A microsatellite analysis identifies global pathways of movement of *Phytophthora cinnamomi* and the likely sources of wildland infestations in California and Mexico

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Abstract

The genetic structure of a sample of isolates of the oomycete plant pathogen *Phytophthora cinnamomi* from natural and agricultural outbreaks, and the long-distance movement of individual genotypes, were studied using four microsatellite markers to genotype 159 isolates of Californian, Mexican, and worldwide origin. Allelic profiles identified 75 multilocus genotypes; STRUCTURE analysis placed them in three groups characterized by different geographic and host ranges, different genic and genotypic diversity, and different reproductive modes. When relationships among genotypes were visualized on a minimum spanning network (MSN), genotypes belonging to the same STRUCTURE group were contiguous with rare exceptions. A putatively ancestral Group 1 had high genic diversity, included all A1 mating type isolates and all Papuan isolates in the sample, was rarely isolated from natural settings in California and Mexico, and was positioned at the center of the MSN. Putatively younger Groups 2 and 3 had lower genic diversity, were both neighbors to Group 1 but formed two distinct peripherical sectors of the

MSN, and were equally present in agricultural commodities and natural settings in Mexico and California. A few genotypes, especially in Group 2 and 3, were isolated multiple times in different locations and settings. The presence of identical genotypes from the same hosts in different continents indicates that long-distance human-mediated movement of *P. cinnamomi* has occurred. The presence of identical genotypes at high frequency in neighboring wildlands and agricultural settings suggests that specific commodities may have been the source of recent wild infestations caused by novel invasive genotypes.

Keywords: California; emergent disease; exotic pathogen; introductions; novel strain; Oomycetes

Introduction

Invasive species, including exotic pathogens and pests, are among the most serious threats to local biodiversity and are a major cause of species extinction (Lowe et al. 2000). Because of these impacts, there is an increasing need to understand specific introduction pathways for exotic organisms in order to develop adequate containment and control protocols. The introduction of plant pathogens into natural ecosystems through the trade of ornamental plants or through agricultural practices is a long-known issue that has recently re-emerged as an important research topic (Lowe et al. 2000; Dehnen-Schmutz et al. 2010; Santini et al. 2013; Jung et al. 2016). Although movement of ornamental and agricultural plants is recognized as a major way of moving pests and pathogens around the world, the emphasis of international phytosanitary containment has been placed mostly on plants infected by recently described or exotic pathogenic species. In contrast, the re-emergence, or emergence in natural ecosystems, of pathogens long established in agricultural settings has mostly and unjustly been overlooked (Garbelotto 2008; Dehnen-Schmutz et al. 2010).

One reason for this selective emphasis is that regulatory agencies do not have a system in place to regulate pathogens already known to have a broad distribution. This lack of regulation is problematic, because broad and even worldwide distributions do not equate to a ubiquitous presence of these biological threats in natural ecosystems. In particular, individual strains or genotypes of invasive pathogens are usually site-specific; thus, there is a real risk that multiple introductions will result in the introduction of novel strains still absent in a given region (Garbelotto 2008). There is an urgent need to understand the risks associated with the introduction of new genotypes of the same pathogen/pest: these risks are well understood for

diseases affecting humans, but the same is not true for plant pathogens and pests (Desprez-Loustau et al. 2007). Most published cases in this area of research have had to do either with the insurgence of resistance to chemical control agents, or with increases in the number of highly susceptible hosts (Dixon et al. 1996).

In this study, we used *Phytophthora cinnamomi* Rands as a model system to study: a)- the worldwide movement of a pathogen through human activities; b)- the pathways of introduction of a pathogen from agricultural into natural settings, and; c)- the emergence of new invasive strains. *Phytophthora cinnamomi* is a soilborne Oomycete pathogen associated with a large number of hosts worldwide (Zentmeyer 1983; Erwin and Ribeiro et al. 1996; Hardham 2005); it is currently listed as one of the 100 worst invasive organisms in the world (Lowe et al. 2000). First isolated in Sumatra (Rands 1922), this heterothallic organism is thought to be indigenous to Papua New Guinea where maximum genetic diversity is encountered (Linde et al. 1999, Old et al. 1984, 1988). However, its center of origin may include other parts of East and Southern Asia (Arentz, 2017; Arentz and Simpson 1986). The current global distribution of this organism appears to be the result of the intercontinental movement of infected soil and plant material associated with the horticultural trade in the last 100+ years (Zentmeyer 1988; Linde et al. 1999; Jung et al. 2016; Arentz 2017).

In addition to being a significant pathogen of horticultural crops (Erwin and Ribeiro 1996), *P. cinnamomi* has also been identified as a pathogen in natural ecosystems (Brasier 1996; Tainter et al. 1997, 2000; Swiecki et al. 2003; Hardham 2005; Garbelotto et al. 2006; Nagle et al. 2010; EPPO/CABI 2011). The impact of its presence in natural settings varies depending on the ecosystem and the inherent susceptibility of the plant species involved (Hayden et al. 2013). The impact of *P. cinnamomi* can be dramatic in ecosystems such as the Jarrah forests of Western Australia (Shearer et al. 2004), the white oak forests of Central Mexico (Tainter et al. 1997, 2000), and Manzanita populations in the foothills of the Sierra Nevada in California (Swiecki et al. 2003). In other ecosystems, including oak woodlands in Iberia (Brasier 1996; Sánchez et al. 2002; Gómez-Aparicio et al. 2012), in the Eastern US (Nagle et al. 2010; Balci et al. 2010; Eggers et al. 2012; McConnell and Balci 2014), in Southern California (USA) (Garbelotto et al. 2006), and in pine stands of the eastern US (French 1989; Griffin et al. 2009; Mckeever and Chastagner 2016), the presence of *P. cinnamomi* is associated with a condition known as “oak decline” in oaks (Brasier 1996) or “littleleaf disease” in pines (French 1989). In these cases, *P. cinnamomi* acts like a less aggressive pathogen, mostly responsible for pruning the fine roots of

infected hosts (Brasier 1996; Garbelotto et al. 2006). Although not directly leading to plant mortality, infection of the fine roots significantly reduces the resilience of trees and leads to mortality at the onset of limiting conditions such as a persistent drought (Eggers et al. 2012; Garbelotto et al. 2006), or results in premature senescence and a short lifespan (French 1989; Griffin et al. 2009). Although mortality in these cases is cyclical and linked to environmental and site conditions (Garbelotto 2008; Griffin et al. 2009; Nagle et al. 2010), the decline of infected trees may occur over large areas, with obvious deleterious ecological and economic effects. A third scenario consists of spatially limited infestations, such as those reported for Kauris in New Zealand (Beever et al. 2009), Pacific madrones in California (Fichtner et al. 2009), and sweet chestnuts in Southern Europe (Vannini and Vettraino 2001; Vettraino et al. 2001). In these cases, mortality of individual trees or of small clusters of trees has been reported; it is not clear whether this more limited effect may be due intrinsically to mixed host composition and diversity in these ecosystems, or may simply result from the fact that the pathogen was only recently introduced in these ecosystems (Vannini and Vettraino 2001).

The presence of *P. cinnamomi* in three different natural California ecosystems has been reported relatively recently (Swiecki et al. 2003; Garbelotto et al. 2006; Rizzo and Fichtner 2009). California may therefore be an ideal region to understand the pathways through which a soilborne pathogen of agricultural importance may be released in nature, and to confirm the insurgence of new strains as reported for agricultural commodities (Pagliaccia et al. 2013). The identification of founder individuals responsible for new wildland infestations may be easier in California because in younger infestations, founder effects should still be strong and genetic similarity should be high between those founder individuals that were the source of the outbreak and the invasive individuals currently causing the outbreak (Garbelotto 2008). The California example is also particularly interesting because *P. cinnamomi*, although clearly exotic, is not regulated due to its abundance in agricultural and horticultural settings. One may assume that the sources of invasions of natural ecosystems may all be identified in populations already established in non-natural systems throughout the state. This presumption, although reasonable, needs to be tested by evaluating whether identical pathogen genotypes show evidence for a link between commodities and natural ecosystems.

In this study, we adopted a population genetics approach first on a California and worldwide collection of *P. cinnamomi* both from natural ecosystems and from commodities. Second, we performed the same analysis on a Mexican collection of isolates to identify the possible source of

some California outbreaks. This second analysis was prompted by the observation that some novel California outbreaks were seemingly concurrent with novel Mexican outbreaks.

Our specific aims were to:
1)- Use microsatellite analysis to draw inferences about the broad genetic structure of *P. cinnamomi* at the worldwide level, and to determine the host and geographic range of individual genotypes, and

2)- Use multilocus genotyping to identify: i)- long distance movement of the pathogen through the movement of infested commodities, ii)- cross-contamination among commodities, iii)- the specific sources for the release of the pathogen from commercial commodities into natural settings in California and Mexico, and iv)- emergent young "invasive" genotypes affecting multiple commodities and present in different world regions

Materials and methods

Isolates

We employed a two-tiered sampling approach. Our study of pathways of worldwide movement of *P. cinnamomi* used isolates available in historical collections, some dating back to 1966, emphasizing geographic breadth over depth within any given geographic region. Conversely, intensive sampling of California and Mexico populations after the year 2000 was designed to examine both recent wildland outbreaks and chronic infestation of agricultural commodities in order to understand the number and sources of introductions of this pathogen in natural settings. Together, these studies allowed us to obtain a satisfactory picture of instances of long distance global movement of the pathogen, as well as of its short movement from commodities into natural settings in California and Mexico.

Table 1 summarizes the host or substrate, the geographic provenance and the mating type of all isolates employed in the first study. In summary, 75 isolates were used from 8 distinct countries, including 61 from the USA. A total of 44 isolates were collected from natural or 'wild' settings comprising all three major reports of *P. cinnamomi* in the wild in California, namely oak woodlands in San Diego county (n=6), Manzanita-dominated communities in serpentine soils of Stanislaus County in the Sierra Nevada foothills (n=23), and woodlands in the San Francisco Bay Area (n=15). The sample also included 17 USA isolates from agricultural and nursery commodities located in California (n=15) and Florida (n=2). Worldwide isolates were collected

from a natural setting in Taiwan (n=1), from Papua New Guinea (n=4), Australia (n=1), and from an oak infestation in the state of Colima, Mexico (n=1) (Tainter et al. 2000). Seven additional isolates used in the study were from agricultural commodities in China (4), South Africa (2) and Madagascar (1). Table 2 lists all Mexican isolates used for the second analysis, including 64 isolates from five different states: Colima (7), Jalisco (7), Guerrero (6), Estado de Mexico (7), and Michoacán (37), with 27 from natural settings and 37 from agricultural commodities. A total of 12 isolates from the first analysis were re-analyzed together with Mexican isolates, allowing us to compare the two analyses. The 12 isolates used in both analyses included six pairs of closely related genotypes, with each pair being genetically distant from the others. The reasons for performing two distinct analyses are detailed in the section below.

DNA extraction and SSR amplification

Culture collections were maintained on 1.7% Corn Meal Agar (CMA) and subcultured on selective Pimaricin-Ampicillin-Rifampicin-Pentachloronitrobenzene agar (PARP) (Erwin and Ribeiro 1996), incubated at room temperature in the dark for 3 weeks, and transferred into 12% pea broth (120 g peas/liter) liquid medium (Eyre and Garbelotto 2015) at room temperature for 7 days. Mycelia were harvested by filtering the broth through Whatman paper and lyophilizing the filtrites for 24 hours. DNA was extracted from 20 mg of lyophilized mycelium using the Gentra Puregene Tissue DNA kit (Qiagen, MD, USA) and eluted in 50 µl ultrapure water as described by Ivors et al. (2006).

Four di-nucleotide SSR (Simple Sequence Repeat, or microsatellite) loci described by Dobrowolski et al. (1998, 2002) were amplified: d39, e16, g10, and g13. Due likely to a mutation in the g13 priming site for some isolates, two primer pairs – g13(1) and g13(4) – are needed to genotype this locus. The d39 and g13 loci exhibit genetic linkage (Dobrowolski et al. 2002). The amplification reactions were performed in a final volume of 10 µl using 10 ng of genomic DNA, 200 µM of dNTPs, 1.5 mM $MgCl_2$, 0.1 µM of each primer and 1U Taq polymerase. All loci except g13(4) were amplified using the following PCR conditions: initial denaturation of 2 min at 96 ºC; 6 cycles of denaturation at 96ºC for 30 s, annealing at 66ºC for 30 s, and extension at 72ºC for 30 s; followed by 20 cycles of denaturation for 30 s at 96ºC, annealing for 30 s at 60ºC and extension for 30 s at 72ºC. The microsatellite g13(4) was amplified using an initial denaturation for 2 min at 96ºC; 6 cycles of denaturation for 30 s at 96ºC, annealing for 30 s at 64ºC and extension for 30 s at 72ºC; followed by 20 cycles of denaturation for 30 s at 96ºC, annealing for 30 s at 58ºC, and extension for 30 s at 72ºC. The forward primer was labeled with 6-FAM and

size determination of the PCR products was conducted on an ABI377 sequencer (Applied Biosystems, CA, USA) using GeneScan 500 LIZ (Thermo Fisher Scientific, MA, USA) as the size marker. Amplifications were conducted in 96-well plates in a MiQ Single Color Real-Time PCR Detection System thermal cycler (Bio-Rad, CA, USA), and negative and positive controls (isolates of known genotype) were included in each plate. For the Mexican analysis, amplifications were conducted three years later in a CFX96 thermal cycler (Bio-Rad, CA, USA), and fragments were sized on an ABI3730 DNA Analyzer using GeneScan 500 LIZ as the size marker. For statistical analysis, allele fragment length was substituted with the number of repeats corresponding to the allele size.

Genetic and Statistical Analyses

Cumulative allelic profiles were used to identify multilocus genotypes (MG), each characterized by a unique combination of alleles, using the R package poppr, version 2.5.0 (Kamvar et al. 2014). In order to ensure that sampling was sufficiently saturated in the worldwide/California set of isolates, given the resolution of the genetic markers employed, we constructed a genotype accumulation curve as described by Grünwald et al. (2017).

Statistical confidence of identifying unique individuals with the selected microsatellite loci was assessed by calculating the probability of identity, $P_{(ID)}$. However, *P. cinnamomi* has three characteristics that may violate the Hardy-Weinberg equilibrium and linkage equilibrium assumptions of $P_{(ID)}$ calculation: occurrence of clonality, possible population substructure, and linkage between two of the loci used in this study (d39 and g13). To address these issues, we (1) performed complete clone correction of each dataset (worldwide/California and Mexico); (2) included a more conservative $P_{(ID)}$ measure; and (3) calculated the $P_{(ID)}$ values with and without one of the two linked loci. We therefore calculated four values of P(ID) for each dataset, for all four loci vs. one locus removed, using two formulas: the more conservative measure for siblings described by Waits et al. (2001):

$$P_{(IDsib)} = 0.25 + \left(0.5\,\Sigma p_i^2\right) + \left[0.5\left(\Sigma p_i^2\right)^2\right] - \left(0.25\,\Sigma p_i^4\right)$$

where p_i is the frequency of the ith allele, as well as the commonly-used measure of Paetkau and Strobeck (1994):

$$P_{(ID)} = \Sigma p_i^4 + \Sigma\Sigma(2p_i p_j)^2$$

where p_i and p_j are two allele frequencies, $p_i \neq p_j$.

For each dataset, the two $P_{(ID)}$ measures were calculated for each locus; the multilocus genotype was calculated as the product of the individual per-locus genotype probabilities. For calculations removing one of the linked loci, the locus with the lower heterozygosity (d39 for both datasets) was removed. Allele frequencies were calculated for each clone-corrected dataset using the round robin method of Parks and Werth (1993) as implemented in poppr 2.5.0.

Relationships among individual multilocus genotypes were visualized by calculating the matrix of pairwise genetic distances using the software Genodive (Meirmans and Van Tienderen 2004) using the repeat number-based metric of Bruvo (2004). The distance matrix was used to generate a minimum spanning network (MSN) using poppr 2.8.1 (Kamvar et al. 2014) in order to visualize the relatedness among the multilocus genotypes. One MSN tree was generated for the worldwide/California set of isolates, and one for the Mexican set of isolates. The analysis of the Mexican isolates also included 12 *P. cinnamomi* isolates representing the different clusters obtained in the first SSR analysis, re-genotyped for consistency with the protocols and technology used in the latter analysis in order to avoid batch effects.

Inference of population genetic structure was conducted using the software SRUCTURE (Pritchard et al. 2000) with genome admixing allowed, and with linkage assumed between SSRs g13(1) and g13(4) (Dobrolowski et al. 2002). Both the worldwide/California and the Mexican datasets were clone corrected by eliminating any identical genotypes that were isolated from the same site, to eliminate any obvious bias in sampling intensity across sites. We maintained identical genotypes from distant locations, in the analyses, because we believe this clonal component is key to understanding the broader genetic structure and pathways of spread of this plant pathogen.

All Structure runs employed a burn-in of 1,000,000 iterations and a sample of 5,000,000 iterations, and were automated using StrAuto version 1.0 (Chhatre and Emerson 2017). The optimal value of K (number of populations) was determined from 10 replicate runs of K values from 1 to 8 using STRUCTURE HARVESTER (Earl and von Holdt 2011) to implement the ΔK method of Evanno et al. (2005). STRUCTURE output files were merged in CLUMPP v.1.1.2 (Jakobson and Rosenberg 2007) and graphed using DISTRUCT v. 1.1 (Rosenberg 2004).

To infer the most likely mode of reproduction of different *P. cinnamomi* populations, we calculated the index of association I_A and the standardized index of association $r_{bar}D$ using poppr v.2.8.1 independently for each STRUCTURE group in both datasets. For the

worldwide/California analysis, calculations were made both for the two groups identified by the k= 2 scenario, and for the 3 groups identified by the k= 3 scenario (see results below), for a total of 4 groups because one group perfectly overlapped between the two analyses. Calculations were performed on fully clone corrected sets, where only a single representative per genotype was left in the analysis. Hypothesis tests of linkage equilibrium were conducted using the one-sided permutation test implemented in poppr v.2.8.1.

The following diversity indices were also calculated as described by Mascheretti et al. (2009) using the R package poppr, version 2.5.0 (Kamvar et al. 2014): (i) eMLG = the number of expected MLGs based on rarefaction with a minimum sample size of 10 individuals (Hurlbert 1971); (ii) H = Shannon-Wiener index of MLG diversity (Shannon 2001); (iii) Stoddart and Taylor's index, $G= 1/\Sigma p_i^2$, (Stoddart and Taylor 1988) where p_i is the frequency of the i^{th} MG; (iv) lambda = Simpson's index (Simpson 1949); (v) E_5 = genotypic evenness (Grünwald 2003), and (vi) H_{exp} = genic diversity (expected heterozygosity) (Nei, 1978). Calculations were performed on the STRUCTURE groups of isolates described above for the I_A analysis, subjected to partial clone correction in which identical genotypes from distant locations were retained in the dataset, but identical genotypes from the same site were excluded to avoid sampling bias.

Results

Worldwide variability and genetic diversity in *Phytophthora cinnamomi*

All four SSRs were highly polymorphic; two were trisomic (i.e. included three alleles for some genotypes), and cumulatively 44 alleles differentiated 23 multilocus genotypes (MGs) in the worldwide/California analysis (Tables 1 and 3). Thirteen MGs were singletons represented by a single isolate, while the most common MGs were MG18 (n=24) and MG08 (n=15). Several isolates belonging to the same MG were found at great distance, often on different continents, on the same or on different hosts (Table 1). The genotype accumulation curve indicated that sampling was close to saturation (Figure 1), and thus adequate to answer our research questions. Probability of identity values ranged from 2.46×10^{-3} ($P_{(ID)sib}$ for three loci) to 5.62×10^{-5} ($P_{(ID)}$ for four loci) for the worldwide / California dataset, and from 5.15×10^{-3} ($P_{(ID)sib}$ for three loci) to 5.62×10^{-5} ($P_{(ID)}$ for four loci) for the Mexico dataset (Table S1), thus, it can be assumed with reasonable confidence that these microsatellite loci are capable of distinguishing individuals.

The optimal value of K=2 was determined using the ΔK method for the worldwide/California samples (Figure S1); however, we used K=3 for the final analysis in order to show additional potential substructure (Figure 2A). The presence of three distinct groups was confirmed by the Mexican analysis, which, by including a broad representation of genotypes belonging to the group identified here as group WW2 (represented by a single genotype and thus weakly supported in the worldwide analysis), clearly identified this group as statistically significant and distinct from the other groups. Each of the three STRUCTURE groups consist of genotypes that are also contiguous in the MSN, with the exception of a single sample (P-6493 from *Rhododendron* spp. in China); due to its inconsistent location on the MSN, this sample was excluded in the discussion (Figure 3). STRUCTURE group WW1 (worldwide 1) included four isolates belonging to mating type A2 from two locations in California (n=3, MG 10) and one location in China (n=1, MG11), and all 16 A1 isolates from the Southern Hemisphere, China, and California. Group WW1 was centrally located in the MSN with Group WW2 emerging from one side and Group WW3 emerging from the other. All A1 isolates were contiguous in the MSN, with the isolates from Papua New Guinea forming a distinct subgroup of contiguous genotypes within the A1 cluster. Isolates in Group WW2 all belonged to a single genotype with mating type A2, derived directly from a PNG genotype in Group WW1; this group was isolated both from wild and commodity hosts in California and Mexico. Group WW1 isolates with the A2 mating type were located at another edge of Group WW1 in the MSN; these isolates were found in China and California, and appeared to be more closely related to an A1 genotype isolated from *Camellia japonica* in China. STRUCTURE Group WW3 appeared to emerge from one A2 MG belonging to Group WW1. Group WW3 included multiple MGs, both from wild and commodity hosts, but all isolated in the USA. The presence of multiple isolates from distant locations and various hosts, but belonging to the same MG, was more evident in STRUCTURE groups WW2 and WW3 (see below), while Group 1 included mostly singletons.

Genotypic analysis reveals examples of long distance movement, cross-commodity spread, and pathogen release in wild settings

Examination of genotypes comprising multiple isolates uncovered a number of likely links between geographic areas, commodities, and between agricultural and wild settings. STRUCTURE group WW1 contains 12 genotypes and is defined as the "Old World Group" because it includes all Papuan isolates, presumed to be from within the native range of the pathogen. This group contains 4 different genotypes from Papua New Guinea wildlands, 5 genotypes isolated from 7 agricultural or plantation forestry hosts in China, Australia, South

Africa, and Madagascar (avocado, pineapple, grapes, camellia or rhododendron, and eucalyptus). The observed genetic and geographic patterns provide strongly suggest the occurrence of long-distance human-mediated movement of *P. cinnamomi* both within and between commodities (Table 1). Within-commodity long-distance movement is evidenced by the identical genotype MG13 found both on Chinese and Californian *Camellia*. Between-commodity movement is indicated by an identical genotype found on California avocado and Taiwanese pineapple (MG20), by genotype MG22 found on South African grapes and Australian eucalyptus, and by genotype MG20 being necessarily derived from genotype MG13, the latter isolated from Chinese and California *Camellia* (Figure 3). Transmission from commodities to wild habitats is also suggested by our results: genotype MG10, found on Chinese and Californian *Rhododendron*, was also found on wild manzanitas in the foothills of the Sierra Nevada, California, identifying ornamental rhododendrons as one of the likely sources for this wild infestation.

STRUCTURE Group 2 (both WW2 in the worldwide/California analysis and MEX2 in the Mexican analysis; see below) appears to be derived directly from a PNG genotype in Group WW1 (Figure 3), and is "contained" between genotypes belonging to STRUCTURE group MEX1 in the Mexican analysis (Figure 4), meaning that genotypes at both ends of Group 2 cluster are related to MEX1 genotypes. In the worldwide/California analysis, this group is the only one to comprise a single MG (Figure 3, Table 1), and contains a broad geographic and host distribution. This group/MG provides evidence of long-distance movement between California and Central Mexico, having been isolated from a severe disease outbreak on oaks in the Mexican state of Colima and on Christmas trees in both countries (true firs and Douglas firs; see results of the Mexican analysis below), and on two wild manzanita species (*Arctostaphylos viscida* and the endangered *A. myrtifolia*) in California. Infested Christmas tree farms and manzanita woodlands were both located in the Sierra Nevada foothills; this geographic proximity suggests a link between wild and agricultural outbreaks. The discovery that this genotype was associated with the a large outbreak on oaks in Colima, Mexico (Tainter et al. 2000) and to the recent Manzanita outbreak in California discussed in this paper, prompted us to investigate whether isolates belonging to Group 2 may have arrived to California from Mexico. To answer this question, we performed a second genetic analysis on a large collection of *P. cinnamomi* isolates from Mexico (see below).

Group WW3 appeared to be closely related to New World A2 genotypes belonging to Group WW1 rather than to the Papuan genotypes that represent the presumed native range of *P.*

cinnamomi (Old et al. 1984; Arentz and Simpson 1986; Arentz 2017). This group included 8 genotypes (Figure 3, Table 1); as all isolates are from North America, we refer to WW3 as the North American Group. Three isolates belonging to genotypes MG04 and MG18 came from the California Christmas tree industry: two from two different true fir species and one from Monterey pine. Genotype MG04 was isolated both from a true fir species in a Christmas tree farm in the Sierra Nevada foothills (California) and from wild manzanitas growing in the same foothills, thus indicating a possible agricultural source for this wild infestation. Multiple Group WW3 isolates belonging to genotypes MG15 and MG18 were found in avocado orchards, indicating a close link to this industry. The discovery of MG18 in avocado orchards in California and Florida suggests a role of this industry in the long-distance movement of *P. cinnamomi*. MG18 was also isolated 24 times from a variety of wildland hosts including oaks in Southern California, manzanitas in the Sierra Nevada foothills, and Pacific madrones in the greater San Francisco Bay Area, as well as in additional agricultural contexts including blueberries from Florida, white fir Christmas trees in the Sierra Nevada Foothills, and Monterey pine Christmas trees in the San Francisco Bay Area. The presence of this same genotype on multiple hosts and locations suggests it is an aggressive, invasive clonal genotype. Its presence in Christmas trees and wild manzanitas in the Sierra Nevada foothills of California, in avocados and wild oaks in San Diego County (California), and finally in Christmas trees and wild Pacific madrones in the San Francisco Bay Area is indicative of the potential movement of this pathogen from specific agricultural settings into natural habitats, facilitating expansion in host range.

Analysis of Mexican isolates shows occurrence of unique genotypes, links to worldwide and California isolates, and evidence for inter-host transmission

Mexican samples were processed three years after the processing of worldwide/California samples, and using different batches of reagents and different equipment. Results from the 12 reference isolates processed in both analyses indicated allelic profiles were similar between analyses, but not identical. This was in contrast with results of the first worldwide/California analysis, in which all samples were processed twice with identical outcomes. Hence, we opted to perform all analyses on both sets separately, using the positioning of the 12 reference isolates to draw comparisons between the two analyses (Tables 2 and 5).

Based on a total of 41 different alleles, 64 Mexican isolates and the 12 reference isolates from the worldwide/California analysis were assigned to 52 MGs (Tables 2 and 5). The optimal K value

for the Mexico analysis was determined using the Δ*K* method to be K=2 (Figure S1). A K=3 analysis of the Mexican samples resulted in all individuals appearing as admixed, suggesting overestimation of the true number of populations; thus, the optimal value of K=2 was used here in contrast to the K=3 value used in the worldwide analysis. STRUCTURE analysis of these isolates identified two groups (Figure 2B): Mexican Group MEX1 included 11 Mexican genotypes, all consisting of singletons (i.e., 1 isolate per genotype), as well as all reference A1 and Papuan isolates belonging to the Worldwide/California STRUCTURE Group WW1, two California A2 isolates belonging to STRUCTURE Group WW3, and the only two A2 isolates from California belonging to SRUCTURE group WW1. However, when STRUCTURE group assignment was overlaid on the Mexican MSN (Figure 4), it became apparent that STRUCTURE group MEX1 included three subgroups 1a, 1b, and 1c; these subgroups were not contiguous on the MSN, and match well with worldwide/California STRUCTURE Groups WW1 (MEX1b and 1c) and WW3 (MEX1a). Subgroup MEX1a includes 7 genotypes: the two genotypes connecting Mexican subgroup 1a with the rest of the network are from avocados cultivated in Michoacán, while the remaining 5 genotypes all came from wild oaks in the Mexican state of Jalisco. Subgroup MEX1b includes a single isolate with mating type A2 from a wild oak in the state of Guerrero; this isolate appears to be a close relative of MG06 from avocado in Madagascar and MG07 from eucalyptus in Australia, both carrying mating type A1 and belonging to the worldwide/California STRUCTURE group WW1. Subgroup MEX1c includes Papuan A1 isolates and Californian A2 isolates belonging to STRUCTURE Group WW1. The vast majority of Mexican isolates belong to STRUCTURE group MEX2, matching the worldwide/California STRUCTURE group WW2 and including 28 different genotypes. Six genotypes included multiple isolates; for four of these genotypes, isolates came from different locations, suggesting these are clonal invasive genotypes that have been spread by humans. Mexican MG38 matches perfectly California MG08. These genotypes were both isolated from multiple hosts, some wild and some cultivated; however, one host – Douglas fir in Christmas tree farms – was common to both, providing evidence of a likely international pathway of movement for this pathogen.

A comparison of population genetic indices between STRUCTURE groups WW3 (mostly including isolates from California) and MEX1a, and between WW2 (again with isolates exclusively from California) and MEX2 shows two inverse trends (Table 4). California's WW2 has minimal genotypic diversity (1 genotype) and low genic diversity, while MEX2 has extremely high genotypic diversity and higher genic diversity, suggesting Mexico may be a primary or secondary center of origin for this group that may have arrived in California only

recently. In contrast, Group WW3 shows higher genic diversity in California than in Mexico; thus, its presence may be older in California. The comparable level of genotypic diversity observed between the two populations may be due to the fact that evenness is reduced in California due to the presence of clonally reproducing genotypes present in different locations.

Several Mexican genotypes (MG21, MG38, MG39) were present in agricultural commodities (e.g. avocados or Douglas-firs grown as Christmas trees) and in natural habitats (e.g. oaks). The same was true for the following two pairs of genotypes, with one MG necessarily deriving from the other in each of the two pairs, based on their location on the MSN: MG26 (oak)-MG23 (avocado), and MG48 (oak)-MG22 (avocado) (Figure 4, Table 2). No Mexican study site included both wild and cultivated hosts, so it was not possible to provide direct evidence in favor of contagion between the two types of hosts.

***Phytophthora cinnamomi* outbreaks in California wild populations exhibit links to agricultural commodities**

In addition to the wildland outbreaks sampled as part of the Mexican study described above, our sampling scheme included intensive sampling from three wildland outbreaks in California: oak woodland mortality in San Diego County, Manzanita die-back in the Sierra Nevada foothills, and Pacific madrone mortality in the greater San Francisco Bay Area. Each of these three cases shows clear genetic links to an agricultural outbreak located in close proximity. The outbreak on wild oaks in San Diego County was associated with 3 genotypes (MG01, MG16. MG18), all from STRUCTURE Group WW3. MG18 was found both on avocados and oaks growing in the same general area. Additionally, the MSN shows oak genotype MG16 from San Diego County as a terminal genotype (i.e. at the outer edge of the MSN) necessarily derived from MG15 from avocado, also in San Diego County (Figure 3). The outbreak on Manzanitas in the Sierra Nevada Foothills (Amador and Eldorado Counties) was associated with at least 6 genotypes: MG10 from STRUCTURE group WW1, MG08 from group WW2, and MG02, MG04, MG17 and MG18 from group WW3. MG10 has been previously isolated from an ornamental *Rhododendron*; MG08 has been previously isolated from a true fir and from a Douglas-fir in a Christmas tree farm in Eldorado County, MG04 and MG18 have also been previously isolated from true firs in a Christmas tree farm in Eldorado County. The outbreak on wild Pacific madrones in the San Francisco Bay Area (California) was associated with the single genotype MG18 belonging to

group WW3, which, by including multiple isolates from different hosts and sites, appears to be an emerging invasive strain linked to the avocado and Christmas tree industries in the same region.

***Phytophthora cinnamomi* strains differ in reproductive modes**

Linkage disequilibrium, as indicated by significant values of the index of association I_A (Brown et al. 1980; Smith et al. 1993; Agapow and Burt 2001) ($P<0.0001$), was characteristic of STRUCTURE Group WW1 in the worldwide/California datasets (Table 4). It is noteworthy that this cluster is predominantly characterized by mating type A1 genotypes. STRUCTURE Group WW3 and STRUCTURE Group MEX2, exclusively characterized by the A2 mating type, showed no Linkage Disequilibrium in the clone corrected sets, a result suggestive of sexual reproduction. In both analyses, several genotypes had admixed haplotypes (Figure 2). These results cumulatively suggest that sexual reproduction, although rare, may not be common where mating type A1 is predominant, but may occur where mating type A2 occurs.

Comparisons of population genetic indices among STRUCTURE groups suggests three broad categories (Table 4): 1)- High genotypic diversity, high genotypic evenness (i.e. reduced presence of clonal genotypes) and high gene diversity not necessarily paired with sexual reproduction, but maybe associated with older and larger populations, as occurs in STRUCTURE groups WW1 and MEX1; 2)- Reduced genotypic and genic diversity, low genotypic evenness with significant presence of clonally identical genotypes in distant locations, possibly sexually reproducing but younger in age, as occurs in STRUCTURE group WW3 ; 3)- High genotypic diversity, low genic diversity, intermediate genotypic evenness with some clonally reproducing genotypes but with possible sexual reproduction, young and experiencing large population growth, as shown in STRUCTURE Group MEX2. We do not include WW2 in this summary because represented by a single genotype.

Discussion

Human activities play a pivotal role in the introduction of exotic organisms both in novel regions and in previously uninfested natural ecosystems (Wingfield et al. 2001; Garbelotto 2008; Dehnen-Schmutz et al. 2010; Garbelotto and Pautasso 2012; Croucher et al. 2013; Jung et al. 2016; Garbelotto et al. 2018), and specific introduction histories can be reconstructed using the powerful tools provided by population genetics and genetic epidemiological studies (Wingfield et al. 2001; Mascheretti et al. 2008; Garbelotto 2008; Garbelotto and Gonthier 2013; Croucher et al.

2013). Accurate knowledge of pathways of spread of plant pathogens is pivotal to prevent further introductions.

Like several other *Phytophthora* species, *P. cinnamomi* is a pathogen of global concern (Hayden et al. 2013; Jung et al. 2016), and has recently been reported as the cause of significant and novel disease outbreaks both in natural ecosystems and in a variety of cultivated commodities (Hardham 2005; Rizzo and Fichtner 2009; Quynh et al. 2017; Jung et al. 2016; Jung et al. 2017). Genetic epidemiological studies in this organism are facilitated by knowledge of the putative native range of the pathogen (Old et al. 1984; Arentz and Simpson 1986; Arentz 2017) and by the existence of genetic markers previously developed for local population studies (Linde et al. 1997, 1999; Dobrowolski et al. 1998, 2002, 2003; Pagliaccia et al. 2013). The present study extends this previous knowledge by examining links within and between agricultural and forest disease outbreaks on a global scale and in detail for two regions of North America. The value of the present study is in genotyping recent intensively-collected samples from natural ecosystems and agricultural settings in California and Mexico together with historical collections (some dating back to 1966), incorporating wildlands and agricultural settings from a wide geographic range, and including areas such as Papua New Guinea and Taiwan presumed to be within the native range of *P. cinnamomi*.

While the use of four SSR markers provides somewhat limited discrimination potential, we provide evidence that the probability of a given multilocus genotype occurring by chance alone based on underlying allele frequencies of the four SSR markers used in this study is sufficiently low. Our calculations do not take into account rapid convergence events associated with loss of heterozygosity, gene duplication or trisomy and other genetic events, all reported to occur in *Phytophthora* species (Dobrowolski 2002; Kasuga et al. 2016). However, the conclusions of this study are based on multiple examples provided by isolates obtained in different times and from different world regions, enhancing the robustness of these conclusions. Finally, given the discriminating power of the SSRs employed, we show that our sampling was scaled adequately, and genotypic diversity was saturated. We should also clarify that differently from other authors who base their conclusions on the presence and distribution of clonal lineages (Dobrowolski et al. 2003), we base all of our inferences almost exclusively on the presence of identical genotypes in different sites and on different commodities. Occasionally, inferences were made on the presence of two genotypes that are closest relatives and positioned in such a way on the edges of the MSNs, that the distal one at the very end of a branch in the MSN has to be derived from the other.

Origin and spread of *P. cinnamomi* through agriculture

Given that it is the only group: a)- including isolates from the putative native range of the pathogen, b)- including both A1 and A2 mating types, c)- displaying the highest level of genic diversity, and, d)- positioned in the center of the worldwide/California MSN, Group WW1 is strongly supported as ancestral within the context of the sample analyzed in this study. It is interesting to note that all Papuan A1 isolates are contiguous in the MSN, and, furthermore, that all A1 isolates are also contiguous. This distribution pattern supports the hypothesis that *P. cinnamomi* ancestrally was characterized by A1 mating type populations that evolved in a broad region stretching from Papua New Guinea to East Asia, as suggested by Arentz (2017). The appearance of the A2 mating type (whether by mating type switch or by a different unknown mechanism) may have occurred later and at least twice independently, because A2 genotypes are positioned in two distinct portions of the MSN, at two different edges of STRUCTURE Group WW1. Sexual reproduction seems to be present only in groups generated after the emergence of the A2 mating type. Group WW1 genotypes from wild populations within the putative native range of the pathogen are closely related to genotypes isolated from many widespread agricultural commodities, highlighting the likely role of agriculture in the initial diffusion of this pathogen from its native range to a global scale (Hayden et al. 2013). The presence of identical genotypes within a commodity even in distant regions of the world provides further evidence of long-distance dispersal through the plant trade; additionally, the presence of identical genotypes between commodities indicates that pathogen transfer between commodities has also occurred.

Agriculture as a source of *P. cinnamomi* spread to Californian and Mexican wildlands

Several lines of evidence suggest that disease outbreaks in California and Mexico forests originated from agricultural sources. First, most genotypes present in the wild were also detected in agricultural commodities. In the case of wildland infestations in California, not only did we identify the same genotype in commodities and in the wild, but, additionally, both were identified in the same geographical region, providing even stronger support for a commodity source of wildland infestations. Reports from agricultural settings always preceded reports in the wild, a strong indication that pathogen movement occurred from agricultural into wild settings, and not vice versa. This order of events is further supported by the observation that California wildland outbreaks are rarely associated with the presence of genotypes from the presumed ancestral STRUCTURE Group WW1, but are predominantly associated with genotypes in the more derived Groups WW2 and WW3.

Genotype specificity of invasions: evidence for multiple introductions and implications for disease management

The genetic patterns shown in this study – particularly the association of specific pathogen genotypes with specific hosts and locations – suggest that individual specific *P. cinnamomi* genotypes are historically shared within and sometimes among commodities, and that individual wildland outbreaks have different histories and are caused by different strains of the pathogen. For example, while commodities such as grapes, ornamental plants, and avocados are associated with Group WW1 genotypes, the Christmas tree industry in California is not, suggesting that it may have acquired the infection later. This result is in agreement with the fact that outbreaks of *P. cinnamomi* in California Christmas tree farms were first reported as recently as the early 2000s (Mckeever and Chastagner 2016).

The presence of identical genotypes, isolated multiple times from different hosts and distant locations (e.g. MG08 and MG18 in the worldwide/California analysis), suggests the recent emergence of particularly invasive microbial genotypes in Groups WW2 and WW3 that are currently being actively spread both within commodities and from commodities into the wild. Because not all genotypes are everywhere, and because these novel emergent genotypes appear to be particularly invasive, it is important to determine which specific genotypes should not be introduced or further spread in any given region. For instance, Group WW2 genotypes are common in Mexico, but absent in our sample from most of California except for Christmas tree farms and manzanita stands in two counties in the foothills of the Sierra Nevada mountains. Conversely, the emergent invasive genotype MG18 is not present in Mexico but it is dominant in California. Likewise, its spread into Mexico from California should be prevented by well-designed regulations. An additional concern is that release in the wild of A1 and A2 genotypes could lead to sexual reproduction, thus accelerating the adaptive potential of this already invasive and aggressive pathogen.

Summary

Figure 5 is a schematic reconstruction of the recent history and movement of *P. cinnamomi* based on our results. In brief, from a native asexual population with mating type A1, individual genotypes became founders of populations associated with different commodities. These commodities were responsible for the worldwide movement of genotypes associated with them, as documented by the fact that identical or very similar genotypes were found in the same

commodity but in distant locations of the world (Oudemans and Coffey 1991; Linde et al. 1999; Pagliaccia et al. 2013). In a relative early stage of the modern history of *P. cinnamomi*, cross-contamination among commodities occurred as evidenced by the presence of identical genotypes in different agricultural commodities. Without excluding commodities that were not sampled in this study, four commodities have clearly played an important role in the long-distance movement of *P. cinnamomi*: avocado, ornamental plants, grapes, and, more recently, Christmas tree farms. Mexico appears to be an early recipient of this pathogen compared to California, especially of genotypes of Group 2, which is more genotypically diversified and has a much broader distribution in Mexico than in California. These same commodities may have recently been responsible for the introduction of *P. cinnamomi* in wildland settings. Our California and Mexican analyses identified some likely sources for wild outbreaks. Genotypes from avocados appear as the likely source of outbreaks responsible for the death of large numbers of oaks in several Mexican states (Tainter et al. 2000) and for infecting oaks in Southern California (Garbelotto et al. 2006). The bulk of the manzanita outbreak in California is caused by a single genotype in Group 2 likely to have arrived in California from Mexico through the trade of Douglas-firs produced as Christmas trees. Direction of movement here is presumed based on the much greater abundance and diversity of Group 2 genotypes in Mexico. The pathway of movement (i.e. through infected Douglas fir Christmas trees) instead is inferred based on a conversation with the owner of the infested Christmas tree farm in Mexico, who had a history of plant trading with California Christmas tree facilities (Garbelotto, personal communication). While plausible, this hypothesis needs to be confirmed by a more widespread sampling of California infestations. One of the manzanita species affected, *Arctostaphylos myrtifolia*, is on the list of endangered US plants (USDA 2017) and likely to become extinct due to the devastating effects of *P. cinnamomi* (Swiecki et al. 2003). A disease outbreak on highly prized Pacific madrones in the San Francisco Greater Bay Area (Rizzo and Fichtner 2009) is caused by a single genotype in Group WW3 present in several commodities that is clearly invasive and recently emerged. Interestingly, even if Group WW3 was present both in California and Mexico (where it was defined as Group MEX1a), the invasive genotype in question was absent in Mexico, suggesting that its emergence is recent and occurred only in California.

Phytophthora cinnamomi has long been known to affect agricultural crops and wild populations of plants (Zentmeyer 1976; Garbelotto et al. 2006), and consequently it is currently not regulated in the US. However, this study uncovered the presence of emergent invasive genotypes strongly associated with three newly reported outbreaks in California oaks, manzanitas, and Pacific

madrones (Swiecki et al. 2003; Garbelotto et al. 2006; Rizzo and Fichtner 2009). The discovery of emergent invasive genotypes warrants further research to determine whether significant phenotypic variability exists within *P. cinnamomi* to require a different regulatory approach for different strains. Given recent results showing that invasive populations of pathogens can rapidly evolve and become strikingly different from their source populations (Garbelotto et al. 2015), the introduction of multiple genotypes from source populations may result in different outbreaks of a disease. Thus, the need to prevent multiple introductions of the same pathogen may warrant a change in the regulatory world and in international trading practices.

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Table 1. Information on the 75 isolates used in the California and worldwide study.

Isolate Nº (alternate code)	Collector[1], date	Host	Origin	US County or Mexican State	Mating type	W/C[2]	MG[5]	STRUCTURE group
mc03	MG, 2001	*Quercus agrifolia*	CA, USA	San Diego	A2	W	MG01	WW3
mc07	MG, 2001	*Quercus* sp.	CA, USA	San Diego	A2	W	MG01	WW3
mc21 (3a2)	TS, 2003	*Arctostaphylos myrtifolia*	CA, USA	Amador	A2	W	MG02	WW3
mc12	MG, 2003	*Abies nordmanniana*	CA, USA	El Dorado	A2	C	MG03	Admixed
mc16	MG, 2003	*Abies* sp.	CA, USA	-	A2	C	MG04	WW3
mc19 (1b2)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG04	WW3
mc29 (7b1)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG04	WW3
mc31 (15 0)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG04	WW3
mc35 (20a1)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG04	WW3
mc17	MG, 2003	Soil	CA, USA	Alameda	A2	W	MG05	WW3
P-2183 (PNG 8062)	DS, 1972	Soil	PNG[1]		A1	W	MG06	WW1
P-3658 (CSIRO A121)	FA, 1988	*Castanopsis* sp.	PNG		A1	W	MG07	WW1
mc04	FT, 2000	*Quercus* sp.	Mexico	Colima	A2	W	MG08	WW2
mc09	MG, 2003	*Arctostaphylos sp.*	CA, USA	Amador	A2	W	MG08	WW2
mc14	MG, 2003	*Pseudotsuga menziesii*	CA, USA	El Dorado	A2	C	MG08	WW2
mc15	MG, 2003	*Abies spp*.	CA, USA	El Dorado	A2	C	MG08	WW2
mc18 (1c0)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG08	WW2
mc20 (2a1)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG08	WW2
mc23 (5b1)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG08	WW2
mc24 (10a2)	TS, 2003	*Arctostaphylos viscida*	CA, USA	Amador	A2	W	MG08	WW2
mc25 (11b2)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG08	WW2
mc26 (12a2)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG08	WW2
mc27 (13a2)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG08	WW2
mc30 (9a1)	TS, 2003	*A. viscida*	CA, USA	Amador	A2	W	MG08	WW2
mc34 (19a5)	TS, 2003	*A.myrtifolia*	CA, USA	Amador	A2	W	MG08	WW2
mc37 (24 1)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG08	WW2
mc39 (26 25)	TS, 2003	*A.myrtifolia*	CA, USA	Amador	A2	W	MG08	WW2
P-3656 (CSIRO A118)	FA, 1988	*Nothofagus* sp.	PNG		A1	W	MG09	WW1
mc33 (17a1)	TS, 2003	*A. viscida*	CA, USA	Amador	A2	W	MG10	WW1
mc38 (25 2)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG10	WW1
P-2301 (ATCC 46686)	GAZ, 1976	*Rhododendron* sp.	CA, USA		A2	C	MG10	WW1
P-3232	PT, 1986	*Rhododendron* sp.	China		A2	C	MG11	WW1
P-3233	PT, 1986	*Camellia japonica*	China		A1	C	MG12	WW1
P-2096 (ATCC 46667)	WT, 1968	*C. japonica*	CA, USA		A1	C	MG13	WW1
P-2100 (ATCC 46668)	GAZ, 1969	*C. japonica*	CA, USA		A1	C	MG13	WW1

P-2170	GAZ, 1972	*C. japonica*	CA, USA		A1	C	MG13	WW1
P-3237	PT, 1986	*C. japonica*	China		A1	C	MG13	WW1
P-6493 (Shen B14)	PT, 1989	*Rododendron* sp.	China		-	C	MG14	WW1
mc06	LM, 2001	*Persea americana*	CA, USA	San Diego	A2	C	MG15	WW3
mc08	MG, 2001	*Q. agrifolia*	CA, USA	San Diego	A2	W	MG16	WW3
mc10	MG, 2001	*Q. agrifolia*	CA, USA	San Diego	A2	W	MG16	WW3
mc22 (4b2)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG17	WW3
mc32 (16 0)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG17	WW3
A4	TS, 2005	*Arbutus menziesii*	CA, USA	San Mateo	A2	W	MG18	WW3
D2-2	TS, 2005	*A. menziesii*	CA, USA	San Mateo	A2	W	MG18	WW3
D8-3A	TS, 2005	*A. menziesii*	CA, USA	San Mateo	A2	W	MG18	WW3
D904	TS, 2005	*A. menziesii*	CA, USA	San Mateo	A2	W	MG18	WW3
mc01	MG, 2001	*Quercus agrifolia*	CA, USA	San Diego	A2	W	MG18	WW3
mc02	MG, 2001	*Q. agrifolia*	CA, USA	San Diego	A2	W	MG18	WW3
mc05	n/a	*Vaccinium corymbosum*	FL, USA		A2	C	MG18	WW3
mc11	MG, 2003	*Abies concolor*	CA, USA	El Dorado	A2	C	MG18	WW3
mc28 (6b1)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG18	WW3
mc36 (22a2)	TS, 2003	*A. myrtifolia*	CA, USA	Amador	A2	W	MG18	WW3
P-2288 (ATCC 46685)	GAZ, 1975	*Pinus radiata*	CA, USA	Santa Cruz	A2	C	MG18	WW3
P-2428	SC, 1985	*P. americana*	CA, USA		A2	C	MG18	WW3
P-2444	TD, 1985	*P. americana*	CA, USA		A2	C	MG18	WW3
mc40 (29a2)	TS, 2003	*A. viscida*	CA, USA	Amador	A2	W	MG18	WW3
P-543	TS, 2005	Soil[4]	CA, USA	Santa Cruz	A2	W	MG18	WW3
P-544	TS, 2005	Soil[4]	CA, USA	San Rafael	A2	W	MG18	WW3
P-545	TS, 2005	Soil[4]	CA, USA	San Rafael	A2	W	MG18	WW3
P-546	TS, 2005	Soil[4]	CA, USA	Sonoma	A2	W	MG18	WW3
P-547	TS, 2005	Soil[4]	CA, USA	Sonoma	A2	W	MG18	WW3
P-549	TS, 2005	Soil[4]	CA, USA	Sonoma	A2	W	MG18	WW3
P-6490 (Collier 26)	RP, 1989	*P. americana*	FL, USA		A2	C	MG18	WW3
PC004	TS, 2005	*A. menziesii*	CA, USA	Marin	A2	W	MG18	WW3
P-541	TS, 2005	*A. menziesii*	CA, USA	Santa Cruz	A2	W	MG18	WW3
P-542	TS, 2005	Soil[4]	CA, USA	Santa Cruz	A2	W	MG18	WW3
P-3662 (CSIRO A126)	FA, 1988	*Castanopsis* sp.	PNG[1]		A1	W	MG19	WW1
P-2138 (ATCC 38581)	JR/MJ, 1970	*P. americana*	CA, USA		A1	C	MG20	WW1
P-6379 (Pcip1-2)	PJA, 1989	*Ananas comosus*	Taiwan		A1	W	MG20	WW1
P-2121 (ATCC 46672)	JB, 1966	*P. americana*	Madagascar		A1	C	MG21	WW1
P-2159 (ATCC 46678)	HB,1971	*Vitis vinifera*	South Africa		A1	C	MG22	WW1
P-2160 (ATCC 46679)	HB,1971	*V. vinifera*	South Africa		A1	C	MG22	WW1
P-3664 (CSIRO A138)	n/a	*Eucalyptus* sp.	Australia		A1	W	MG22	WW1
P-2021	GAZ, 1966	*C. japonica*	CA, USA		A1	C	MG23	WW1

(ATCC46660)

[1]Collectors: MG= M. Garbelotto, TS= T. Swiecki, DS= D. Shaw, FA= F. Arentz, FT= F. Tainter, GAZ= G.A. Zentmyer, PT= P. Tsao, WT= W. Thorne, LM= L. Marais, SC= S. Campbell, TD= T. Dolan, RP= R. Ploetz, JR= J. Reid, MJ= M. Jackson, PJA= P-J. Ann, JB= J. Brun, HB= H. Brodrick

[2] PNG = Papua New Guinea.

[3]Collected in the wild (W) or from an agricultural commodity (C).

[4] Soil collected near symptomatic California bay laurels (*Umbellularia californica*) or symptomatic Pacific madrones (*Arbutus meziesii*)

[5]MG determined by allele frequencies in Table 3.

Table 2. The 64 Mexican isolates and 12 worldwide reference isolates included in the second study. Precise location within each Mexican State is provided in the "origin" column. Isolates were collected by A. Almaraz Sánchez, D. Alvarado Rosales and S. Ochoa.

Isolate Nº	Host	Origin	Mating type	W/C[1]	MXMG /WWMG[2]	STRUCTURE group[3]
Me64	*Persea americana*	Michoacán (Me.), Uruapan	A2	C	MG01	MEX1
P2183	*Soil*	Papua New Guinea	A1	W	MG02/ MG06	MEX1/ WW3
Me36	*P. americana*	Michoacán (Me.), Jicalán	A2	C	MG03	MEX1
P3662	*Castanopsis* sp.	Papua New Guinea	A1	W	MG04/ MG19	MEX1/ WW1
Me37	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG05	MEX2
P2121	*Persea americana*	Madagascar	A1	C	MG06/ MG21	MEX1/ WW1
P3664	*Eucalyptus* sp.	Australia	A1	W	MG07/ MG22	MEX1/ WW1
Me29	*P. americana*	Michoacán (Me.), Peribán	A2	C	MG08	MEX1
Me41	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG09	MEX2
Me31	*P. americana*	Michoacán (Me.), Tacambaro	A2	C	MG10	Admixed
Me35	*P. americana*	Michoacán (Me.), Tijerias	A2	C	MG11	MEX1
Me14	*Quercus peduncularis*	Jalisco (Me.), El Mango	A2	W	MG12	MEX1
Me13	*Q. peduncularis*	Jalisco (Me.), El Mango	A2	W	MG13	MEX1
Me62	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG14	MEX2
Me33	*P. americana*	Michoacán (Me.), Tacambaro	A2	C	MG15	MEX2
Me34	*P. americana*	Michoacán (Me.), Tijerias	A2	C	MG15	MEX2
Me44	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG16	MEX2
Me46	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG17	MEX2
Me9	*Q. peduncularis*	Jalisco (Me.), Sierra de Manantlán	A2	W	MG18	MEX2
Me15	*Quercus elliptica*	Guerrero (Me.), San Francisco	A2	W	MG19	MEX2
Me50	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG20	MEX2
Me57	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG20	MEX2
Me61	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG20	MEX2
Me2	*Quercus salicifolia*	Colima (Me.), Arrayanal	A2	W	MG21	MEX2
Me25	*Pseudotsuga menziesii*	Estado de México (Me.), Florencio	A2	C	MG21	MEX2
Me30	*P. americana*	Michoacán (Me.), Tacambaro	A2	C	MG21	MEX2
Me45	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG22	MEX2
Me59	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG23	MEX2
Me51	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG24	MEX2
Me63	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG25	MEX2
Me6	*Q. salicifolia*	Colima (Me.), Arrayanal	A2	W	MG26	MEX2
P2301	*Rhododendron* sp.	California, USA	A2	C	MG27/ MG10	MEX1/ WW1
Me20	*Q. elliptica*	Guerrero (Me.), El Charco	A2	W	MG28	MEX1
Me40	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG29	MEX2
Me7	*Q. salicifolia*	Colima (Me.), Arrayanal	A2	W	MG30	MEX2
Me53	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG31	MEX2

Mc08	*Quercus agrifolia*	San Diego Co., California, USA	A2	W	MG32/ MG16	MEX1/ WW3
Me10	*Q. peduncularis*	Jalisco (Me.), Sierra de Manantlán	A2	W	MG33	MEX2
Me16	*Q. elliptica*	Guerrero (Me.), San Francisco	A2	W	MG34	MEX2
Me60	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG35	MEX2
Me47	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG36	MEX2
Me48	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG36	MEX2
Me58	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG36	MEX2
Mc20	*Arctostaphylos myrtifolia*	Amador Co., California, USA	A2	W	MG37/ MG08	MEX2/ WW2
Mc39	*A.myrtifolia*	Amador Co., California, USA	A2	W	MG38/ MG08	MEX2/ WW2
Me19	*Q. elliptica*	Guerrero (Me.), Magueyitos	A2	W	MG38	MEX2
Me22	*P. menziesii*	Estado de México (Me.), Mesa Rica	A2	C	MG38	MEX2
Me27	*P. menziesii*	Estado de México (Me.), Florencio	A2	C	MG38	MEX2
Me3	*Q. salicifolia*	Colima (Me.), Arrayanal	A2	W	MG38	MEX2
Me4	*Q. salicifolia*	Colima (Me.), Arrayanal	A2	W	MG38	MEX2
Me42	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG38	MEX2
Me5	*Q. salicifolia*	Colima (Me.), Arrayanal	A2	W	MG38	MEX2
Me17	*Q. elliptica*	Guerrero (Me.), Xalpatláhuac	A2	W	MG39	MEX2
Me18	*Q. elliptica*	Guerrero (Me.), Xalpatláhuac	A2	W	MG39	MEX2
Me21	*P. menziesii*	Estado de México (Me.), Mesa Rica	A2	C	MG39	MEX2
Me24	*P. menziesii*	Estado de México (Me.), Mesa Rica	A2	C	MG39	MEX2
Me28	*P. americana*	Michoacán (Me.), Cerritos	A2	C	MG39	MEX2
Me49	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG39	MEX2
Me52	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG39	MEX2
Me55	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG39	MEX2
Me54	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG40	MEX2
Me38	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG41	MEX2
Me12	*Q. peduncularis*	Jalisco (Me.), Sierra de Manantlán	A2	W	MG42	MEX1
Me8	*Q. peduncularis*	Jalisco (Me.), Sierra de Manantlán	A2	W	MG43	MEX1
Mc16	*Abies* sp.	California, USA	A2	C	MG44/ MG04	MEX1/ WW3
Me43	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG45	MEX2
Me56	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG46	MEX1
Me23	*P. menziesii*	Estado de México (Me.), Mesa Rica	A2	C	MG47	MEX2
Me26	*P. menziesii*	Estado de México (Me.), Florencio	A2	C	MG47	MEX2
Me39	*P. americana*	Michoacán (Me.), Uruapan	A2	C	MG47	MEX2
Me1	*Q. salicifolia*	Colima (Mexico), Arrayanal	A2	W	MG48	MEX2
Me32	*P. americana*	Michoacán (Me.), Ario de rosales	A2	C	MG49	MEX1
Me11	*Q. peduncularis*	Jalisco (Me.), Sierra de Manantlán	A2	W	MG50	MEX1
P2100	*Camellia japonica*	California, USA	A1	C	MG51/ MG13	MEX1/ WW1
P3237	*C. japonica*	China	A1	C	MG51/ MG13	MEX1/ WW1
Mc38	*A. myrtifolia*	Amador Co., California, USA	A2	W	MG52/ MG10	MEX1/ WW1

[1]W= Wild host, C= Host grown as a commodity.

[2]Mutilocus genotype in the Mexican analysis/ Multilocus genotype in the Worldwide analysis, based on alleles in Table 5.
[3]Structure group in the Mexican analysis/ Structure group in the Worldwide analysis. For admixed genotypes, the sample was assigned to a group if the genome corresponds mostly to that group. Isolates with equal or nearly equal admixture proportions between Structure groups are denoted as Admixed.

Table 3: The 23 multilocus genotypes (MGs) (expressed as number of repeats) produced by the 4 SSRs for the Californian and worldwide isolates.

MG	Origin/Hosts	n (Σ=75)	d39 (Σ alleles=11)	e16 (Σ alleles=6)	g10 (Σ alleles=9)	g13 (Σ alleles=18)
MG01	USA (CA)	2	19/19	14/15	10/29	16/25/28
MG02	USA (CA)	1	17/17	14/15	10/30	16/25/28
MG03	USA (CA)	1	17/17	14/15	10/29	12/18/28
MG04	USA (CA)	5	17/17	14/15	10/29	16/25/28
MG05	USA (CA)	1	17/17	14/15	10/31	16/25/28
MG06	Papua New Guinea	1	14/20	10/14	9/10/11	14/22
MG07	Papua New Guinea	1	13/13	10/14	9/10/11	14/23/28
MG08	USA (14, CA), Mexico (1)	15	12/34	11/11	8/9	12/18/28
MG09	Papua New Guinea	1	12/18	10/14	9/10/11	14/28
MG10	USA (CA)	3	12/12	14/15	10/31	13/16/27
MG11	China	1	12/12	14/14	10/31	13/16/27
MG12	China	1	12/12	14/14	8/10	23/null
MG13	USA (3, CA), China (1)	4	12/12	14/14	8/10	23/31
MG14	China	1	15/15	14/14	5/12	15/15
MG15	USA (CA)	1	11/17	13/15	10/29	16/25/28
MG16	USA (CA)	2	11/17	12/13	10/29	16/25/28
MG17	USA (CA)	2	11/17	14/15	10/30	16/25/28
MG18	USA (22, CA), (2, FL)	24	11/17	14/15	10/29	16/25/28
MG19	Papua New Guinea	1	11/15	10/13	9/10/11	14/26
MG20	Taiwan (1) USA (1, CA)	2	11/11	14/14	5/11	31/38
MG21	Madagascar	1	9/11	14/14	9/10	21/53
MG22	Australia (1), South Africa (2)	3	9/11	14/14	9/10	21/51
MG23	USA (CA)	1	9/11	14/14	8/10	23/31

Table 4. Diversity indices for worldwide/California (WW) and Mexican (MEX) STRUCTURE groups. See text for explanation of indices, STRUCTURE grouping, and references.

Pop	N[1]	MLG[2]	eMLG	SE	H	G	lambda	E.5	Hexp	Ia*	rbarD*
WW1,k=3	17	13	8.68	0.794	2.51	11.56	0.913	0.937	0.72	0.888*	0.2991*
WW2, k=3	4	1	1	0	0	1	0	NaN	0.468	NaN	NaN
WW1+2, k=3 (= WW1, k=2)	21	14	12.7	0.789	2.52	10.76	0.907	0.857	0.772	1.127*	0.3791*
WW3, k=3 (=WW2, k=2)	18	8	5.15	1.021	1.53	2.95	0.66	0.535	0.6	-0.106	-0.0554
Total WW (1+2+3)	**39**	**22**	**7.79**	**1.184**	**2.75**	**10.07**	**0.901**	**0.617**	**0.772**	**1.455**	**0.5143**
MEX1	12	12	12	0	2.48	12	0.917	1	0.793	0.9102*	0.32703*
MEX1a =WW3	6	6	6	0	1.79	6	0.833	1	0.511	-0.0333	-0.0346
MEX2= WW2	37	29	10.9	0.936	3.25	21.7	0.954	0.84	0.614	0.0258	0.00886
MEX Total (1+2)	**49**	**41**	**11.3**	**0.769**	**3.62**	**32**	**0.969**	**0.857**	**0.701**	**0.6743**	**0.22655**

[1] Number of isolates.
[2] Number of multilocus genotypes.

Table 5. The 52 multilocus genotypes (MGs) (expressed in number of repeats) produced by the 4 SSRs for the Mexican isolates and international reference specimens.

MG	Origin	n (Σ=76)	d39 (Σ alleles =12)	e16 (Σ alleles =8)	g10 (Σ alleles =8)	g13 (Σ alleles =13)
MG1	Michoacán	1	13/13	13/13	9/9	28/28
MG2	Papua New Guinea	1	13/21	12/12	10/11	23/28
MG3	Michoacán	1	9/21	10/15	9/9	16/28
MG4	Papua New Guinea	1	11/15	10/13	8/9	14/26
MG5	Michoacán	1	11/13	10/15	8/9	18/18
MG6	Madagascar	1	9/11	14/14	9/10	21/21
MG7	Australia	1	9/11	14/14	8/10	21/21
MG8	Michoacán	1	11/11	14/32	10/29	18/25
MG9	Michoacán	1	11/11	10/15	9/9	18/27
MG10	Michoacán	1	11/11	10/15	8/9	19/28
MG11	Michoacán	1	10/10	14/14	7/7	18/28
MG12	Jalisco	1	10/17	15/15	10/29	26/26
MG13	Jalisco	1	17/31	15/15	10/29	26/26
MG14	Michoacán	1	19/32	10/15	8/9	27/27
MG15	Michoacán	2	19/32	10/15	8/9	18/27
MG16	Michoacán	1	11/32	10/15	8/9	28/28
MG17	Michoacán	1	32/32	11/15	8/9	27/27
MG18	Jalisco	1	32/32	10/15	10/10	18/18
MG19	Guerrero	1	32/32	10/15	9/9	18/26
MG20	Michoacán	3	32/32	10/15	8/9	28/28
MG21	Colima (1), Estado de México (1), Michoacán (1)	3	32/32	10/15	8/9	18/27
MG22	Michoacán	1	11/34	10/15	8/9	18/18
MG23	Michoacán	1	34/34	10/15	8/9	28/28
MG24	Michoacán	1	34/34	10/15	8/9	18/27
MG25	Michoacán	1	34/34	10/15	8/9	18/18
MG26	Colima	1	34/34	10/15	8/8	18/27
MG27	USA (CA)	1	10/12	14/15	10/31	27/27
MG28	Guerrero	1	12/32	12/12	8/9	19/19
MG29	Michoacán	1	12/32	10/10	8/9	18/28
MG30	Colima	1	12/32	10/10	8/8	17/17
MG31	Michoacán	1	12/32	10/18	8/9	18/29
MG32	USA (CA)	1	12/32	15/17	10/29	25/28
MG33	Jalisco	1	12/32	10/15	9/30	18/27
MG34	Guerrero	1	12/32	10/15	9/9	18/18

MG35	Michoacán	1	12/32	10/15	8/9	28/28
MG36	Michoacán	3	12/32	10/15	8/9	27/27
MG37	USA (CA)	1	12/32	10/15	8/9	18/21
MG38	Colima (3), Guerrero (1), Estado de México (2), Michoacán (1), USA (1, CA)	8	12/32	10/15	8/9	18/28
MG39	Guerrero (2), Estado de México (2), Michoacán (4)	8	12/32	10/15	8/9	18/27
MG40	Michoacán	1	12/32	10/15	8/9	18/18
MG41	Michoacán	1	12/32	10/15	8/8	18/27
MG42	Jalisco	1	12/32	15/15	10/29	16/26
MG43	Jalisco	1	12/32	15/15	10/29	17/26
MG44	USA (CA)	1	12/32	15/15	10/29	25/27
MG45	Michoacán	1	12/34	10/10	8/9	18/28
MG46	Michoacán	1	12/34	10/15	9/9	16/16
MG47	Estado de México (2), Michoacán (1)	3	12/34	10/15	8/9	18/28
MG48	Colima	1	12/34	15/18	8/8	18/18
MG49	Michoacán	1	12/34	15/15	10/29	17/17
MG50	Jalisco	1	12/34	15/15	10/29	18/26
MG51	USA (1, CA), China (1)	2	12/12	11/14	8/10	23/31
MG52	USA (CA)	1	12/12	14/14	10/30	27/27

Fig. 1 Genotype accumulation curve for the worldwide/California study.

Fig. 2 STRUCTURE admixture barplots indicating group assignment for isolates in the worldwide/California (A) and Mexican (B) analyses. Datasets were partially clone corrected for the analysis; i.e., only one isolate per multi locus genotype (MG) per site was included. The worldwide/California analysis is shown for K= 3 (see text); when run using K= 2, isolates in Groups 1 and 2 merged into the same group. The Mexican analysis is shown for K=2.

Fig. 3 Minimum Spanning Network based on the matrix of pairwise Bruvo genetic distances, visualizing relatedness among multi locus genotypes (MGs) in the worldwide/California analysis.

Fig. 4 Minimum Spanning Network based on the matrix of pairwise Bruvo genetic distances, visualizing relatedness among multi locus genotypes (MGs) in the Mexican analysis.

Fig. 5 5a. Schematic reconstruction of the historical movement of *Phytophthora cinnamomi* based on the presence of identical or quasi-identical multi locus genotypes in different world regions. 5b Recent cross contamination between agricultural and wild hosts in California and Mexico, inferred by tracking the presence of identical multi locus genotypes in agricultural commodities and in native flora in the same region.

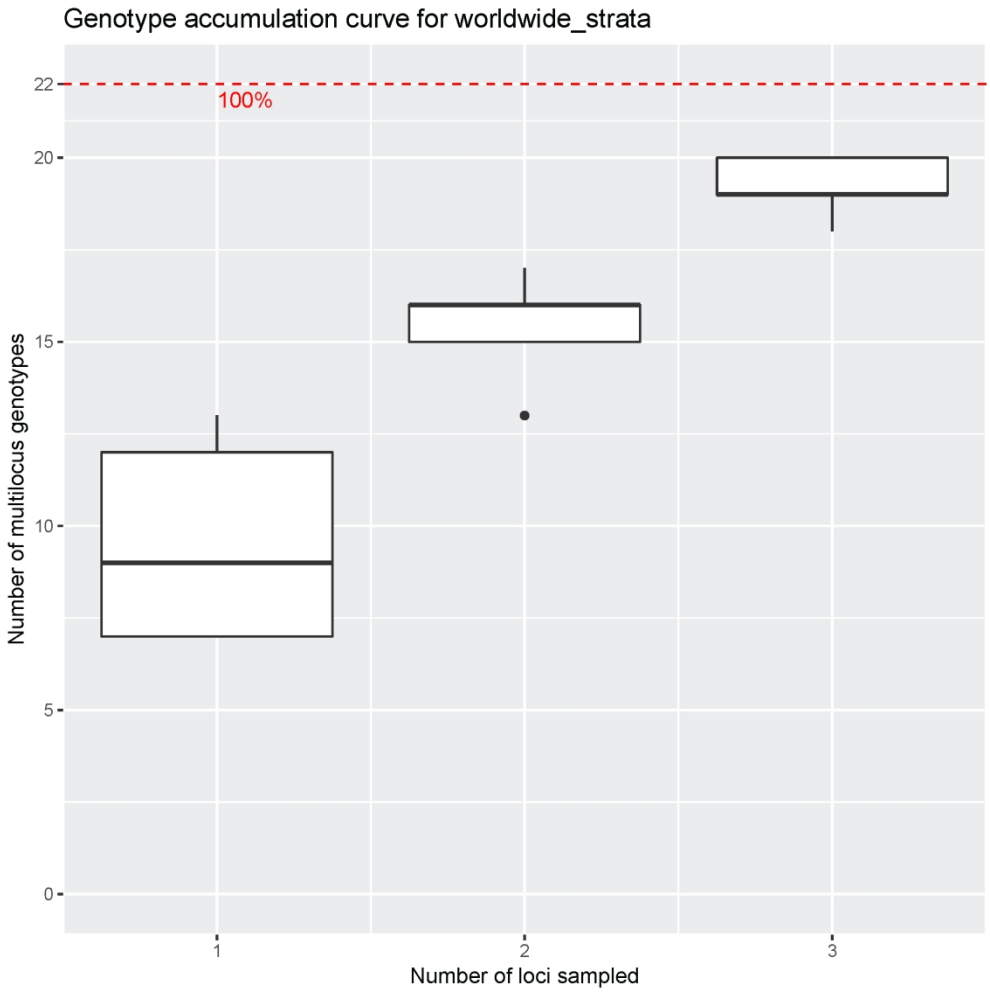

Fig. 1 Genotype accumulation curve for the worldwide/California study.

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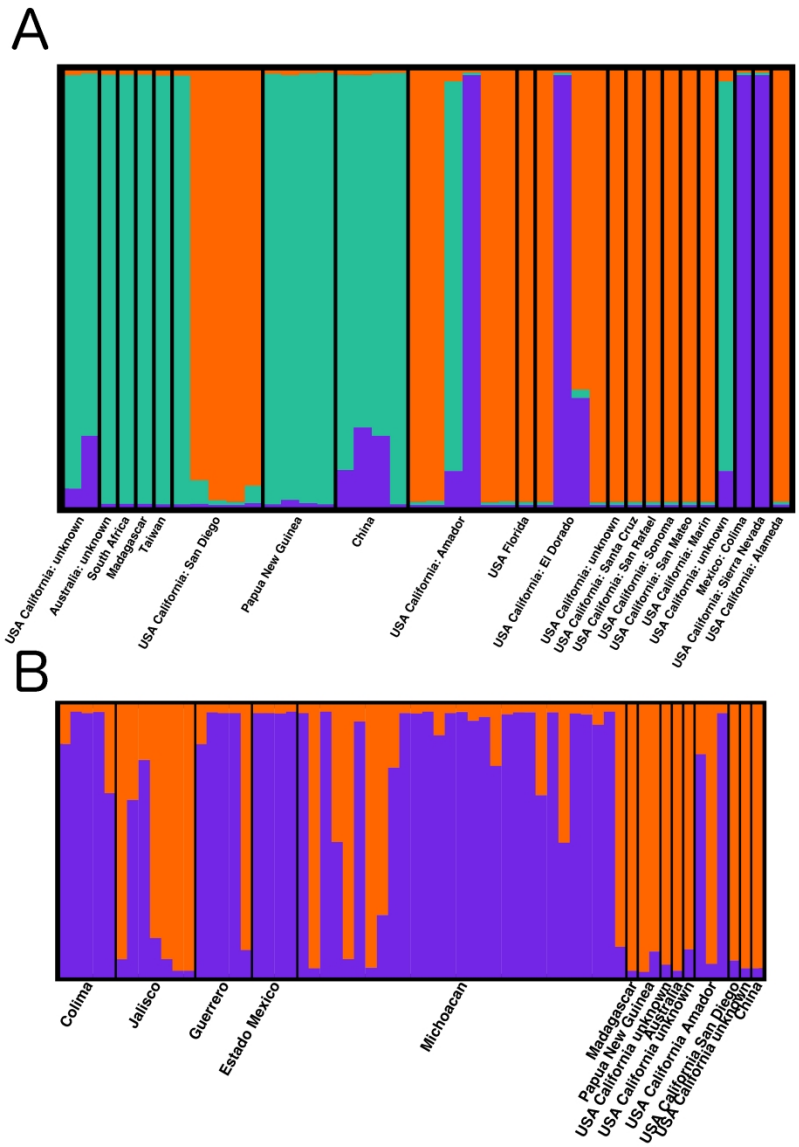


Fig. 2 STRUCTURE admixture barplots indicating group assignment for isolates in the worldwide/California (A) and Mexican (B) analyses. Datasets were partially clone corrected for the analysis; i.e., only one isolate per multi locus genotype (MG) per site was included. The worldwide/California analysis is shown for K= 3 (see text); when run using K= 2, isolates in Groups 1 and 2 merged into the same group. The Mexican analysis is shown for K=2.

215x279mm (300 x 300 DPI)

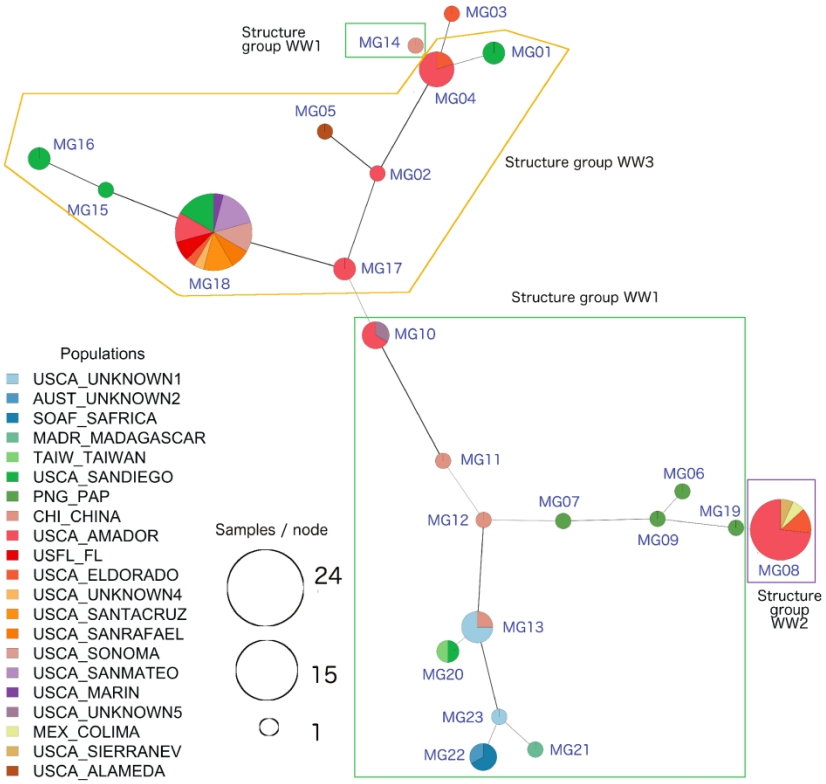


Fig. 3 Minimum Spanning Network based on the matrix of pairwise Bruvo genetic distances, visualizing relatedness among multi locus genotypes (MGs) in the worldwide/California analysis.

215x279mm (300 x 300 DPI)

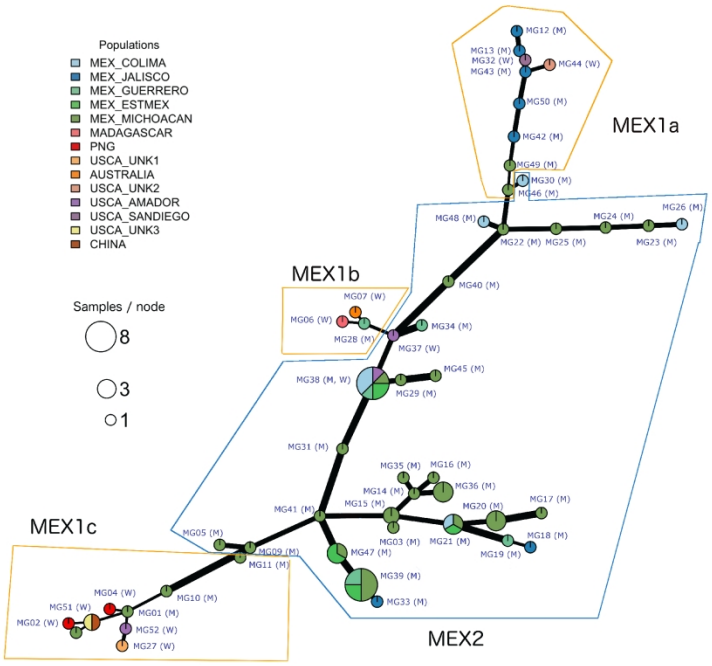


Fig. 4 Minimum Spanning Network based on the matrix of pairwise Bruvo genetic distances, visualizing relatedness among multi locus genotypes (MGs) in the Mexican analysis.

215x279mm (300 x 300 DPI)

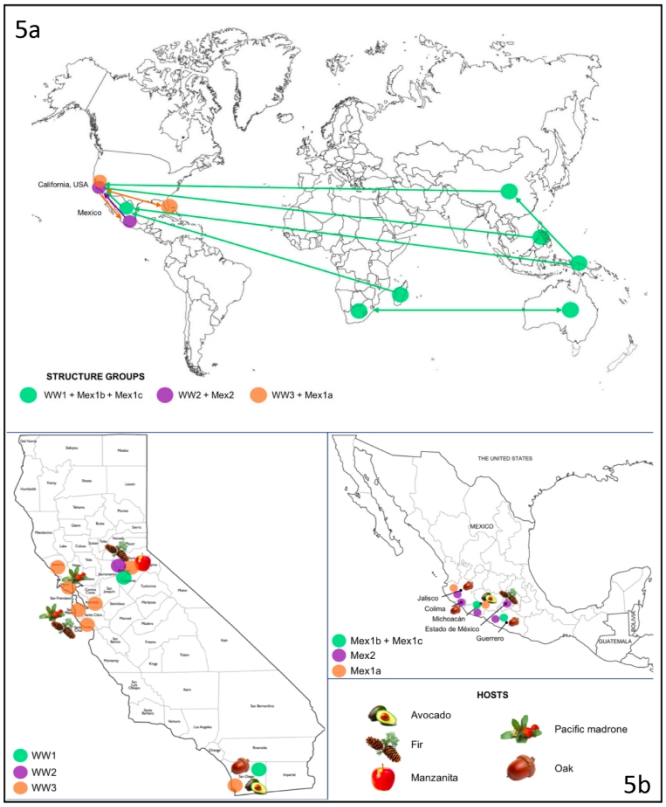


Fig. 5 5a. Schematic reconstruction of the historical movement of Phytophthora cinnamomi based on the presence of identical or quasi-identical multi locus genotypes in different world regions. 5b Recent cross contamination between agricultural and wild hosts in California and Mexico, inferred by tracking the presence of identical multi locus genotypes in agricultural commodities and in native flora in the same region.

215x279mm (300 x 300 DPI)

Supplemental Information

Table S1. Theoretical probability of identity values based on clone-corrected data for the worldwide/California and Mexico datasets. See main text for explanation of the measures used.

Worldwide/California

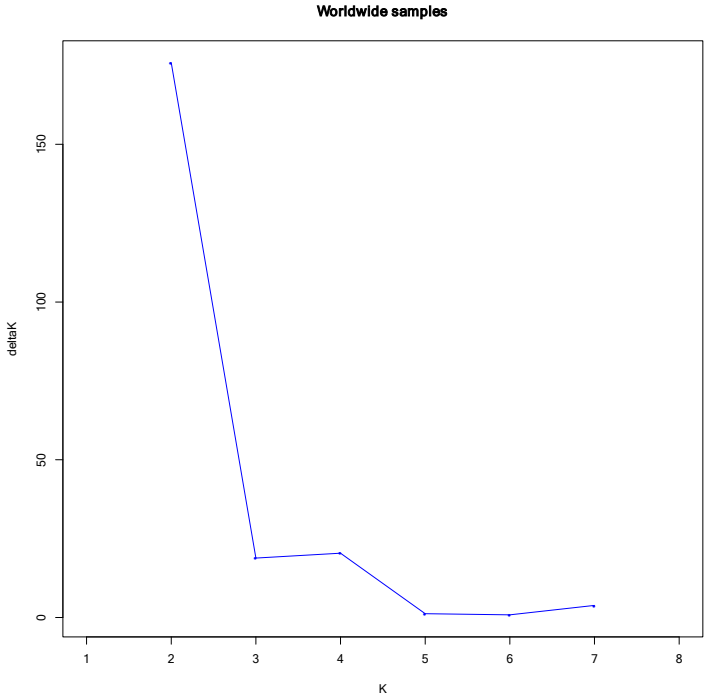
Measure	Loci	Probability
$P_{(ID)sib}$	e16, g10, g13	0.002464
$P_{(ID)sib}$	all	0.000331
$P_{(ID)}$	e16, g10, g13	0.000838
$P_{(ID)}$	all	0.000056

Mexico

Measure	Loci	Probability
$P_{(ID)sib}$	e16, g10, g13	0.005150
$P_{(ID)sib}$	all	0.000736
$P_{(ID)}$	e16, g10, g13	0.000838
$P_{(ID)}$	all	0.000056

Figure S1. Plots of DeltaK (= mean(|L''(K)|)/ sd(L(K))) for the **A**. worldwide/California and **B**. Mexico analyses.

A.



B.

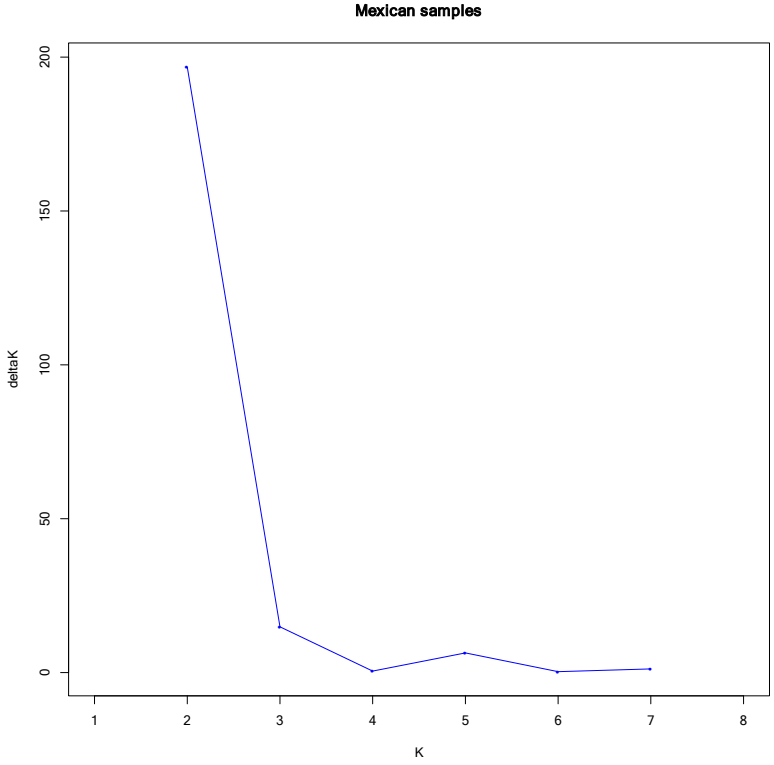


Table S2. The 23 multilocus genotypes (MGs) produced by the 4 SSRs for the Californian and worldwide isolates, expressed as amplicon lengths in nucleotides.

MG	Origin/Hosts	n (Σ=75)	d39 (Σ alleles=11)	e16 (Σ alleles=6)	g10 (Σ alleles=9)	g13 (Σ alleles=18)
MG01	USA (CA)	2	138/138	169/171	116/154	151/169/175
MG02	USA (CA)	1	134/134	169/171	116/156	151/169/175
MG03	USA (CA)	1	134/134	169/171	116/154	143/155/175
MG04	USA (CA)	5	134/134	169/171	116/154	151/169/175
MG05	USA (CA)	1	134/134	169/171	116/158	151/169/175
MG06	Papua New Guinea	1	128/140	161/169	114/116/118	147/163
MG07	Papua New Guinea	1	126/126	161/169	114/116/118	147/165/175
MG08	USA (14, CA), Mexico (1)	15	124/168	163/163	112/114	143/155/175
MG09	Papua New Guinea	1	124/136	161/169	114/116/118	147/175
MG10	USA (CA)	3	124/124	169/171	116/158	145/151/173
MG11	China	1	124/124	169/169	116/158	145/151/173
MG12	China	1	124/124	169/169	112/116	165/null
MG13	USA (3, CA), China (1)	4	124/124	169/169	112/116	165/181
MG14	China	1	130/130	169/169	106/122	149/149
MG15	USA (CA)	1	122/134	167/171	116/154	151/169/175
MG16	USA (CA)	2	122/134	165/167	116/154	151/169/175
MG17	USA (CA)	2	122/134	169/171	116/156	151/169/175
MG18	USA (22, CA), (2, FL)	24	122/134	169/171	116/154	151/169/175
MG19	Papua New Guinea	1	122/130	161/167	114/116/118	147/171
MG20	Taiwan (1) USA (1, CA)	2	122/122	169/169	106/118	179/195
MG21	Madagascar	1	118/122	169/169	114/116	161/???
MG22	Australia (1), South Africa (2)	3	118/122	169/169	114/116	161/???
MG23	USA (CA)	1	118/122	169/169	112/116	165/181

Table S3. The 52 multilocus genotypes (MGs) produced by the 4 SSRs for the Mexican isolates and international reference specimens, expressed as amplicon lengths in nucleotides.

MG	Origin	n (Σ=76)	d39 (Σ alleles =12)	e16 (Σ alleles =8)	g10 (Σ alleles =8)	g13 (Σ alleles =13)
MG1	Michoacán	1	126/126	167/167	114/114	175/175
MG2	Papua New Guinea	1	126/142	165/165	116/118	165/175
MG3	Michoacán	1	118/142	161/171	114/114	151/175
MG4	Papua New Guinea	1	122/130	161/167	112/114	147/171
MG5	Michoacán	1	122/126	161/171	112/114	155/155
MG6	Madagascar	1	118/122	169/169	114/116	161/161
MG7	Australia	1	118/122	169/169	112/116	161/161
MG8	Michoacán	1	122/122	169/206	116/154	155/169
MG9	Michoacán	1	122/122	161/171	114/114	155/173
MG10	Michoacán	1	122/122	161/171	112/114	157/175
MG11	Michoacán	1	120/120	169/169	110/110	155/175
MG12	Jalisco	1	120/134	171/171	116/154	171/171
MG13	Jalisco	1	134/162	171/171	116/154	171/171
MG14	Michoacán	1	138/165	161/171	112/114	173/173
MG15	Michoacán	2	138/165	161/171	112/114	155/173
MG16	Michoacán	1	122/165	161/171	112/114	175/175
MG17	Michoacán	1	165/165	163/171	112/114	173/173
MG18	Jalisco	1	165/165	161/171	116/116	155/155
MG19	Guerrero	1	165/165	161/171	114/114	155/171
MG20	Michoacán	3	165/165	161/171	112/114	175/175
MG21	Colima (1), Estado de México (1), Michoacán (1)	3	165/165	161/171	112/114	155/173
MG22	Michoacán	1	122/168	161/171	112/114	155/155
MG23	Michoacán	1	168/168	161/171	112/114	175/175
MG24	Michoacán	1	168/168	161/171	112/114	155/173
MG25	Michoacán	1	168/168	161/171	112/114	155/155
MG26	Colima	1	168/168	161/171	112/112	155/173
MG27	USA (CA)	1	120/124	169/171	116/158	173/173
MG28	Guerrero	1	124/165	165/165	112/114	157/157

MG29	Michoacán	1	124/165	161/161	112/114	155/175
MG30	Colima	1	124/165	161/161	112/112	153/153
MG31	Michoacán	1	124/165	161/177	112/114	155/177
MG32	USA (CA)	1	124/165	171/175	116/154	169/175
MG33	Jalisco	1	124/165	161/171	114/156	155/173
MG34	Guerrero	1	124/165	161/171	114/114	155/155
MG35	Michoacán	1	124/165	161/171	112/114	175/175
MG36	Michoacán	3	124/165	161/171	112/114	173/173
MG37	USA (CA)	1	124/165	161/171	112/114	155/161
MG38	Colima (3), Guerrero (1), Estado de México (2), Michoacán (1), USA (1, CA)	8	124/165	161/171	112/114	155/175
MG39	Guerrero (2), Estado de México (2), Michoacán (4)	8	124/165	161/171	112/114	155/173
MG40	Michoacán	1	124/165	161/171	112/114	155/155
MG41	Michoacán	1	124/165	161/171	112/112	155/173
MG42	Jalisco	1	124/165	171/171	116/154	151/171
MG43	Jalisco	1	124/165	171/171	116/154	153/171
MG44	USA (CA)	1	124/165	171/171	116/154	169/173
MG45	Michoacán	1	124/168	161/161	112/114	155/175
MG46	Michoacán	1	124/168	161/171	114/114	151/151
MG47	Estado de México (2), Michoacán (1)	3	124/168	161/171	112/114	155/175
MG48	Colima	1	124/168	171/177	112/112	155/155
MG49	Michoacán	1	124/168	171/171	116/154	153/153
MG50	Jalisco	1	124/168	171/171	116/154	155/171
MG51	USA (1, CA), China (1)	2	124/124	163/169	112/116	165/181
MG52	USA (CA)	1	124/124	169/169	116/156	173/173