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Source or sink? The role of soil and water borne inoculum in the dispersal of *Phytophthora ramorum* in Oregon tanoak forests

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ABSTRACT

Management of invasive species requires confidence in the detection methods used to assess expanding distributions, as well as an understanding of the dominant modes of spread. Lacking this basic biological information, during early stages of invasion management choices are often driven by available resources and the biology of closely related species. Such has been the case for the management of the phytopathogen, *Phytophthora ramorum*, causal agent of sudden oak death (SOD) of oaks and tanoaks. To detect *P. ramorum*, The Oregon SOD eradication program has relied upon the aerial observation of dead, overstory tanoak (*Notholithocarpus densiflorus*), an easily infected host widely distributed throughout the range of *P. ramorum* in Oregon. At risk is the possibility of misrepresenting the distribution of SOD, particularly if inoculum is predominately moved in soil and water, common dispersal pathways for other *Phytophthora* spp. To assess this risk, we performed surveys of understory vegetation in areas with a high risk of establishment of understory infection from soil and water sources: along roadsides within heavily trafficked areas with a history of SOD, and along streams known to contain *P. ramorum* inoculum. Additionally, we tested the alternative hypothesis of aerial dispersal, whereby infection in the understory would be spatially correlated with overstory mortality. Consistent with prior studies into the spatial structure of *P. ramorum* in Oregon, we found no evidence of understory infection in close proximity to roads in the absence of overstory mortality. Similarly, *P. ramorum* was only isolated from understory vegetation associated with streams when within close proximity to overstory sources, and more commonly further away from stream edges than within the splash and flood line. Both disease patterns are inconsistent with a dominate soil and water mediated dispersal mechanism. Rather, we found evidence supporting our alternative hypothesis of aerial dispersal whereby recovery of *P. ramorum* in the understory declined with increasing distance from the only known overstory source. These results support the use of aerial detection in describing the distribution of SOD in Oregon, and give further support to dispersal of inoculum in blowing fog or rain at scales not yet described for other forest *Phytophthora* species.

1. Introduction

Biotic invasions have the capacity to drive landscape scale changes in community diversity and ecosystem function, changes commonly associated with severe environmental and economic consequences (Crooks, 2002; Ehrenfeld, 2010; Loo, 2009; Vilà et al., 2011). Preventative or mitigation measures implemented to avoid adverse effects associated with the introduction of invasive species tend to be labor and financially costly, and are often handicapped by limited understanding of species biology (Holdenrieder et al., 2004; Leibhold et al., 1995; Myers et al., 2000). Understanding the long range dispersal methods of an invasive species is a basic requirement for the control of existing populations, as well as preventing the spread of these invasive organisms into new areas (Suarez et al., 2001; Wilson et al., 2009).

Invasion is inherently a spatial process and if captured before an invasive has colonized the full extent of its potential range, the spatial distribution of an invasive organism may indicate dominant mechanisms of spread (Johnson and Carlton, 1996; McIntire and Fajardo, 2009). For plant pathogens, spatial patterns are often manifested as disease gradients, where new infections are concentrated closer to the source of inoculum production or introduction (Madden et al., 2007).

Soil-borne pathogens, typically carried in infested soils on vehicles, equipment or shoes, are often limited to road, trail, or stream

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introductions, amplifying the spatial relationship between these organisms and their dispersal pathways. Classically thought to be soil and water borne, forest *Phytophthora* species are excellent candidates for studying the invasion dynamics of soil-borne pathogens. Species in this genus are emerging as an increasing threat to forest health (Hansen et al., 2012); regardless, relatively few studies have investigated the spatial structure of epidemics caused by *Phytophthora* spp. in heterogeneous environments.

Exceptions include mortality caused by *Phytophthora lateralis*, causal agent of Port-Orford cedar root disease, which in North America is associated either with roads or with streams downstream of where roads cross waterways (Hansen et al., 2000; Jules et al., 2002). Correspondingly, proximity to roads and streams increases the risk of exposure to *P. lateralis* inoculum (Jules et al., 2002; Kauffman and Jules, 2006). Similar results have been recorded for *P. cambivora*, one species responsible for ink disease of *Castanea* spp., where disease severity and rates of tree mortality decrease as one moves away from water drainages located in areas where human activities are limited (Vannini et al., 2010). These data have been used to make generalizations about the dispersal epidemiology and management of other species, including the more recently introduced *Phytophthora ramorum*, causal agent of sudden oak death (SOD) in oaks and tanoaks.

Since its introduction to coastal Californian forests in the 1990s, *P. ramorum* (Werres, DeCock & Man in't Veld) has been implicated in the decline of native acorn-producing species, particularly tanoak (*Notholithocarpus densiflorus*, syn. *Lithocarpus densiflorus*) and some red oak species (*Quercus* section Lobatae) (Ellison et al., 2005; McPherson et al., 2010; Rizzo et al., 2002). SOD is characterized by profuse bleeding from cankers on the stems of mature trees ultimately leading to identifiable crown flaring as the tree dies (Rizzo et al., 2002; Rizzo and Garbelotto, 2003). *P. ramorum* also causes a non-lethal leaf blight on over 100 hosts, from which sporangia, the asexual propagules responsible for dispersal and infection, are produced (Animal and Plant Health Inspection Service, 2012; Werres et al., 2001). While also present infecting Japanese larch plantings in Great Britain, and more widely distributed in nurseries and gardens in the United States and Europe, *P. ramorum's* distribution within native forests occurs only patchily along the coast of the Western United States (Brasier and Webber, 2010; Grünwald et al., 2012; Rizzo and Garbelotto, 2003).

Despite the large number of hosts, a few are more epidemiologically important due to their abundance, ease of infection, and ability to support ample sporulation (Davidson et al., 2008, 2011). Pacific rhododendron (*Rhododendron macrophyllum*) and evergreen huckleberry (*Vaccinium ovatum*), but especially tanoak are the most common foliar hosts associated with *P. ramorum* infection in Oregon (Hansen et al., 2008). California bay laurel (*Umbellularia californica*), an important component of the Californian epidemic (Davidson et al., 2008, 2011), is also regionally abundant in stream drainages, however this host is not as commonly found infected at Oregon SOD sites in comparison to tanoak (Hansen et al., 2008). Within its range, tanoak is commonly found in the understory, as a codominant species mixed with emergent conifers, or in dense, pure tanoak stands (Tappeiner et al., 1990). This species also produces prolific basal sprouts at all ages (Tappeiner et al., 1990), which are easily infected. *N. densiflorus* is the only host known to produce inoculum from leaf and twig lesions, as well as develop stem cankers, which do not support sporulation (Davidson et al., 2005; Rizzo et al., 2002).

P. ramorum was first identified in Oregon in 2001 within the Douglas-fir/tanoak forests outside the coastal town of Brookings in Curry County (Hansen et al., 2008). Immediately after detection a multi-agency eradication program was implemented with the goal of eliminating *P. ramorum* from Oregon forests (Goheen et al., 2002). For this ongoing effort, dead or dying overstory tanoaks are identified via aerial flights, which are then assessed for infection by *P. ramorum* via culture and PCR. When the pathogen is present the site is treated, typically with a cut and burn treatment of all major hosts within a 100 m buffer around symptomatic plants (Hansen et al., 2008).

The capacity for early-detection and thorough local eradication has greatly reduced the size of infected sites. Nevertheless, *P. ramorum* has continued to spread away from the areas of its initial introduction, producing new infection foci every year of the eradication program (Hansen et al., 2008). Much of this spread has been in drainages with no residential development and minimal public access, particularly the watershed of the North Fork of the Chetco River (Fig. 1). Spread has been predominately north of the originally infested sites, despite near uniformity in host and environmental suitability within the region (Hansen et al., 2008; Václavík et al., 2010). While most infections have been within 400 m of infections of a previous year, new *P. ramorum* sites have been identified in the North Chetco watershed up to 4 km away from the nearest known inoculum source (Hansen et al., 2008). Multiple hypotheses exist to explain the long distance dispersal of inoculum between sites, including the movement of inoculum within soils, streams, or blowing fog or rain.

Given the precedence for soil-mediated spread in this genus, a substantial amount of research has focused on the infection of understory foliage from soil and water sources. *P. ramorum* is regularly recovered from soils beneath infested host trees, from footwear of hikers leaving infested areas, and from sites after eradication (Cushman and Meentemeyer, 2008; Davidson et al., 2005; Goheen et al., 2008). Under experimental conditions soil inoculum may cause infection of low-lying vegetation (Fichtner et al., 2009). *P. ramorum* can also be recovered from waterways downstream of areas with known infection (Davidson et al., 2005; Sutton et al., 2009) and, rarely, irrigation water drawn from infested streams has been implicated in the infection of ornamental plants (Tjosvold et al., 2008).

Contrary to this evidence, landscape-scale spatial analysis showed no association between tanoak mortality and roads, a feature inconsistent with soil dispersal (Peterson et al., 2014). New SOD sites were closely associated with streams, however, a pattern which may be consistent with two competing hypotheses: the dispersal of inoculum within stream waters and subsequent infection of streamside vegetation, or through the movement of sporangia in air currents as modulated by the topography associated with stream valleys.

While poorly studied for forest *Phytophthora* spp., dispersal of sporangia in wind is a well documented phenomenon contributing to the spread of some agricultural *Phytophthora* spp. (Aylor, 1990; Ristaino and Gumpertz, 2000). Sporangia of *P. ramorum* are caducous (Werres et al., 2001) and are readily dislodged by rain splash and perhaps by turbulent air. While not definitive by itself, disease gradients between SOD sites in Oregon and Northern California epidemics are consistent with turbulent dispersal, also suggestive of an aerial mechanism (Filip et al., 2012; Hansen et al., 2008). Lacking direct evidence for streamside infection or aerial dispersal, however, studies are required to indirectly measure which mechanism contributes most to the continuing expansion of SOD in the Oregon landscape.

Which dispersal pathway, aerial or soil/stream, dominates long distance transport will largely determine the best mode of control, or, in retrospect, may explain why soil containment has not wholly stopped the spread of SOD. As leaf and petiole infection does not kill foliar hosts, aerial detection is an ineffectual means of discerning the extent of understory infection in Oregon. To assess this risk, we measured host and pathogen distribution in three separate surveys: along roads, along streams, and around recently identified tanoak trees infected by *P. ramorum*.

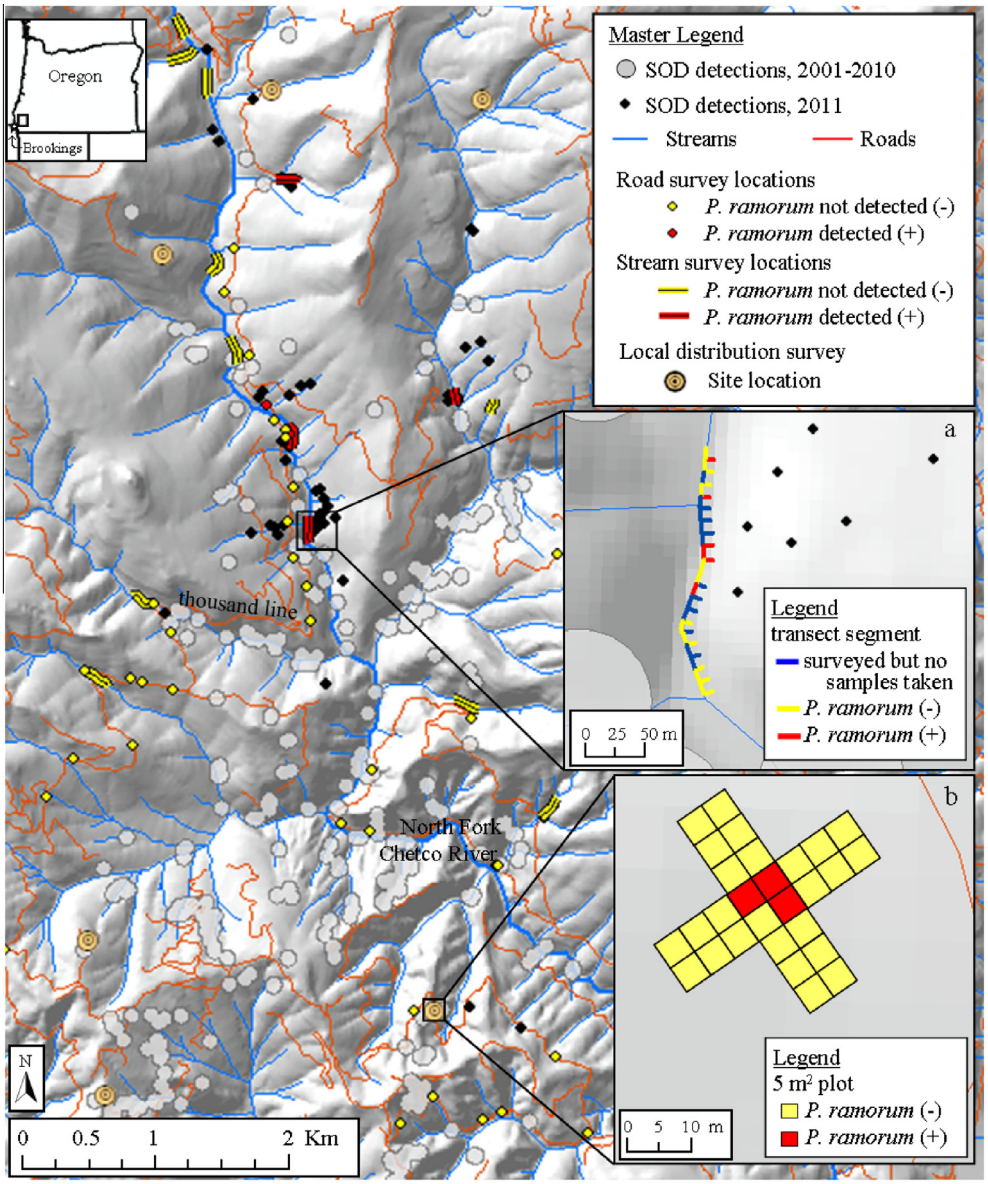

Fig. 1. Location of sites for the local distribution, road, and stream surveys. For the stream surveys (inset a, depicting Strm4) host and pathogen distribution was assessed in 10 m intervals along the stream or in 5 m transects moving away from the stream. In the local distribution survey (inset b, depicting Site 1) host and pathogen presence were assessed in 5 m^2 plots located in 20 m transects oriented uphill, downhill, and laterally around a center, dead mature tanoak assumed to be the source of secondary inoculum. Pictured are all sites within the North Chetco and Joe Hall Creek drainages, an area with the longest disease history and where the majority of surveys were performed.

Soil and stream mediated dispersal requires that in early stages of local establishment, understory infection near the ground level precedes canopy infection. Davidson et al. (2005) documented a strong dispersal gradient from infected trees resulting from local spread in rain splash, with consistent recovery of *P. ramorum* only up to 10 m from infected canopies. Provided we can assess the distribution of infection in the understory during early stages of local spread, we expect to see similarly strong dispersal gradients around the point of inoculum introduction. That is, if soils and streams are sources of primary inoculum, then we should observe understory infection occurring in patterns independent of overstory mortality but spatially dependant upon roads or streams. Alternatively, if *P. ramorum* is dispersing in air currents and establishing in canopies before subsequent dispersal into surrounding vegetation, understory infection should be spatially associated with diseased, mature tanoaks. Assessing patterns of understory infection furthermore allows us to challenge an assumption central to the eradication program: the distribution of *P. ramorum* infection in Oregon can be detected and described by overstory mortality.

2. Methods

2.1. Presence within roadside puddles and vegetation (dispersal in soils)

While the lack of spatial association between roads and SOD sites suggests roads are not an important dispersal pathway (Peterson et al., 2014), no direct attempt has yet been made to isolate *P. ramorum* from road surface waters and roadside vegetation in Oregon. To accomplish this, road-associated waters were surveyed during the rainy seasons of 2011 (February through April) and 2012 (January and February). Eight actively used roads passing through concentrations of SOD sites were selected. Water was collected along each road from mud puddles on the road

surface (for dirt roads) or roadside drainages (for paved roads), and then was then baited for *P. ramorum* with rhododendron leaf disks in lab.

In 2012, symptomatic roadside vegetation was also collected from the splash zone on both sides of the road along 100 m transects associated with each puddle. Plants were tested for *P. ramorum* infection by isolation in *Phytophthora*-selective media. A total of 113 puddles and 135 vegetation samples were collected and tested (Table 1). In addition to the six roads located in the North Chetco watershed (Fig. 1), we also surveyed two roads in the more heavily infected area north of the town of Brookings (Duley Creek and Ostenberg Roads). In contrast to the North Chetco watershed, which is an intermix between the Bureau of Land Management and large parcels of privately owned timber land, Duley Creek and Ostenberg Roads are within a rural residential area characterized by smaller ownership parcels and greater road access and density.

2.2. Distribution of infection in relation to streams (dispersal in streams)

Another survey was performed to assess the distribution of host and pathogen adjacent to and moving away from streams. Surveys were performed along major and minor waterways known to contain *P. ramorum* inoculum. Starting locations preferentially included water bait stations established as part of the early detection network. To be included in the survey, a bait station must have had either a *P. ramorum* culture positive, or, when culture negative, a PCR positive and known *P. ramorum* infection at any location upstream.

To increase our sample size and ensure equal representation of land ownership (publicly or privately owned) and stream size (river or tributary), additional locations within the study area were used. These locations were randomly selected along the same waterways as the bait stations and were downstream of recent infection. Potential starting points were excluded if we lacked the ability to survey 200 m without encountering a clear cut harvest unit or known active infection. Locations were also not surveyed if more than half the length of the survey would pass through a previously eradicated area on both sides of the stream. As this study was performed in areas at relatively high risk for *P. ramorum* infection during the time of aerial surveys, July and August 2011, some transects were later confirmed to have infection on uphill vegetation after the surveys were completed.

Two sets of transects were completed at each of 15 surveyed locations. The first comprised a survey of the understory and overstory vegetation along the stream ('main transect'); the second focused only on major foliar host species located perpendicularly away from the stream ('side transect'). Additionally, any tanoak observable during the surveys that displayed crown dieback or fading was inspected for symptoms of *P. ramorum* infection. When symptoms were present we sampled foliage and cankers and recorded the tree's location with a global positioning system.

2.2.1. Main transect methods

To assess vegetation and pathogen abundance in streamside foliage, at each site we ran a 100–200 m long transect, total length depending upon the topography. The presence or absence of all major riparian plant species with canopies within 2 m of the waters' edge (applicable to smaller tributaries) or bank (applicable to rivers with gravel bars due to seasonal flooding) was recorded in 10 m intervals. The species recorded included: understory tanoak (either basal sprouts or immature trees), California bay laurel, evergreen huckleberry and rhododendron, and overstory tanoak, red alder (*Alnus rubra*), big leaf maple (*Acer macrophyllum*) and Douglas-fir (*Pseudotsuga menziesii*). Of these species alder is the only non-host, while big leaf maple, Douglas-fir and evergreen huckleberry foliage is only rarely found infected by *P. ramorum*.

Despite the potential for asymptomatic infection, prior sampling in SOD sites before and after eradication has shown that *P. ramorum* is preferably isolated from symptomatic tissues, especially from key foliar hosts. In this study, we collected up to five symptomatic leaves each from tanoak and California bay laurel per 10 m interval as a means to detect *P. ramorum* or other *Phytophthora* spp.

2.2.2. Side transect methods

To assess host and pathogen presence out of the splash and flood line, at each 10 m interval along the main transect we started additional 2 m wide transects perpendicular to the stream. Transects were established on both sides of the stream when possible, and extended away from the stream for a horizontal distance of 5 m. Side transects were not installed when the slope exceeded 120°, or when located within a previously eradicated area. Tanoak and bay laurel located within the side transect but not the main transect were inspected for symptoms. As with the main transect, up to five leaves from each species were gathered for isolation. When cankers were present on mature tanoaks a bark sample was taken for isolation in lab.

2.2.3. Statistical analysis

A standard Bonferroni correction was applied to all statistical tests with a common hypothesis. Differences between host (understory tanoak, overstory tanoak, or bay) abundance along streams (main transect) and away from streams (side transects) were tested with a Wilcoxon signed-rank test comparing proportion of 10 m stream segments to proportion of side transects in which each host was present at each site ($\alpha = 0.0167$ for each comparison).

P. nemorosa was the most common *Phytophthora* species recovered, and was included in our analysis to test for differences in *Phytophthora* abundance between hosts and locations. Preferential isolation of *P. ramorum* or *P. nemorosa* from either tanoak or bay

Table 1
Recovery of *P. ramorum* from puddles on roads by baiting and from roadside vegetation subject to splash from the roads by direct isolation.

Road	Puddle baits		Road vegetation	
	Sampled	*P. ramorum* detected	Sampled	*P. ramorum* detected
Lewis creek	14	0	4	0
Thousand line	43	1	43	0
Duley creek	10	1	15	11
Mountain view drive	8	0	17	0
Bean creek	14	0	1	0
Ostenburg road	14	0	27	6
Bravo creek	4	0	4	0
Ransom Ridge	6	0	24	0
Sum:	113	2	135	17

was analyzed with a Pearson chi-square statistic on contingency tables built separately for each pathogen ($\alpha = 0.025$). Preferential isolation of *P. nemorosa* from main and side transects was tested with a Wilcoxon signed-rank test comparing proportion of transect lengths in which a host was present and *P. nemorosa* was isolated, for *P. nemorosa* positive locations only. An identical analysis was attempted for main and side transect recovery of *P. ramorum*. All analyses were performed in S + statistical software.

2.3. Distribution of local infection in relation to overstory mortality (dispersal in air currents)

To assess the distribution of *P. ramorum* in understory vegetation around positive overstory tanoaks, we assumed that the first tree(s) to die at a SOD positive site were among the first infected by primary inoculum and were the source of secondary inoculum contributing to subsequent understory infection. Survey locations were selected from aerial maps of overstory SOD mortality under the criterion of having an identifiable 'first' overstory tree on which to base the spatial sampling. We included isolated sites located at the periphery of the developing epidemic as well as within heavily infested areas, with no *a priori* information on the extent of understory infection. Limiting our focus to small sites with minimal overstory mortality allowed us to avoid having to scale sampling distances to account for the relative size of infested areas; however, it also reduced the number of potential sites available for this study, as at the time of detection most sites were too large to approximate the point of introduction.

Six locations were sampled to assess the spatial relationship between overstory mortality and understory infection: one in 2007, four in 2008 and one in 2011, between the months of May and August. For each of the six sites, four belt transects were constructed extending 20 m uphill, downhill, and laterally centered around the overstory tanoak identified as the first infected. Each transect was 10 m wide, and was divided into 5 m by 5 m plots. All distances were corrected for slope, such that lengths measured on the ground represent horizontal distance to the center of the plot. At distances from 0 to 5 m from the center of the site we sampled four 5 m^2 plots; at distances from 5 to 10 m, 10 to 15 m, and 15 to 20 m we sampled eight 5 m^2 plots for each distance interval (Fig. 1 inset b).

In each 5 m^2 plot the presence or absence of rhododendron and tanoak sprouts was recorded. Up to 5 symptomatic leaf samples were taken from each host to determine if *P. ramorum* was present in the understory at that location. Due to the infrequency with which we recovered *P. ramorum* from other foliar hosts (e.g. evergreen huckleberry) in earlier surveys, we limited this study to rhododendron and tanoak. California bay laurel was rarely encountered, but was recorded and sampled when present.

2.3.1. Statistical analysis

Recovery of *P. ramorum* in each distance interval (0–5 m, 5–10 m, 10–15 m, or 15–20 m) at each location was visualized as the proportion of plots with understory hosts present in which the pathogen was recovered. A spline curve was added to illustrate trends in recovery of *P. ramorum* from vegetation collected at increasing distance away from the presumed source of secondary inoculum. Statistical significance of a decline in recovery from the center of the site was tested by first fitting a logistic regression model to the binary recovery response for each 5 m^2 plot against distance interval for each location. Fitted slope values from each model ($n = 6$) were used to test for a decline in recovery with increasing distance from the center of the plot with a one-sided, one-sample Wilcoxon signed-rank test (H_o: $\mu = 0$; $\alpha = 0.025$).

2.4. Isolation and identification of Phytophthora species

All vegetation samples were stored in a cooler for a maximum of 4 days and returned to lab. Within 5 days of collection one lesion per sample was plated onto cornmeal agar–ampicillin–rifampicin–pimaricin selective media (CARP) (Osterbauer, 2004) and incubated in the dark for 7–12 days at 20 °C. Culture identification was based upon morphology of hyphae and spore structures. Any cultures lacking diagnostic features at the time of the first observation were incubated for another week and re-examined. In the road and local distribution studies we only attempted to identify *P. ramorum* to species. We additionally identified *P. nemorosa* from isolates recovered from stream surveys. Any other *Phytophthora* species present were noted but not identified further.

3. Results

3.1. Presence on roads and adjacent vegetation

Over the 2 years of road sampling *P. ramorum* was recovered from only 2 of the 113 water samples taken from roads (Table 1). Both were within areas of active infestations, either where a recently detected SOD site spanned the road (Duley Creek) or where a roadside drainage containing runoff from an adjacent eradication site crossed the road (Thousand Line). *P. ramorum* was isolated from 17 of the 135 roadside vegetation samples collected along six transects from two roads (Table 1). Only one puddle associated with positive vegetation was positive for *P. ramorum*, at Duley Creek. All infected roadside plants were growing in close proximity to infected overstory tanoak trees, in areas with a heavy amount of canopy infection. Absent overstory sources, *P. ramorum* was not recovered from puddles or roadside vegetation.

3.2. Distribution of infection in relation to streams

3.2.1. Host distribution

California bay laurel was the most common host at all locations (Fig. 2). There was significantly more bay present along the main transects than the side transects ($z = 2.6126$, $p = 0.009$). Overstory tanoak was present at all locations, however in comparison to bay, alder and big leaf maple, it was a minor component of the streamside forest (Fig. 2). Overstory tanoak was present in an average of 11% of the 10 m segments observed in the main stream transects (range by location: 0–62%), and 13% of all side transects (range by location: 0–24%). Understory tanoak was more abundant,

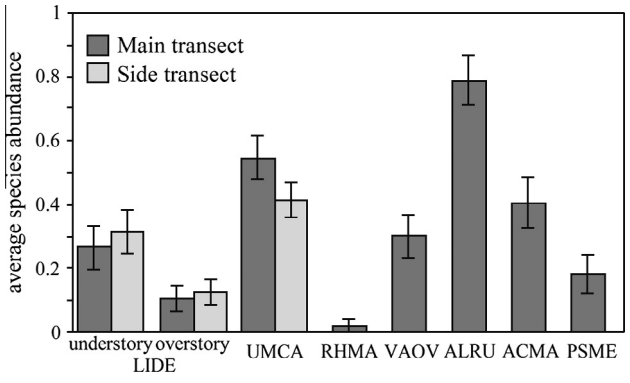

Fig. 2. Relative abundance of streamside vegetation. Abundance is quantified as either the average proportion of 10 m segments along the main transect or average proportion of side transects in which the host was present at each site. Error bars represent standard error. LIDE = tanoak; UMCA = California bay laurel; RHMA = Pacific rhododendron; VAOV = evergreen huckleberry; ALRU = red alder; ACMA = big leaf maple; PSME = Douglas-fir.

present in an average of 26% of the 10 m segments along the main stream transect (range by location: 0–58%), and 31% of the side transects (range by location: 0–88%). There was no significant difference in the abundance of understory tanoak ($z = -0.2841$, $p = 0.7763$) or overstory tanoak ($z = -0.2841$, $p = 0.7547$) between main and side transects.

3.2.2. Pathogen recovery

Phytophthora species were recovered from all locations. *P. nemorosa* was the most common species recovered and was isolated with equal probability from California bay laurel and tanoak ($\chi^2 = 1.79$, d.f. = 1, $p = 0.181$) (Fig. 3). *P. nemorosa* was recovered at 12 of the 15 locations, from an average of 26.5% of main transect segments and 24.9% of side transect segments in which either host was present. There was no significant difference in recovery of *P. nemorosa* between main or side transects ($z = 0.6676$, $p = 0.5044$).

We isolated *P. ramorum* from 28 leaves collected at 4 sites (Fig. 3, Table 2). All 4 sites were in close proximity to current, active infection (Fig. 1). *P. ramorum* was disproportionally isolated from tanoak (93% of all *P. ramorum* isolates; $\chi^2 = 72.5$, d.f. = 1, $p < 0.0001$), and side transects (9% of main transect segments vs. 34% of side transects with hosts sampled within locations in which *P. ramorum* was recovered). Due to the small number of *P. ramorum* positive locations ($n = 4$) we lacked sufficient power to determine statistical significance between recovery of *P. ramorum* in main vs. side transects.

3.3. Distribution of infection in relation to overstory mortality

Understory hosts (tanoak sprouts or rhododendron) were present in all four 5 m^2 plots between 0 and 5 m, and all eight 5 m^2 plots between 5 and 10 m at all sites. At distance intervals 10–15 m and 15–20 m, hosts were present in an average of 7.83 and 7.5 plots (of 8 plots possible), respectively.

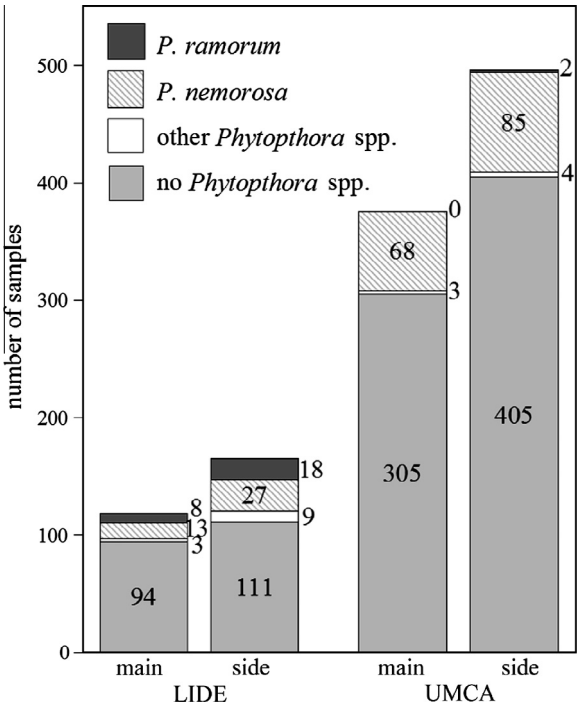

Fig. 3. *Phytophthora* spp. recovered in stream surveys from tanoak (LIDE) and California bay laurel (UMCA), separated by main and side transects. Total number of samples taken of tanoak = 118 from main and 165 from side transects; total number of samples taken of bay laurel = 376 from main and 496 from side transects.

At three sites (# 1, 4, and 5) *P. ramorum* was only recovered from understory vegetation within 0–5 m from the center of site (Figs. 1 inset b and 4). Recovery at the remaining sites was greatest up to 10 m from the center, and then declined between 10 and 20 m. Fitted slope values were negative for all sites (range: −0.0335 to −2.4521), with a significantly negative trend between pathogen recovery and distance from the center of each location ($p = 0.0156$).

4. Discussion

The expansion of global trade in plants and, inadvertently, their pests has resulted in the introduction of tree diseases having major impacts on native forest ecosystems (Leibhold et al., 1995; Loo, 2009). *P. ramorum* is one recent example of this continuing exotic pathogen problem. Although *P. ramorum* causes mortality on only a few hosts, as a generalist pathogen with non-descript symptoms on understory foliage, the distribution of this species is difficult to assess at a landscape scale in the absence of SOD mortality. As such, research has relied upon extensive (but ultimately limited) monitoring programs, statistical modeling, and epidemiological theory to best direct management efforts. Much of this effort has been put towards documenting the presence of *P. ramorum* in soils and streams; however, no prior studies have been able to investigate if inoculum in these understory sources significantly contributes to long distance spread and establishment of new SOD sites under natural conditions.

Additional difficulties arise due to the multiple pathways responsible for movement at different scales. Locally *P. ramorum* moves between plants in rain splash (Davidson et al., 2005). Regionally and nationally *P. ramorum* has been moved with infected nursery stock (Grünwald et al., 2012). Between these scales, Californian epidemiology in more heavily infected and populous areas suggests soil movement has contributed to the intensification, if not introduction, of *P. ramorum* (Cushman and Meentemeyer, 2008; Fichtner et al., 2009).

Prior epidemiological studies in California have been limited by the extensive distribution of SOD at the time of this species' description, reducing the ability to differentiate between primary and secondary spread. In contrast, the SOD eradication program has resulted in a distribution of disease resulting solely from primary introductions. But for yearly aerial detections the remaining forest is assumably free of *P. ramorum*. Due to the limitations of the eradication program, however, there remains a continuous (albeit reduced) level of infection contributing to the further spread of disease. The persistence of inoculum in streams and soils at eradication areas, and the great amount of traffic within the North Chetco area, has posed a significant risk to missing infection and subsequent dispersal of inoculum into new areas. The risk of missed understory infection is greatly enhanced if soil and stream inoculum should be a major pathway of introduction.

In contrast to other forest *Phytophthora* species, however, we found no evidence that soil or stream borne inoculum is significantly contributing to the long distance dispersal of inoculum between sites in Oregon. Given the availability of hosts and pathogen presence in some stream segments included in our surveys for as long as 6 years, the hypothesis of stream dispersal would have predicted greater streamside infection than was observed. Other *Phytophthora* species, particularly *P. nemorosa*, were not absent from streamside vegetation, and were isolated from both bay and tanoak. While understory tanoak, the host from which *P. ramorum* was preferentially isolated, was equally as common in transects adjacent to streams as away from streams, we isolated *P. ramorum* more commonly from vegetation in transects away from the splash or flood line. All recoveries were found in

Table 2
Characteristics of locations used to test the hypothesis that *P. ramorum* is preferentially established in streamside vegetation. Host and pathogen presence were surveyed in 10 m intervals along the stream (main transect; maximum length = 200 m), or in 5 m long transects moving away from the stream edge (side transects, located at every 10 m interval along the stream). *Note:* no vegetation at site WA90S displayed any symptoms.

Site name	Stream size	Ownership	Length of main transect (m)	Length of all side transects (m)	# Leaf samples taken	# Samples *P. ramorum* positive
WA29	Tributary	Private	200	200	152	2
WA33	River	Private	200	195	45	0
Strm12	River	Private	200	200	64	0
1000Rd	River	Public	200	135	37	7
WA90	River	Public	120	120	32	6
WA90S	Tributary	Public	130	130	0	0
WA67	Tributary	Public	200	200	85	0
WA11	Tributary	Public	200	165	118	0
WA35	Tributary	Public	130	165	105	0
WA83	River	Private	200	190	73	0
WA83S	Tributary	Private	200	190	87	0
WA44	Tributary	Private	200	200	46	0
Strm52	Tributary	Private	200	165	14	0
Strm4	River	Public	200	95	106	13
Strm9	River	Private	200	190	191	0
		Sum	2780	2540	1155	28

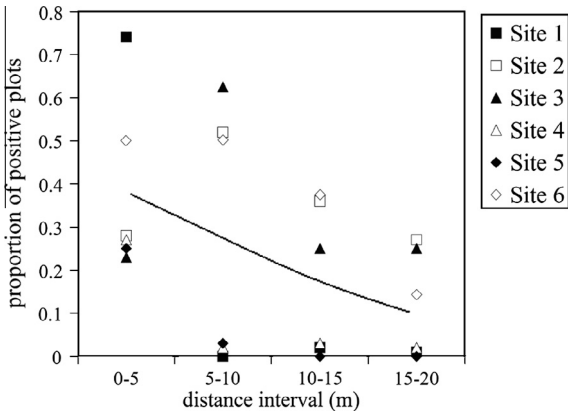

Fig. 4. Local distribution of *P. ramorum* in the understory around SOD positive trees. Pathogen presence is presented as proportion of 5 m^2 plots in which either tanoak or rhododendron were present and *P. ramorum* was recovered at each distance (# positive 5 m^2 plots/# of 5 m^2 plots with hosts present). A spline curve has been included to illustrate trends in recovery moving away from the presumed secondary inoculum source at the center of the site. Locations with an identical recovery at a given distance have been jiggered.

areas of known, active SOD infection, and could be attributed to sporulation from upslope, overstory trees identified in the summer of 2011. In the absence of these overstory inoculum sources we failed to recover *P. ramorum*, even immediately downstream of positive samples (Fig. 1 inset a, for example). Similarly, we also failed to isolate *P. ramorum* from road surface puddles or road-side vegetation, except when within areas with abundant infected, overstory tanoaks.

Phytophthora species are not uncommon in Oregon forests. Overall, the infrequency with which we recovered *P. ramorum* was surprising, especially in our stream vegetation surveys. Similarly confounding observations have been noted in other areas with a history of *P. ramorum* introduction. While *P. ramorum* has only established in the forests of Oregon and California, shipment of infected nursery stock has moved this pathogen to other regions of North America containing both a suitable environment and susceptible hosts (Grünwald et al., 2012; Kelly et al., 2007; Tooley and Browning, 2009). Nursery containment programs have minimized the further distribution of these plants, but *P. ramorum* can sometimes be isolated from soils on nursery grounds, irrigation pond water, and creeks running adjacent to contaminated nurseries, even after infected plants are removed (Jeffers et al., 2010). With the exception of two highly localized *P. ramorum* detections adjacent to infested streams or ditches, both within meters of the positive nursery sources, *P. ramorum* has also not been isolated from stream-side vegetation and no new epidemics have developed (Chastagner et al., 2010, 2011). Such anecdotal evidence has suggested that streams are not an important dispersal pathway (as mentioned in Grünwald et al., 2012), though this is the first study testing this hypothesis.

In contrast to a soil or water borne pathways, the alternative hypothesis of aerial dispersal was also tested. Whereas understory establishment should have produced patterns of infection closer to roads or streams and independent of overstory mortality, the inverse would be observed if inoculum is establishing first in overstory trees before dispersing locally in rain splash. This process would have resulted in a gradient whereby the greatest amount of understory infection should be observed closest to the source tree, provided one could assess the pattern during the first stages of secondary spread.

Overall, there was a strong spatial dependence of understory infection on overstory mortality. Despite a high abundance of understory hosts in the forests surrounding these locations, recovery of *P. ramorum* in understory vegetation declined as one moved away from the presumed source at all sites (Fig. 4). Lacking patterns in understory infection consistent with soil or stream dispersal, we conclude that the sources of primary inoculum at these sites are best attributed to aerial sources. Importantly, this suggests that new SOD sites in Oregon are isolated and have been properly identified with the aerial detection of overstory mortality (and subsequent work to confirm infection by *P. ramorum*), without missing significant understory infection.

The question remains why hosts in proximity to understory inoculum sources are not more commonly found infected in Oregon, and if these results can aid the management of the epidemic in California. Road and stream conditions may not be conducive for spore survival and infection. Inoculum in soil loses viability upon drying (Fichtner et al., 2007), and comparative analyses between soil and foliar pathogen populations suggest rates of spread by soil are slower than that from foliar infections (Eyre et al., 2013). Despite the moist conditions and sampling within heavily infested watersheds, however, we failed to recovery *P. ramorum* from soils on roads, or, more telling, from roadside hosts.

Most likely the lack of streamside infection is due to low risk of exposure to inoculum during times critical to dispersal of *P. ramorum*. Infection of leaf baits placed within streams for extended periods can be used to detect inoculum in all seasons, although detection rates increase over the summer with increasing temperatures and a drop in water levels (Sutton et al., 2009). While streamside hosts were abundant and samples were gathered within the splash and flood line expected during winter flooding, little foliage was in direct contact with water over the course of our surveys during the summer months. We propose the risk of stream-borne inoculum coming into contact with susceptible foliage is relatively minor, especially in contrast to *P. lateralis* infection of Port-Orford cedar whose roots actually grow within the water (Kauffman and Jules, 2006).

Alternatively, the eradication program may have kept inoculum levels beneath a threshold required for soils and streams to be a significant source of primary inoculum. We expect inoculum density to play a large part in the risk of pathogen introduction, particularly if the road or stream environment is not conducive to successful infection. The low-probability events supporting primary introduction in soils may be sufficiently infrequent as to be undetectable during eradication. The reduction in inoculum due to the eradication and, importantly, the low frequency of bay infection, may also explain why soils are implicated in the movement of inoculum in California, but not Oregon. Bay laurel, with its abundance in coastal forests and capacity to produce copious amount of inoculum (Davidson et al., 2008), has been the focus of all major studies of the Californian SOD epidemic. For example, infected bay laurel leaf counts are common measures of disease severity, and bay presence is a common indicator used to predict the risk of *P. ramorum* establishment (Meentemeyer et al., 2008a,b).

While bay is common within the Douglas-fir/tanoak stands of Oregon, especially within stream drainages, we found very little infection on bay in comparison to tanoak, a pattern that has been consistent throughout the eradication program. This may be due to small differences in pathogen lineages (Prospero et al., 2009) or seasonal variation in bay susceptibility (Hüberli et al., 2012) between California and Oregon. More likely, the greater susceptibility of tanoak (Hansen et al., 2005) makes infection of this species more likely under the low inoculum conditions of primary introduction with substantial infection of bay only after the epidemic has established.

This makes Californian epidemiology an important descriptor of *P. ramorum* severity in established infestations, but ineffectual at assessing the risk of primary establishment with the detail we are able to accomplish in Oregon. With the recent cessation of eradication in some areas within southwest Oregon, studies should be performed to assess if infection and sporulation rates on bay become more prevalent over time, and if an increase in understory infection is subsequently observed.

While the eradication program has aided the detection of these spatial patterns through our ability to identify sites early and maintain pathogen free areas within heavily infested watersheds, it has also limited the scope of inference for these surveys. For our local distribution study, most infestations were too large at the time of detection to be surveyed and, usually being located on the periphery of the quarantine zone, were top priorities for prompt eradication treatment. Similarly, streams had to have been surveyed in heavily infested areas to ensure that stream inoculum was present, but significant portions of streamside forest had been altered by the eradication program at the time of this study. Selection of sites and small sample sizes may have affected our results; however, our results are consistent with field observations in infested areas that, for reasons of practicality, we were unable to survey with these methods.

While *P. ramorum* can infect over 100 species, including many less common understory plants in the Douglas-fir/tanoak forests of southwest Oregon, practicality also necessitated focusing on a few hosts key to the epidemiology of SOD in other systems. Given their wide distribution, higher incidence of infection within SOD-infested areas, and ability to support sporulation, the hosts sampled in this study, California bay laurel, rhododendron and especially tanoak, are the best descriptors of understory infection. The likelihood of other hosts contributing to spread independently of these three species is improbable.

The lack of evidence for dispersal along roads or from streams, and evidence for establishment in tanoak canopies all support our alternative hypothesis of aerial dispersal of inoculum. This study adds to a growing body of literature suggesting the natural dispersal of inoculum occurs aerially at distances greater than rain splash alone (Eyre et al., 2013; Mascheretti et al., 2008; Metz et al., 2012). Mechanisms of aerial dispersal are highly variable in the *Phytophthora* genus. No evidence exists supporting the hygroscopic detachment of sporangia in drying air as in the case of *P. infestans* (Aylor et al., 2001). Rather, the alternative mechanisms of movement in blowing fog or rain, analogous to dispersal by *P. capsici* (Granke et al., 2009), seems more likely. Contrary to the questionable importance of movement in air currents for *P. capsici* (Granke et al., 2009), however, it has been our observation that the range and frequency at which aerial dispersal is possible has contributed significantly to the establishment of *P. ramorum* in Oregon.

We cannot eliminate the risk of soil borne inoculum in other systems. Prudent management practices should therefore minimize the movement of infested soils and utilization of infested waters, especially if spread by these understory sources is more likely under higher inoculum densities. This remains especially relevant as the control program in Oregon changes its objective from complete eradication to containment. Regardless, management aimed at preventing the movement of infested soils – trail and road closures or washing stations – will be ineffective at preventing the dispersal of inoculum into new stands once *P. ramorum* has established regionally. This conclusion is in sharp contrast to those made by researchers documenting roadside associations with other invasive *Phytophthoras*. Jules et al. (2002) found that while foot and animal traffic was responsible for moving inoculum of *P. lateralis* away from streams, vehicle traffic could best explain the introduction of inoculum into new watersheds, especially early in the epidemic. As such these authors suggested that watersheds without roads have a relatively minimal risk of exposure to inoculum (Jules et al., 2002). Unfortunately, this has not been our observation of the distribution of *P. ramorum* in Oregon.

Aerial dispersal has not been conclusively demonstrated for any forest *Phytophthora* species, although interest in aerial dispersal of sporangia has recently come to include two other species: *P. pinifolia* (Durán et al., 2008), a pathogen of radiata pine, and *P. lateralis* (Robin et al., 2010). While *P. lateralis* is known as a root pathogen of Port-Orford cedar, it can cause foliar infections on low lying branches (Trione and Roth, 1957). Recent infection in European windbreak plantings of Port-Orford cedar has occurred not only at ground level, but as cankers in the upper boles of trees (Robin et al., 2010). This circumstantial evidence supports the hypothesis that otherwise soil-bound *Phytophthora* spp. can disperse in air currents under specific conditions.

Owing to the low probability of successful dispersal and infection over long distances, new infections resulting from aerial dispersal often appear sporadically and randomly distributed across the landscape (Aylor, 2003). While these events are difficult to predict, they do occasionally happen at distances now documented up to 4 km from the nearest known inoculum source (Hansen et al., 2008). Any management decisions designed to limit spread or pro-

tect individual trees from infection (e.g. host-free zones or removal of adjacent foliar hosts) must take into account the possibility that inoculum may span greater distances than expected from splash dispersal independent of human movement, and commit to management practices that deal with these rare new foci as they develop.

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