Phytophthora ramorum and Congenerics: Global Threats to Oaks

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ABSTRACT

Phytophthora ramorum, a microscopic pathogen belonging to Phylum Oomycota, has been causing sudden oak death in California forests for over 25 years. In the U.S., this pathogen primarily kills *Quercus agrifolia* (coast live oak) and other oaks in genus *Quercus*, section *Lobatae*, as well as *Notholithocarpus densiflorus* (tanoak); in the UK, Ireland and France, it also kills *Larix kaempferi* (Japanese larch) and causes stem cankers and/or foliar blight on a variety of native and non-native hosts including *Fagus sylvatica* (beech), *Castanea sativa*, (sweet chestnut), *Q. falcata* (southern red oak) and *Q. rubra* (northern red oak). In nurseries, the pathogen has been detected on popular ornamental plants (i,e., *Rhododendron* and *Camellia*), and eradication is mandated by quarantines in over 60 countries in Asia, Europe and North America. In the past several years the estimate of the number of trees killed by the pathogen in California, has increased 10 fold to over 50 million. The apparent increase in estimated mortality underlines both our increasingly sophisticated understanding of this pathogen's effects as well as its continued spread and infection of trees in western North America. This paper summarizes gains in pathogen understanding, new developments in pathogen distribution and activity, management approaches and research progress since 2014. In many ways we have learned a lot about *P. ramorum*. However, in terms of tree mortality, recent developments suggest that we are just beginning to foresee its potential to alter landscapes.

Introduction

Phytophthora ramorum, a microscopic pathogen belonging to Phylum Oomycota within the kingdom-level *Stramenopiles-Alveolata-Rhizaria* "supergroup" (McCarthy and Fitzpatrick 2017), has been causing sudden oak death in California forests for over 25 years. In the U.S., this pathogen primarily kills *Quercus agrifolia* (coast live oak), *Q. kelloggii* (California black oak), *Q. parvula* var. *shrevei* (Shreve oak), *Q. chrysolepis* (canyon live oak), and *Notholithocarpus densiflorus* (tanoak), although it can also kill *Arbutus menziesii* (madrone) and small individuals of other species; in the UK, Ireland and France, it also kills *Larix kaempferi* (Japanese larch) and causes stem cankers and/or foliar blight on a variety of native and non-native hosts including *Fagus sylvatica* (beech), *Castanea sativa* (sweet chestnut), *Q. falcata* (southern red oak) and *Q. rubra* (northern red oak). In nurseries, the pathogen has been detected on popular ornamental plants (i,e, *Rhododendron* and *Camellia*), and eradication is mandated by quarantines in over 60 countries in Asia, Europe and North America (Kliejunas 2010).

In California, a recent estimate puts the number of trees killed by this plant pathogen since its introduction at nearly 50 million (California Oak Mortality Task Force 2018). In 2014, at the time of the most recent summary of pathogen activity to appear in this Journal (Frankel and Palmieri 2014), rough estimates found that only 5 million California trees had been killed. The apparent increase in estimated mortality underlines both our increasingly sophisticated understanding of this pathogen's effects as well as its continued spread and infection of trees in western North America. This paper summarizes gains in pathogen understanding, new developments in pathogen distribution and activity, management approaches and research progress since 2014. In many ways we have learned a lot about *P. ramorum*. However, in terms of tree mortality, recent developments suggest that we are just beginning to foresee its potential to alter landscapes.

Frankel and Palmieri (2014) summarized *P. ramorum*'s appearance in California during the 1990s, its basic biology, the regulatory and management actions taken to curtail its spread, and its variable emergence in coastal California and other ecosystems. Monitoring of *P. ramorum* symptoms and impacts since 2014 has reinforced for observers the importance of local climatic conditions in disease development. Following a very wet winter in 2016-2017 on the U.S. West Coast and a very wet set of summer and autumn conditions in the UK, increasing numbers of symptoms and increasing tree mortality caused by *P. ramorum* have been observed up to the present day (California Oak Mortality Task Force 2018). As one example, the increase in the number of new outbreaks in Scotland has been so large that attempts to fell all infected trees had to be abandoned in favor of a priority zone at the periphery of the infested areas (Forestry Commission Scotland 2018).

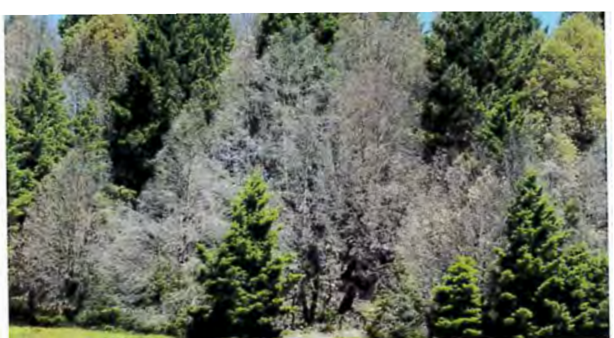

Photo 1/ *Notholithocarpus densiflorus* mortality along the first ridge inland from the ocean in Sonoma County,

Monitoring and new detections

The years 2017 and 2018 saw the detection of *P. ramorum* in at least two noteworthy places. The pathogen was detected for the first time in France in May 2017 on *L. kaempferi* in the Saint-Cadou forest in the Finistère department in western Brittany. By autumn of that year, the pathogen was affecting 47% of the *L. kaempferi* in the forest (Schenck et al. 2018). Genetic analysis could not trace the probable source of the *P. ramorum* population in this French forest, but it strongly suggested that it did not come from the nearest likely source in the UK (California Oak Mortality Task Force 2018). Additionally, researchers from the UK and mainland Europe detected *P. ramorum* on natural vegetation and in water in the Lào Cai province of Vietnam. Preliminary information suggested that the isolate did not match any known genetic lineage, fueling speculation that this location could represent part of the pathogen's native range (California Oak Mortality Task Force 2018).

Scientific name	Scientific name
Arctostaphylos glandulosa	Eastwood manzanita
Arctostaphylos hooveri	Hoover's manzanita
Arctostaphylos montaraensis	Montara manzanita
Arctostaphylos montereyensis	Monterey manzanita, Toro manzanita
Arctostaphylos morroensis	Morro manzanita
Arctostaphylos pallida	Alameda manzanita, Oakland Hills manzanita, pallid manzanita
Arctostaphylos pilulosa	La Panza manzanita, Santa Margarita manzanita
Arctostaphylos pumila	dune manzanita, sandmat manzanita
Arctostaphylos rainbowensis	rainbow manzanita
Arctostaphylos silvicola	Bonny Doon manzanita, silverleaf manzanita
Arctostaphylos virgata	Bolinas manzanita, Marin manzanita
Chrysolepis chrysophylla	golden chinquapin
Cornus nuttallii	Pacific dogwood
Lophostemon confertus (=Tristania conferta)	Brisbane box
Notholithocarpus densiflorus var. *echinoides*	shrub tanoak
Pickeringia montana	chaparral pea
Rubus ursinus	blackberry, trailing blackberry
Trillium ovatum	Western wake robin
Vaccinium ovatum	red huckleberry
Vinca minor	common periwinkle

Table 1/ *Phytophthora ramorum* host plants discovered in the U.S. since 2011. Koch's postulates have not been completed for some of these species, and they are pending USDA APHIS action to be added to the official U.S. host or associated host list.

Surveyors and diagnosticians continue to detect the pathogen on unexpected hosts. Some of the most severe impacts have appeared on *Arctostaphylos* spp. (manzanita), several of which are rare, threatened, or endangered (California Native Plant Society since USDAAPHIS last published a list of official hosts in 2012-2013 (Table 1; California Oak Mortality Task Force 2018; Rooney-Latham et al. 2017; Swiecki and Bernhardt 2017b). Two other developments have also emerged concerning hosts that have been known for many years. First, it was discovered that *P. ramorum* can cause cryptic bole cankers on *Q. chrysolepis*. These cankers produce almost no external symptoms, so that infected trees can go undetected for many years before death (Swiecki et al. 2016). Second, concern arose about the potential impacts of the EU1 genetic lineage on conifers in the western U.S. Up until 2015, this lineage was only found in Europe and in certain U.S. nurseries and associated waterways, but it was detected on a *N. densiflorus* in its natural environment in Oregon in February of that year (Grünwald et al. 2015).

The discovery of EU1 in Oregon wildlands prompted researchers to follow two lines of inquiry motivated by concern about this lineage's introduction and impacts. Microsatellite alleles of the *N. densiflorus* isolate nearly but inexactly matched those of an isolate previously detected at a nearby retail nursery (which was subsequently closed), supporting the suggestion of Kamvar et al. (2015) that multiple independent introductions were responsible for the geographic extent and patterns of the sudden oak death epidemic in Oregon. Motivated by the possibility that the EU1 lineage could be more aggressive on conifers than the North American lineages (NA1 and NA2) – based on the EU1 lineage's increased virulence on conifers in the U.K. and Ireland – researchers confirmed Koch's postulates for this lineage on *Abies grandis* (grand fir) and *Pseudotsuga menziesii* (Douglas-fir) (LeBoldus et al. 2017) in preparation for more detailed pathogenicity studies (Association of Oregon Counties 2017).

Research and management

Despite waning allocations from large institutions and governmental organizations for *P. ramorum* investigations, researchers continue to learn valuable new information from both basic and applied projects. We highlight several examples below.

(1) *Phytophthora ramorum* and fire. Several research projects elucidated the interactions of *P. ramorum,* fire and vegetation. Forrestel et al. (2015) documented increased fuel loading in stands dominated by *P. menziesii* and *Sequoia sempervirens* (redwood) in coastal California, potentially leading to increased fire behavior for some period of time, and Shaw et al. (2017) found similar increases in a *Q. agrifolia*-dominated type. Varner et al. (2017) found that dead hardwood foliage is more flammable than *P. menziesii* foliage and that as infected hardwoods such as *N. densiflorus* die, accumulated surface fuels in resulting *P. menziesii*-dominated stands are expected to be less flammable. This process resembles mesophication trends in other situations where *P. menziesii* has increased in stand dominance, such as encroached oak woodlands in the north coast (Engber et al. 2011). In a series of investigations over the past decade in the Big Sur area of California, where data on *P. ramorum*-infested and -noninfested plots were available both before and after two large wildfires, Metz et al. (2011; 2013; 2017) showed that wildfire severity and impacts to subsequent vegetation succession depend heavily on stage of disease development and its year-to-year effects on the fuels profile. These researchers documented that trees resistant to either wildfire or sudden oak death alone can suffer unexpectedly high damage from the convergence of both disturbances. Meanwhile, Simler et al. (2018)

showed more robust growth because of release from competition. In the period from 2015-2018, several large wildfires in both California and Oregon burned in *P. ramorum*-infested landscapes, including wildland-urban interface areas, providing future opportunities for more research into pathogen-fire interactions and effects (California Department of Forestry and Fire Protection 2018).

(2) *Phytophthora ramorum* in watercourses. Although *P. ramorum* is readily detected in stream water, we know little about its persistence or epidemiology in aquatic environments. Aram and Rizzo (2018) filled some of this knowledge gap by showing that one mode of *P. ramorum* persistence in streams is by colonization of naturally occurring, fallen green leaves and other fresh floating litter, although the pathogen does not effectively compete with other *Phytophthora* species for occupation of this material over the long term. Morgan (2017) made progress toward clarifying another infection route with the observation that such floating debris can cause infections on susceptible streamside vegetation when floodwaters strand the debris against trunks, branches, and twigs.

(3) *Phytophthora ramorum* management. Applied, adaptive management projects in several locations over the last five years have clarified the potential of various techniques to slow the spread of *P. ramorum* outbreaks, prevent or delay infection onset, and cope with pathogen impacts on vegetated landscapes. Notable among these are *Umbellularia californica* (California bay laurel), the main sporulating host in California) removal projects undertaken in Jack London State Park (Sonoma County, CA), in 2014 and the UC Big Creek Reserve and Los Padres National Forest in Big Sur (Monterey County, CA) in 2015 (California Oak Mortality Task Force 2018). The objective of these *U. californica* removal projects is to prevent or delay initial infection by removing the primary inoculum

Photo 2/ *Notholithocarpus densiflorus* mortality

are often cost-effective as they discourage *U. californica* dominance and promote greater tree species diversity in the managed stand. In Redwood National Park in northern California (Humboldt County), management projects focused on eradication by removal of infected *N. densiflorus* and *U. californica* to create a large (100-400 m) host-free buffer zone around infected trees (California Oak Mortality Task Force 2018), but the project was abandoned in 2017 amid evidence that showed that even these large buffer zones were insufficient for eradication (Morgan 2017). Other projects that began as eradication attempts have also transitioned into broader-scale efforts to slow pathogen spread and/or learn optimal techniques for removing susceptible hosts, preventing resprouting, and utilizing host woody material for environmental sustainability and carbon capture (Twieg et al. 2017). Restoration projects have also been undertaken that focus both on impact alleviation and future stand structure enhancement (e.g., Cobb et al. 2017).

Oregon remains committed to slowing the spread of the outbreaks; but continued pathogen spread has forced the state to concentrate on the periphery of the infested area, with intense focus on eradication efforts in areas known to harbor the EU1 lineage (California Oak Mortality Task Force 2018; Kanaskie et al. 2017). In England, Wales, Scotland, and Ireland, similar choices have had to be made for eradication projects in *L. kaempferi* plantations (Forestry Commission Scotland 2018; California Oak Mortality Task Force 2018). Meanwhile, research on management techniques elsewhere has made important discoveries related to such topics as efficacy and best practices for oak and tanoak treatment using phosphonate fungicides (Garbelotto 2018; Swiecki and Bernhardt 2017a); the survival of *P. ramorum* propagules in compost (Swain and Garbelotto 2015); and new geospatial methods of visualizing the effects of sudden oak death management decisions on the landscape (Meentemeyer et al. 2017).

These selected topics only begin to describe the variety of ongoing *P. ramorum* research. New areas in research and management have been opened because of the detection in many places of a nursery-wildland connection for a variety of *Phytophthora* species, not only *P. ramorum* (Garbelotto et al. 2018; Jung et al. 2016). These detections have led to vigorous public awareness campaigns designed to transmit best practices for prevention of *Phytophthora* transmission to native trees, shrubs, and herbaceous plants (Frankel et al. 2018). Political action campaigns and the consideration of legislation relating to invasive species (e.g., California Senate Bill 287, which has not passed, to address habitat restoration projects and *Phytophthora* introductions; Assembly Bill 2470, which passed, to provide a legislative code basis and money to fund invasive species activities; California State Legislature 2019) show some progress in demonstrating to policymakers, vegetation managers, and others that invasive plant pathogens represent a substantial threat to public values and plant health and that the conservation of native habitat is worth a high level of public investment. Through its continued visibility as a threat to iconic oaks and tanoaks, the case of *P. ramorum* is likely to draw attention to this important point for years to come.

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Works cited

Aram, K., and D.M. Rizzo. 2018. Distinct trophic specializations affect how *Phytophthora ramorum* and Clade 6 *Phytophthora* spp. colonize and persist on *Umbellularia californica* leaves in streams. *Phytopathology* 108: 858-869.

Association of Oregon Counties. 2017. *Sudden Oak Death Task Force Strategic Action Plan*. www.oregonlegislature.gov/smithd/documents/sodtaskforce_actionplan_june2017_final.pdf. Accessed December 18, 2018.

California Department of Forestry and Fire Protection. 2018. CA.GOV. CAL FIRE. Incident information. www.fire.ca.gov/current_incidents Accessed December 18, 2018.

California Native Plant Society. 2019. Inventory of rare and endangered plants. www.rareplants.cnps.org. Accessed January 11, 2019.

California Oak Mortality Task Force. 2018. Newsletter archive. www.suddenoakdeath.org/library/newsletter-archive. Accessed December 18, 2018.

California State Legislature. 2019. California legislative information. leginfo.legislature.ca.gov/faces/home.xhtml. Accessed January 11, 2019.

Cobb, R.C., D.M. Rizzo, K. Frangioso, P. Hartsough, J. Klein, M. Swezy, A. Williams, C. Sanders, and S.J. Frankel. 2017. Restoration of Mount Tamalpais forests destroyed by the sudden oak death pathogen. In *Proceedings of the sixth sudden oak death science symposium, Gen. Tech. Rep. GTR-PSW-255,* coordinated by S.J. Frankel and K.M. Harrell, p.23. Albany, CA: US Department of Agriculture Forest Service, Pacific Southwest Research Station.

Engber, E.A., J.M. Varner, L.A. Arguello, and N.G. Sugihara. 2011. The effects of conifer encroachment and overstory structure on fuels and fire in an oak woodland landscape. *Fire Ecology* 7(2): 32-50.

Forestry Commission Scotland. 2018. *Phytophthora ramorum* in Scotland. scotland.forestry.gov.uk/supporting/forest-industries/tree-health/phytophthora-ramorum. Accessed December 18, 2018.

Forrestel, A.B., B.S. Ramage, T. Moody, M.A. Moritz, and S.L. Stephens. 2015. Disease, fuels and potential fire behavior: Impacts of sudden oak death in two coastal California forest types. *Forest Ecology and Management* 348: 23-30.

Frankel, S.J., J.M. Alexander, D. Benner, and A. Shor. 2018. Coordinated response to inadvertent introduction of pathogens to California restoration areas. *California Agriculture* 72: 205-207.

Frankel, S.J., and K.M. Palmieri. 2014. Sudden oak death, *Phytophthora ramorum*: a persistent threat to oaks and other tree species. *International Oaks*: 43-56.

Garbelotto, M. 2018. Sudden oak death disease management. UC Berkeley Forest Pathology and Mycology Lab. https://nature.berkeley.edu/garbelottowp. Accessed December 18, 2018.

Garbelotto, M., S.J. Frankel, and B. Scanu. 2018. Soil- and waterborne *Phytophthora* species linked to recent outbreaks in northern California restoration sites. *California Agriculture* 72: 208-216.

Grünwald, N.J., M.M. Larsen, Z.N. Kamvar, P.W. Reeser, A. Kanaskie, J. Laine, and R. Wiese. 2015. First report of the EU1 clonal lineage of *Phytophthora ramorum* on tanoak in an Oregon forest. *Plant Disease* 100: 1024-1024.

Jung, T., L. Orlikowski, B. Henricot, P. Abad-Campos, A. G. Aday, O. Aguín Casal, J. Bakonyi, S. O. Cacciola, T. Cech, D. Chavarriaga, T. Corcobado, A. Cravador, T. Decourcelle, G. Denton, S. Diamandis, H.T. Doğmuş-Lehtijärvi, A. Franceschini, B. Ginetti, S. Green, M. Glavendekić, J. Hantula, G. Hartmann, M. Herrero, D. Ivic, M. Horta Jung, A. Lilja, N. Keca, V. Kramarets, A. Lyubenova, H. Machado, G. Magnano di San Lio, P.J. Mansilla Vázquez, B. Marçais, I. Matsiakh, I. Milenkovic, S. Moricca, Z. Á. Nagy, J. Nechwatal, C. Olsson, T. Oszako, A. Pane, E.J. Paplomatas, C. Pintos Varela, S. Prospero, C. Rial Martínez, D. Rigling, C. Robin, A. Rytkönen, M. E. Sánchez, A. V. Sanz Ros, B. Scanu, A. Schlenzig, J. Schumacher, S. Slavov, A. Solla, E. Sousa, J. Stenlid, V. Talgø, Z. Tomic, P. Tsopelas, A. Vannini, A.M. Vettraino, M. Wenneker, S. Woodward, and A. Peréz-Sierra. 2016. Widespread *Phytophthora* infestations in European nurseries put forest, semi-natural and horticultural ecosystems at high risk of *Phytophthora* diseases. *Forest Pathology* 46: 134-163.

Kamvar, Z N., M.M Larsen, A.M. Kanaskie, E.M. Hansen, and N.J. Grünwald. 2015. Spatial and temporal analysis of populations of the sudden oak death pathogen in Oregon forests. *Phytopathology* 105: 982-989.

Kanaskie, A., R. Wiese, D. Norlander, J. Laine, S. Navarro, E.M. Goheen, R. Rhatigan, E. Hansen, W. Sutton, P. Reeser, N. Grunwald, Z. Kamvar, and N. Osterbauer., 2017. Slowing spread of sudden oak death in Oregon forests, 2001-2015. In *Proceedings of the Sixth Sudden Oak Death Science Symposium, Gen. Tech. Rep. GTR-PSW-255,* coordinated by S.J. Frankel and K.M. Harrell, p.1. Albany, CA: US Department of Agriculture Forest Service, Pacific Southwest Research Station.

Kliejunas, J. T. 2010. *Sudden oak death and* Phytophthora ramorum*: a summary of the literature. Gen. Tech. Rep. PSW-GTR-234.* Albany, CA: US Department of Agriculture Forest Service, Pacific Southwest Research Station.

LeBoldus, J.M., K.L. Sondreli, W. Sutton, P. Reeser, S. Navarro, A. Kanaskie, and N.J. Grünwald. 2017. First report of *Phytophthora ramorum* lineage EU1 infecting Douglas-fir and grand fir in Oregon. *Plant Disease* 102: 455-455.

McCarthy, C.G.P., and D.A. Fitzpatrick. 2017. Phylogenomic reconstruction of the oomycete phylogeny derived from 37 genomes. Msphere. 2(2):e00095-17.

Meentemeyer, R.K., F. Tonini, D. Shoemaker, R.C. Cobb, B.A. Harmon, V. Petras, V., and H. Mitasova. 2017. Collaboratively managing sudden oak death using tangible geospatial modeling. In *Proceedings of the Sixth Sudden Oak Death Science Symposium, Gen. Tech. Rep. GTR-PSW-255,* coordinated by S.J. Frankel and K.M. Harrell, pp. 9-10. Albany, CA: US Department of Agriculture Forest Service, Pacific Southwest Research Station.

Metz, M.R., K.M. Frangioso, R.K. Meentemeyer, and D.M. Rizzo, D.M. 2011. Interacting disturbances: wildfire severity affected by stage of disease invasion. *Ecological Applications* 21(2): 313-320.

Metz, M.R., J.M. Varner, K.M. Frangioso, R.K. Meentemeyer, and D.M. Rizzo. 2013. Unexpected redwood mortality from synergies between wildfire and an emerging infectious disease. *Ecology* 94(10): 2152-2159.

Metz, M.R., J.M. Varner, A.B. Simler, K.M. Frangioso, and D.M. Rizzo. 2017. Implications of sudden oak death for fire management. *Forest Phytophthoras* 7: 30-44.

Morgan, L.A. 2017. Modeling the spread of sudden oak death across a heterogeneous landscape in Redwood National Park using a spatially explicit epidemiological model. https://digitalcommons.humboldt.edu/cgi/viewcontent.cgi?article=1029&context=etd

GTR-PSW-255, coordinated by S.J. Frankel and K.M. Harrell, pp. 83-84. Albany, CA: US Department of Agriculture Forest Service, Pacific Southwest Research Station.

Schenck, N., C. Saurat, C. Guinet, C. Fourrier-Jeandel, L. Roche, A. Bouvet, C. Husson, F.-X. Saintonge, and R. Ioos.. 2018. First Report of *Phytophthora ramorum* Causing Japanese larch Dieback in France. *Plant Disease* 102: 2045-2045.

Shaw, D.C., T. Woolley, R.G. Kelsey, B.A. McPherson, D. Westlind, D.L. Wood, and E.K. Peterson. 2017. Surface fuels in recent *Phytophthora ramorum* created gaps and adjacent intact *Quercus agrifolia* forests, East Bay Regional Parks, California, USA. *Forest Ecology and Management* 384: 331-338.

Simler, A.B., M.R. Metz, K.M. Frangioso, R.K. Meentemeyer, and D.M. Rizzo. 2018. Novel disturbance interactions between fire and an emerging disease impact survival and growth of resprouting trees. *Ecology* 99: 2217-2229.

Swain, S., and M. Garbelotto. 2015. *Phytophthora ramorum* can survive introduction into finished compost. *California Agriculture* 69: 237-241.

Swiecki, T.J., and E.A. Bernhardt. 2017a. Field studies evaluate methods to prevent sudden oak death in oaks and tanoak. *Forest Phytophthoras* 7: 15-29.

Swiecki, T.J., and E.A. Bernhardt. 2017b. *Phytophthora cinnamomi* diagnostic testing in pallid manzanita populations. Final Report. Prepared for East Bay Regional Park District. www.phytosphere.com.

Swiecki, T.J., and E.A. Bernhardt. 2017c. Testing and implementing methods for managing *Phytophthora* root diseases in California native habitats and restoration sites. In *Proceedings of the Sudden Oak Death Sixth Science Symposium. Gen. Tech. Rep. GTR-PSW-255*, coordinated by S.J. Frankel and K.M. Harrell, pp. 53-55. Albany, CA: U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station.

Swiecki, T.J., E.A. Bernhardt, K. Aram, D.M. Rizzo, T. Kasuga, and M. Bui. 2016. *Phytophthora ramorum* causes cryptic bole cankers in canyon live oak. *Plant Health Progress* 17: 20-26.

Twieg, B., Y. Valachovic, R. Cobb, and D. Stark. 2017. Reducing CO_2 emissions by managing for sudden oak death . . . is it possible? In *Proceedings of the Sudden Oak Death Sixth Science Symposium. Gen. Tech. Rep. GTR-PSW-255*, coordinated by S.J. Frankel and K.M. Harrell, pp. 19-22. Albany, CA: U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station.

Varner, J.M., H. G. Kuljian, and J.K. Kreye. 2017. Fires without tanoak: the effects of a non-native disease on future community flammability. *Biological Invasions* 19(8): 2307-2017.