



Spatial relationship between *Phytophthora ramorum* and roads or streams in Oregon tanoak forests



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ABSTRACT

The pathogen, *Phytophthora ramorum*, causal agent of sudden oak death (SOD) of oaks and tanoaks, continues to expand its range within Oregon despite an effort to eradicate it from native forests. With its early detection and prompt removal of infected hosts, the Oregon SOD eradication program has produced a landscape distribution of disease resulting predominantly from the long distance (100 m to 4 km) dispersal of inoculum between sites. Using a regionally restricted randomization test reflecting the south to north intensification of the SOD epidemic in Oregon, we assessed if the movement of *P. ramorum* between sites was spatially dependant upon roads and streams, topographic features associated with the landscape-scale movement of soil and water borne inoculum of related *Phytophthora* spp. Dissimilar to other forest *Phytophthora* spp. we found no association between SOD sites and the road network. We did, however, determine that SOD sites are occurring closer to streams than would be expected by chance, especially in regions with microclimates less conducive to establishment. Environmental conditions and/or dispersal mechanisms associated with streams may contribute to the distribution of SOD in Oregon tanoak forests. Monitoring and management should therefore concentrate on susceptible forests in close proximity to streams, especially in stands further inland from a coastal climate.

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1. Introduction

The invasion of non-native species is inherently a spatial process, and movement can be mapped over time following an invasive's introduction. Resultant spatial patterns can be used to generate or test hypotheses about the processes driving spread and establishment of invasive species, and may suggest ways to mitigate their effects (McIntire and Fajardo, 2009). The relationship between an invasive species and distinct landscape features can also identify areas at risk of introduction, at spatial scales which are difficult to assess by other means (Johnson and Carlton, 1996; Jules et al., 2002; Levin, 1992). In the case of phytopathogens, the landscape distribution of disease may indicate which aspects of host or environmental heterogeneity are contributing to the observed patchiness of pathogen distribution (Condeso and Meentemeyer, 2007; Holdenrieder et al., 2004; Kauffman and Jules, 2006). Nevertheless, because of cryptic infection and an inability to obtain a large enough dataset to effectively analyze spatial distribution, in practice spatially-explicit landscape analyses can be difficult to interpret.

The phytopathogen *Phytophthora ramorum* (Werres, DeCock & Man in't Veld) is one invasive whose distribution has been

monitored and mapped since its detection in Oregon, USA in 2001. *P. ramorum*, causal agent of Sudden Oak Death (SOD), has caused extensive harm to forest communities by killing tanoak (*Notholithocarpus densiflorus*) and other ecologically important trees (Ellison et al., 2005; McPherson et al., 2010; Rizzo and Garbelotto, 2003). *P. ramorum* is present in nurseries and gardens in the United States and Europe, including a recent epidemic in Japanese larch plantings in Great Britain (Grünwald et al., 2012; Braiser and Webber, 2010). Infestations of native forests, however, have been limited to the western United States (Rizzo and Garbelotto, 2003).

This pathogen has spread relatively unimpeded in California, where it was first identified infecting tanoak trees in the mid-1990s (Rizzo et al., 2002, 2005). When SOD was detected in the Douglas-fir/tanoak forests outside the coastal town of Brookings (Curry County, Oregon), a multi-agency eradication program was initiated with the goal of eliminating *P. ramorum* from Oregon forests (Goheen et al., 2002; Hansen et al., 2008). The distribution of *P. ramorum* within its range in southwestern Oregon has been mapped annually by locating recently killed tanoak trees and determining a cause of death. Until 2010 new SOD areas were eradicated within a year of detection; nevertheless, new, geographically isolated sites have been detected every year of the eradication program (Hansen et al., 2008).

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Understanding the modes of dispersal responsible for the spread of inoculum is an essential component of any disease management system (Ristaino and Gumpertz, 2000). *P. ramorum* has been dispersed between states and countries on horticultural nursery stock, particularly on *Rhododendron* spp., with rare movement into surrounding forested ecosystems (Grünwald et al., 2012; Croucher et al., 2013). Once established in overstory foliage, short distance (within 10 m) dispersal in rain splash is responsible for local intensification (Davidson et al., 2005). In Oregon, however, new SOD sites occurring in areas with limited public access range between 100 m and 4 km to the nearest known inoculum source (Hansen et al., 2008), dispersal not explained by either mechanism. Different dispersal processes are evidently responsible for disease spread between sites on the landscape.

Between-site movement of forest *Phytophthora* spp. is classically attributed to the transport of infested soils. Well studied examples include *P. lateralis*, an invasive pathogen of Port-Orford cedar in northern California and southwestern Oregon (Hansen et al., 2000) and sister species to *P. ramorum* (Ivors et al., 2004), *P. cambivora*, one species associated with ink disease of *Castanea* spp. (Vettraino et al., 2001), and *P. cinnamomi*, a second contributor to ink disease and causal agent of jarrah dieback in Australia (Crandall et al., 1945; Weste and Marks, 1987). These species may be moved between sites in infested soil on vehicles, boots, and equipment (Hansen et al., 2000; Kliejunas and Ko, 1976). When infested soil enters waterways inoculum is carried downstream, where it may be recovered from stream baits (Kliejunas and Ko, 1976; Reeser et al., 2011). Dispersal gradients favor new infections closer to the source of inoculum introduction (Madden et al., 2007). Risk of infection by these soil-associated *Phytophthora* spp. therefore increases with proximity to roads, trails, or streams resulting in patterns of disease closely associated to their dispersal pathways (Jules et al., 2002; Kauffman and Jules, 2006; Vannini et al., 2010; Weste and Taylor, 1971).

Due to this history, the emphasis of research and control of SOD has logically focused on the importance of movement of infested soil by people. Indeed, *P. ramorum* is regularly recovered from soils beneath infested host trees 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 in low-lying vegetation (Fichtner et al., 2009). Proximity to trails and land ownership (private versus public, presuming public access increases rates of spread of inoculum-infested soils) have been included as significant variables in models describing the incidence of disease in an area (Cushman and Meentemeyer, 2008; Kelly and Meentemeyer, 2002).

Inoculum introduced into waterways from soil or plant sources may also pose a risk of disease spread. *P. ramorum* can 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 infection of ornamental plants (Tjosvold et al., 2008). There is no direct evidence, however, that either soil or water borne inoculum is important in starting new SOD infestations in the forests of Oregon and California. To date no studies have demonstrated soil or stream borne inoculum to be important in the primary establishment of *P. ramorum* in new areas.

In Oregon the eradication program, with its prompt removal of infected vegetation and a buffer of surrounding trees, has eliminated the intensification of local spread beyond the time between the primary infection and detection. We have the unique opportunity to view the spatial distribution of *P. ramorum* exclusively as a result of long distance (>100 m) dispersal between SOD sites. The objective of this study is to discern if the movement of *P. ramorum* in Oregon forests is spatially dependant upon roads or streams, landscape features associated with the movement of soil and water

borne inoculum, particularly over long distances. Our approach assesses if the distribution of *P. ramorum* deviates from spatial independence to roads or streams by using a regionally restricted randomization test reflecting the south to north intensification of this epidemic in Oregon.

Control measures for soil-borne pathogens focus on reducing the rate of transport of infested soils, including closing roads at times deemed high risk for soil movement (e.g. *P. lateralis*, Hansen et al., 2000; Goheen et al., 2012), or through the use of vehicle and equipment washing stations (e.g. *P. cinnamomi*, Cahill et al., 2008). Similar measures are suggested by California regulators for *P. ramorum* control, whereby the public is advised to stay out of areas of wet soils, and clean personal clothing and equipment of soil when entering or leaving infested areas (Cushman and Meentemeyer, 2008; California Oak Mortality Task Force (COMTF) website). It remains unclear if these measures have reduced the spread of *P. ramorum* between stands within California, or if road closures could have prevented the long distance dispersal events observed in Oregon. As an indication of whether these actions would have prevented spread we expect to see *P. ramorum* occurring closer to roads or streams than expected by chance. Any association to landscape features may furthermore identify areas with a higher risk for establishment and priority for treatment.

2. Methods

2.1. Confirmation of SOD distribution

Tanoak is an easily infected and widely distributed host within the coastal forests of southwestern Oregon, and mortality is visible from a distance. Recently killed trees are located in systematic aerial surveys covering the entire distribution of tanoak within Oregon (Kanaskie et al., 2011). Flights are conducted annually (more frequently in areas of special concern) and global position system (GPS) coordinates are recorded for each suspect tree. Follow up ground surveys confirm the coordinates of potentially infected tanoak trees and ascertain cause of death by collecting samples of inner-bark, leaves and stems with symptoms of *Phytophthora* infection from each suspect tree. All samples are transported to lab, and are plated in *Phytophthora*-selective media for identification. Culture negative samples are subjected to molecular diagnosis using a PCR technique (Winton and Hansen, 2001) to verify the absence of *P. ramorum*. When *P. ramorum* is confirmed the site is treated with the goal of local eradication of infected vegetation. Symptomatic tanoak and other host plants are cut and burned in a treatment area extending at least 100 m beyond symptomatic plants to include recently infected trees that were not yet symptomatic.

This methodology has proven over time to adequately identify and contain new SOD sites in Oregon. The limited size of SOD sites at the time of detection indicates most are identified before a substantial amount of local spread has occurred. For this study we used coordinates for all *P. ramorum* positive samples identified between 2001 and 2010 within the study areas of interest.

2.2. Description of study areas

We identified two study areas for our analyses, differentiated by topography, disturbance history, and the amount of public access and use. The first area, representing relatively limited public access, includes the watersheds of Ferry Creek, Joe Hall Creek and the North Fork Chetco River (North Chetco study area), where *P. ramorum* was first identified in 2001 (Fig. 1). Much of the North Chetco study area is managed for timber production by private companies. Mixed with private timber lands and accounting for

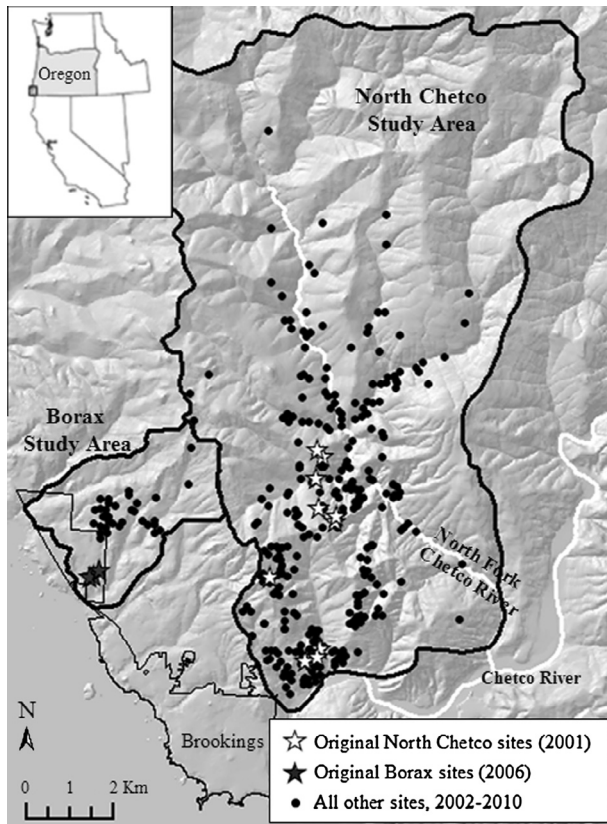


Fig. 1. Map of the Oregon SOD infestation, showing all SOD sites identified between 2001 and 2010 within the North Chetco and Borax study areas. Study area boundaries were defined by the encompassing topography around the North Fork Chetco River, Joe Hall Creek and Ferry Creek watersheds, where *P. ramorum* was first identified in 2001 (North Chetco study area), and the infestation originating from the Borax site, first identified in 2006 (Borax study area). Site locations have been enlarged on the map for clarity.

most of the remaining infestation in this study area are lands owned by the Bureau of Land Management. Most roads within the North Chetco lie behind locked gates with very limited access to the general public, although roads are heavily used by vehicles associated with logging and land management. Due to the difficult terrain and large area, travel within the North Chetco study area requires road use to access relatively remote parts of this landscape.

The Borax study area was included to validate the methods we used in the North Chetco area in an area with different disease history, topographical orientation, and land ownership. First identified in 2006, the epidemic developing initially from the Borax

site (Fig. 1) has proceeded relatively independently west of the ridge bounding the North Chetco study area. The Borax area is largely forested rural-residential with smaller ownership parcels and greater road access and density (Table 1). Borax has a comparable forest composition, but with a lower elevation and lying closer to the coast this area has a stronger maritime influence compared to the North Chetco.

The borders of both study areas were defined by the topography of the watersheds containing SOD (Fig. 1). A single clonal lineage comprises the SOD epidemic in Oregon forests, of which one genotype dominates both the Borax and North Chetco areas (Prospero et al., 2009). While we cannot distinguish either population genetically, the infrequency in which *P. ramorum* has moved south, east, and west from the North Chetco watershed suggests movement outside of major drainage systems is relatively rare. Any SOD positive coordinates located east of the north–south ridge on the westernmost edge of the North Chetco watershed were assumed to originate from dispersal from sites in the North Chetco study area; those coordinates on the west side of the ridge were assumed to have originated from dispersal from sites in the Borax study area.

2.3. Topographical and landscape features

Using a 10 m digital elevation model obtained from the USDA National Resources Conservation Service (<http://datagateway.nrcs.usda.gov/>), we generated a stream network with the program tauDEM 5.0 (<http://hydrology.usu.edu/taudem/taudem5.0/index.html>). This was accomplished with the ‘Stream Definition by Threshold’ tool whereby a raster cell was classified as a waterway if it had a minimum contributing area of 300 upslope grid cells (threshold = 300). The resultant stream rasters were then converted to vector format and screened for anomalies before analysis.

Road layers were obtained from the Port-Orford cedar-GIS regional distribution maps compiled on September 6th, 2006 (courtesy USDA Forest Service SW Oregon Forest Health Service Center, Medford Oregon). Maps relating to the Rogue River Siskiyou region included all major roads and most logging roads within the study areas. Roads not in this dataset but evident in aerial photographs taken in 2005 or 2009 were added manually.

Topographic descriptors were defined for each of the study areas with the zonal statistics tool in ArcMap. We characterized average slope for the terrain, as well as the average elevation for all streams within each study area.

2.4. Site definition

For analysis, clusters of positive trees were reduced to a single site coordinate defined as the centroid of all isolations located with 60 m of one another (Fig. 2). This minimized the bias of over-sampled locations, and approximated the point of primary inoculum introduction. The centroid instead of the point closest to the road or stream was selected for ease of computation and because prior spatial studies had confirmed focal spread (Peterson, 2011). From the 709 positive trees within the North Chetco study area we defined 294 sites for analysis; from the 80 positive trees within the Borax study area we defined 36 sites (Table 2).

All datasets were projected in the OR NAD83 Lambert coordinate system and analyzed in ArcGIS (version 9.3; ESRI). To quantify the minimum distance of each of the SOD sites to the nearest road or stream a spatial join was performed relating points (site) to each line feature (either roads or streams). This analysis created a field containing the minimum Euclidean distance between the point and the closest line. Twenty-five points were checked manually with the distance tool to verify accuracy.

Table 1
Topographical characteristics and road and stream features within the North Chetco and Borax study areas.

	North Chetco Study area	Borax Study area
Total area (square (sq.) km)	111.48	10.71
SOD density, all years (# sites/sq. km)	2.64	3.36
Total road length (m)	74,908	12,741
Road density (m/sq. km)	672	1190
Total stream length (m)	334,671	31,033
Stream density (m/sq. km)	3002	2898
Average stream elevation (m)	96	49
Range in stream elevation (m)	0–276	0–144
Average slope of the terrain (% $\pm$ s.d.)	29.48 $\pm$ 19.05	28.64 $\pm$ 19.03

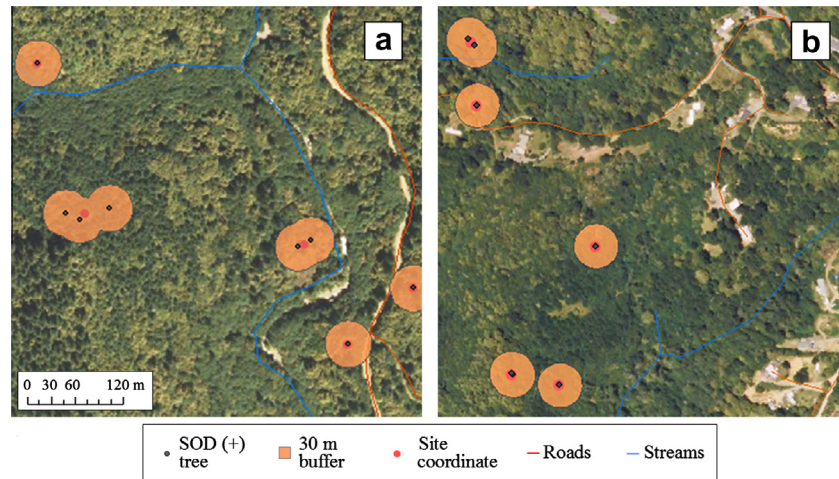


Fig. 2. Example of how sites were defined for analysis, as well as the forest, road and stream structure within the North Chetco (a) and Borax (b) study areas. A 'site' was defined as the centroid of the coordinates for all SOD positive isolations within 60 m of one another; when only one positive isolation was made in the immediate area the site coordinate equals that of the positive isolation. The lighter vegetation distributed throughout both aerial photographs is overstory tanoak.

Table 2

Spatial relationships by year for all sites identified as positive for *P. ramorum* infection within the North Chetco and Borax study areas. Median distance to road or stream was calculated as horizontal distance to the closest road or stream for all sites detected in that year, or as the 10 year median for all sites detected between 2001 and 2010.

Year of detection	North Chetco study area				Borax study area			
	# of new positive sample	# of new sites	Median distance to road (m)	Median distance to stream (m)	# of new positive sample	# of new sites	Median distance to road (m)	Median distance to stream (m)
2001	50	10	102	128	n/a	n/a	n/a	n/a
2002	79	17	73	94	n/a	n/a	n/a	n/a
2003	56	18	111	102	n/a	n/a	n/a	n/a
2004	28	10	62	160	n/a	n/a	n/a	n/a
2005	60	17	124	65	n/a	n/a	n/a	n/a
2006	128	46	111	45	5	3	291	40
2007	132	61	96	44	12	2	130	40
2008	79	50	104	89	20	6	85	113
2009	68	44	93	59	31	16	93	60
2010	29	21	141	91	12	9	101	143
All years:	709	294			80	36		
Median distance for all years:			100	71			102	74

2.5. Statistical analysis

We performed a geographically restricted randomization procedure to test the null hypothesis that sites are no closer to roads or streams than would be expected by chance (spatial independence). First, a dataset of random points was constructed in ArcMap with the goal of approximating the overall south to north distribution of observed *P. ramorum* sites. A south to north stratification was necessary to account for the differences in exposure to the pathogen from the original sites and variation in road or stream density within each study area. To accomplish this, random points were differentially distributed within 1-km wide regions spaced horizontally throughout each study area (Appendix Fig. 1). The proportion of random points created was equal to the proportion of actual SOD sites within each region; the total number of random points created over the entire North Chetco study area was equal to the number of sites present multiplied by 5 000, generating 1.47×10^6 random points total. A random dataset was similarly produced in the Borax study area generating a set of 1.8×10^5 ($= 36 * 5\,000$) random points.

The distance of each random point to the nearest road and stream was calculated with a spatial join as with the true dataset. To test for a spatial association between roads and SOD sites within the North Chetco area, for example, using code implemented in

MATLAB (ver. 7.14; Mathworks) we randomly sampled 294 distances from the random dataset (each representing the distance of a random point to the nearest road; Appendix Box 1). We then calculated the median distance to the nearest road for that run. Median distance was preferred over the mean to reduce the effect of extreme outliers present in the random dataset. Due to computational constraints no attempt was made to enforce a minimum distance between random points. This was repeated 10,000 times, and all statistics were tabulated to generate a distribution of median distances to roads expected under the null hypothesis of spatial independence.

Statistical likelihood of observing the true median distance under randomness was computed with a 1-tailed randomization test where $\text{pseudo-}p = k/N$; k = the number of random data sets which had median distances less than or equal to the true median distance to roads (those with a median distance closer than observed), N = the total number of randomizations performed (Manly, 1991).

An identical process using the same initial dataset of random points, but a new set of 10,000 randomizations was performed to assess the spatial dependence of *P. ramorum* to streams within the North Chetco study area. We repeated the analysis in the Borax study area in which for each of the 10,000 randomizations we sampled 36 points.

3. Results

3.1. Statistics for observed sites

From the 709 positive samples observed in the North Chetco study area between 2001 and 2010 we identified 294 sites, ranging from <1 to 610 m to the nearest road (median = 100 m), and <1 to 414 m to the nearest stream (median = 71 m) (Table 2 and Fig. 3a, b).

From the 80 positive samples observed in the Borax study area between 2006 and 2010 we identified 36 sites, ranging from 5 to 393 m to the nearest road (median = 102 m), and 20 to 252 m to the nearest stream (median = 74 m) (Table 2 and Fig. 4a and b).

3.2. Randomization results

Of the 10,000 randomizations used to assess spatial dependence to roads in the North Chetco study area, the average median distance to roads was 101 m; 4 733 randomizations had a median distance to road that was closer than observed. Sites were not significantly closer to roads than expected by chance (pseudo- $p = 0.4733$) (Fig. 5a). Of the 10,000 randomizations used to assess spatial dependence to streams in the North Chetco study area, the average median distance to streams was 88 m; only 14 of the 10,000 randomizations were closer to streams than observed. Sites were significantly closer to streams than expected by chance (pseudo- $p = 0.0014$) (Fig. 5b).

Of the 10,000 randomizations used to assess spatial dependence to roads in the Borax study area, the average median distance to roads was 78 m; 9 005 randomizations had a median distance to road that was closer than observed. Sites were not

significantly closer to roads than expected by chance (pseudo- $p = 0.9005$) (Fig. 6a). Of the 10,000 randomizations used to assess spatial dependence to streams in the Borax study area, the average median distance to streams was 91 m; 1 446 of the 10,000 randomizations were closer to streams than observed. Sites were not significantly closer to streams than expected by chance (pseudo- $p = 0.1446$) (Fig. 6b).

4. Discussion

Numerous models have been built to describe the real or potential distribution of *P. ramorum* in both nursery and forest environments. Much of the work on the Californian epidemic has focused upon the conditions contributing to severity, not necessarily risk of introduction, of SOD by incorporating the environmental and host factors for which there is evidence to support their epidemiological importance (Meentemeyer et al., 2004; Condeso and Meentemeyer, 2007; Cushman and Meentemeyer, 2008). Others have tested for aggregations in population structure or *P. ramorum* detections as indices of range of spread (Xu et al., 2009; Mascheretti et al., 2008).

The SOD early detection and local eradication program has produced a spatially explicit dataset of the distribution of *P. ramorum* in Oregon. The restriction of our analysis to the North Chetco, an area with minimal public access and required road use, has minimized confounding patterns of spread due to different dispersal mechanisms, particularly extensive recreational movement and the transportation of nursery stock. Collapsing clusters of adjacent infected trees into one site coordinate for analysis also eliminates local splash dispersal from consideration. The resulting point pattern is unique amongst the datasets used in previous models of *P. ramorum* spread, and describes the distribution of SOD solely

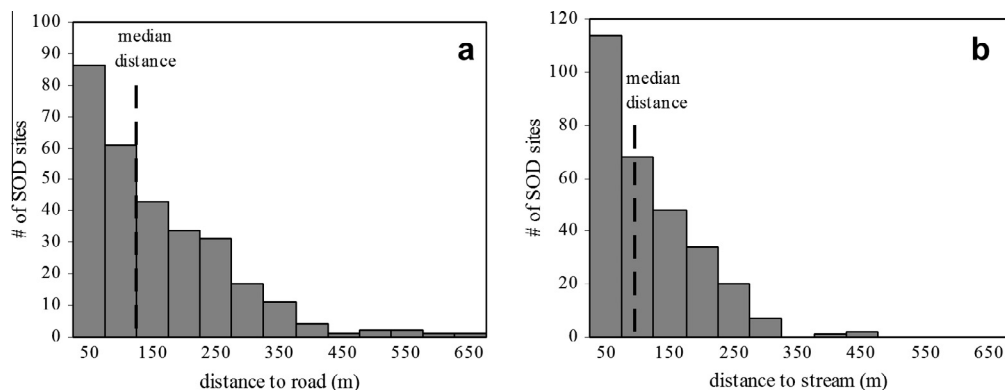


Fig. 3. Distribution of observed distances to the nearest road (a) or stream (b) for all SOD positive sites identified between 2001 and 2010 in the North Chetco study area ($n = 294$).

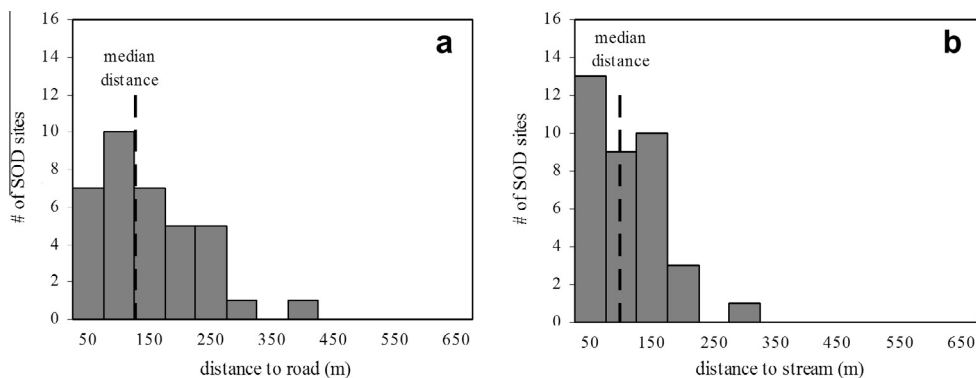


Fig. 4. Distribution of observed distances to the nearest road (a) or stream (b) for all SOD positive sites identified between 2006 and 2010 in the Borax study area ($n = 36$).

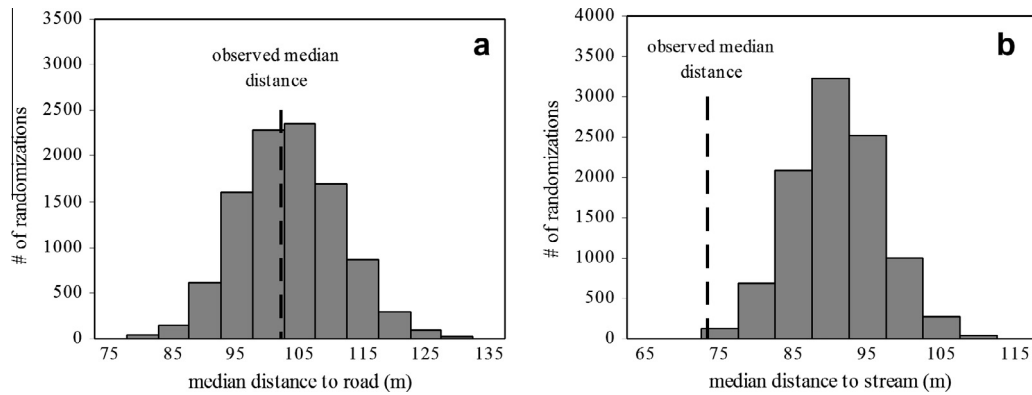


Fig. 5. Distributions of median distances to the nearest road (a) or stream (b) calculated for each of the 10,000 randomizations used to assess the spatial independence of SOD sites to roads or streams within the North Chetco study area. The observed median distance to road or streams calculated for the actual 294 SOD positive sites is indicated by the dashed line.

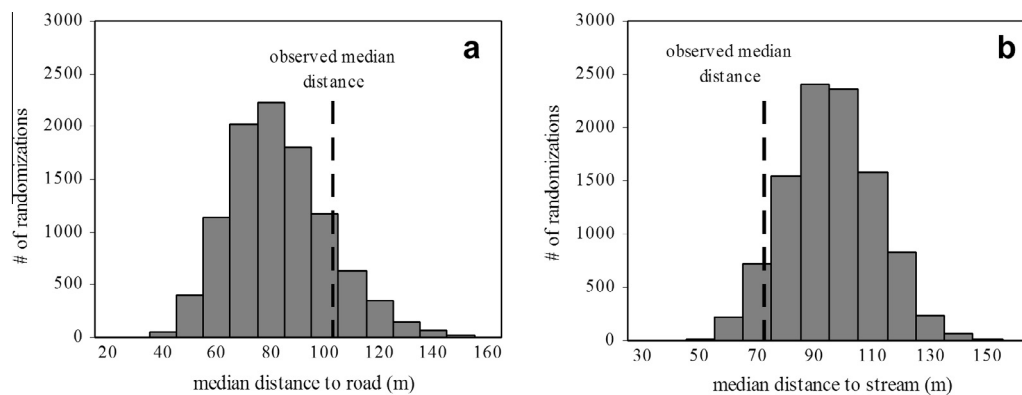


Fig. 6. Distributions of median distances to the nearest road (a) or stream (b) calculated for each of the 10,000 randomizations used to assess the spatial independence of SOD sites to roads or streams within the Borax study area. The observed median distance to road or streams calculated for the actual 36 SOD positive sites is indicated by the dashed line.

as a result of dispersal between sites. Randomization tests are well suited for relating point pattern relationships to discrete landscape components, provided each randomization approximates other sources of heterogeneity occurring independently of the spatial feature to be analyzed (for example, the concentration of sites in the southern edge of *P. ramorum*'s range due to the dispersal gradient of inoculum from the areas of its original introduction) (Fortin and Jacquez, 2000; Fortin and Payette, 2002; Roxburgh and Chesson, 1998).

Comparable spatial analyses done for other forest pathogens (and those on *P. ramorum*) have all taken different statistical approaches best suited for the available datasets, including survival analysis combined with dendrochronologically-dated mortality (used by Jules et al. (2002) to describe risk of infection of Port-Orford cedar by *P. lateralis*), or geostatistics (used by Vannini et al. (2010) to describe the distribution of ink disease caused by *P. cambivora*). Regardless of dissimilar methodology, both Jules et al. (2002) and Vannini et al. (2010) described statistically a pattern that was apparent visually, as first documented by Hansen et al. (2000) and Saavedra et al. (2007), respectively. Similarly, our results within the North Chetco study area are consistent with prior observations that new SOD sites are typically not roadside, but do appear to occur more often along stream ways.

Given the examples for road-mediated dispersal among other forest *Phytophthora* species, however, road use was considered to present a high risk for long distance spread of inoculum. Statistical methodology is furthermore required given the frequency distribution of SOD sites to roads. While many SOD sites were relatively close to roads – 50% of SOD sites within the North Chetco

study area were within 100 m of the nearest roadway (Fig. 3a) – sites were no more likely to occur closer to roads than expected by chance (Fig. 5a). The independence between the distribution of sites and the road network suggests that the movement of inoculum in infested soils along roads has not contributed to the northerly spread of SOD within the North Chetco watershed. Rather, the frequency with which we observe *P. ramorum* close to roads is likely due to the overall high road density within this study area.

Little prior work has been performed assessing the relationship between SOD and roads, specifically. Regardless, implicit in Californian epidemiology is the risk that movement of inoculum by people using roads contributes to spread of SOD. It remains possible that roads are a dispersal pathway in Oregon, but that current disease management protocols have maintained inoculum levels below a threshold that could contribute to the significant movement of *P. ramorum* in Oregon. Alternatively, soil movement by people may contribute more to the local intensification of SOD post-introduction, not the means by which inoculum is introduced into new areas. Local intensification by hikers is consistent with prior studies of the spread of *P. lateralis*, where dispersal of soil-borne inoculum by foot and hoof was independent of roads and relatively short ranged, contributing more to inoculum movement within a site than between watersheds (Jules et al., 2002).

While dispersal along roads cannot account for the landscape distribution of *P. ramorum*, the North Chetco area results did indicate that SOD sites occurred significantly closer to waterways than expected by chance. Host distribution is an unlikely explanation

for this strong stream association. Overstory tanoaks are readily identified in aerial photographs (Fig. 2), and it is evident that tanoaks are generally abundant at all elevations within the study area with the exceptions of recent clear cuts on industrial forest lands. Additional surveys within the heavily infested area have shown tanoak to be a common component of understory vegetation as well. More likely the stream association results from some combination of abiotic factors and alternative dispersal mechanisms.

P. ramorum has demonstrated tolerance to a wide variety of environments in Oregon, though studies in California have shown a strong preference for moister conditions. Recovery of *P. ramorum* in soils, foliage, and rainwater is typically higher in wetter seasons and locations (Davidson et al., 2011; Fichtner et al., 2009). Changes in vegetation cover have also increased inoculum load and disease prevalence through a decrease in solar insolation and temperature (Meentemeyer et al., 2008). We do expect these conducive conditions to be more prevalent in riparian areas close to streams, either due to topography or increased overall hardwood canopy cover (Chen et al., 1999; Rambo and North, 2008). Fog is also commonly observed in basins in the North Chetco area, likely providing a cooler and moister microclimate more favorable for pathogen establishment closer to the streams.

Alternatively, the distribution of SOD may indicate other dispersal mechanisms are contributing to the spread of *P. ramorum*. The potential for alternative dispersal methods contributing to spread at this scale (multiple km) was identified by Mascheretti et al. (2008), whereby the degree of spatial autocorrelation between sampled loci declined within the range of splash dispersal, but reached a high degree of similarity at distances greater than 1 km. Two often cited options remain possible: the dispersal of inoculum in stream water itself, or aerial dispersal in blowing fog, rain, or wind. *P. ramorum* is regularly recovered from stream baits deployed downstream of infested tanoak stands and stream baiting is incorporated in the SOD early detection program in Oregon (Sutton et al., 2009). Perhaps terrestrial infections originate when host leaves are immersed during high water, or by water splash in areas with turbulent stream flow. Anecdotal evidence has suggested stream-borne inoculum to be a relatively unimportant dispersal pathway in natural ecosystems (as mentioned by Grünwald et al., 2012), but surveys of riparian vegetation should be performed to determine if *P. ramorum* is established in stream-side foliage as an indication of stream-dispersal.

There is a general tendency for winds to blow parallel to valley axes without gaining vertical height (Eckman, 1998) and, as mentioned, fog is often observed drifting up and down the stream valleys in the North Chetco study area while the ridges remain clear. While poorly studied for forest *Phytophthora* spp., dispersal of sporangia in wind currents is a well documented phenomenon contributing to the spread of some agricultural *Phytophthora* spp. (Aylor, 1990; Ristaino and Gumpertz, 2000). No direct evidence has surfaced supporting the detachment of *P. ramorum* sporangia with a mechanism analogous to these agricultural species, although they are borne on stalks similar to other aerially dispersers. 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, the dispersal gradient observed for SOD in southwest Oregon (Hansen et al., 2008) is consistent with turbulent dispersal, also suggestive of an aerial mechanism.

While we did not detect any significant relationships, spatial simulations in the Borax study area produced results similar to simulations in the North Chetco area. There was no association between SOD and roads. Rather, there was a tendency for SOD sites to be further from roads in the Borax area than by chance alone. Although *P. ramorum* was less limited to stream side habitat, SOD sites tended to be closer to streams than further away, again similar to our results in the North Chetco. These results may be

indicative of the same mechanisms that explain the distribution of SOD in the North Chetco, however modulated to the specific conditions present in the Borax area.

Although immediately adjacent to one another, the Borax study area differed from the North Chetco area in several ways. Borax was characterized by disturbance associated with rural residential development rather than industrial forestry. Unlike the more uniform forest cover of the North Chetco area, land was often cleared immediately adjacent to the houses and roads, with tanoak concentrated further away (Fig. 2). Our analysis could also not account for possible local movement in soils along trails or old skid roads, which within the Borax study area tend to radiate away from the houses and roadways. Either may explain why infections occurred preferentially further away from roads than near them in the Borax study area (albeit not significantly). This within-stand establishment would be consistent with our hypothesis that if indeed soil movement is responsible for the spread of SOD, it contributes more to local intensification than long distance movement.

At lower elevations closer to the ocean, Borax was also under a stronger maritime climate influence than the North Chetco. Observations suggest that fog was more frequent and more uniform in the Borax area than to the east across the ridge separating it from the North Chetco. Under the low-inoculum conditions of primary establishment successful infection should be more sensitive to microclimate than spread post-establishment. In areas with an overall greater distribution of suitable environment, such as a greater degree of fog cover, the distribution would thus be significantly less limited. Alternatively, the stream association observed in the North Chetco area may not be as strong in Borax where the topography is not oriented perpendicular to the coast resulting in spread that, while also to the north, was not confined to a single drainage system. This would most likely impact the distribution of *P. ramorum* if it indeed disperses long distances aerially, whereby in the North Chetco winds would be channeled up the drainage system but in the Borax area winds would impact the flanking ridges. Overall our use of spatially-explicit randomizations may be better suited for the North Chetco area, where the movement of *P. ramorum* has been more constrained by topography, and where lack of public access and a wider range of microclimate variation produced a stronger spatial signature.

In neither area was there any indication that deposition of infested soils along roads has significantly contributed to the movement of *P. ramorum*. It remains unlikely, then, that road closures would have prevented the spread of SOD in Oregon. Additional studies should be conducted in California to confirm this conclusion, particularly considering the great differences in epidemiology between these two locales that may affect the risk of soil inoculum. Notably this includes the greater incidence of infection of bay laurel (*Umbellularia californica*) in Californian forests, a species which supports a significantly greater quantity of inoculum production compared to tanoak (Davidson et al., 2008).

Lacking dispersal along roads in Oregon other mechanisms must have contributed to the spread of inoculum, at scales documented up to 4 km from the nearest known source. Both dispersal and environment may produce spatial patterns of disease associated with streams (or more precisely, topography), and by itself a landscape analysis cannot distinguish between either explanation (Real and McElhany, 1996). The utility of these methods best direct future research needs and identify areas at a higher or lower risk of introduction. The strong stream-association, especially as seen in the North Chetco area, suggests that concentrating monitoring efforts to host areas in closer proximity to streams may improve detection of SOD. With a more restrictive range, pre-emptive treatment in stream-associated forests in proximity to known infection may also be suggested in areas with environmental conditions less conducive to the establishment of *P. ramorum*.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.10.002>.

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