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# Landscape variables influence *Phytophthora cinnamomi* distribution within a forested Kentucky watershed

Kenton L. Sena[a,*], Jian Yang[b], Alysia J. Kohlbrand[b], Tyler J. Dreaden[c], Christopher D. Barton[b]

[a] Lewis Honors College, University of Kentucky, 1120 University Drive, Lexington, KY 40526-0104, USA
[b] Department of Forestry, University of Kentucky, 730 Rose Street, Lexington, KY 40546-0073, USA
[c] USDA-Forest Service, Southern Research Station, Forest Health Research and Education Center, Lexington, KY, USA

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ABSTRACT

Invasive pests and pathogens have contributed to widescale forest change around the world, but especially in the eastern US. *Phytophthora cinnamomi*, one such introduced pathogen, causes root rot in American chestnut (*Castanea dentata*) and shortleaf pine (*Pinus echinata*), among other eastern forest species of interest, and has inhibited chestnut restoration efforts in some cases. Traditionally, *P. cinnamomi* has been associated with low landscape positions and moister soils; however, its distribution patterns in the eastern US are poorly understood. Improved understanding of *P. cinnamomi* distribution may enable forest managers to prioritize sites with low risk of *P. cinnamomi* presence for chestnut restoration. To elucidate landscape factors associated with *P. cinnamomi* distribution, two sets of soil samples from an eastern Kentucky forest (representing two levels of sampling intensity) were screened for *P. cinnamomi* incidence, and data were analyzed for spatial distribution patterns. In general, sites in which *P. cinnamomi* was detected tended to be warmer (higher annual solar radiation) and drier (lower moisture indices), than sites in which *P. cinnamomi* were not detected. *P. cinnamomi* incidence was also found to be associated with oak (*Quercus* spp.) abundance and (weakly) negatively associated with soil microbial activity under certain conditions. Overall, *P. cinnamomi* was found to be distributed across a wide range of landscape variables, including both drier ridge-top sites and moister streamside sites, contrary to traditional associations. In addition, the association with oak abundance suggests that the drier upland sites preferred by oak species in eastern Kentucky are not "safe" from *P. cinnamomi*. Given that *P. cinnamomi* was found distributed across a range of environmental conditions, forest managers cannot assume that any landscape position is phytophthora-free, and soil screening should be used for site selection to inform restoration of chestnut and other susceptible species.

## 1. Introduction

*Phytophthora cinnamomi* is a soilborne oomycete pathogen causing disease in a wide variety of forest tree species around the world (Sena et al., 2018a). Thought to have originated in southeast Asia (Ko et al., 1978; Arentz & Simpson, 1986), *P. cinnamomi* has been introduced throughout the world, and in forests has been associated with dramatic declines in Eucalyptus trees in Australia (Podger, 1972; Shearer and Dillon, 1996; McDougall et al., 2002), and oaks and chestnuts in Europe (Vannini & Vettraino, 2001; Vettraino et al., 2002). In eastern U.S. forests, *P. cinnamomi* is primarily associated with root rot in American chestnut (*Castanea dentata*) (Anagnostakis, 2001) and littleleaf disease in shortleaf pine (*Pinus echinata*) (Campbell and Copeland, 1954), but has also been associated with fine root loss in white oak (*Quercus alba*) (McConnell & Balci, 2015; McConnell & Balci, 2014).

American chestnut, once a dominant forest canopy species throughout the eastern U.S., has suffered greatly at the hands of introduced pathogens (Paillet, 2002; Rigling and Prospero, 2018). In the early 1900s, the fungal pathogen *Cryphonectria parasitica*, causal agent of chestnut blight, swept through the eastern U.S. forests, killing chestnut back to the ground and functionally eliminating it from forest ecosystems (Anagnostakis, 2001). *P. cinnamomi* had been introduced to the southeast U.S. in the mid-late 1800s (Corsa, 1896), but was subtler in its impacts and was not the subject of intensive study in eastern U.S. forests until relatively recently (Hwang et al., 2009; Meadows et al., 2011; Meadows and Jeffers, 2011). Thanks to extensive breeding efforts introducing disease resistance from Chinese chestnut, blight-resistant American chestnut varieties are now becoming available for

* Corresponding author.
*E-mail addresses:* kenton.sena@uky.edu (K.L. Sena), jian.yang@uky.edu (J. Yang), alysia.kohlbrand@uky.edu (A.J. Kohlbrand), tdreaden@fs.fed.us (T.J. Dreaden), barton@uky.edu (C.D. Barton).

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outplanting (Diskin et al., 2006), and are the subject of further selection targeting *P. cinnamomi* resistance (Jeffers et al., 2009; Zhebentyayeva et al., 2013; Santos et al., 2015). In addition to developing host genetic resistance to *P. cinnamomi*, restoration efforts should be informed by improved understanding of how *P. cinnamomi* is distributed on the landscape in eastern U.S. forests (Sena et al., 2018a, 2018b). If areas on the landscape where *P. cinnamomi* is unlikely to be found can be characterized, these may be identified as high-priority areas for chestnut restoration.

In the southern Appalachians, *P. cinnamomi* was isolated from 12% of samples in mountain pine/hardwood stands and 45% of samples from coastal pine stands (Campbell and Hendrix, 1967), and from 34% of forest soil samples in another study in south-central Appalachia (Sharpe, 2017). A recent study in an American chestnut planting site in eastern Kentucky found *P. cinnamomi* in 100% of soil samples collected prior to chestnut planting (Pinchot et al., 2017). While these studies suggest that *P. cinnamomi* is widespread in the southern and central Appalachians, they did not provide insight into factors influencing its distribution.

*P. cinnamomi* distribution is influenced by many factors interacting across multiple spatial scales, including climatic variables (e.g., temperature), edaphic variables (e.g., soil water availability), and biotic variables (e.g., presence/absence of host species, competition from other microbes), as well as anthropogenic variables (e.g., management or restoration efforts introducing the pathogen to a new area). With respect to climate, *P. cinnamomi* has poor tolerance for freezing temperatures (Bergot et al., 2004); in the eastern U.S., *P. cinnamomi* has been detected in forests ranging as far north as southern Pennsylvania and Ohio (Balci et al., 2013; McConnell and Balci, 2014). *P. cinnamomi* has previously been found throughout the central Appalachian region; therefore, we do not anticipate that cold temperatures will be an important factor influencing distribution. Rather, *P. cinnamomi* activity is known to increase (up to a point) with temperature, reducing *Quercus ilex* radicle length up to 26 °C (Martín-García et al., 2014) and causing more severe infection in *Eucalyptus marginata* up to 30 °C (Halsall and Williams, 1984). Thus, in eastern Kentucky, *P. cinnamomi* may be favored by warmer areas on the landscape. (For a thorough treatment of current and potential future impacts of climate on *P. cinnamomi* distribution, see Burgess et al., 2017).

With respect to soil, *P. cinnamomi* survival has been reported to be higher in moist soils than dry or flooded soils (Kuhlman, 1964; Hwang and Ko, 1978; Weste and Vithanage, 1979), although *P. cinnamomi* can survive prolonged periods of drought by producing survival structures such as chlamydospores (McCarren et al., 2005), stromata, or oospores (Crone et al., 2013a, 2013b), or by colonizing roots (Old et al., 1984; Jung et al., 2013). In parts of Australia and Mediterranean Europe, disease caused by *P. cinnamomi* has frequently been associated with moist, low-lying areas, such as drainages (Dawson and Weste, 1985; Wilson et al., 2003; Vannini et al., 2010; Keith et al., 2012), but the pathogen has also been isolated from drier ridgetop soils in some cases (Shea and Dell, 1981). Because eastern Kentucky receives plenty of annual precipitation (117.5 cm average [Cherry, 2006]), it is unclear whether moisture will influence *P. cinnamomi* distribution in this region.

Biotic factors that may limit distribution include presence of susceptible host species and intensity of competition from other members of the soil microbial community. *P. cinnamomi* is known to be a poor saprophyte (McCarren, 2006); thus, distribution is thought to be related to occurrence of host species (Crone et al., 2014). However, a recent study in Australia found that *P. cinnamomi* infects herbaceous understory plants (both annual and perennial) without causing disease (Crone et al., 2013a, 2013b), suggesting that the relationship of *P. cinnamomi* and hosts is more complex than previously thought. In the eastern U.S., host tree species of concern include white oak (*Quercus alba*), shortleaf pine (*Pinus echinata*), and especially American chestnut. Because shortleaf pine and American chestnut are uncommon in the study area, we anticipate that white oak may be an important host species in this study. With respect to microbial competition, a significant body of research has related *P. cinnamomi* survival to soil microbial communities (Halsall, 1982; Malajczuk et al., 1983), suggesting that presence of microbes including endospore-forming bacteria (Aryantha et al., 2000) and actinomycetes (Broadbent and Baker, 1974; You et al., 1996), or even microbial activity in general (Nesbitt et al., 1979), can suppress *P. cinnamomi* growth or survival. Additionally, some studies suggest that infection of host roots by ectomycorrhizal fungi can reduce host vulnerability to infection by *P. cinnamomi* (Corcobado et al., 2014). A previous study in a Robinson Forest watershed found that potential soil respiration rates were greater on the northeast-facing slope than the southwest-facing slope, suggesting a strong aspect effect on microbial activity (Abnee et al., 2004). Because *P. cinnamomi* may be competitively excluded by some microbial groups, it is possible that *P. cinnamomi* distribution will be restricted from more north-facing slopes.

Finally, *P. cinnamomi* is an introduced species in the eastern U.S. and may not yet be present in all watersheds where environmental and biological conditions are suitable. A recent study in California tied spread of *P. cinnamomi* into a previously uninfested area to use of infected nursery stock in restoration plantings (Swiecki and Bernhardt, 2017). While *P. cinnamomi* was previously documented in Robinson Forest (Rhoades et al., 2003; Sena et al., 2018b), it is unknown whether the pathogen was relatively recently introduced. If the pathogen were a recent introduction, we would expect its distribution to be related to potential invasion pathways, particularly roads and streams.

This study was initiated to characterize the distribution patterns of *P. cinnamomi* within two watersheds at different spatial scales in eastern Kentucky, with specific interest in identifying climatic, edaphic, biotic, and anthropogenic factors that may influence *P. cinnamomi* distribution.

## 2. Methods and materials

This study evaluated soils from Robinson Forest, an approximately 6000 ha research forest located in portions of Breathitt, Knott, and Perry Counties, Kentucky, in the Appalachian Coalfields. This section of the Cumberland Plateau is characterized by steep slopes (25–60%), with elevation differences ranging from 150 to 300 m (Smalley, 1986) and well-drained residuum or colluvial soils derived from sandstone, shale, and siltstone parent material (Kalisz et al., 1987). The underlying geology in the region consists of interbedded sandstone, siltstone, shale, and coal of the Breathitt formation of the Lower to Middle Pennsylvania age (McDowell et al., 1981; Wunsch, 1993). Vegetation in Robinson Forest is characterized as mixed-mesophytic forest (Braun, 1950) and dominated by more than 50 woody species including oak (*Quercus* spp.), hickory (*Carya* spp.), yellow poplar (*Liriodendron tulipifera*), and American beech (*Fagus grandifolia*) (Carpenter and Rumsey, 1976). Robinson Forest was clearcut between 1910 and 1920, but has since been managed by the University of Kentucky for research and teaching. Robinson Forest is not open for public recreation, and thus sustains very little foot and vehicle traffic.

Due to the high degree of topographic variability across this dissected landscape, we employed two sampling strategies to capture spatial variability at multiple scales. First, samples were collected (in late October to early November 2016) from 47 Continuous Forest Inventory (CFI) plots in the 1500 ha Clemons Fork watershed, Robinson Forest (Sena et al., 2018b). These plots are arranged in a systematic random design, appropriate for capturing broad patterns of spatial variability. Second, samples were collected (in early November 2017) from Little Millseat, a 79 ha subwatershed of Clemons Fork (Abnee et al., 2004). In Little Millseat, plots follow a random transect design, better suited than grid sampling for capturing smaller-scale variability. Briefly, Abnee et al. (2004) identified clusters of potential sampling points stratified by aspect (northeast/southwest), slope curvature (concave/convex), and landscape position (downslope/midslope/upslope). Sampling points were selected near the center of each selected

cluster, with each combination of landscape variables (12 combinations) replicated four times. Four soil samples were collected from the upper 5 cm of mineral soil in 50 ml tubes (Falcon© Corning Inc., Corning, NY, USA) from the corners of a square meter plot centered on the coordinates from each plot (48 plots total) identified in Abnee et al. (2004). For both sample sets, sampling occurred shortly after rain events, when soil moisture was generally expected to be suitable for P. cinnamomi growth.

All samples from the first set (hereafter, Clemons Fork) were screened using methods described by Sena et al. (2018b), and considered positive if screened as positive by any of the three detection methods performed. Samples from the second set (hereafter, Little Millseat) were screened using the leaf disc bait and PCR method (Sena et al., 2018b). Briefly, ~40 ml samples in 50 ml tubes were flooded with sterile water and baited with rhododendron leaf discs for 5 days. Leaf discs were stored at −4 °C until it was convenient to proceed with DNA extraction. DNA was extracted from leaf discs using QIAGEN DNeasy UltraClean Microbial DNA extraction kit, with an added proteinase K digestion step. Presence of amplifiable DNA was confirmed in every sample using ITS1-ITS4 primers, which amplify DNA from many taxa, including plants, oomycetes and fungi (White et al., 1990). Samples were screened for *P. cinnamomi* using published primers Ycin3F and Ycin4R (Schena et al., 2008; Kunadiya et al., 2017). Samples were screened in duplicate with positive controls, *P. cinnamomi* isolate RF5 (isolated from Robinson Forest, GenBank Accession #MF966152) at $1.5 \times 10^{-2}$ ng/PCR, and no-template negative controls.

The size of these sample sets was insufficient to support sophisticated species distribution modeling approaches, so a hypothesis-testing approach was adopted to screen candidate predictor variables. Data were grouped by *P. cinnamomi* screening results into “detected” or “not detected” groups and tested for differences between groups for each potential predictor variable using Welch two sample t-tests. Annual solar radiation (a climatic variable) derived from a fine spatial resolution (5 ft or 1.52 m) digital elevation data (DEM) using the ArcGIS *Solar Radiation* tool (Fu and Rich, 2002) was tested to assess potential temperature influence on *P. cinnamomi* distribution. Topographic position index (TPI), which describes the difference between the elevation at a central point and the mean elevation within a predetermined neighborhood (Weiss, 2001; De Reu et al., 2013) was assessed to consider landform effects. Edaphic GIS variables derived from topographic data that were assessed included topographic wetness index (TWI; Beven and Kirkby, 1979) and integrated moisture index (IMI; Iverson et al., 1997), which are indicators of soil water availability. For the Clemons Fork sample set, oak abundance data (a biotic variable) from the most recent (2013–2014) forest inventory were available, including abundance of oaks overall (*Quercus* spp.) and white oak particularly (*Quercus alba*)—these data were assessed to identify potential associations with host species or communities. For the Little Millseat dataset, soil respiration rates (another biotic variable) reported by Abnee et al. (2004) were assessed as a proxy for soil microbial activity. These included potential respiration at two incubation temperatures (15 °C and 25 °C) and moisture levels (native moisture content and field capacity), abbreviated FN (15 °C at native moisture), FFC (15 °C at field capacity), TWN (25 °C at native moisture), and TWFC (25 °C at field capacity). Finally, to estimate whether *P. cinnamomi* is a recent invader to these watersheds or has reached distribution equilibrium, distance to road and distance to stream were also assessed as distribution predictor variables.

## 3. Results

In Clemons Fork, *P. cinnamomi* was detected in 21 of 47 plots screened (45%) (Fig. 1). These plots exhibited lower IMI and TWI, but no significant differences in annual radiation, TPI, or distance to roads or streams. While there was no significant association of *Quercus alba* abundance with *P. cinnamomi* detection, plots in which *P. cinnamomi* was detected were characterized by higher *Quercus* spp. abundance.

In Little Millseat, *P. cinnamomi* was detected in 12 of the 48 plots screened (25%), three on the northeast-facing slope and nine on the southwest-facing slope (Fig. 1). Plots in which *P. cinnamomi* was detected received higher annual solar radiation and were characterized by lower IMI, but were not different from plots in which *P. cinnamomi* was not detected for TWI, TPI, distance to road, or distance to stream. In addition, differences in soil microbial respiration data from Abnee et al. (2004) between detected and not detected groups were not significant. However, difference in potential respiration rates at 25 °C and native soil moisture was nearly significant ($p = 0.0578$) (see Table 1).

## 4. Discussion

In this study, *P. cinnamomi* was detected in 25% and 45% of samples collected in the Little Millseat and Clemons Fork watersheds, respectively. These detection levels are similar to other studies in the southern and south-central Appalachians that reported detection frequencies of 12–45% (Campbell and Hendrix, 1967; Sharpe, 2017). However, this frequency is less than that reported by Pinchot et al. (2017), who found *P. cinnamomi* in all samples screened in a site in the Daniel Boone National Forest, Kentucky.

In Little Millseat, *P. cinnamomi* was positively associated with annual solar radiation, suggesting that it is favored by warmer sites in this steeply dissected watershed. Similarly, while *P. cinnamomi* distribution has traditionally been associated with moist, low-lying soils in drainages (Vannini et al., 2010), it was also detected in drier landscape positions (lower IMI and/or TWI) in both Little Millseat and Clemons Fork. These results suggest that *P. cinnamomi* distribution is not necessarily associated with wetter landscape positions in these watersheds.

In Clemons Fork, *P. cinnamomi* exhibited an association with abundance of *Quercus* species overall, but not with *Quercus alba* abundance specifically. White oak is a species of interest in the eastern U.S., particularly because of increasing demand for white oak for production of bourbon barrels. In light of this, white oak is the subject of the White Oak Initiative and other collaborative efforts to favor restoration and improved management (https://forestry.ca.uky.edu/white oak). A number of studies have demonstrated that *P. cinnamomi* causes infection in white oak (McConnell and Balci, 2014), but *P. cinnamomi* has not been conclusively identified as a driver of white oak mortality. The lack of *P. cinnamomi* association with white oak suggests that white oak is not an important host species in this system. However, the association of *P. cinnamomi* with oak species overall suggests either that *P. cinnamomi* distribution is related to distribution of oaks as susceptible hosts, or that *P. cinnamomi* distribution is related to the types of sites typically dominated by oak species. Regardless, our survey clearly demonstrates that *P. cinnamomi* occurs on oak-dominated sites, and thus presents potential risk to susceptible oak species.

In Little Millseat, soils from sites in which *P. cinnamomi* was detected weakly exhibited ($p < 0.10$) lower respiration rates under certain conditions (data from Abnee et al., 2004). Soils favorable for microbial activity (and especially activity of actinomycetes, endospore-forming bacteria) can be unfavorable for *P. cinnamomi* (Broadbent and Baker, 1974; Nesbitt et al., 1979; Halsall, 1982; Malajczuk et al., 1983; You et al., 1996; Aryantha et al., 2000). In this watershed, *P. cinnamomi* distribution may be restricted to drier upslope sites by competition from other microbes.

In addition, *P. cinnamomi* presence in these watersheds was not associated with distance to roads or streams, suggesting that the pathogen is not a recent invader to these watersheds. While it is possible that *P. cinnamomi* was inadvertently anthropogenically introduced to Robinson Forest during forest management in the past, the pathogen has spread across the landscape since introduction, and has likely spread across its suitable habitat by now.

Finally, our tiered sampling strategy uncovered varying degrees of

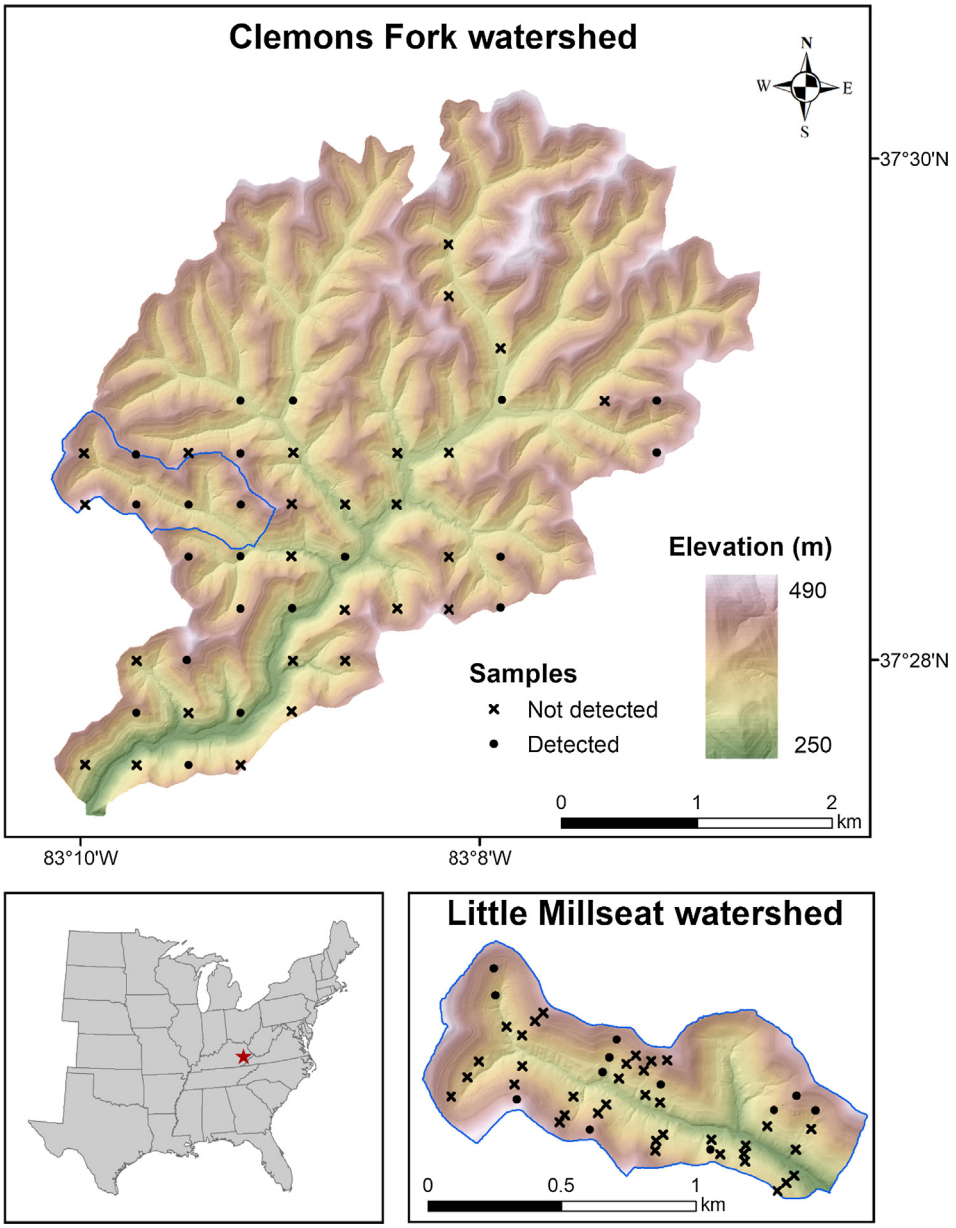


**Fig. 1.** *P. cinnamomi* distribution within two watersheds in Robinson Forest, Kentucky, USA.

consistency in distribution patterns at multiple spatial scales. Differences in IMI between detected and undetected plots were similar across scales (Clemons v. Little Millseat), suggesting a strong association of *P. cinnamomi* incidence with this landscape variable. Similarly, annual radiation exhibited consistent trends across spatial scales (although the difference between detected and undetected plots was significant only in Little Millseat). In contrast, nonsignificant trends toward higher TWI and lower TPI in detected plots in Little Millseat were not consistent with observed significantly lower TWI and nonsignificantly higher TPI in detected plots in Clemons Fork, suggesting that *P. cinnamomi* incidence is not closely related to these landscape variables.

## 5. Conclusions

The association of *P. cinnamomi* with drier sites (low TWI and/or IMI) is unexpected, differing from the traditional association of *P. cinnamomi* and diseases it causes with low-lying soils in drainages. It is likely that eastern Kentucky receives sufficient rainfall to permit *P. cinnamomi* survival even in drier sites; however, the precise mechanisms whereby *P. cinnamomi* appears to prefer drier sites must be elucidated. It is possible, given the slight negative association of *P. cinnamomi* with microbial respiration rates, that microbial competition may exclude *P. cinnamomi* from sites with higher moisture availability.

*P. cinnamomi* was also not associated with abundance of white oak, although it was associated with abundance of oak species overall. In other studies, *P. cinnamomi* was found at high incidence rates in American chestnut plantings (Brosi, 2001; Rhoades et al., 2003), suggesting that the presence of highly susceptible species could lead to increased abundance of *P. cinnamomi* in some forest systems. The association of *P. cinnamomi* with oak-dominated sites may present challenges to conservation and management of susceptible oak species under certain environmental scenarios, but almost certainly presents challenges to restoration of the highly susceptible American chestnut.

While *P. cinnamomi* is not native to eastern Kentucky, our data suggest that it is not a recent invader in our sampled watersheds. Newly introduced species tend to exhibit distribution patterns clustered around invasion points, but our data showed no spatial relationship

**Table 1**
Candidate predictor variables were classified as "detected" or "not detected," and differences between groups were detected using Welch two-sample t-tests. Bold indicates $p < 0.05$.

| | Mean (d.)* | Mean (n.d.) | t | df | p-value |
|---|---|---|---|---|---|
| *Little Millseat* | | | | | |
| Radiation (annual) (WH/m$^2$) | 1,303,000 | 1,153,000 | −2.499 | 24.0 | **0.0197** |
| IMI | 35.44 | 41.75 | 2.185 | 34.5 | **0.0358** |
| TWI | 5.26 | 5.14 | −0.358 | 20.4 | 0.7241 |
| TPI (ft) | 3.91 | 4.59 | 0.111 | 17.2 | 0.9131 |
| FN | 14.73 | 18.04 | 0.950 | 40.3 | 0.3461 |
| FFC | 13.21 | 15.03 | 0.560 | 32.2 | 0.5766 |
| TWN | 22.46 | 31.33 | 1.970 | 29.9 | 0.0578 |
| TWFC | 18.71 | 23.56 | 1.320 | 22.7 | 0.2006 |
| Distance to Road (m) | 92.60 | 80.64 | −0.704 | 25.0 | 0.4880 |
| Distance to Stream (m) | 206.51 | 200.16 | −0.168 | 17.8 | 0.8682 |
| *Clemons Fork* | | | | | |
| Radiation (annual) (WH/m$^2$) | 1,215,602 | 1,143,771 | −1.268 | 40.8 | 0.2122 |
| IMI | 35.90 | 41.70 | 2.311 | 44.4 | **0.0255** |
| TWI | 4.78 | 5.54 | 2.020 | 43.1 | **0.0497** |
| TPI (ft) | 10.10 | 2.77 | −1.371 | 41.7 | 0.1779 |
| *Quercus* abundance | 8.48 | 5.46 | −2.133 | 42.4 | **0.0387** |
| *Q. alba* abundance | 3.62 | 2.23 | −1.169 | 34.6 | 0.2503 |
| Distance to Road (m) | 207.58 | 214.48 | 0.119 | 37.4 | 0.9057 |
| Distance to Stream (m) | 250.48 | 218.04 | −0.878 | 40.8 | 0.3851 |

* d. = "detected," n.d. = "not detected," t = t-stat returned by Welch two-sample *t*-test, df = degrees of freedom calculated by Satterthwaite method, IMI = Integrated Moisture Index, TWI = Topographic Wetness Index, TPI = Topographic Position Index, FN = potential respiration rate at 15 °C and native moisture content, FFC = Potential respiration rate at 15 °C and field capacity moisture, TWN = Potential respiration rate at 25 °C and native moisture content, TWFC = Potential respiration rate at 25 °C and field capacity moisture (FN, FFC, TWN, TWFC from Abnee et al. (2004); respiration given as μg C/g soil/day). *Quercus* spp. and *Quercus alba* abundance given as number of stems > 5" DBH per tenth-acre.

with the most likely invasion routes in our watersheds—streams or roads. These data suggest that *P. cinnamomi* has reached an equilibrium distribution constrained by climatic, edaphic, and biotic factors. However, this question should be further explored by additional sampling for *P. cinnamomi* incidence over time, especially capturing seasonal variability. In addition, studies in other regions have reported that *P. cinnamomi* propagules can be transported by animals (e.g., Li et al., 2014); however, the potential for wildlife species present in Robinson Forest (e.g., black bear, elk, white-tailed deer, Virginia opossum, racoon, etc.) to move *P. cinnamomi* propagules has not been investigated and presents opportunity for further research.

Finally, *P. cinnamomi* is not associated with disease across all environmental conditions. In Europe, researchers found that disease caused by *P. cinnamomi* is typically associated with moist soils in drains (Vannini et al., 2010). Similarly, in Australia, *P. cinnamomi* was detected across a reclaimed mine site, but jarrah dieback (*Eucalyptus marginata*) was associated with poorly drained landscape areas where rainwater ponded (Hardy et al., 1996). While this study documents that *P. cinnamomi* is distributed across a wide range of environmental conditions, further research in the region will be necessary to clarify the environmental conditions in which *P. cinnamomi* will cause disease in susceptible species (especially American chestnut and white oak). Further research is also necessary to evaluate the potential role of microbial community competition in restricting *P. cinnamomi* distribution.

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