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Cataloging *Phytophthora* Species of Agriculture, Forests, Horticulture, and Restoration Outplantings in California, U.S.A.: A Sequence-Based Meta-Analysis

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Abstract

California contains a diverse flora, and knowledge of the pathogens that threaten those plants is essential to managing their long-term health. To better understand threats to California plant health, a meta-analysis of *Phytophthora* detections within the state was conducted using publicly available sequences as a primary source of data rather than published records. Accessions of internal transcribed spacer (ITS) ribosomal DNA were cataloged from 800 Californian *Phytophthora* isolates, analyzed, and determined to correspond to 80 taxa, including several phylogenetically distinct provisional species. A number of *Phytophthora* taxa not previously reported from California were identified, including 20 described species. Pathways of introduction and spread were analyzed by categorizing isolates' origins, grouped by land-use: (i) agriculture, (ii) forests and other natural ecosystems, (iii) horticulture and nurseries, or (iv) restoration outplantings. The pooled *Phytophthora* metacommunities of the restoration outplantings and horticulture land-use categories were the most similar, whereas the communities pooled from forests and agriculture were least similar. *Phytophthora cactorum, P. pini, P. pseudocryptogea*, and *P. syringae* were identified in all four land-use categories, while 13 species were found in three. *P. gonapodyides* was the most common species by number of ITS accessions and exhibited the greatest diversity of ITS haplotypes. *P. cactorum, P. ramorum*, and *P. nicotianae* were associated with the greatest number of host genera. In this analysis, the *Phytophthora* spp. most prevalent in California differ from those compiled from the scientific literature.

Keywords: barcoding, California, diagnostics, disease management, meta-analysis, nursery, *Phytophthora*, restoration, species complex

A remarkably diverse array of plants grow in California (United States). The state is geographically large and physically diverse, with the second-most protected wilderness of any U.S. state after Alaska (Riddle and Hoover 2019). California is the state with the greatest documented biodiversity and endemism, with the most vascular plant records in the United States Department of Agriculture PLANTS database (USDA-NRCS 2020). The Jepson eFlora lists 8,649 vascular plant taxa occurring in the state (including subspecies and varieties), 7,287 of which are considered California natives (Jepson Flora Project 2020); these numbers place California's documented flora as more diverse than most countries, including almost all European countries (Hassler 2020). Although the state only ranks 14th in the United States by total agricultural land area, California is the highest-grossing agricultural state and grows the greatest number of crops (USDA-ERS 2020; USDA-NASS 2017). In addition, California's horticulture industry is the largest by sales value (USDA-NASS 2017). As the most populous U.S. state, the opportunities for human-mediated dispersal of plant pathogens are great across California. The spatial distribution of agriculture, wildlands (including newly restored areas), and peri-urban areas potentially allows for pathogen spillover between plant communities (Jung et al. 2016; Redondo et al. 2018; Sims and Garbelotto 2021).

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Californian-grown plants are potential or known hosts for species of *Phytophthora* (a genus of oomycete plant pathogens). *Phytophthora* spp. have been documented in agricultural and horticultural settings in California for over a century (Mills 1902; Smith and Smith 1906). Over this time, a great body of research has amassed, particularly in regards to the diagnosis and management of Phytophthora root rot, a complex of diseases that may affect most crops, ornamentals, and wildland plants (Garbelotto et al. 2018; Trouillas et al. 2022; Weiland 2021). Interest in *Phytophthora* spp. in California's natural ecosystems has intensified, driven by the onset of sudden oak death (SOD) around the turn of the 21st century (Rizzo et al. 2002). Caused by the nonnative pathogen *Phytophthora ramorum*, SOD has killed tens of millions of trees in California and Oregon (Cobb et al. 2020; Rizzo et al. 2002). SOD increased regulation and monitoring of the U.S. horticultural industry because of evidence that *P. ramorum* was transported to the United States (Jung et al. 2020; Mascheretti et al. 2009) and between states on living plants (Goss et al. 2009; Kamvar et al. 2015). These regulations focus solely on *P. ramorum* (Frankel 2008) despite horticulture being a hotspot for *Phytophthora* spp. (Molnar et al. 2020; Prigigallo et al. 2015; Redekar et al. 2019), and the plant trade is the most important pathway of plant pathogens worldwide (Liebhold et al. 2012; Migliorini et al. 2015).

In addition to the plant trade pathway, *Phytophthora* spp. may be introduced to nurseries via irrigation draws of local waterways, then amplified in the nursery (Redekar et al. 2019, 2020). Having had potential exposure to a diverse community of pathogenic *Phytophthora* spp. while in the nursery, infested stock may be sources of introduction for *Phytophthora* regionally, when infested nursery plants are inadvertently purchased and planted (Frankel et al. 2020; Rooney-Latham et al. 2015, 2019; Weiland et al. 2020). Restoration projects often deploy nursery-origin plants into landscape settings (Li and Gornish 2020), making restoration a risky activity in regards to local transmission and escape of plant pathogens into the environment.

Developing a baseline knowledge of the *Phytophthora* community is critical for the accurate identification and control of potentially invasive members of the genus. To understand which species are

newly introduced and at high risk for invasion and, therefore, warrant regulation or eradication, a record of past detections and the diseases they caused is needed. Without a baseline understanding of *Phytophthora* spp. diversity in California, the origin and biology of species encountered in surveys or inspections is difficult to discern.

Genus *Phytophthora* was first described in 1876. Since then, the diagnostics and identification of its species have changed several times, based first on a series of morphological keys (Stamps 1990; Tucker 1931; Waterhouse 1963) and now with sequence-based molecular "barcodes" (Abad et al. 2019; Cooke et al. 2000; Förster et al. 2000; Robideau et al. 2011). The molecular species determination era, which has coincided with increasing surveys of horticulture and landscapes, has made clear that the diversity of *Phytophthora* spp. has been greatly underestimated, and many of these species have been inadvertently moved great distances before they were known to researchers (Hansen et al. 2012; Scott et al. 2019). Ecosystem surveys have also highlighted the saprotrophic ability of some *Phytophthora* spp., expanding the genus not only in terms of number of species but also ecologically, beyond plant parasitism (Aram and Rizzo 2018; Brasier et al. 2003; Marano et al. 2016). Despite this great expansion of the genus, our understanding of its biogeography and, therefore, the potential risk of most *Phytophthora* spp. in native plant communities is still limited.

Although molecular barcoding (i.e., sequence-based identification) methods have the potential to be both more accurate and more precise than previous methods of species determination, the new, primarily phylogenetically defined species (i.e., phylospecies) often do not agree with the older morphospecies (i.e., morphologically defined species). Most commonly, historical morphospecies are carved into many cryptic (morphologically similar or indistinguishable) phylospecies, which can invalidate or confuse much of the pre-21st century diagnostic knowledge. Less commonly, and less problematic in regards to record keeping, is when morphospecies are combined into morphologically variable phylospecies such as *P. bilorbang* (including *P.* taxon oaksoil) (Aghighi et al. 2012). Molecular studies have been conducted for more than two decades, long enough for molecular-based determinations to become outdated; as novel species are added, particularly within complexes, older phylospecies may be split into several new phylospecies, and molecular determinations made at the time of deposition become outdated (Bily et al. 2022; Burgess et al. 2018; Hansen et al. 2009; Jung et al. 2002, 2017). The lists kept by plant pathologists and regulators linking known species of pathogens to particular hosts and geographic areas need updating, because this knowledge is essential to inform management and prevent additional invasions by all plant pathogens but particularly for the cryptic and high-risk *Phytophthora* spp. (Jung et al. 2016; Scott et al. 2019). This sequence-based meta-analysis (Page et al. 2021) aims to improve management and research by listing the diversity of genus *Phytophthora* in California and its plant associations by both species and molecular barcode. We hope to provide a tool that can serve regulators and researchers, is reproducible, and is able to be easily updated during the ongoing taxonomic revision of the genus.

Materials and Methods

Information sources

Our survey was conducted using publicly available DNA sequence accessions (Supplementary Table S1) gathered between June and October 2020. As the most widely employed barcoding locus for *Phytophthora* (Abad et al. 2019; Robideau et al. 2011), internal transcribed spacer (ITS) ribosomal DNA (rDNA) sequences were the focus of the survey. A contemporaneous search of the fungus-host-distribution database at the Agricultural Research Service Germplasm Resources Information Network (ARS-GRIN) (Farr and Rossman 2020) for genus "*Phytophthora*" and locality "California" aided the literature search and served as a source of published records of *Phytophthora* in California.

Search strategy

Because sequence accessions may or may not be encoded with source metadata, several types of searches were employed to create a combined list of accessions that could be reliably identified as derived from both *Phytophthora* spp. and California. The NCBI nucleotide collection (https://www.ncbi.nlm.nih.gov/nucleotide/) was searched for sequence accessions with "*Phytophthora*" in the organism field that also were documented as deriving from "California" or "CA" in the country field. The World *Phytophthora* Genetic Resource Collection (WPC) database was polled for isolates known to be from California, which was crossed-checked against available sequence accessions. In addition to the sequence accession databases, literature searches were conducted to find additional studies that detected *Phytophthora* spp. in California and deposited sequences but did not include location metadata with them (Supplementary Table S1); this was aided by the results from the GRIN database. The accessions were verified as derived from *Phytophthora* strains isolated in California, and their associated metadata was compiled and sorted into unique ITS haplotypes based on BLASTn (https://blast.ncbi.nlm.nih.gov/Blast.cgi) searches (Supplementary Table S1).

Selection process

No sequence accessions were observed to contain sequence characteristics that resulted in their rejection on the basis of quality. Several accessions did not cover the entire ITS locus (i.e., ITS1, 5.8S rDNA, and ITS2 regions); these were still included but their truncated length and any resulting species determination uncertainty was noted (Supplementary Table S1).

Based on origin information associated with the GenBank accessions, each *Phytophthora* detection was assigned to one of four land-use categories (Fig. 1): (i) agriculture (mostly from nonnative plants grown as crops, for consumption or utilization); (ii) forests and other natural ecosystems, including waterways that flow through such landscapes; (iii) horticulture and nonagricultural plant production settings, including native plant nurseries (native and nonnative plants, typically sold as live plants for gardens, landscaping, and restoration); and (iv) restoration sites (native, mostly nursery-grown stock, outplanted within natural ecosystem settings). Pairwise Sørensen similarity coefficients were calculated between the metacommunities pooled from each land-use category using the R package vegan (Oksanen et al. 2019).

Species determinations

Molecular species determinations were made for each ITS haplotype beginning with BLASTn searches and aided by BLAST-generated distance-based phylogenetic trees. Most haplotypes were successfully determined to describe species based on unambiguous BLAST matches, using the well-curated Animal and Plant Health Inspection Service Center for Plant Health Science and Technology (CPHST) strains deposited by IDphy (Abad et al. 2019) as a guide although, in some cases, there was unresolved ambiguity in regards to the species associated with an ITS haplotype. For species complexes, determinations were also aided by recent work (Brazee et al. 2017; Bourret et al. 2018b, c; Dang et al. 2021; Safaiefarahani et al. 2015; Yang et al. 2017). Positive determinations to provisional species were based on consultation with recent phylogenetic and barcoding work (Bourret et al. 2018 a, c; Martin et al. 2014; Robideau et al. 2011; Yang et al. 2017). Note that ITS sequences are currently considered to be sufficient to make determinations of most *Phytophthora* spp. (Robideau et al. 2011), even in most species complexes, with three exceptions relevant to our study. (i) *P. infestans* cannot be separated from *P. andina, P. mirabilis*, and other subclade 1c species based solely on ITS sequences (Robideau et al. 2011). Therefore, for subclade 1c, the published geographic and host distributions, rather than ITS sequence, were primary in determining species identity, and the determinations made at the time the strains were deposited were not reevaluated. (ii) *P. fragariae* and *P. rubi* represent a pair of species that cannot be distinguished based solely on ITS sequences (Man in 't Veld 2007) and, therefore, the single

strain of *P. fragariae* was determined to species based on mitochondrial sequences also available for the isolate. (iii) Californian isolates with ITS sequences matching *P. borealis* do not match *P. borealis* when comparing mitochondrial loci and, instead, match a provisional species with the same pattern, *P*. sp. NJB-2015 (Bourret et al. 2018b).

Several ITS accessions were ambiguous: phylogenetically distinct enough from voucher specimens of their most closely related species to possibly represent a distinct taxon but not distinct enough to clearly represent a separate species. These were given ambiguous species determinations, notated as aff. (Latin *affinis* or "neighboring"), and were counted as separate taxa during the tabulation of the results. When ITS haplotypes were determined to unambiguously derive from putative undescribed species they were given species designations beginning with cf. (Latin *confer* or "compare against") followed by the epithet of a neighboring species. Hybrids were determined based on the presence of polymorphisms (single-nucleotide variants [SNVs]) in the ITS accessions corresponding to differences between the ITS sequences of two putative parent taxa.

Maximum-likelihood phylogenetic trees were inferred, illustrating some of the ITS-based species determinations within the *P. citricola, P. cryptogea, P. megasperma*, and *P. parsiana* species complexes. The alignments consisted of an accession of each ITS haplotype in the complex (Supplementary Table S1), as well as ITS sequences derived from type material as listed by IDphy (http://idtools.org/id/phytophthora/) (Abad et al. 2019). The trees were inferred using IQTREE2 (Minh et al. 2020) following the methods of Bourret et al. (2022).

Results

Eight hundred instances of *Phytophthora* spp. isolated within California were confirmed from the sequence accessions. The accessions were sorted into 272 distinct ITS haplotypes and 80 *Phytophthora* taxa, 61 of which have been formally described (Table 1; Supplementary Table S1). This resulted in three hierarchical lists of *Phytophthora* in California: individual isolates, unique ITS haplotypes, and *Phytophthora* taxa. We determined different species than those listed in the GenBank accession for 59 *Phytophthora* strains (7% of the accessions). In all, 136 (17%) of the isolates were placed in the agriculture land-use category, 373 (47%) in the forest category, 96 (12%) in horticulture, and 117 (15%) in restoration outplantings; 78 (10%) could not be placed into one of the categories and, therefore, were discarded from the Sørensen analysis.

The five most common *Phytophthora* spp. in descending order were *P. gonapodyides, P. pseudosyringae, P. ramorum, P. cactorum*, and *P. crassamura*, with 83, 58, 54, 46, and 44 isolates, respectively (Table 1). The total number of plant host genera was 79, and *P. cactorum, P. ramorum*, and *P. nicotianae* were associated with the greatest number, with 19, 17, and 13 host genera, respectively. The most common host genera were *Quercus* (50 isolates), *Solanum* (30 isolates), *Prunus* (26 isolates), and *Artemisia* (24 isolates). *Quercus* was associated with the most *Phytophthora* spp. (n = 20 species),

Fig. 1. Examples of the four land-use categories of Californian *Phytophthora* spp. Clockwise from upper left: restoration outplantings, an oak and a nursery-origin toyon planted between a road and an urban waterway in a restored area in the San Francisco Bay Area; agriculture, a field of onion in the California Central Valley; forests and forest streams, a Big Sur coast redwood forest affected by both fire and sudden oak death; and nurseries and horticulture, a commercial production nursery in the Central Valley.

followed by *Artemisia* ($n = 14$) and *Diplacus* ($n = 9$); *Citrus*, *Prunus*, and *Rhododendron* were next, each associated with 8 *Phytophthora* spp.

Most common Californian plant hosts were found to be associated with multiple *Phytophthora* spp. Plant genera represented by three or more records (Supplementary Table S1) were always associated with multiple *Phytophthora* spp., with only three exceptions: genera *Capsicum* (*P. capsici*), *Chamaecyparis* (*P. lateralis*), and *Sequoia* (*P. ramorum*). Five *Phytophthora* spp. represented by three or more isolates were only associated with a single host genus: *P. foliorum* (*Rhododendron*), *P. infestans* (*Solanum*), *P. medicaginis* (*Medicago*), *P. mengei* (*Persea*), and *P. quercina* (*Quercus*). At least five species of *Phytophthora* were originally described from California or have Californian type material and ex-type strains: *P. citrophthora, P. mengei, P. nemorosa*, and *P. rosacearum* all have Californian type material and, although the type of *P. drechsleri* is lost, the most official extant strain, based on the work of IDphy (well-authenticated G. Abad selected specimen CPHST BL 17 [A2] = P11637, likely candidate as a neotype), is derived from California. There are also several provisional species known only from California, including *P.* taxon mugwort (Bourret et al. 2018a), *P.* sp. *canalensis* (see WPC database; no published record), and *P.* taxon juncus (Bourret et al. 2018c).

The ARS-GRIN fungus-host-distribution database, which includes published references with or without accompanying

Table 1. List of *Phytophthora* spp. documented in California[a]

	Isolates						
***Phytophthora* spp.**	**Agric**	**For**	**Hortic**	**Restor**	**Total**	**ITS**	**Host**
Clade 1							
cactorum	6	12	10	15	46	8	19
hedraiandra	–	–	1	1	2	1	2
infestans	22	–	–	–	22	7	1
nicotianae	4	–	9	6	20	15	13
pseudotsugae[b]	–	12	–	–	12	1	1
tentaculata	–	–	1	–	1	1	1
aff. *nicotianae*	1	–	–	–	1	1	1
cf. *infestans*	1	–	–	–	1	1	1
xserendipita[b]	–	–	1	–	1	1	1
Clade 2							
capsici	12	–	–		12	10	2
citrophthora	7	–	–	1	8	6	2
insolita[b]	1	–	–	–	1	1	1
mengei	5	–	–	–	5	1	1
siskiyouensis	–	4	–	–	4	1	1
tropicalis	–	–	1	–	1	1	0
aff. *tropicalis*	–	–	1	–	1	2	0
multibullata[b]	1	–	–	–	1	1	1
occultans[b]	–	–	1	1	2	1	2
P. citricola species complex							
acerina[b]	–	–	–	1	1	1	1
citricola	1	–	–	–	1	1	1
multivora	–	13	9	2	24	4	11
pini	1	2	1	2	6	2	4
plurivora	1	–	3	–	4	4	2
sp. *aureomontensis*	–	2	–	–	2	1	0
cf. *citricola*	1	–	–	–	1	1	1
Clade 3							
nemorosa	–	21	–	–	21	1	3
pluvialis[b]	–	17	–	–	17	1	0
pseudosyringae	–	53	–	1	58	4	4
psychrophila[b]	–	–	–	1	1	1	1
Clade 4							
palmivora	–	–	1	1	2	2	2
quercetorum[b]	–	–	–	2	3	2	2
Clade 6							
amnicola[b]	–	–	1	–	1	1	0
asparagi[b]	3	–	–	1	4	2	2
bilorbang[b]	–	3	–	5	8	6	3
chlamydospora[b]	–	39	2	2	43	10	3
condilina[b]	–	–	–	1	1	1	1
crassamura	8	–	2	11	44	2	12
gonapodyides	–	81	1	1	83	18	5
humicola[b]	–	–	–	2	2	1	1
inundata	4	13	–	8	25	3	7
lacustris[b]	1	20	–	3	24	11	3

(*Continued on next page*)

[a] Agric = agriculture isolates, For = forest and forest stream isolates, Hortic = horticulture and plant production isolates, Restor = restoration outplanting isolates, Total = total isolates or strains, ITS = internal transcribed spacer haplotypes, and Host = associated host.

[b] Described species that had not been reported from California in the literature as of August 2020, according to the Agricultural Research Service Germplasm Resources Information Network fungus-host-location database. Summarized from Supplementary Table S1.

sequences, identified a total of 42 described *Phytophthora* spp. detected in California associated with 251 host genera (Farr and Rossman 2020). The GRIN search identified *P. ilicis, P. richardiae, P. rubi*, and *P. sojae*, which were not represented with sequence accessions in our data sources. We also identified 20 described *Phytophthora* spp. occurring in California based on sequence accessions but not identified in the published literature (Table 1). Of 17 phylogenetic clades of *Phytophthora* (Bourret et al. 2018a), 11 were represented (1 to 4, 6 to 9, and 11 to 13).

Of the four *Phytophthora* metacommunities pooled by land-use category (agriculture, forests, horticulture or nurseries, and restoration outplantings), the restoration outplantings community had the greatest richness, with 42 *Phytophthora* taxa, 13 of which were only found in that category (Table 1). Agriculture yielded 35, 14 of which were only found in that category, while horticulture and nurseries yielded 33 total, 9 unique to the category. Despite having more than twice as many isolates as any of the other pooled communities, the forest *Phytophthora* community had the lowest richness, with 26 *Phytophthora* spp., 9 of which were only found in that category. *P. cactorum, P. pini, P. pseudocryptogea*, and *P. syringae* were identified in all four land-use categories, while 13 taxa were found in three of the four (Supplementary Fig. S1). The pairwise Sørensen similarity measures were highest between the restoration outplantings and horticulture metacommunities at 0.48, followed by the restoration and forests at 0.46, while agriculture and forests were the least similar at 0.26 (Table 2).

The majority of *Phytophthora* spp. were represented by more than one unique ITS haplotype. For well-represented species, one haplotype was typically dominant (Supplementary Figs. S2 to S5), and

Table 1. (*Continued from previous page*)

	Isolates						
***Phytophthora* spp.**	**Agric**	**For**	**Hortic**	**Restor**	**Total**	**ITS**	**Host**
aff. *lacustris*	1	–	–	–	1	1	1
megasperma	–	–	1	4	5	3	4
riparia	–	17	–	1	18	6	2
rosacearum	5	–	–	10	15	14	7
thermophila[b]	–	2	1	1	4	2	2
sp. *canalensis*	–	–	1	–	1	1	0
sp. NJB-2015	–	5	–	–	5	1	1
taxon raspberry	–	–	1	1	2	1	2
taxon walnut	4	–	–	1	5	4	5
humicola × *inundata*	–	–	–	1	1	1	1
lacustris × *riparia*	–	11	–	–	11	8	0
sp. xWS	–	–	–	2	2	2	1
Clade 7							
cinnamomi	4	4	13	–	40	11	7
mediterranea	2	–	1	–	3	2	2
fragariae	1	–	–	–	1	1	1
niederhauserii	6	–	2	–	8	7	3
cf. *niederhauserii*	–	–	2	–	2	1	2
parvispora	–	–	1	–	1	1	0
sp. *cadmea*	–	1	–	2	3	1	2
× *cambivora*	1	–	–	9	11	5	4
Clade 8							
foliorum	–	–	3	–	4	4	1
hibernalis	1	1	1	–	3	1	2
lateralis	–	1	–	–	7	1	2
medicaginis	3	–	–	–	3	6	1
ramorum	–	21	15	1	54	6	17
syringae	11	11	1	1	24	5	4
aff. *syringae*	–	4	–	–	4	3	0
P. cryptogea species complex							
cryptogea	2	–	2	–	4	3	4
drechsleri	2	–	–	–	2	2	2
aff. *drechsleri*	1	–	–	–	1	1	1
erythroseptica		–	–	1	2	2	1
kelmania	4	–	2	2	8	8	5
pseudocryptogea[b]	6	3	3	2	15	6	8
Clade 9							
hydropathica[b]	–	–	–	1	1	1	1
parsiana species complex	2	–	1	1	4	5	3
taxon xguadalupesoil	–	–	–	2	2	2	1
Clade 11							
taxon juncus	–	–	–	1	1	1	1
Clade 12							
quercina[b]	–	–	–	4	4	1	2
Clade 13							
taxon mugwort	–	–	–	1	1	1	1
Totals							
Isolates or strains	136	373	96	117	800	272	72
Total species	35	26	33	42	80	–	–
Unique species	14	9	9	13	–	–	–

these common haplotypes were also found across the land-use categories—this was the pattern for species such as *P. multivora, P. pini*, and *P. pseudosyringae*. This was not the pattern for the haplotypes of *P. cactorum*: four of the seven isolates with the CAC1 haplotype were from agriculture, with CAC1 also detected in forests and horticulture; isolates with haplotype CAC2 ($n = 12$) were only found in restoration and horticulture, and CAC3 ($n = 17$) was found in all categories except agriculture. CAC4 ($n = 6$), CAC5 ($n = 1$), and CAC8 ($n = 1$) were only found in forests, while CAC6 ($n = 1$) and CAC7 ($n = 1$), each represented by a single isolate, were from agriculture. One *P. cinnamomi* haplotype was relatively widespread (CIN1, $n = 29$) but CIN2 to CIN7 ($n = 7$) were only found in horticulture, CIN8-10 ($n = 3$) were only found in forests, and CIN11 ($n = 1$) was only found in agriculture. Within *P. syringae*, isolates with the SYR1 haplotype ($n = 6$) were only found in agricultural fields; SYR2 ($n = 15$) was found across agriculture, forests, and restoration; SYR3 ($n = 1$) was only in horticulture; and SYR4 to SYR8 ($n = 6$) only in forests.

Discussion

Phytophthora in California

Knowing the distribution and diversity of plant pathogens is critical to sustain worldwide plant health, and the detections assembled here can be used to inform *Phytophthora* management, regulation, and research worldwide. As the list of putatively nonnative plant pathogens detected in California expands, the task of protecting California's plants, whether in forests or production, increases in difficulty; continual *Phytophthora* prevention and management efforts are needed to maintain plant health. The plant diversity of California is a treasured resource in need of protection.

It is no surprise to find a long list of Californian *Phytophthora* spp. Not only does California boast great plant biodiversity but also within its borders are several universities involved in *Phytophthora* research, including the University of California, Riverside, which houses the WPC. California's forests have also been greatly impacted by SOD, a disease that has compelled considerable research and regulation, as well as plant mortality (Cobb et al. 2020; Hansen et al. 2012; Wickland et al. 2008). Nevertheless, 80 taxa, including 60 described species, is a large number, considering that the total number of species in the genus was approximately 70 just prior to the molecular era, circa 1996 (Brasier 2009; Erwin and Ribeiro 1996). A model-based study found the United States to have the highest predicted *Phytophthora* diversity, with 81 to 90 species (Scott et al. 2019). For comparison, a recently published assessment of a large, historical collection of Pennsylvanian *Phytophthora* isolates reported 36 species (Molnar et al. 2020). A large survey of continental Europe listed 68 *Phytophthora* spp. (Jung et al. 2016), although considerable systematic work has been done since. A metabarcoding survey across the continent of Australia detected 68 *Phytophthora* taxa (Burgess et al. 2019), while a specimen- and literature-based study found 99, 80 of which were described (Burgess et al. 2021).

The similarities of the communities derived from the four *Phytophthora* land-use categories (agriculture, forests, horticulture, and restoration outplantings) (Table 2) suggest that horticulture exerts a slightly stronger influence on the *Phytophthora* spp. found in restoration outplantings than that of the surrounding forests but that the *Phytophthora* community associated with agriculture contributes the least to the restoration areas. The two highest-similarity pairings, nurseries–restoration and restoration–forests, reflect a common and problematic pathway of invasive *Phytophthora* infestation (i.e., nursery → outplanting → natural ecosystem) and fortify findings that there are few buffers preventing *Phytophthora* spp. from moving between these locations (Jung et al. 2016; Sims and Garbelotto 2021). This confirms the importance of strict phytosanitation practices in nurseries (Swiecki et al. 2021). Of the 15 possible combinations of the four land-use categories, only forests + agriculture and forests + horticulture were depauperate (Supplementary Fig. S1). That restoration outplantings supported the most diverse *Phytophthora* communities of the four land-use categories is without question a cause for concern; however, sampling was unequal across the four categories, particularly in regards to soilborne *Phytophthora* spp. Also, the number of detections for each species reflects the level of survey activity, particularly so for *P. ramorum*, a regulated pathogen with mandated ongoing inspections. More study and *Phytophthora* surveys are needed across all land-use categories to evaluate these results.

Table 2. Sørensen similarity between the four pooled metacommunities of the land-use categories

Metacommunities	Restoration outplantings	Horticulture, nurseries	Forests
Horticulture, nurseries	0.48	–	–
Forests	0.46	0.37	–
Agriculture	0.39	0.41	0.26

Cataloging barcodes

This sequence-based meta-analysis, comprising curated, publicly available sequence accessions, differs considerably from literature-based lists because all of the data (sequence accessions) used are listed in Supplementary Table S1; much of the report-based literature relies on morphological determinations that are not repeatable, because the specimens no longer exist. Another major benefit of the sequence-based method is that the compiled data serve as a barcoding tool: the Supplementary Table S1 spreadsheet can be downloaded and consulted by researchers and regulators as a barcoding guide. Future work may incorporate the data into a website that can be easily modified and updated by other researchers and perhaps be expanded to other geographic areas. Even if subsequent systematic work updates the nomenclature, because the accessions are organized by ITS haplotype, updating species names would be straightforward. In the case of several important species, particularly *P. cactorum*, ITS haplotypes may provide clues into ecologically significant intraspecific groupings (Bourret et al. 2022).

The greater number of *Phytophthora* spp. in this meta-analysis compared with the number from the literature search demonstrates the benefit of molecular barcoding in its precision at separating *Phytophthora* spp. The list of 80 species is undoubtedly incomplete and biased, because more than a third of the sequence accessions could be attributed to just two *Phytophthora* surveys (Bourret et al. 2018c, b). However, the number of host genera found through the sequence accessions, 79 (Table 1; Supplementary Table S1), is dwarfed by the number of host genera in the GRIN database, which is in the hundreds. In this context, the efforts of culture collections and barcoding projects—namely, IDphy, WPC, and Robideau et al. (2011)—allow some unification of these two systems and enable researchers to see backward in time. Nevertheless, it will likely be a long time before an accession-based analysis can list even half the number of hosts as are compiled from more than a century of published records.

Despite over a century of research, our knowledge of actual *Phytophthora* diversity is limited and greatly biased. It is thought that many pathogens are rare or difficult to detect in their native range and there is no question that many if not most *Phytophthora* spp. are described from locations where they are not indigenous; *P. ramorum*, one of the most common species in this meta-analysis, is known to have been recently introduced to North America and Europe, where it was described (Jung et al. 2021; Werres et al. 2001). Some species in clade 6 that may have less pathogenic and more saprotrophic lifestyles appear to be exceptions, in that they appear to be commonly encountered but putatively indigenous, based on high levels of intraspecific diversity. Taxa known from only a few or single local detections deserve attention, because these might be recently introduced (potentially capable of becoming naturalized or causing an epidemic) or possibly rare, indigenous microbes.

Because they are a measure of intraspecific diversity, the number of ITS haplotypes detected for each species can be informative,

although undetected sequencing errors artificially inflate these numbers. Heterozygosity has the potential to increase the number of ITS haplotypes observed; if two parental sequences that differ by a single substitution are simultaneously present in a progeny, the SNV present at that site will be counted as a third, separate ITS haplotype. Of the six species with more than 10 observed ITS haplotypes, two (*P. cinnamomi* and *P. gonapodyides*) are heterothallic, two (*P. chlamydospora* and *P. lacustris*) are sterile or weakly heterothallic, *P. rosacearum* is homothallic, and *P. nicotianae* is known as both homothallic and heterothallic depending on isolate (Abad et al. 2019); SNVs contributed to the observed ITS haplotype diversity of all of these species.

When reporting *Phytophthora* detections, it would be beneficial, although not always tractable, for all researchers to provide each unique ITS sequence found for each host–species combination, with data in the "country" source modifier and the publication information provided for each accession. Although environmental DNA (eDNA) research holds great promise for quickly extending our knowledge of *Phytophthora* ecology, current metabarcoding methods result in sequences that are shorter than the full ITS amplicons employed for diagnostic barcoding, and it is rare that these metabarcoding sequencing results are deposited into the nucleotide collection to be matched during BLAST searches along with source metadata. Therefore, eDNA detections do not constitute any of the data in this meta-analysis.

Species complexes

***P. citricola* species complex.** *P. pini* was synonymized with *P. citricola* by Waterhouse (1963) and, prior to the use of molecular data, the single species *P. citricola* was regarded as one of the most widespread and important species in the genus. Now *P. citricola* sits within what is known to be a diverse species complex (Brazee et al. 2017; Ginetti et al. 2014; Henricot et al. 2014; Jung and Burgess 2009; Robideau et al. 2011), including the resurrected *P. pini* (Hong et al. 2011). According to our results, the *P. citricola* species complex is phylogenetically and ecologically diverse in California. Despite many accessions deposited as *P. citricola*, only one instance of *P. citricola* sensu stricto in California was documented; most accessions instead correspond to *P. multivora* and *P. pini*, which both appear to be relatively widespread (Supplementary Fig. S2). Although *P. multivora* and *P. pini* were found in several different land-use categories, *P. citricola* and *P.* cf. *citricola* were only found within agricultural sites, *P.* sp. *aureomontensis* only in forests, and *P. acerina* only in restoration; the species complex was most diverse in agricultural settings, with four documented taxa. *P. acerina, P.* cf. *citricola*, and *P. plurivora* are members of the complex that have been documented in California but appear to be more widespread in Europe (especially *P. plurivora*) (Jung et al. 2016), which, until more is known about the biogeography of this species complex, suggests that they should be seen as species of concern in California. Additional work on the pathogenicity of these species on a range of hosts is needed.

***P. cryptogea* species complex.** We cataloged all five described species of the *P. cryptogea* species complex, as well as a putative undescribed taxon related to *P. drechsleri* (Supplementary Fig. S3). The three earliest-described taxa in the complex (*P. cryptogea, P. drechsleri*, and *P. erythroseptica*) were relatively uncommon, while the recently described cryptic species *P. pseudocryptogea* was the most common and widespread, followed by the closely related *P. kelmania*. Five taxa in the species complex were found in agricultural settings, while three each were found in restoration outplantings and horticulture or nurseries. *P. pseudocryptogea* was one of the most pathogenic species in a recent study of ornamental trees in Western Australia (Khdiar et al. 2020). Until more is known, it would be beneficial if all members of the *P. cryptogea* species complex were considered species of concern in California.

***P. megasperma* species complex.** *P. megasperma* has probably been split most frequently into other *Phytophthora* spp., giving rise to many cryptic look-alikes (Erwin and Ribeiro 1996; Förster and Coffey 1993; Hansen and Maxwell 1991; Hansen et al. 2009, 1986; Scanu et al. 2015). Although many of the cryptic species split from *P. megasperma* are phylogenetically distant and, therefore, do not constitute a species complex, the recently described *P. crassamura* and *P. megasperma* sensu stricto are sister species (Supplementary Fig. S4). Based on the current survey, *P. megasperma* is rare in California, with only five confirmed isolations, whereas *P. crassamura* has been in the state for at least 100 years, widely associated with agriculture (but known as *P. megasperma*), more recently associated with restoration activities (as *P. crassamura*), including restoration nurseries, as well as detected in riparian areas of the Angeles National Forest (Supplementary Table S1). Sims et al. (2019) found many isolates of *P. crassamura* from California to be mefenoxam resistant, suggesting that this resistance may have developed during time spent in a nursery, where mefenoxam is commonly used.

Conclusions

Although essential, understanding Californian let alone worldwide *Phytophthora* diversity remains a daunting challenge and outstanding need. This meta-analysis provides evidence of considerable diversity but, to the extent that it differs methodologically from previous lists of *Phytophthora* spp., also serves as a tool or model to facilitate further research and guide management. Based on our results, some widely held beliefs about which *Phytophthora* spp. are the most prevalent and pathogenic in California need to be updated. We confirm that *P. cactorum, P. cinnamomi, P. nicotianae,* and *P. ramorum* have been frequently recorded in the state across a range of hosts but, based on sequence accessions, *P. citricola* has not. The most widespread member of the *P. citricola* species complex detected in the state appears to be *P. multivora.* Likewise, *P. cryptogea* and *P. drechsleri* have been uncommonly reported but *P. pseudocryptogea* recoveries have been relatively widespread, whereas *P. megasperma*, while not rare, has not been as commonly detected as the look-alikes *P. crassamura* and *P. rosacearum*. Continued research is needed regarding the impacts of not only these more commonly detected *Phytophthora* spp., but also species not yet reported on California native plant species. The impacts of this research are not restricted to California but are part of an ongoing global effort to manage a wide and complex range of Phytophthora diseases of agriculture, forests, and horticulture—everywhere that plants grow.

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