

## Host heterogeneity influences the impact of a non-native disease invasion on populations of a foundation tree species

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**Abstract.** Invasive pathogens are becoming increasingly important in forested ecosystems, yet they are often difficult to study because of their rapid transmission. The rate and extent of pathogen spread are thought to be partially controlled by variation in host characteristics, such as when host size and location influence susceptibility. Few host-pathogen systems, however, have been used to test this prediction. We used Port Orford cedar (*Chamaecyparis lawsoniana*), a foundation tree species in riparian areas of California and Oregon (USA), and the invasive oomycete *Phytophthora lateralis* to assess pathogen impacts and the role of host characteristics on invasion. Across three streams that had been infected for 13–18 years by *P. lateralis*, we mapped 2241 trees and determined whether they had been infected using dendrochronology. The infection probability of trees was governed by host size (diameter at breast height [DBH]) and geomorphic position (e.g., active channel, stream bank, floodplain, etc.) similarly across streams. For instance, only 23% of trees <20 cm DBH were infected, while 69% of trees ≥20 cm DBH were infected. Presumably, because spores of *P. lateralis* are transported downstream in water, they are more likely to encounter well-developed root systems of larger trees. Also because of this water-transport of spores, differences in infection probability were found across the geomorphic positions: 59% of cedar in the active channel and the stream bank (combined) were infected, while 23% of trees found on higher geomorphic types were infected. Overall, 32% of cedar had been infected across the three streams. However, 63% of the total cedar basal area had been killed, because the greatest number of trees, and the largest trees, were found in the most susceptible positions. In the active channel and stream bank, 91% of the basal area was infected, while 46% was infected across higher geomorphic positions. The invasion of Port Orford cedar populations by *P. lateralis* causes profound impacts to population structure and the invasion outcome will be governed by the heterogeneity found in host size and location. Models of disease invasion will require an understanding of how heterogeneity influences spread dynamics to adequately predict the outcome for host populations.

**Key words:** *Chamaecyparis lawsoniana*; disease ecology; foundation species; host heterogeneity; invasion ecology; *Phytophthora lateralis*; Port Orford cedar; riparian areas; Siskiyou Mountains.

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## INTRODUCTION

In spite of the importance of invasive pathogens in forested ecosystems, our ability to study their dynamics is often surprisingly limited due to their rapid rates of spread. Several important invasive pathogens are well-known by ecologists because of their dramatic consequences, including some oft-cited examples: the reduction of American chestnut (*Castanea dentata*) by the fungal pathogen, *Cryphonectria parasitica* (Anagnostakis 1987, Burke 2012), jarrah dieback by *Phytophthora cinnamomi* in Australian eucalyptus forests (Gregory 1983, Cahill et al. 2008), and the loss of five-needle pines due to white pine blister rust (*Cronartium ribicola*; Keane et al. 2011). These and many other emerging pathogens, especially those with air-borne or insect-transmitted propagules, spread over vast areas quickly (Liebhold et al. 1995, Aukema et al. 2010) making documenting the details of their spread rates and ecological impacts challenging.

And yet, it is precisely the details of the rate at which individuals within host populations are infected by pathogens that are needed to test some of the most important predictions about what governs the rate and extent of disease invasions. As with nondisease invasions, the initial spread of a disease through a host population is driven by pathogen production, dispersal rates, and host susceptibility (Mollison 1986). Host susceptibility is influenced by numerous factors that can vary considerably within a population, including local site conditions, genetic variation, and physical host traits such as size (Jarosz and Burdon 1988, Alexander and Antonovics 1995, Morrison 1996, Cobb et al. 2012). Theoretical work suggests that the magnitude of heterogeneity in these characteristics can control the rate of disease spread (Dwyer et al. 1997, Hastings et al. 2005), and a few empirical studies have shown this for non-plant disease systems (May and Anderson 1988, Dwyer et al. 2000, Park et al. 2001, Lloyd-Smith et al. 2005, Kilpatrick et al. 2006). For example, Neri et al. (2011) showed that the invasion of experimental populations (laboratory arrays) of sites (individual agar dots) by the fungal pathogen, *Rhizoctonia solani*, was slower when nutrient content varied more among dots within a population. For forest pathogens, however, few studies report variation

in susceptibility that can be related to host tree characteristics, and instead focus on describing mean infection rates for a given population (Gibbs 1978, Gibbs et al. 1999, Kizlinski et al. 2002). For example, the well-studied invasion of white pine blister rust across the range of whitebark pine (*Pinus albicaulis*) is usually described using the mean infection rate within a population (Larson 2011, Maloney et al. 2012). Campbell and Antos (2000), however, show that mortality due to blister rust can be related to tree size and that the relationship varies depending on stand age. Given the clear potential for heterogeneity in host susceptibility in driving invasion dynamics, the development of population models that can predict the outcome of disease invasions for forest trees will require careful descriptions of how infection rates are influenced by host characteristics. The study presented here describes the way in which a forest pathogen is influenced by the size and position of its host tree.

Port Orford cedar (*Chamaecyparis lawsoniana*) is a long-lived species that dominates riparian habitats in northern California (USA) and southwestern Oregon (USA; Figs. 1 and 2). Because Port Orford cedar is locally common and therefore defines overall forest structure, and because individual cedar play important roles by increasing soil-surface calcium, providing shade, and strongly controlling stream geomorphology, the species has been described as a foundation species (Ellison et al. 2005). Port Orford cedar is also host to an invasive oomycete, *Phytophthora lateralis*, that was first detected within the natural range of the cedar in 1952 and is almost always fatal for the host (Roth et al. 1957, Hansen et al. 2000). The pathogen is known to infect only one other species, Pacific yew (*Taxus brevifolia*), although at much lower rates than are found for Port Orford cedar (Hansen et al. 2000). *P. lateralis* infects the root system of cedars and eventually leads to host mortality by causing phloem necrosis extending from the roots to the lower stem of the tree (Zobel et al. 1985). Spores of the pathogen are spread over long distances primarily by vehicles that transport infected soil and carry it along roads where it can be deposited near a stream, and secondarily by foot traffic (e.g., elk, bears, and humans; Jules et al. 2002). Once the pathogen successfully infects





Fig. 1. Stream dominated by large a Port Orford cedar in the study area (Elder Creek in southwestern Oregon, USA). The largest tree visible is a Port Orford cedar that is stabilizing the stream bank, and the riffle in the foreground was formed by a fallen cedar. Port Orford cedar is important in structuring the shape of streams by stabilizing active channels, stream banks, and floodplains and by forming long-lived pools. Pools can be formed both by large, living root systems extending across streams or by fallen dead wood. Photo by E. S. Jules.

roots in a previously uninfected stream, mortality of cedars spreads downstream in flowing water and is amplified by production of additional spores on dying trees that are then carried to susceptible roots downstream (Kauffman and Jules 2006). Cedar that do not have their roots directly in the active channel or on the stream

bank (see icons in Fig. 3) can become infected either during frequent winter flooding events or by foot traffic carrying spores uphill. There is evidence for heritable variation in resistance (i.e., time until death after infection) but there is no known immunity of Port Orford cedar to *P. lateralis* (USDA Forest Service and USDI Bureau

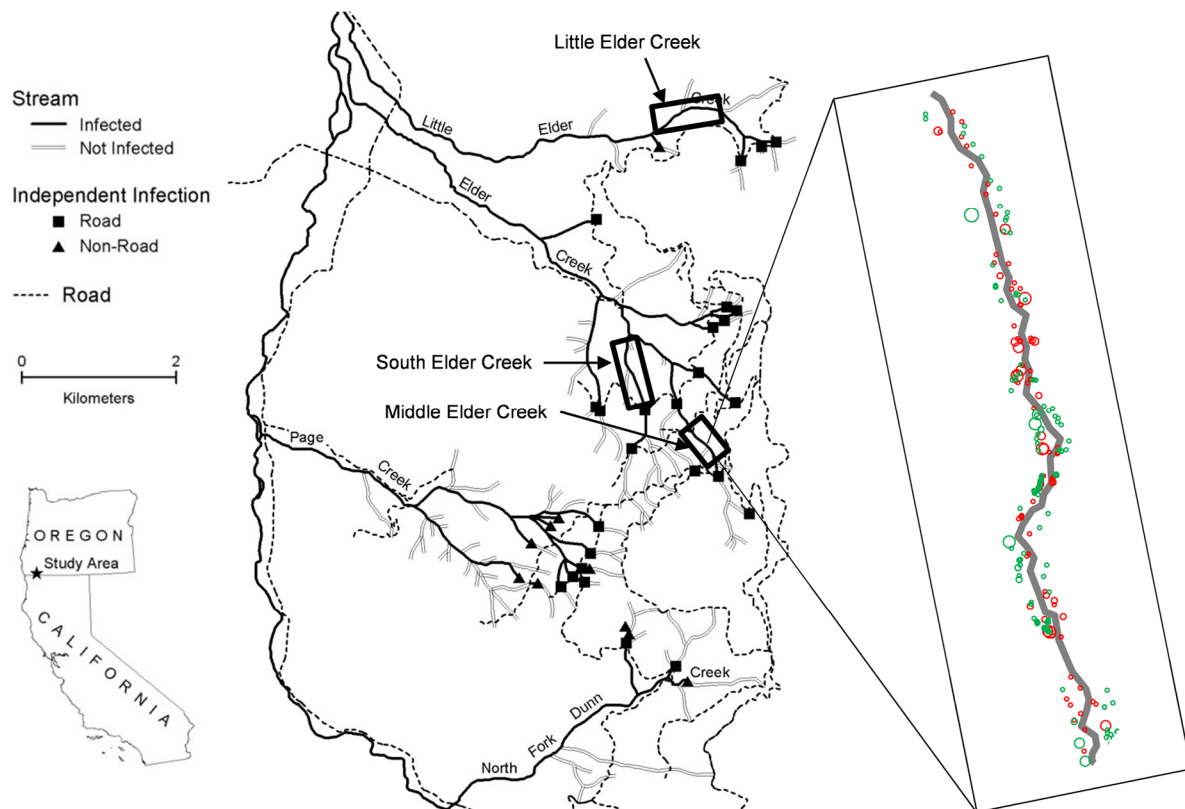


Fig. 2. Distribution of Port Orford cedar and the associated root pathogen, *Phytophthora lateralis*, in the study area of southwestern Oregon and northwestern California, USA. Cedars within the study area are generally restricted to riparian areas, such that their distribution follows the network of creeks. Both infected and uninfected streams are shown, as well as the road system along which the pathogen is dispersed. Filled squares indicate infection initiation locations along roads, and triangles indicate infection locations initiated by animal and foot traffic. Infections from these events spread downstream in water. Open rectangles show the three stream segments surveyed intensively for this study. The inset (right) shows a small segment of Middle Elder Creek. Green circles are healthy cedar and red are infected with *P. lateralis* (symptomatic or dead). Five size classes of cedar are shown for the segment, as well as their distance from the active channel (grey line).

of Land Management 2000). Whether living cedar in infected streams have remained healthy because of elevated resistance, the chance that spores have not contacted a root, and/or the presence of microsites that are relatively safe from infection, is unknown.

Port Orford cedar and *P. lateralis* provide an ideal system in which both the pattern of mortality and the heterogeneity in host characteristics can be described, even many years after the initial infection within a population (Kauffman and Jules 2006). Because the wood of Port Orford cedar is remarkably rot-resistant, dead trees remain standing and intact for many

decades (Carroll and Jules 2005), allowing for populations to be assessed long after pathogen invasion. This decay resistance not only allows for dead trees to be counted, but more importantly it allows the date of mortality for dead trees to be determined using the dendrochronological technique of crossdating (Stokes and Smiley 1968). Detecting the date of mortality makes it possible to eliminate trees that died prior to the initial infection from analyses, and we are unaware of any other host-disease system in which this technique has been used. In addition, there is evidence that host characteristics mediate infection by the disease, in particular



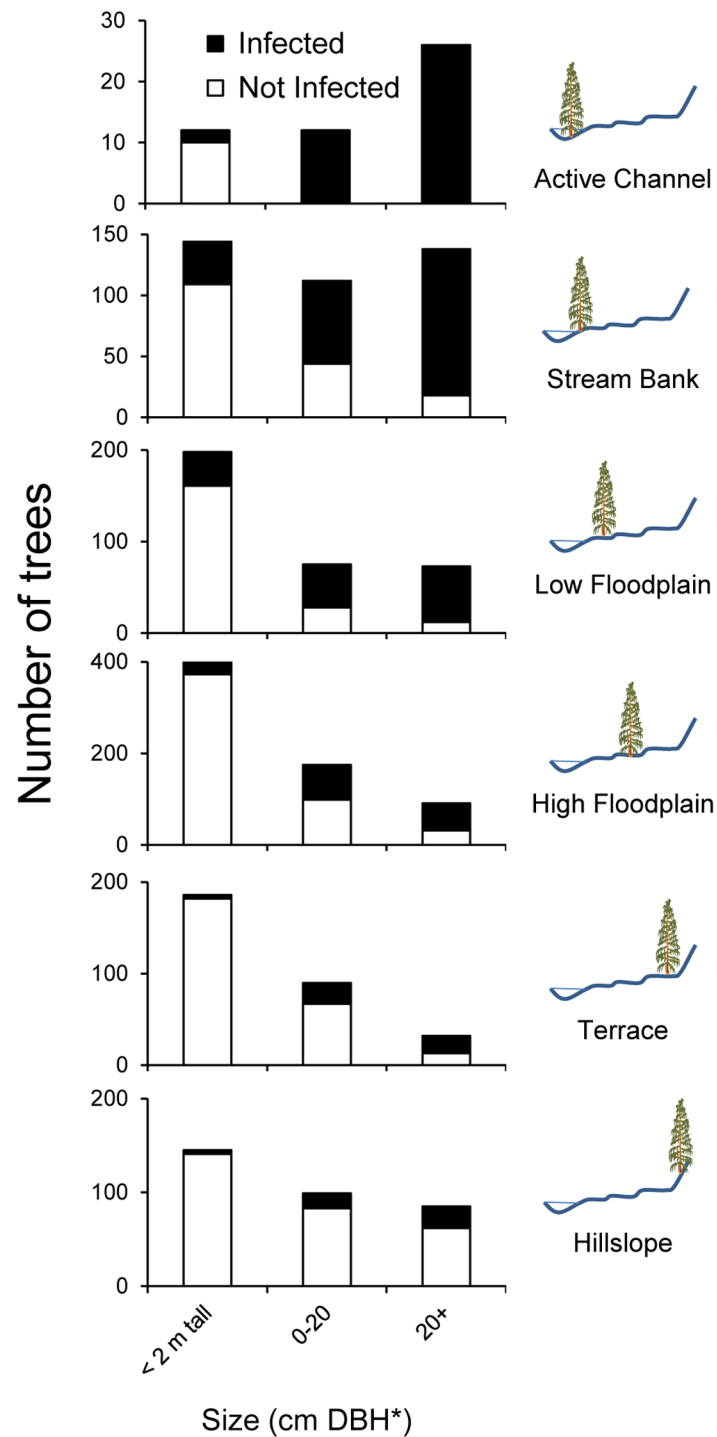


Fig. 3. The number of Port Orford cedar individuals uninfected or infected by the pathogen *Phytophthora lateralis* across size classes and geomorphic positions (panels). Data shown are all individuals summed across three stream study sites (see text for descriptions). Note that scales on the y-axes differ among rows. \*Size is diameter at breast height (DBH, cm) except the first group, which is for trees <2 m tall.

host proximity to the stream and host size (Kauffman and Jules 2006). Lastly, previous work has shown that most mortality within a stream segment occurs during a pulsed epidemic over ten years following initial exposure, such that most mortality resulting from *P. lateralis* within a population can be characterized after that time (Kauffman and Jules 2006). On average, ~40% of cedar within the riparian area die in the study area during this pulse, followed by low, but continual mortality (Kauffman and Jules 2006).

Our study had two goals. First, we provide an in-depth description of how Port Orford cedar populations are impacted by *P. lateralis*. We conducted precise mapping and a complete census of all trees (2241 individuals total) in all size categories throughout three separate stream segments. This component of our work is the most comprehensive description of the amount of Port Orford cedar lost due to this invasive pathogen. Second, we assess the role of host heterogeneity in mediating the invasion of *P. lateralis* and the ensuing pattern of mortality across the three stream segments. In particular, we assess the host's size and position on the stream—the latter a direct measure of a tree's exposure to stream-borne spores. Our previous work in this system has shown the importance of these two factors using a single stream (Kauffman and Jules 2006), where larger trees had higher infection probabilities than small trees and trees found near the stream had higher infection probabilities than those found further from the stream. Because the spores of *P. lateralis* are transported downstream in water, they are more likely to encounter the well-developed root systems of large trees and those trees near the active stream channel. Here we extend this work using three streams to test whether or not the role of host size and position are generalizable across the study area. Our results are necessary for the development of future models that could use population structure and differential mortality rates to predict the long-term outcome of *P. lateralis* invasions on Port Orford cedar populations.

## METHODS

### Study system

The study area is located in the Siskiyou Mountains of southwestern Oregon and northern

California, within the boundaries of the Rogue River-Siskiyou National Forest. Most of the study area is dominated by a mixed conifer forest comprised of Douglas-fir (*Pseudotsuga menziesii*), incense cedar (*Calocedrus decurrens*), tanoak (*Notholithocarpus densiflorus*), and Pacific madrone (*Arbutus menziesii*). The most common resource management activity has been timber harvesting; by the time of our initial field sampling (1998 and 1999), 35% of the area had been logged (USDA Forest Service and USDI Bureau of Land Management 2000). Within the study area, Port Orford cedar is primarily restricted to wet areas near streams, seeps, and other mesic sites, and is the dominant tree in riparian areas (Zobel et al. 1985, Jules et al. 2002).

We studied three independent stream segments that were infected with *P. lateralis* where the pathogen had been transported into the stream by vehicles traveling along logging roads (Fig. 2; Jules et al. 2002). The three segments vary somewhat in length and elevation: Little Elder Creek was 1150 m in length and ranged from 770 to 820 m elevation; middle tributary of Elder Creek (called Middle Elder Creek hereon) was 703 m in length and ranged from 1040 to 1130 m elevation; and southern tributary of Elder Creek (called South Elder Creek hereon) was 1098 m in length and ranged from 720 to 800 m elevation. Each stream segment shared similar topography, gradients and surrounding vegetation.

### Data collection

We surveyed all Port Orford cedar within a plot delineated along each stream that was wide enough to include all cedars within the portion of the watershed exposed to dispersing spores (usually  $\leq 10$  m from the stream center; Kauffman and Jules 2006). Because epidemic spread had occurred in all three streams since the early 1980s, and most mortality caused by *P. lateralis* occurs within ten years of initial stream infection (Kauffman and Jules 2006), we used the spatial distribution of infected cedars in combination with local stream topography to delineate the plot boundaries (Kauffman and Jules 2006). The study plot was of variable width; the plot was wider in areas with a large floodplain and narrower in stream sections with steep banks. Because of the local restriction of Port Orford cedar to moist sites, most (~70–90%) of the cedar

population falls within our study plots, with the remainder inhabiting upland sites that are too far from the inoculum carried in streams to become infected. For each tree >2 m tall, we determined their disease status (healthy, dead, or dying [symptomatic]), geomorphic position (active channel, stream bank, low floodplain, high floodplain, terrace, or hillslope), and diameter at breast height (DBH). Geomorphic position estimates the amount of water flowing near roots, and thus inoculum, reaching a given tree during normal flows or flood events. For trees <2 m tall we determined their disease status (healthy, dead, or dying), geomorphic position, and we measured their height. Highly decayed snags where their mortality predated the *P. lateralis* infection and dead trees with apparent causes of death other than *P. lateralis* (e.g., fire) were identified as natural mortality. Because DBH was not recorded for trees that were <2 m tall, we converted height to a meaningful measure that could be used in analyses of host size. To make this conversion, we first noted that trees very close to 2 m tall for which we did record DBH (e.g., 2.0–2.3 m height) had a DBH of approximately 1.0 cm. Thus, we assigned trees that were 2 m in height a DBH of 1.0 cm by dividing height by 200, and we used the same approach for all trees <2 m tall (i.e., height/200).

We determined the calendar year of death for all dead trees by extracting 2–3 increment cores from each tree and using the dendrochronological method of crossdating, which relies on shared climatic signatures that trees display in their annual rings (Douglass 1939, Swetnam et al. 1985). Cores were crossdated by visually aligning ring-width patterns and then statistically confirmed using the program COFECHA (Holmes 1983). A master ring-width chronology was created and used to crossdate dead trees (see also Carroll and Jules 2005). We were able to estimate the year of infection (which may predate death by several years) by recording the beginning of growth reduction of rings that results from invading mycelium (see Jules et al. 2002, Kauffman and Jules 2006 for further details). The invasion of a stream by *P. lateralis* results in a clear and dramatic increase in mortality that can be used to date the initial infection in a particular stream. Thus, for our three study stream segments, we omitted all trees that had died prior to

the time of pathogen invasion by using the mortality and infection dates determined using crossdating. The dates of initial *P. lateralis* invasion used for the three streams were as follows: Little Elder Creek, 1980; Middle Elder Creek, 1986; South Elder Creek, 1981.

### Statistical analyses

To assess the effects of size, geomorphic position, and stream site on infection status, an information theoretic approach (Burnham and Anderson 2002) based on Akaike's Information Criterion (AIC) was used to determine support for eight a priori models. The candidate model set included: (1) a model that includes tree size, geomorphic position, and stream site with an size  $\times$  geomorphic position interaction; (2) a model that includes tree size, geomorphic position, and stream site with an size  $\times$  stream site interaction; (3) an additive model that includes tree size, geomorphic position, and stream site; (4) a model that includes tree size, geomorphic position, and stream site, and all possible interaction terms; (5) a model that includes geomorphic position, tree size, and an interaction term; (6) an additive model that includes geomorphic position and tree size; (7) an additive model that includes tree size and stream site; and (8) an additive model that includes geomorphic position and stream site. We include the size  $\times$  position interaction because Kauffman and Jules (2006) found that the decrease in infection risk of trees in higher geomorphic positions was less pronounced for large trees, presumably because large trees have extensive root systems that can better contact inoculum regardless of position.

We modeled the infection status of each tree as a function of the explanatory variables. All models were fit using general linear models (GLMs) assuming a binomial error distribution and logit link in R (R Core Team, 2013). AIC, corrected for small sample size (AIC<sub>c</sub>), was applied to determine which model, among our candidate set, was best supported by the data. AIC<sub>c</sub> minimizes loss of information in the data by relating the maximum likelihood to the number of parameters in the model (Anderson 2008). Akaike weights ( $w_i$ ) are the relative likelihood of the model given the data, which are normalized across the set of candidate models to sum to one,



and can be interpreted as ‘model probabilities’. A model whose Akaike weight approaches 1 is unambiguously supported by the data. Multi-model inference is typically employed where there is no single model that is strongly supported by the data (i.e., best model  $w < 0.9$ ) (Johnson and Omland 2004, Anderson 2008). Model coefficients are considered significantly different from zero based upon likelihood profile confidence intervals. We inspected binned residual plots for indications of a non-linear relationship between the predicted values and the residuals and to check for constant variance (Gelman and Hill 2007). No signs of non-linearity or non-constant variance were detected. Logistic regression is non-linear on the probability scale and thus cannot be simply interpreted on the scale of the data. Therefore, average predictive comparisons are presented, which give the expected, or average difference in the probability of infection corresponding to a unit difference in an input variable (Gelman and Hill 2007).

In order to determine the relative importance of the three predictor variables included in the best supported model for infection (i.e., tree size, geomorphic position, and site) we used a likelihood ratio test, which evaluates the loss of model fit from elimination of one or more terms from a model. The likelihood ratio test statistic ( $D$ , equivalent to deviance) is calculated as twice the difference of the log likelihood of a base model (here, the best AIC model) and the alternative (here, a set of models that exclude either site, tree size, or geomorphic position).  $D$  is asymptotically  $\chi^2$  distributed with degrees of freedom equal to the difference in degrees of freedom between the alternative and base model (Faraway 2006). We use the magnitude of  $D$  for each alternative model to assess the relative contribution of three predictors (stream site, tree size, geomorphic position) to the prediction of infection status.

To assess the impact of *P. lateralis* on the reduction of Port Orford cedar basal area across the geomorphic positions, we calculated basal area as the area of the circular bole of the tree (area =  $\pi r^2$ , where  $r = \text{DBH}/2$ ). For trees <2 m tall we used their estimated DBH for basal area calculations (see above description). For each of the three stream segments, we used separate  $\chi^2$  tests to assess differences in the proportion basal

area killed across the six geomorphic positions. We opted not to use allometric equations to convert our basal area ( $\text{cm}^2$ ) measures to an estimate of biomass (kg) for two reasons. First, no study has specifically mensurated Port Orford cedars for use in an allometric equation and we do not consider the available biomass estimators robust. Second, and more importantly, since a primary goal in our analysis was to compare the relative amount of infected and uninfected material among geomorphic positions, basal area offers a direct measure with greater precision than a biomass estimator.

## RESULTS

We surveyed a total of 2241 trees, of which 611 were found in Little Elder Creek, 609 in Middle Elder Creek, and 1021 in South Elder Creek. In total, we found 779 dead trees (35% of total) across the three streams. Crossdating was successful for determining the date of mortality for most dead Port Orford cedars. Only 36 of the 779 dead trees could not be confidently crossdated, of which 14 were snags, suggesting their death predated infection. Trees for which crossdating demonstrated they had been dead before the arrival of *P. lateralis* infection reduced the total number of trees to 2124 (i.e., 555, 581, and 988 for Little Elder Creek, Middle Elder Creek, and South Elder Creek, respectively). Overall, the proportion of trees that had been infected (killed or dying) at the time of our survey was 44%, 30%, and 27% for Little Elder Creek, Middle Elder Creek, and South Elder Creek, respectively. Overall, 32% of cedar had been infected across the three streams. Across the three streams, 59% of cedar in the active channel and the stream bank were infected, while 23% of trees found on higher geomorphic types were infected.

The risk of cedar individuals becoming infected by *P. lateralis* varied depending on their size (Figs. 3 and 4), geomorphic position (Figs. 3 and 5), and site (Table 1). Model 1, which includes a size  $\times$  geomorphic position interaction and creek site as parameters received strong support ( $w_1 = 0.959$ ; Table 1) when compared with the other seven models in the candidate set using AIC<sub>c</sub>. The weight of evidence for this model ( $w_1 = 0.959$ ) strongly suggests that differences in tree size, geomorphic position, and creek site are

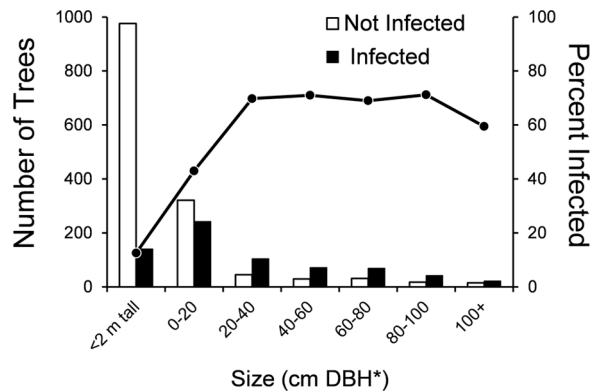


Fig. 4. The number of Port Orford cedar individuals uninfected or infected by the pathogen *Phytophthora lateralis* across size classes and the percentage of cedar individuals infected (secondary y-axis). \*Size is diameter at breast height (DBH, cm) except the first group, which is for trees <2 m tall. Data shown are all individuals summed across three stream segments (see text for descriptions).

predictive of infection status. Given the weight of evidence for the best fit model, we judged other models as unlikely to implausible (e.g.,  $w_2 = 0.006$ ) and did not employ model averaging techniques. We found that most of the main effects parameter estimates were significant predictors of infection (e.g., size and geomorphic

position), while the effect size and significance of interaction effects were less consistent (Appendix: Table A1).

Likelihood ratio test results and AIC model ranking suggest that while stream site is a statistically significant predictor of infection status, its effect size compared to other predictors is small. Model 5, which does not contain stream site as a predictor (see Table 1 for model specifications), but retains all other predictors from Model 1 has a change in deviance ( $D$ ) of 12.52 ( $P < 0.01$ ,  $df = 2$ ; Appendix: Fig. A1). In contrast, Models 7 and 8, which drop geographic position and tree size as predictors, respectively, have changes in deviance ( $D$ ) of 270.05 ( $P < 0.0001$ ,  $df = 8$ ) and 272.87 ( $P < 0.0001$ ,  $df = 4$ ; Appendix: Fig. A1). Further, if the effects of geomorphology or tree size varied spatially, we would expect that models with strong AIC support would include site interactions with the other predictors. However, the best-supported model including a site interaction, Model 4, received an AIC weight of <1% ( $w_5 = 0.005$ ; Table 1). These results provide evidence for generality of tree size and geomorphology effects on the infection process.

Increasing tree size corresponded to an increase in infection risk across all geomorphic positions and creek sites (Fig. 6; Appendix: Table A1). For example, a 20 cm DBH cedar at the

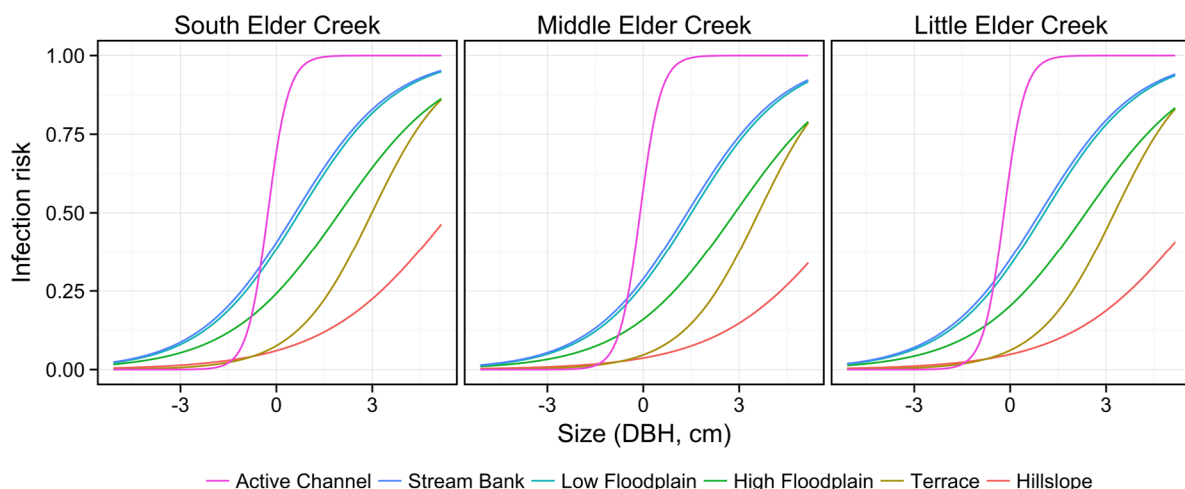


Fig. 5. The probability of infection by *Phytophthora lateralis* for cedars found in three creeks (panels) and across six geomorphic positions (color codes). Geomorphic positions are ordered in the color codes from most exposed to least exposed (left to right) to water-borne spores of *P. lateralis*. Infection probabilities are a product of general linear models assuming a binomial error distribution and logit link. The x-axis (host size) uses a log scale.

Table 1. Candidate set of logistic regression models used to evaluate risk of Port Orford cedar infection by *Phytophthora lateralis*. Models considered the effects of tree size, geomorphic position, and stream site on infection risk. Model structure, number of parameters ( $K$ ), change in Akaike's Information Criterion, adjusted for sample size ( $AIC_c$ ), and  $AIC_c$  weights are provided. An asterisk (\*) indicates the model includes both main and interaction effects.

| No. | Model   | $K$ | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weights |
|-----|---|-----|---------|----------------|-----------------|
| 1   | Size + position + size $\times$ position + site | 14  | 1844.72 | 0.00           | 0.959           |
| 3   | Size + position + site                          | 9   | 1853.03 | 8.31           | 0.015           |
| 5   | Size + position + size $\times$ position        | 12  | 1853.18 | 8.47           | 0.014           |
| 2   | Size + position + size $\times$ site            | 11  | 1854.69 | 9.97           | 0.007           |
| 4   | Size $\times$ position $\times$ site            | 36  | 1855.04 | 10.31          | 0.005           |
| 6   | Size + position                                 | 7   | 1862.51 | 17.79          | 0.000           |
| 7   | Size + site                                     | 4   | 2107.1  | 262.38         | 0.000           |
| 8   | Position + site                                 | 8   | 2388.02 | 543.3          | 0.000           |

stream bank was, on average, 19% more likely to be infected than a 5 cm tree at the same location. The geomorphic position of the cedar also strongly influences its risk of infection. A cedar in a geomorphic position relatively isolated from the creek had a lower average risk of infection. For example, on average, a cedar at the stream bank was 26% more likely to be infected than a tree on a terrace. The effect of creek site on infection was less obvious; on average, a cedar on a terrace at South Elder Creek was only about 5% more likely to be infected than a similar tree at Middle Elder Creek, though a similar comparison including Little Elder Creek is not informative due to the degree of uncertainty associated with its coefficient estimate (Appendix: Table A1).

The basal area infected was 63% of the total basal area found across the three streams, and the proportion of basal area infected varied significantly across the geomorphic positions at all three sites (Little Elder Creek:  $\chi^2 = 199648$ ,  $df = 5$ ,  $P < 0.0001$ ; Middle Elder Creek:  $\chi^2 = 76828$ ,  $df = 5$ ,  $P < 0.0001$ ; South Elder Creek:  $\chi^2 = 87245$ ,  $df = 5$ ,  $P < 0.0001$ ). Specifically, geomorphic positions farther from the active channel had less basal area infected than those closer to the moving water (Fig. 6). For example, in the active channel, ~100% of the basal area had been infected, and 88% of the basal area had been infected in the stream bank position. In contrast, 45% of the basal area on terrace sites and 25% of the basal area on hillslope positions were infected.

## DISCUSSION

This study details a substantial impact of an invasive disease epidemic on a riparian foundation tree species. Summed across three independent stream segments, 32% (690 of 2124) of Port Orford cedar individuals censused and 63% of the total Port Orford cedar basal area had been killed by *P. lateralis*. The study also demonstrated that the dynamics of this invasive disease will be strongly controlled by host heterogeneity: individual cedar were not equally at risk of infection. Larger trees, and those located on geomorphic positions with greater exposure to spores (i.e., nearer stream water), were more likely to be killed. For instance, only 23% of trees <20 cm DBH were infected, while 69% of trees  $\geq 20$  cm DBH were infected. Fifty-nine percent of cedar in the active channel and on the stream bank were infected, while only 23% of trees found on other, higher geomorphic types were infected. In agreement with theoretical work suggesting host and site characteristics can influence disease invasions (Mollison 1986, Burdon et al. 1989, Swinton and Anderson 1995), our work suggests that the development of models used to forecast the outcome of the cedar-*Phytophthora* system will rely on the characterization of these differential mortality rates across gradients of host characteristics. Specifically, a model developed to predict how *P. lateralis* invades and impacts Port Orford cedar forests would perform poorly if it could not account for the characteristics of the particular cedar populations being modeled, such as population size structure and the relative amount of cedar on the various geomorphic



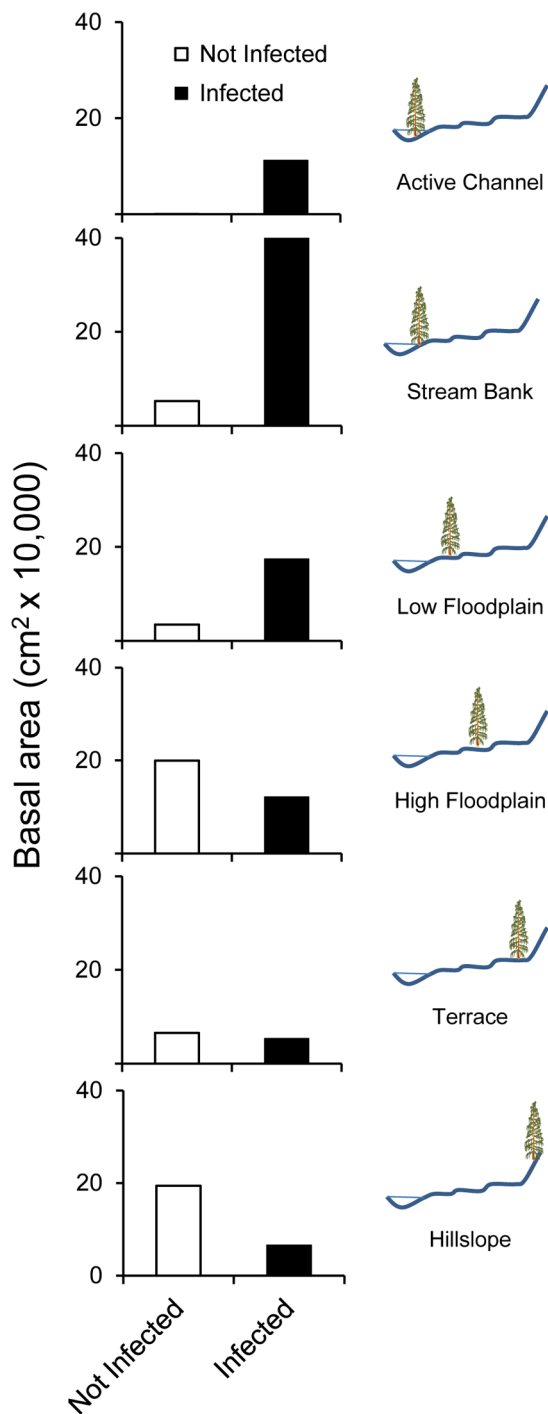


Fig. 6. Basal area ( $\text{cm}^2 \times 10,000$ ) of Port Orford cedar uninfected or infected by the pathogen *Phytophthora lateralis* across six geomorphic positions. Data shown are all individuals summed across three stream study sites (see text for descriptions).

positions.

In the cedar-*Phytophthora* system, the causes for differences in mortality among size and position of hosts are relatively simple, though the result is one that will likely produce complex future population dynamics. Large trees have larger root systems and are thus bigger targets for spores moving in water from upstream infections, and trees closer to the stream are more likely to have roots in the water or near floodwater levels. E. M. Hansen (*unpublished manuscript*) noted the same pattern of Port Orford cedar mortality caused by host size and position in his survey of infected Port Orford cedar forests, though his work did not include an analysis of the strength of either relationship. In previous work (Kauffman and Jules 2006), we showed similar results using one of the three creeks (Little Elder Creek) described in this paper. Our current study tested the generality of previous results using three independent streams, and also used a more useful measure of exposure to inoculum. Kauffman and Jules (2006) used linear distance to the stream center rather than geomorphic position to characterize the likelihood of an individual tree contacting a *P. lateralis* spore moving downstream, as did E. M. Hansen (*unpublished manuscripts*). However, because the topography in the region of Port Orford cedar is complex, the functional role of distance will differ markedly within and between streams. Geomorphic position, on the other hand, is easily assigned to individual trees in all sites, and is a better predictor of water reaching a given tree during flood events. In addition, geomorphic position should allow for easier estimation of simple demographic parameters to be used in future epidemiological models.

The reduction of the Port Orford cedar by *P. lateralis* has large population-level consequences. Infected stands are comprised of fewer large trees; the proportion of an infected population comprised of trees  $>20$  cm is half of an uninfected population (10% vs. 21%). Importantly, because larger trees tend to be found closer to the stream, and because they are therefore more likely to be infected, *P. lateralis* has a larger impact on cedar biomass than on population size per se. In the active channel and stream bank combined, 91% of the basal area was infected, while only 50% was infected among all other,

higher geomorphic types.

Our work adds to a wealth of empirical work that has been done on the impacts of invasive plant pathogens, in particular for tree diseases (Liebhold et al. 1995, Orwig 2002, Holdenrieder et al. 2004, Condeso and Meentemeyer 2007, Filipe et al. 2012, Boyd et al. 2013). For well-known systems, such as Dutch elm disease and chestnut blight, population-level mortality rates have been estimated, which are often coarse measures of the proportion of individuals infected or killed across broad areas (Gibbs 1978, Anagnostakis 1987, Kizlinski et al. 2002). Though they are less common, studies that describe separate infection or mortality rates for different size classes of hosts yield significantly more information, and have recently been conducted for a number of well-known diseases such as sudden oak death and white pine blister rust (e.g., Campbell and Antos 2000, Cobb et al. 2012).

Theoretical work in disease ecology points to the need for understanding the role of host heterogeneity in controlling susceptibility because heterogeneity per se can drive both the rate and extent of pathogen invasions (Holdenrieder et al. 2004). Size structured models of host populations, for instance, require size-specific mortality rates to forecast the impact of disease on population viability. Spatial heterogeneity in susceptibility would further strengthen these models. In the cedar-*Phytophthora* system, we have now described variation in susceptibility due to host size and spatial position, precursors for model development. Similar size structured models have been produced for sugar pine (*Pinus lambertiana*) infected by the invasive white pine blister rust (*Cronartium ribicola*; van Mantgem et al. 2004), and for whitebark pine (*Pinus albicaulis*) infected by white pine blister rust (Field et al. 2012). For Port Orford cedar, additional work will be needed to describe how reproductive effort and recruitment of seedlings is impacted by the *P. lateral*is pathogen.

The unique autecology of Port Orford cedar allowed us to describe the cedar-*Phytophthora* relationship, even though the field data for our analysis was collected almost two decades after initial infection. Individual cedars are remarkably decay resistant, such that all but the smallest dead cedars remained intact between mortality and sampling. For instance, in 1998, Carroll and

Jules (2005) collected cores from one dead Port Orford cedar that had died in 1738 and was still standing with intact wood. Standing individuals in our sites that have died over the past 200 years are common (Kauffman and Jules 2006). In addition, it is unlikely that conducting the study at a later date when the streams had been infected for longer periods would yield significantly different results; previous work suggests that most mortality occurs within the first ten years of infection (Kauffman and Jules 2006). Our three study stream segments had been infected for 13–19 years. On the other hand, it will be important to assess whether the factors that governed the initial pulse of high mortality during the first decade or two of *P. lateral*is invasion will remain important in subsequent phases of the epidemic.

Besides the direct impacts of *P. lateral*is on Port Orford cedar, the disease invasion we describe is likely to have large community-wide impacts (Ellison et al. 2005), and these effects will also be partly determined by the differential mortality of cedars resulting from heterogeneity in host size and position. In the riparian zone of infected streams, increases in light, soil temperature, water temperature, and decomposition rates can be expected, as well as changes in understory flora and calcium levels in surface soils. To date, none of these potential changes have been measured in the cedar-*Phytophthora* system. Douglas-fir may increase in importance in parts of the riparian area when cedars die, but our observation suggests that Douglas-fir cannot establish in the active channel or on the stream bank; if true, this means that the *P. lateral*is invasion may reduce the physical restrictions on the stream course that are often established by large cedars adjacent to the active channel. Furthermore, large Douglas-fir snags that fall into the stream will not produce long-lived pools because they decay much faster than Port Orford cedar. Other disease invasions have resulted in large community-wide changes, such as those caused by the loss of American chestnut and the huge mast resource those forests produced (Elliott and Swank 2008). Recent work on sudden oak death has demonstrated large directional changes in plant community composition in infected forests as a result of the disease invasion and the loss of susceptible taxa (Cobb et al. 2012,

Metz et al. 2012). In addition, sudden oak death also appears to change the fire regime in these forests (Kuljian and Varner 2010, Valachovic et al. 2011, Metz et al. 2013).

The long-term prognosis of Port Orford cedar across its range seems unclear. Some earlier mapping projects attempted to describe the extent of the *P. lateralis* invasion, and are useful at a very coarse level (e.g., USDA Forest Service and USDI Bureau of Land Management 2003). Unfortunately, Jules et al. (2002) demonstrated, using detailed censuses of the same study area used in this paper, that these maps probably underestimate the actual distribution of the pathogen greatly (see also Ritts 2003). Our casual observation suggests that the number of new infections (sites or streams) has declined in the last ten years, perhaps because of the sharp reduction in timber harvest (and concomitant loss of heavy vehicle traffic) or because of the continued reduction in the number of high risk sites. Regardless, there continue to be observations of low-probability, high-impact invasions into previously uninfected areas, such as the Kalmiopsis Wilderness (a mostly roadless area), the upper Sacramento River watershed (the cedar's eastern range boundary), and Willow Creek (near the cedar's southern range boundary). Our results suggest that mortality in these newly infected sites will be high, as the sites are similar to our own in that cedars are highly restricted to riparian areas.

Among the growing number of invasive species, exotic pathogens have initiated some of the most dramatic and well-known alterations to ecological systems (Orwig 2002, Liu et al. 2007, Burke 2012, Fisher et al. 2012). The rapid movement of many pathogens, especially those with air-borne or insect-transmitted propagules, coupled with often virulent effects, have in some cases produced significant transformations of natural assemblages over vast areas (Liebhold et al. 1995). The need for a better understanding of these invasions is driven, in part, by the tantalizing possibility of making better predictions about disease impacts across heterogeneous environments and of making better predictions of what interventions are needed to maintain host populations at stable sizes. Either of these tasks requires descriptions of how host and site variability drive infection rates. For the cedar-

*Phytophthora* system, we have shown that these two forms of variability are critical in producing differences in disease incidence, and, perhaps more importantly, that coarse measures of disease incidence could not be used to successfully explore the impact of the disease on long-term cedar population dynamics.

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## SUPPLEMENTAL MATERIAL

### APPENDIX

Table A1. Coefficient estimates and coefficient standard errors for the top logistic regression model (tree size + geomorphic position + (tree size  $\times$  geomorphic position) + creek site) as evaluated by Akaike's Information Criterion (AIC). Residual deviance = 1816.5, null deviance = 2677.5.

| Parameter                          | Estimate | 95% CI       |
|------------------------------------|----------|--------------|
| Intercept                          | −2.50    | −3.12, −1.98 |
| Tree size (log DBH)                | 0.84     | 0.63, 1.08   |
| Geomorphic position                |          |              |
| Hillslope                          | −0.25    | −1.08, 0.57  |
| High floodplain                    | 1.36     | 0.80, 2.00   |
| Low floodplain                     | 2.03     | 1.44, 2.69   |
| Stream bank                        | 2.12     | 1.52, 2.79   |
| Active channel                     | 3.32     | 1.34, 6.17   |
| Creek site                         |          |              |
| Middle Elder Creek                 | −0.52    | −0.80, −0.23 |
| Little Elder Creek                 | −0.23    | −0.53, 0.07  |
| Interactions                       |          |              |
| Hillslope $\times$ tree size       | −0.33    | −0.63, −0.04 |
| High floodplain $\times$ tree size | −0.26    | −0.52, −0.02 |
| Low floodplain $\times$ tree size  | −0.18    | −0.45, 0.07  |
| Stream bank $\times$ tree size     | −0.18    | −0.45, 0.06  |
| Active channel $\times$ tree size  | 2.25     | 0.33, 8.43   |

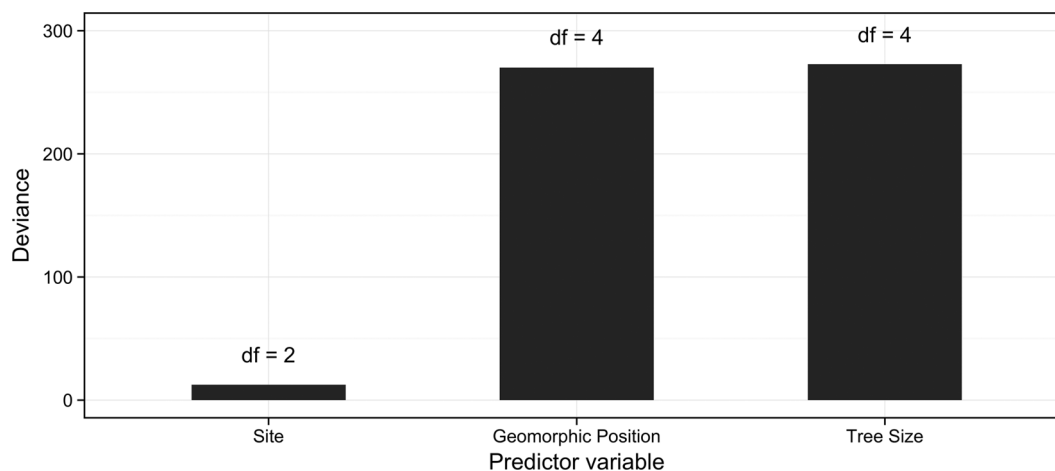


Fig. A1. The magnitude of the deviance ( $D$ ) is used to assess the relative contribution of predictor variables to prediction of infection status. Models that drop geographic position or tree size variables show much greater deviance than the model where site is dropped. This suggests that the effect size of site is relatively weak compared to other predictor variables.