b, Matusick et al. 2008, 2010, Matusick and Eckhardt 2010a, b, Singh et al. 2014). In fact, the virulence of the same isolates for each species tested and applied in these different studies indicates they are no more virulent than our native *L. terebrantis.*

Incidence of *H. irregulare*, the pathogen responsible for Heterobasidion root disease (HRD), was over twice as high in unhealthy as in healthy stand conditions. HRD can occur throughout eastern North America, so its presence in our study sites was not surprising. HRD incidence is tightly linked to soil properties, and hazard maps exist for the southeastern United States (e.g., Dreaden et al. 2016). A closer examination of where *H. irregulare* was found in our study did not provide clarity as to the causal agents of SPD. In fact, we found the highest incidences of *H. irregulare* on sites with a low (e.g., those in Clay, Cleburne, and Talladega Co., AL, or Talbot Co., GA) or medium (e.g., those in Burke or Jenkins Co., GA) HRD hazard rating. We also found high incidences at sites with a high hazard for HRD (e.g., Stewart Co., GA). This information suggests that whereas HRD hazard maps exist, they provide guidance only and are not definitive. Unlike the *Leptographium* spp. encountered in our study, *H. irregulare* is a primary pathogen that will cause tree sickness and death if conditions are suitable (Driver and Dell 1961, Applegate 1971, Bradford et al. 1978, Blanchette et al. 2015). Roots must be excavated to diagnose HRD accurately. Although this activity is simple in concept, it is rarely done in practice, likely because it is laborious and time-consuming. Unfortunately, this could result in these symptoms being attributed to SPD, particularly to the untrained eye, when there may be a distinct and legitimate root-disease issue. Further complicating matters, visual aboveground symptoms of HRD also mirror those associated with SPD: thinning, chlorotic crowns, and reduced growth, sometimes with dead trees present. In short, it is highly likely that many of the previously reported instances of SPD may have actually been attributed to HRD. This particular forest disease shows how identifying the correct cause of forest health issues is a critical step in determining proper and effective management actions. Early HRD damage can easily be confused as abiotic (often drought) stress or SPD, and as the disease progresses *Ips* spp. bark beetles often attack the weakened tree, garnering their own blame for the tree's demise. Careful examination of the roots—including root excavation—is often required to confirm the presence of HRD. Simply calling an unidentified forest health issue a "decline" or lumping multiple primary causal factors into a general "decline" category (e.g., Cohen et al. 2016) is inaccurate and may lead to mismanagement.

Site history likely played a role in stand health (e.g., Worrall et al. 2010, Ryu et al. 2013), but obtaining accurate historical information about our study sites proved incredibly difficult and, in some cases, impossible. Knowing previous site history can be helpful in making management recommendations (e.g., old-field sites generally have different soil physical and chemical properties from the agricultural activities compared to cutover forest sites) or determining the potential for a pathogen like *H. irregulare* to become established. Unfortunately, records were often lost when land changed hands. Determining the exact age of individual trees was possible via tree cores, but more difficult in uneven aged stands because of a limited capacity to sample trees. With the exception of recent prescribed fires, it was almost impossible to determine the timing of silvicultural activities. This problem is likely an issue throughout the region and beyond whenever forest land changes ownership.

While the scale for which weather data were available was too large to make any meaningful determinations for a particular site, we do know that all sites (and most of the southeastern United States) experienced a severe drought in the late 2000s (Supplemental Figure 1). Drought is a well-documented stress agent on many tree species, often leading to reductions in growth, shedding of ephemeral tissues, branch and root dieback (i.e., three symptoms often associated with declines), and mortality (Hanson and Weltzin 2000, Allen et al. 2010, Worrall et al. 2013, Vose et al. 2016). Drought can increase a tree's susceptibility to fungi and other biotic organisms (Desprez-Loustau et al. 2006, Sturrock et al. 2011, Jactel et al. 2012). Pines are known to be sensitive to water stress, especially as trees age, and in stands with higher basal areas and on steeper slopes (Mitchell et al. 1999, Tang et al. 2004, Klos et al. 2009, Will et al. 2015, Bottero et al. 2017). It is possible that some of the unhealthy tree conditions in our study were simply a result of this weather pattern.

It is also possible that loblolly pine was not the optimal tree to be planted (all of our stands were planted at one point; none were old growth) or growing on all of these sites. For instance, longleaf pine is known to perform better than loblolly on deep, sandy soils, presumably because the taproot growth pattern of longleaf allows them to reach deeper sources of moisture (Heyward 1933). Our sites in Burke and Jenkins Co., GA, were such sites. Likewise, shortleaf pine is known to be more tolerant than loblolly on drier, more well-drained sites (Zak 1961); sites in Clay, Cleburne, and Talladega Co., AL may have been be more suited to shortleaf than loblolly pine. Off-site planting (i.e., planting a suboptimal tree species on a site) can contribute to declines in tree health as the trees age.

This large-scale field study showed the complex nature associated with "decline" syndromes. Many factors are often at play, and whether a specific area has an issue usually comes down to the particular abiotic and biotic characteristics of that site. Certainly, human activities (especially management) have an impact, but all these factors interact to produce what is manifested as the overall health and vitality of that forest area. Our data strongly suggest a variety of single primary agents and multiple factors involved in causing a decrease in the overall health of individual pine stands in the South. We recommend using caution when describing decline syndromes, and especially when suggesting generalized management recommendations.

Supplementary Materials

Supplementary data are available at *Forest Science* online.

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