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Tanoak conservation: a role for the California Department of Fish and Wildlife

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Tanoak trees and forests are ecologically, culturally, and economically important, providing valued wildlife habitat and forest products. Since the horticultural trade accidentally introduced the sudden oak death pathogen (*Phytophthora ramorum*) to North America, well over a million tanoaks (*Notholithocarpus densiflorus*) have died, and an unknown number are infected. In roughly twenty years, the lethal disease has spread extensively south and north of San Francisco with disjunct outbreaks as far as southwestern Oregon, despite efforts to contain it. Currently no cure exists for infected trees, and thus far tanoak exhibits little genetic resistance to the exotic water mold that causes the disease. Fortunately large areas remain uninfected, but computer models rank uninfected areas on the north coast of California as high risk for infection. The current sudden oak death epidemic warrants concern because tanoak provides food and habitat for many wildlife species. People also value this evergreen, flowering tree as a source of nuts, edible fungi, and hardwood.

Key words: tanoak, *Notholithocarpus densiflorus, Lithocarpus densiflorus,* sudden oak death, *Phytophthora ramorum*

The dramatic decline of American chestnut (*Castanea dentata*), reminds us that even common plants can rapidly become threatened. A century ago in North America's eastern deciduous forests the exotic plant disease chestnut blight began to spread after its inadvertent introduction on an infected, imported Chinese chestnut. Within thirty years after horticulturalists accidentally introduced the causal pathogen from Asia to North America, American chestnuts were virtually destroyed "through most of their natural range" (Brasier 2008). Today computer models indicate that tanoak (*Notholithocarpus densiflorus*) may experience a similar, massive die off on the west coast of North America due to the introduction of *Phytophthora ramorum*, a plant pathogen that causes sudden oak disease (Meentemeyer et al. 2011). The non-native water mold (or oomycete) was first detected in

North America in the mid-1990s and has been spreading in wildlands of central and northern California via garden plants, firewood, wind-blown rain, and moving waterbodies.

Ecosystem change can occur rapidly after the introduction of novel pathogens (Anderson et al. 2004, Brasier 2008, Desprez-Loustau et al. 2007, Loo 2009). Although it is unlikely that *P. ramorum* will cause tanoak extinction, it will likely cause "the rapid and extensive loss of overstory trees … within 30 years of pathogen establishment in many forests" (Figure 1; Cobb et al. 2012). Our current understanding of tanoak resistance to *P. ramorum* is incomplete but, given observed levels of susceptibility, a "risk of extirpation" exists (Hayden et al. 2011). Along the Big Sur coast in central California, some sites have already experienced 100% tanoak mortality after infestation (Davis et al. 2010). "In the absence of extensive control," a team of seven university scientists predicted "a ten-fold increase in disease spread between 2010 and 2030 with most infection concentrated along the north coast between San Francisco and Oregon" (Meentemeyer et al. 2011). As a result, "substantial tree mortality, particularly of tanoak, is likely to follow." Based on their computer model, they predicted "explosive growth in [*P. ramorum*] infection and disease … to occur around 2016." For more discussion of the threat sudden oak death poses to tanoak, see Bowcutt (2013), Cobb et al. (2013), and Dillon et al. (2013).

FIGURE 1.—Tanoak killed by *Phytophthora ramorum* and photographed circa 2001 at Joe Hall Creek in Curry County, Oregon, one of the first confirmed sudden oak death sites in that state. Photograph by and courtesy of Everett Hansen.

Given its mission "to manage California's diverse fish, wildlife, and plant resources, and the habitats upon which they depend, for their ecological values and for their use and enjoyment by the public," the California Department of Fish and Wildlife (CDFW) is the logical and appropriate agency to become a leader in tanoak conservation (CDFW 2014). In addition to providing food and habitat for numerous native and naturalized animals including important game species, tanoak produces delectable acorns, edible fungi, and beautiful hardwood. Efforts are already underway to develop conservation strategies using science-based management practices that foster tanoak wellness and minimize *P. ramorum* infection risks (Cobb et al. 2013).

Distribution

As California's most abundant hardwood or flowering tree, tanoak serves as a foundational species in a variety of ecosystems, from mixed forests to those dominated by coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*), to prairie balds with scattered trees. Tanoak trees grow from southwestern Oregon through the California Coast Range to near Santa Barbara, with inland populations occurring through the Siskiyou Mountains and from the southern tip of the Cascade Range along the western slopes of the Sierra Nevada to Yosemite National Park (Figure 2; Munz 1973, Baldwin et al. 2012). Much of its coastal distribution overlaps with that of coast redwood, but due to

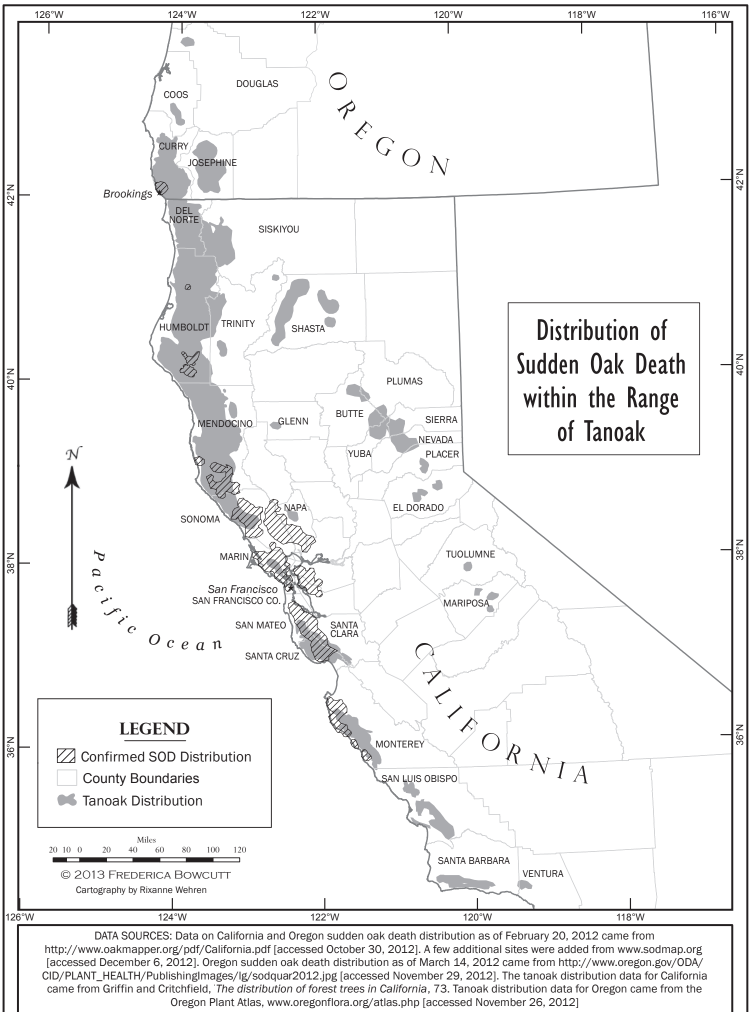

Figure 2.—Distribution of sudden oak death, caused by *Phytophthora ramorum*, in relationship to tanoak distribution. Data sources: California and Oregon distribution as of February 20, 2012 came from Geospatial Innovation Facility (2012); a few additional sites were added from U.C. Berkeley Forest Pathology and Mycology Laboratory (2012). Oregon sudden oak death distribution as of March 14, 2012 came from the Oregon Department of Agriculture (2012). The tanoak distribution data for California came from Griffin and Critchfield (1976). Tanoak distribution data for Oregon came from the Oregon Flora Project (2012).

its greater tolerance of drought, tanoak extends further inland. The shrub variety, *Notholithocarpus densiflorus* var. *echinoides*, occurs from southwestern Oregon to parts of northern California's Klamath Range, Cascade Range, and Sierra Nevada. It tolerates poorer soils and extends tanoak distribution to higher elevations (McDonald and Huber 1995). A mutant shrub-like form grows within Yuba County in the northern Sierra Nevada (*N. densiflorus* forma 'attenuato-dentatus') (Tucker et al. 1969). This mutant is used in horticulture due, in part, to its rarity and its unusual leaves, which are deeply toothed and taper to a very narrow apical tip. Despite being abundant in much of its range, tanoak's global distribution is limited.

Evolutionary Relationship to Chestnuts

For over a century, botanists viewed tanoak as an evolutionary link between oak (*Quercus*) and chestnut (*Castanea*) based on morphological features. Tanoak acorns resemble those of *Quercus*, but its upright male catkins echo those of *Castanea*. In 1840, two British botanists, W. J. Hooker and G. A. W. Arnott, wrote the original description for tanoak and assigned it to *Quercus* but described tanoak as a "remarkable plant *[that]* has very much the appearance of a *Castanea*" (Hooker and Arnott 1840). W. L. Jepson (1909) adopted the revised tanoak name that placed it in the southeast Asian genus *Pasania*, claiming it to be "equally related to" oaks and chestnuts. Currently, *Pasania* is included within *Lithocarpus*. C. S. Sargent's 1922 manual of North American trees called tanoak an oak-chestnut "intermediate" and favored its inclusion in the genus *Lithocarpus* (Sargent 1965). Modern molecular genetic research indicated that oaks, chestnuts, and Asian chinquapin (*Castanopsis*) are more closely related to tanoak than to the southeast Asian genus *Lithocarpus* and its sister taxon, the North American chinquapin, in the genus *Chrysolepis* (Manos et al. 2008). Consequently, a new monospecific genus was established for the North American tanoak, *Notholithocarpus*.

Climate Change and Evolutionary History

Climate change is projected to impact tanoak resilience to disturbance. To make predictions about possible impacts, paleobotanical and post-glacial research is used to learn how related species have responded to past changes in climate. Unfortunately, the fossil record of tanoak remains unresolved. When tanoak was moved to *Notholithocarpus*, the North American paleospecies assigned to the genus *Lithocarpus* were not automatically moved to the new genus. To date, paleobotanists have not determined whether the fossils ascribed to the genus *Lithocarpus* in North America require reassignment. In addition, multiple paleospecies are disputed. Because of the extreme range in leaf variation in *Lithocarpus*, macrofossils are difficult to identify with certainty when preserved fruits do not occur with fossilized leaves. For this reason, *L. klamathensis* and *L. weidei* are disputed species (D. Erwin, University of California Museum of Paleontology, personal communication). Based on leaf shape, venation, and acorn cupule characteristics preserved in macrofossils, *Lithocarpus nevadensis* did grow in Nevada 10–15 million years ago at elevations ≥1,830 m (>6,000 ft) under a much warmer and wetter climate than exists at that elevation today (D. Erwin, University of California Museum of Paleontology, personal communication). Based on macrofossil specimens also housed at the University of California Museum of Paleontology that include an acorn cap, *L. coatsi* dated to the Eocene also appears to be a defendable species, and grew in present day Nevada (D. Erwin, University of California Museum of Paleontology, personal communication).

Although helpful in distinguishing other members of the Fagaceae from one another, pollen microfossils are unlikely to further illuminate the current understanding of tanoak evolution. Researchers studying Quaternary vegetation in southwestern Oregon found fossilized pollen of tanoak to resemble North American chinquapin pollen (Briles et al. 2005). This was corroborated based on light microscopic study of extant tanoak and North American chinquapin pollen (E. Leopold, University of Washington, Seattle, personal communication). Two Swedish paleobotanists found pollen ornamentation highly useful in delineating evolutionary lineages within the genus *Quercus* when examined using a scanning electron microscope (Denk and Grimm 2009). However, Denk doubts pollen can be used to distinguish *Notholithocarpus* from *Lithocarpus* (T. Denk, Swedish Museum of Natural History, personal communication). Although pollen micromorphology is "a character of known diagnostic significance in the family," within the chestnut subfamily Castaneiodeae it is "relatively uniform" (Crepet 1989).

The beech family (Fagaceae), to which tanoak belongs, originated in the northern hemisphere. Although widely considered a natural group derived from a shared ancestor, evolutionary relationships among taxa within the family remain "far from resolved" (T. Denk, Swedish Museum of Natural History, personal communication; see also Nixon 1989). Bidirectional migration reputedly occurred between Eurasia and North America via the North Atlantic and Bering land bridges (Manos and Stanford 2001). However, two evergreen taxa, *Castanopsis* and *Lithocarpus,* appear to have migrated only over the Bering Land Bridge; based on the fossil record, this occurred "by at least the mid-Eocene" (Manos and Stanford 2001).

Later isolation allowed for the evolution of novel species including tanoak and North American chinquapin. Uplift of mountain ranges (or down-drop of adjacent land) due to tectonic activity in western North America resulted in a rainshadow effect that probably caused tanoak's range to shrink to areas that still received moisture from storms moving east from the Pacific Ocean. Beginning roughly 4.5 million years ago, the rising elevation of the Sierra Nevada and the Cascade Range resulted in drier summer conditions east of these mountains (Graham 1999). By the late Pliocene and Pleistocene, a Mediterranean climate resembling today's dry-summer, wet-winter regime developed (Graham 1999).

Recent genetic research has reinforced the notion that tanoak is a paleoendemic, a relict of "an ancient and formerly widespread broadleaf evergreen flora, which persists today in the Indochinese tropics" where summer rainfall is the norm and killing frosts are not (Manos et al. 2008). As a climatic relict of a wetter, more temperate period in North America's past, tanoak may be vulnerable to periods of increased drought and erratic frost events, both of which are predicted to occur more frequently with global climate change. Frost can compromise sexual reproduction, and drought stress can reduce its resistance to pathogens and insect pests. Multiple disturbances linked to climate change affect tanoak's resilience. Periodic wetter and warmer conditions will radically increase tanoak's vulnerability to sudden oak death by favoring *P. ramorum* spore production (Meentemeyer et al. 2011). Although snags do not substantially elevate fire risk, areas with many recently killed tanoaks still standing with dead leaves can increase wildfire severity (Metz et al. 2011).

Value to Wildlife

If the predicted massive tree die-off of tanoak occurs due to sudden oak death, many species of vertebrates will be impacted, as will many insects that warrant more study given their significant influence on ecosystem function. For example, filbert weevils (*Curculio uniformis*), filbertworm moth larvae (*Cydia latiferreana*), and other insects can destroy over half of the acorn crop in the absence of frequent fires (Roy 1957a). These nut-bearing trees feed numerous animal species. The relatively large acorns typically exceed the size of a hazelnut. It is one of the more reliable acorn producers in California and southwestern Oregon, rarely failing completely and bearing bumper crops more frequently than species of *Quercus*. Tanoaks "are heavily laden almost every alternate year and complete seed crop failures are rare," helping to give it the reputation of being the heaviest acorn producer of all Pacific Coast oak species (Roy 1962). Tanoak trees typically begin to bear an abundance of acorns when they have reached between 30 and 40 years old, "although 5-year-old [root] sprouts also have produced fairly heavy crops" (Roy 1962). The shorter, often conical shaped mature trees in full sun tend to produce more than full-grown shaded trees (Figure 3). A mature tanoak tree bears more than 90 kg (200 pounds) of nuts on average in a good year, with estimates as high as 454 kg (1,000 pounds) annually for large mature trees (Baumhoff 1963, Radtke 1937).

Figure 3.—Tanoak in open prairie with robust canopy, a legacy of frequent, low intensity fires set by Native people. Ukiah, California circa 1903. Photograph by A. O. Carpenter (also Plate 7 in Jepson, *The silva of California,* 1910). Image courtesy of the University and Jepson Herbaria Archives, University of California, Berkeley.

Many wildlife species cache tanoak acorns for later consumption, including acorn woodpeckers (*Melanerpes formicivorus*), Stellar's jays (*Cyanocitta stelleri*) and at least four species of squirrels (Fryer 2008, Roy 1957a). One tanoak nut hoarder, the dusky-footed woodrat (*Neotoma fuscipes*), is an important prey of the northern spotted owl (*Strix occidentalis caurina*). Other predators of tanoak herbivores include coyote (*Canis latrans*), cougar (*Puma concolor*), and fisher (*Martes pennanti*) (Raphael 1987). Because tanoaks produce their abundant nut crop in the fall, they provide a critically important food source for deer (*Odocoileus* spp.) and black bear (*Ursus americanus*). The now extinct grizzly bear (*Ursus arctos*) likely fed on tanoak acorns given its former distribution (Storer and Usinger 1963). Other important game species benefit from tanoak mast, such as band-tailed pigeon (*Patagioena fasciata*), wild turkey (*Meleagris gallopavo*), and feral pigs (*Sus scrofa*). Various species of native mice (*Peromyscus* spp.) also consume tanoak acorns (Fryer 2008). The abundant nuts are a "vital" food source for many wildlife species (McDonald and Huber 1995).

Tanoak provides more than just an abundance of acorns as food for wildlife. Mule deer (*O. hemionus*) browse its leaves (Fryer 2008). Northern flying squirrels (*Glaucomys sabrinus*) consume ectomycorhizal fungi that grow on tanoak roots (Fryer 2008). Various salamanders and rodents use tanoak for cover or nesting (Raphael 1987). Because tanoaks often grow in the shade of taller coast redwood and Douglas-fir, they help to create forests with multi-layered tree canopies favorable to northern spotted owls and other animals (North et al. 1999). A variety of birds forage for insects on tanoak, including chickadees (*Poecile* spp.) (Fryer 2008).

Although botanists, foresters, and plant pathologists have completed much research on tanoak, a full understanding of the organisms and ecological processes affected by tanoak remains incomplete. As is typical of members of the beech family, tanoak is a monoecious species and produces separate female and male flowers on the same plant. Each small, simple flower lacks petals and typically appears in summer (Roy 1957b), with acorns maturing two years after pollination. Until recently, it was widely believed that tanoak was wind pollinated like true oaks in the genus *Quercus*. Although self-fertilization does occur and some wind pollination is likely, most female tanoak flowers appear to be insect pollinated (Wright and Dodd 2013). However, the insect species involved remain to be systematically identified. Further research is recommended to study the significance of tanoak pollen as a food source in pollinator communities (Wright and Dodd 2013).

Tanoaks host a variety of fungi that grow on its roots (mycorrhizae) that are known to play important roles in ecosystems including as sources of wildlife food. Bergemann and Garbelotto (2006) found 119 taxa of ectomycorrhizal fungi growing on tanoak roots in northern California, which they believed to be an underestimate given their sampling method. Their estimated species richness of root associated fungal taxa was 265. Researchers predict that *P. ramorum* will cause a decline in ectomycorrhizal fungi, which is troubling given their significance in "ecosystem function through their control over decomposition, nutrient acquisition, and mobilization and regulation of succession in plant communities" and their decline "will likely disrupt the function and structure of these forests" (Bergemann et al. 2013). In coast redwood forests, tanoak is the dominant ectomycorrhizal host (Bergemann and Garbelotto 2006).

Native Americans

Many Native Americans are deeply committed to continued use of tanoak acorns as a traditional food, and seek partnerships to address the *P. ramorum* threat (Ortiz 2008). Human use of tanoak acorns for food extends over at least 5,000 to 7,000 years. Most, if not all, tribes within the range of tanoak (Figure 4) consumed its nutritious nuts. Gathering and processing of tanoak acorns for human use continues today, particularly in northern California among Native Americans, and tanoak acorn-based foods are important to cultural identity.

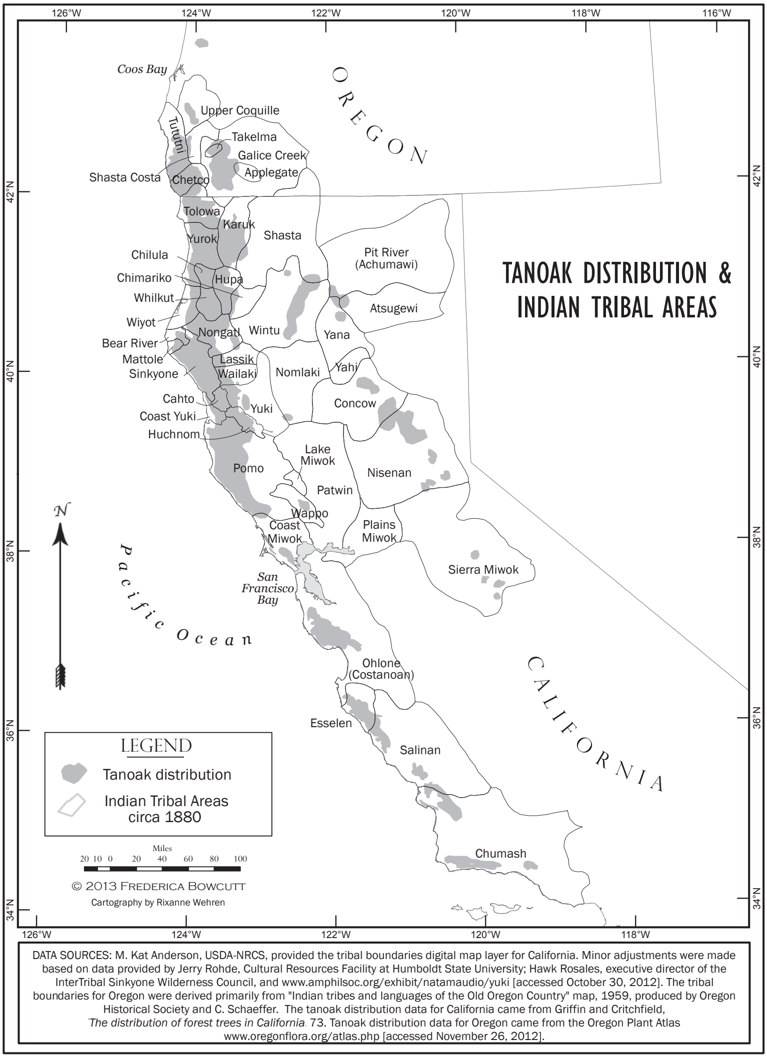

Figure 4.—Tribal territorial map and tanoak distribution. Data sources: M. Kat Anderson, USDA-NRCS, provided the tribal boundaries digital map layer for California. Minor adjustments were made based on data provided by Jerry Rohde, Cultural Resources Facility at Humboldt State University; Hawk Rosales, executive director of the InterTribal Sinkyone Wilderness Council, and the American Philosophical Society (2012). The tribal boundaries for Oregon were derived primarily from Schaeffer (1959). The tanoak distribution data for California are from Griffin and Critchfield (1976). Tanoak distribution data for Oregon are from the Oregon Flora Project (2012).

The anthropological literature documents Native American use of burning to foster tanoak health on a landscape scale; indeed, it was noted by a Karuk woman that annual burning protected tanoak best from infection and insects (Schenck and Gifford 1952). Burning reduces insect populations because trees abort weevil and moth larvae infested acorns during development; thus, a surface fire set after initial acorn drop kills the larvae inside and those already in the leaf litter. The Pomo Indians of Redwood Valley burned annually to maintain widely spaced oaks with a grassy understory; in their "beautiful park landscape," burning controlled the brush while leaving "the larger trees … uninjured" (Kniffen 1939). By decreasing fuel loads, regular burning by tribal peoples reduced the risk of catastrophic wildfire that would destroy mature tanoak trees (Anderson 2005). For a more extensive treatment of tanoak ethnobotany, including traditional ecological knowledge, see Bowcutt (2013).

Tanoak vulnerability to sudden oak death increased with fire exclusion according to a 2005 study using GIS (Moritz and Odion 2005). However, these results have been challenged given the limitations of *P. ramorum* distribution and fire-history maps, which make studying the relationship between "pathogen invasion and persistence" and burning difficult (Lee 2009). Fires do not appear to immunize forests, nor do prescribed burning or catastrophic wildfires eliminate *P. ramorum* from a site, though they can reduce its spread (Lee 2009). Preliminary results from experimental treatments in southwestern Oregon and northern California forests suggest "that burning can be a valuable tool in cleaning up small infectious material in infested sites," even when it does not eliminate the pest (Lee 2009). Thus far, frequent, low-intensity fires that mimic traditional ecological practices of indigenous peoples, have not yet been tested as a prophylactic measure or to treat an infected site.

Traditional burning practices may provide insights into adaptive responses to current climate change, which will likely impact the spread of sudden oak death. Current trends in global climate change indicate that weather patterns are growing "increasingly erratic and extreme" which "could have consequences for ecosystem stability and the control of pests and diseases" (Kelly 2011, Medvigy and Beaulieu 2012). Tanoak acorns ripen in their second autumn, thus increasing their vulnerability to late frost, which can destroy reproductive organs and radically reduce acorn productivity. By clearing underbrush, Native Americans maintained good airflow around harvested tanoaks, which reduced loss of flowers and developing acorns to cold temperatures. Unfavorable climatic conditions also provoked the southwestern Pomo to pray for acorns "when hail comes from the north" (Gifford 1967).

Edible Fungi

In addition to producing edible nuts, tanoak logs, snags, and forests produce a variety of edible fungi. One of the most treasured mushrooms hunted in tanoak stands is the American matsutake (*Tricholoma magnivelare*), also known as tanoak mushroom. It is harvested for local consumption and commercially for export. Multiple northwestern California tribes particularly value the American matsutake, including the Hupa, Karuk, Wailaki, and Yurok (Anderson and Lake 2013). They typically combine autumn mushroom hunting with tanoak acorn and huckleberry harvesting (Anderson and Lake 2013). Native people from northwestern California still consume several other species of fungi associated with tanoak including oyster mushrooms (*Pleurotus cornucopiae*), black trumpet (*Craterellus* *cornucopioide*), and lion's mane (*Hericium erinaceus*) (Anderson and Lake 2013). Choice "oyster mushrooms will repeatedly fruit from rotting … tanoak … snags and logs until the decay is too advanced" (Anderson and Lake 2013). Shiitake mushrooms (*Lentinula edodes*) can be cultivated on wood chips from tanoak logs (Donoghue and Denison 1996).

Hardwood

Tanoak wood is used for heating, flooring, cabinets, furniture, tool handles, wood chips, paper pulp, and biofuel, and it has the potential to become more widely used. The misperception that the wood is inferior to eastern hardwoods persists, in part, due to unskilled producers using milling practices and drying schedules suited for easier to process softwoods (conifers). Consumers developed a negative attitude about tanoak wood and other California hardwoods because poorly manufactured products were of inferior quality (Huber and McDonald 1992). According to the authors of the Hoopa Valley Reservation Hardwood Study Report released in 1968, "A major reason for failure to harvest and manufacture western hardwoods profitably has been a general reluctance to recognize fundamental differences between softwoods and hardwoods requiring the use of different equipment and techniques" (Economic Development Administration 1968).

Leading foresters and others advocated for using tanoak wood beginning in the 1800s. "No other oak begins to vie with it for beauty of grain" according to one booster who claimed that "it will stay exactly where the workman puts it and will stand the roughest knocks without flinching" (Armstrong 1891). A founder of the Society of American Foresters and chief dendrologist for the Bureau of Forestry (later to become the U.S. Forest Service [USFS]), described tanoak in 1908 as "a tree of the greatest importance in Pacific forest, both for its valuable tanbark and for the promise it gives of furnishing good commercial timber in a region particularly lacking in hardwoods" (Sudworth 1967). H. S. Betts conducted timber tests for the USFS and concluded in 1911 "there seems to be no good reason why tanbark oak should not take its place in the Pacific coast hardwood market for many if not all the purposes for which eastern hardwoods are now imported" (Betts 1911). "All things considered," Betts continued, "the seasoning of tanbark oak seems to offer little, if any, more difficulty than is experienced with eastern oaks" (Betts 1911). The wood is particularly well suited for flooring because of its "pleasing grain and color, and the necessary hardness" (Betts 1911). In fact, the Union Lumber Company in Fort Bragg, California had successfully milled tanoak for flooring by 1910 (Huber and McDonald 1992).

The technical ability existed to mill tanoak with no more difficulty than experienced with eastern oaks. Pfeiffer (1956) claimed, "western hardwoods are equally satisfactory as comparable eastern species … and we need not apologize for any of them where care is exercised in their manufacture." In 1977, it was noted that "native California hardwoods, and specifically tanoak, which could provide a major opportunity for increased wood and fiber production, are scarcely utilized" (McDonald 1977). McDonald (1977) also noted that "reliable techniques are available now and are described extensively in the literature.". Tanoak ranked among the densest and stiffest of North American woods (Shelly and Quarles 2013).

Inventories of the tanoak resource indicated that mid-century sawtimber volume was approximately 4.8 million cubic meters or "2,036 million board feet in California" (Roy 1957b). Another estimate from the mid-1980s put the volume of tanoak sawlogs at over

8.6 million cubic meters (3,660 million board feet) in just "the California counties of Del Norte, Humboldt, Mendocino and Sonoma" (Sullivan *circa* 1986). Daniel Oswald (1972) noted that "768,000 acres [310,798 hectares] or 49 percent of the commercial forest land in Mendocino-Sonoma" Counties supported hardwoods, much of which is tanoak. Statewide tanoak dominated over 348,000 hectares (861,000 acres) of California timberlands in 1988, 87% of which was held in private ownership. The same study found that tanoak occurred on over 981,000 hectares (2,425,000 acres) in the state, not including national forests and parks (Bolsinger 1988). The "non-industrial private forestlands of the northern California coast region" alone could potentially sustain extraction of nearly 118 thousand cubic meters (50 million board feet) of tanoak wood annually (Shelly 2001).

Dean Huber and Philip McDonald (1992) asserted that, "Now is the time to develop a philosophy for managing California hardwoods for wildlife, wood, water, and esthetics." According to those authors, California's hardwood resource is significant but "poorly managed and scarcely utilized for lumber and wood products" (McDonald and Huber 1994), and they concluded that in the future tanoaks and other California hardwoods "will contribute significantly to the state's economy … The art of hardwood silviculture in California should enjoy its finest hour" (McDonald and Huber 1994). Quarantines to limit the spread of *P. ramorum* are already limiting commerce in tanoak hardwood; however, Shelly and Quarles (2013) claim the tree remains worthy of use.

Sudden Oak Death Threat

Combined with forestry, catastrophic wildfire, and other disturbances, sudden oak death threatens tanoak "with functional extinction … throughout large portions of its range" (Dillon et al. 2013). Forest management within the range of tanoak focuses almost exclusively on favoring conifers (softwoods) at the expense of hardwood trees. Since the 1950s, use of herbicides has become common practice to weed industrial western forests of these competing species (Bowcutt 2011). Tanoak has demonstrated "substantial resilience under these adverse conditions, but the introduction of *P. ramorum* into tanoak ecosystems presents a new and significant threat to this species" (Dillon et al. 2013). Much like American chestnut today, tanoak could become reduced primarily to populations of asexually reproduced juveniles that never reach sexual maturity because they are killed by resident *P. ramorum* before the trees can begin to bear acorns. Technically they would not be extirpated, but they would no longer function ecologically or culturally as a key acorn producer in a significant portion of its natural distribution.

Diseased and dying tanoak trees were first noticed in the mid-1990s north of San Francisco in Marin County in the vicinity of Mount Tamalpais (McPherson et al. 2005). Plant pathologists ultimately concluded that a previously undescribed species caused the observed bleeding stem cankers. The new lethal tanoak pathogen, *P. ramorum,* probably originated from eastern Asia, but when it arrived in North America remains uncertain. *Phytophthora* means plant destroyer, aptly named given the devastating impact species in this genus have had historically, such as *Phytophthora infestans*, which caused the Irish Potato Famine. *P. ramorum* obstructs xylem cells and reduces water supply to individual branches or the entire crown, which can ultimately kill the host particularly during drought (Parke et al. 2007). By 2002, sudden oak death had "reached epidemic proportions in coastal California" from the Big Sur Coast to Sonoma County (Rizzo et al. 2002a). The water mold has spread through commerce in garden plants (Mascheretti et al. 2008, Rizzo et al. 2005). Although tanoak has proved to be the most susceptible, many native California species and common nursery and landscape plants serve as carriers that help spread the pathogen (Rizzo et al. 2002b). Of the ornamental hosts most prone to spread the disease, plant pathologists list *Rhododendron, Camellia, Viburnum, Pieris,* and *Kalmia* (mountain laurel) (Frankel 2008). While fatal to tanoak and some other related tree species, most of its hosts suffer only shoot die back or leaf spots and blotches. An official list of host plants is maintained by the United States Department of Agriculture (USDA 2012).

Plant pathologists, foresters, and others have developed extensive recommendations for land managers working with tanoak threatened by sudden oak death (California Oak Mortality Task Force 2014). According to plant pathologists actively researching the disease, "landscape management strategies for *P. ramorum* must incorporate prevention, treatment, restoration, and conservation into an overall program" (Rizzo et al. 2005). Unfortunately, the exotic disease poses a serious threat even in preserved public lands. Numerous local parks, roughly thirty state park units, and nine federal land holdings are already infested and many more are at risk (Bowcutt 2013). Given the inability to effectively treat sudden oak death, prevention is the first best response to the current tanoak crisis. Plant pathologists recommend further limiting trade in nursery plants to reduce the risk of spreading *P. ramorum* and other devastating plant diseases (Brasier 2008, Rizzo et al. 2005). Other strategies merit consideration including establishment of refuges or reserves, seed banks, living collections of plantings, and educational outreach.

Existing public lands still provide opportunities for safeguarding tanoak. In anticipation of *P. ramorum* range expansion in North America, some land managers are creating tanoak refuges where infection risks can be reduced. For example, Redwood National and State Parks (RNSP) natural resource managers are preparing for "the inevitable arrival of *P. ramorum* to the parks" by adopting preventive measures to slow its spread once it arrives. Park managers recognize tanoak as a valuable ecological component of the coast redwood forests in the park. "RNSP also has an important cultural legacy of large stands of old tanoak trees that have been managed by Native American families for many generations" (Bueno et al. 2010). Park managers are considering "creating tanoak refuges (defined as tanoak groves that are least likely to become infected due to spatial or temporal factors) and protecting them through the creation of no-host buffers." Grasslands could function as no-host buffers if wide enough around islands of vulnerable tanoaks. Based on epidemiological modeling, widely spaced tanoaks associated with plants that are immune to *P. ramorum* infection "resulted in slow-enough transmission to retain overstorey tanoak" (Cobb et al. 2012). Further, "Recent work identifying heritable disease resistance traits, ameliorative treatments that reduce pathogen populations, and silvicultural treatments that shift stand composition hold promise for increasing the resiliency of tanoak populations" (Cobb et al. 2013). Sudden oak death will probably not get established in the southern end of tanoak's range because suitable hosts for *P. ramorum* are too scattered in the landscape. Also the climatic conditions are less hospitable to the water mold. Sierra Nevada populations of tanoak may also be safe due to climatic conditions. Based on the computer models, however, the area between Mendocino County and southwestern Oregon is at high risk (Meentemeyer et al. 2011).

Conservation of Genetic Diversity

Retaining large tracts of undeveloped land in northern California where extensive tanoak die off without intervention can occur may be important so disease resistance might develop and/or have a chance to express itself. According to Loo (2009), "[m]aintaining large, relatively natural populations of all native tree species will allow natural selection to operate with sufficient intensity to ensure different mechanisms and levels of resistance and tolerance can develop over time, without catastrophic losses of genetic diversity." Liquidating American chestnut trees for lumber, firewood, and tanbark during the chestnut blight crisis potentially contributed to their loss by not allowing the populations to express or develop disease resistance (Freinkel 2007).

Seed saving may be a successful strategy as "reintroduction of material stored ex situ has made the difference between extinction in the wild and continued survival" for some plant species (Guerrant 2012). Unfortunately, tanoak seed saving beyond a year is currently not a viable option because the embryo inside acorns is short lived. Viability plummets with desiccation of the nuts making them resistant "to standard drying and frozen storage, used on species with orthodox seed storage behavior" (E. Guerrant, Portland State University, personal communication). Cryogenic storage of recalcitrant seeds (desiccation resistant) like tanoak may offer an alternative. However, this seed saving approach is labor intensive and more expensive, requiring seed storage at liquid nitrogen temperatures (E. Guerrant, Portland State University, personal communication).

The creation of living collections through plantings could safeguard genetic diversity. American chestnut breeding programs to create chestnut blight resistant individuals relied in part on small-scale plantings in North America that survived outside its natural range (Freinkel 2007). Suitable planting areas outside the natural range of tanoak will likely experience summer drought. For the purpose of conserving genetic diversity and reintroducing tanoak into infested areas, efforts to identify "suitable seed sources will be critical" (Dodd et al. 2013). Seed exchanges could be used as a way to distribute acorns as long as safeguards are in place to ensure that the acorns are disease free. If infected acorns are distributed, this could worsen the current problem. Use of sucker tip layering to reproduce vegetative offshoots of resistant individuals of *P. ramorum* by forcing them to root may be useful in the future (F. Lake, USFS, personal communication).

Educational Outreach

One of the biggest challenges to rallying concern for tanoak is the widespread perception that it is a nuisance species with little value and that it competes with economically important species, like coast redwood and Douglas-fir (Bowcutt 2011). Wildlife biologists, ethnobotanists, environmental historians, and others could contribute to an educational campaign designed to counter this misperception. In addition to its substantial value to wildlife and Native Americans, tanoak has a history of being used to tan leather, feed livestock, and make various wooden products including furniture and cabinets (Bowcutt 2011). Botanic gardens, arboreta, parks, natural history museums, and societies dedicated to conserving California's native plants could provide venues for educational outreach about this indigenous nut tree. Better interpretation about tanoaks is recommended, especially in *P. ramorum* infected parks with high visitation. Efforts to raise awareness of the value of tanoak might include the creation of commemorative U.S. Postal Service stamps modeled on their vanishing wildlife species program. Possibly non-timber forest product collecting permits could be developed modeled on the Federal Migratory Bird Hunting and Conservation Stamps issued by the U.S. Fish and Wildlife Service which have functioned as hunting licenses and a source of revenue for the creation of wildlife refuges. Duck stamps also helped to educate the public about the plight of waterfowl and the importance of defending their wetland habitats and flyways.

Conclusions

In 2000, Dr. Steve Zack with the Wildlife Conservation Society said, "The cascading effect of losing these trees is going to be awesome. We're just waiting for the other shoe to drop" (Yoon 2000). Current efforts to limit the spread of *P. ramorum* are not working adequately. The demise of well over a million tanoaks in less than twenty years suggest it is time more wildlife biologists joined with plant pathologists, botanists, foresters, horticulturalists, landowners, environmental organizations, and tribes in calling for policy changes to accommodate tanoak's needs to thrive. CDFW could work with the California Wildlife Conservation Board to buy conservation easements and land in northern California as mature tanoak ecological reserves. By leading efforts to defend tanoak, CDFW can demonstrate a commitment to ecosystem management and embrace a shift in its priorities to include plants.

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