Phylogeography of the wide-host range panglobal plant pathogen Phytophthora cinnamomi

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Phylogeography of the wide-host range panglobal plant pathogen *Phytophthora cinnamomi*

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Abstract

Various hypotheses have been proposed regarding the origin of the plant pathogen *Phytophthora cinnamomi*. *P. cinnamomi* is a devastating, highly invasive soilborne pathogen associated with epidemics of agricultural, horticultural and forest plantations and native ecosystems worldwide. We conducted a phylogeographic analysis of populations of this pathogen sampled in Asia, Australia, Europe, southern and northern Africa, South America, and North America. Based on genotyping-by-sequencing, we observed the highest genotypic diversity in Taiwan and Vietnam, followed by Australia and South Africa. Mating type ratios were in equal proportions in Asia as expected for a

sexual population. Simulations based on the index of association suggest a partially sexual, semi-clonal mode of reproduction for the Taiwanese and Vietnamese populations while populations outside of Asia are clonal. Ancestral area reconstruction provides new evidence supporting Taiwan as the ancestral area, given our sample, indicating that this region might be near or at the center of origin for this pathogen as speculated previously. The Australian and South African populations appear to be a secondary center of diversity following migration from Taiwan or Vietnam. Our work also identified two panglobal, clonal lineages PcG1-A2 and PcG2-A2 of A2 mating type found on all continents. Further surveys of natural forests across Southeast Asia are needed to definitively locate the actual center of origin of this important plant pathogen.

1. INTRODUCTION

The spread of plant pathogens into both managed and naïve ecosystems has occurred repeatedly via the movement of live plants (C. M. Brasier, 2008; Burgess & Wingfield, 2017; Jung et al., 2016; Liebhold, Brockerhoff, Garrett, Parke, & Britton, 2012; Santini et al., 2013). Classical examples of fungal plant pathogen invasions include ash dieback caused by *Hymenoscyphus fraxineus* (Gross, Holdenrieder, Pautasso, Queloz, & Sieber, 2014; McMullan et al., 2018), chestnut blight caused by *Cryphonectria parasitica* (Rigling & Prospero, 2018), and white pine blister rust caused by *Cronartium ribicola* (Brar et al., 2015). The oomycete genus *Phytophthora* features prominently among invasive plant pathogens (Goss, Larsen, Chastagner, Givens, & Grünwald, 2009; Grünwald, Garbelotto, Goss, Heungens, & Prospero, 2012; T. Jung, Pérez-Sierra, et al., 2018) and includes the potato late blight pathogen *P. infestans*, the sudden oak and sudden larch death pathogen *P. ramorum* (Grünwald et al., 2012) and the Port Orford Cedar pathogen *P. lateralis* (Hansen, Goheen, Jules, & Ullian, 2000). Several species such as *P. infestans*, *P. palmivora* and *P. cinnamomi* have reached panglobal distributions (Erwin & Ribeiro, 1996). Predicting the spread of newly emerging and re-emerging plant pathogens and their management critically depends on knowledge of the origin and distribution of a plant pathogen. This knowledge can be used to harness novel sources of resistance for plant breeding as well as management by quarantine based on monitoring and interception of novel variants.

Phytophthora cinnamomi is the most notorious and invasive member of the genus infecting and causing root rot, bark cankers, dieback and mortality of more than 5,000 woody plant species worldwide (Balci et al., 2007; Erwin & Ribeiro, 1996; Hardham & Blackman, 2018; Shearer, Crane, & Cochrane, 2004). This pathogen is considered to be a major invasive threat to native forest and heathland ecosystems in Australia and South Africa and agricultural, horticultural and forest ecosystems worldwide (Cahill, Rookes, Wilson, Gibson, & McDougall, 2008; Pratt & Heather, 1973; Pratt, Heather, & Shepherd, 1973; Shearer, Crane, Barrett, & Cochrane, 2007). One of the most devastating epidemics caused by *P. cinnamomi* is the dieback of the diverse jarrah (*Eucalyptus marginata*) forests in Western Australia (Cahill et al., 2008; Jung, Colquhoun, & Hardy, 2013; Jung et al., 2018; Shearer & Tippett, 1989) (Fig. 1A). The Australian government has labeled *P. cinnamomi* a "key threatening process to Australia's biodiversity" in the Environmental Protection and Biodiversity Conservation Act 1999 (https://www.environment.gov.au/biodiversity/threatened/key-threatening-processes). *P. cinnamomi* is also causing widespread dieback and mortality of oak, chestnut and pine forests in Europe and North America, Valdivian rainforests in Chile, *Araucaria* forests in Brazil, and numerous orchard and nursery crops including avocado and pineapple (Balci et al., 2007; Beaulieu, Ford, & Balci, 2017; C. M. Brasier, Robredo, & Ferraz, 1993; A. Drenth & Guest, 2004; Eggers, Balci, & MacDonald, 2012; Erwin & Ribeiro, 1996; Jung & Dobler, 2002; Jung, Durán, et al., 2018; Jung, Pérez-Sierra, et al., 2018; Santos, Tessmann, Alves, Vida, & Harakava, 2011; Tainter, O'Brien, Hernández, Orozco, & Rebolledo, 2000; Vettraino et al., 2005) (Fig. 1).

P. cinnamomi groups in phylogenetic Clade 7c of the genus *Phytophthora* which belongs to the oomycetes, a group of water molds within the kingdom *Stramenipila* (Beakes, Honda, & Thines, 2014; Erwin & Ribeiro, 1996; Yang, Tyler, & Hong, 2017). This particular *Phytophthora* species is heterothallic requiring two mating types, A1 and A2, for sexual reproduction via the formation of oospores (Erwin & Ribeiro, 1996). Although both mating types have been found around the world, the global epidemic is driven by the A2 mating type and populations described to date worldwide are clonal (Beaulieu et al., 2017; Eggers et al., 2012; Engelbrecht, Duong, & Berg, 2017; Celeste Linde, Drenth, Kemp, Wingfield, & Von Broembsen, 1997; Celeste Linde, Drenth, & Wingfield, 1999).

The origin of *P. cinnamomi* is still a topic of hot debate while one leading hypothesis, yet to be formally tested, is that *P. cinnamomi* might have originated in different areas of Southeast Asia or in

Taiwan (Arentz, 2017; Arentz & Simpson, 1986; T. Jung et al., 2017; Thomas Jung et al., 2020; Ko, Chang, & Su, 1978; Pratt & Heather, 1973; Shepherd, 1975; Zentmyer, 1988). The pathogen was first described from stripe cankers of the cinnamon tree, *Cinnamomum burmanii*, in Sumatra (Rands, 1922). *C. burmanii* is considered native to Sri Lanka and has been planted widely across Southeast Asia. Therefore, it was suggested that *P. cinnamomi* had spread to the plantations of this introduced tree species from surrounding native forests. Crandall & Gravatt (1967) first advanced the hypothesis that *P. cinnamomi* is native to Southeast Asia. This hypothesis was based on the fact that native plants in this region were resistant to the pathogen. Ko et al. (1978) provided further evidence to support Southeast Asia as a center of origin based on the co-occurrence of both mating types in healthy natural forests of Taiwan. Recently, in a larger survey, *P. cinnamomi* was found in 15 natural forest stands across Taiwan with a balanced overall A1:A2 mating type ratio of approximately 1:1 (T. Jung et al., 2017). Also in Vietnam both mating types of *P. cinnamomi* co-occur in natural forest stands with a mating type ratio near to 1:1 (Thomas Jung et al., 2020). Interestingly, in Taiwan the A2 mating type only occurred in lowland forests and was always associated with dieback of native trees whereas the A1 mating type was distributed in both montane and lowland forests without causing obvious disease symptoms (Fig. 1F). Therefore, it was proposed that the A1 mating type is native to Taiwan while the A2 mating type might be recently introduced (T. Jung et al., 2017). Based on the geographical distribution and host associations of both mating types and their genetic diversity using isozymes, Arentz & Simpson (1986) and Old *et al.* (1984) came to a similar conclusion for Papua New Guinea being a possible center of origin of the A1 mating type with a recent introduction of the A2 mating type. Alternative hypotheses for the origin of *P. cinnamomi* include those put forward by Shepherd (1975) suggesting New Guinea and Indonesia's Sulawesi island (formerly Celebes) as a center based on mating type ratios and absence of disease in the region. Pratt & Heather (1973) argued that *P. cinnamomi* is native to eastern Australia as it was found to be associated with both disturbed and undisturbed geographic regions. However, *P. cinnamomi* samples from Australia and South Africa were shown to be genetically identical suggesting a potential introduction from the same source with low genotypic diversity (Celeste Linde et al., 1997, 1999; Old, Dudzinski, & Bell, 1988). In addition, A1 isolates from eastern Australia showed much lower isozyme diversity than A1 isolates from Papua New Guinea (Old et al., 1984). Generally, most of these earlier works relied on

circumstantial evidence, lacked population samples from critical geographic regions and did not employ population genetic approaches to test the hypothesis of a candidate center of origin.

Identification of a center of origin relies on a range of approaches (Grünwald & Flier, 2005; Grünwald, McDonald, & Milgroom, 2016; Stukenbrock & McDonald, 2008). Mating type ratios are expected to follow approximately a 1:1 ratio (Grünwald et al., 2001). Populations are expected to reproduce sexually (Goss et al., 2014). Genotypic diversity is highest at the center of origin and declines as one moves out of the center of origin (Shakya, Larsen, Cuenca-Condoy, Lozoya-Saldaña, & Grünwald, 2018). Pathogens are found on native plants but do not necessarily cause severe disease (Flier et al., 2003; T. Jung et al., 2017, 2016). This has been well demonstrated for the Irish potato famine pathogen *P. infestans* at its center of origin in Mexico based on support from root state probabilities for phylogeographic analyses (Goss et al., 2014). Similar criteria were used recently by O'Hanlon et al. (2018) to infer East Asia as a geographic hotspot and the center of origin of the chytrid fungus *Batrachochytrium dendrobatidis* causing global declines of amphibian populations.

Ancestral state reconstruction (ASR) infers the ancestral phenotype or ancestral character state. Bayesian Markov chain Monte Carlo (MCMC) is used to obtain the joint probability distributions of characters for ancestral and tip genotypes (Revell, 2012, 2014). This approach relies on the threshold mode of quantitative genetics in which the discrete presentation of an organismal character trait is actually based on an underlying, unobserved continuous trait called "liability" (Revell, 2014). Bayesian MCMC is used to sample the liabilities of ancestral and tip species for the posterior probability distribution. Variations of ASR approaches have been used to infer the geographic origin of organisms including ancestral area reconstructions (Lemey, Rambaut, Drummond, & Suchard, 2009; Ree & Smith, 2008). The Bayesian posterior probabilities of internal nodes can thus support a given geographic region as the candidate center of origin of a genetic cluster.

In this study, we included populations of *P. cinnamomi* from Asia, Europe, North and South America, Africa and Australia to infer the possible center of origin and global population structure of *P. cinnamomi*. We used genotyping by sequencing (GBS), to obtain genome-wide single nucleotide polymorphisms (SNPs) using restriction endonucleases, sample barcoding and high throughput sequencing, to genotype *P. cinnamomi* (Elshire et al., 2011). This technique has been used successfully to ask hypothesis driven questions about key demographic processes such as gene flow,

migration, bottlenecks, mating type systems and other evolutionary processes (Grünwald et al., 2016). Previous studies using different marker systems have shown that *P. cinnamomi* populations are of low diversity with the existence of only a few genotypes (Chang, Yang, & Wang, 1996; Old et al., 1988, 1984; Socorro Serrano et al., 2019). We formally tested the hypothesis that Asia is the ancestral range and thus a candidate center of origin of *P. cinnamomi* (given our sample) and that migration occurred out of Asia leading to clonal expansion of *P. cinnamomi* to the rest of the world.

2. MATERIALS AND METHODS

2.1 Isolates of *Phytophthora cinnamomi* and isolation techniques

A total of 204 *P. cinnamomi* isolates were collected from Africa (Algeria, South Africa and Tunisia), Asia (Taiwan and Vietnam), Australia, Papua New Guinea, Europe (Austria, France, Italy, Hungary, Portugal, Spain and the United Kingdom,), North America (Dominican Republic and the USA), and South America (Chile) (Table S1) representing the most comprehensive global sample evaluated to date. Strains from Oceania (Papua New Guinea) were removed from most analyses due to the low sample size (N = 3) but are included for reference in figures 4 and 5 resulting in a final sample size of 201 isolates. The isolates were obtained from rhizosphere soil samples using different baiting approaches or, less frequently, by direct plating of infected root or bark tissue onto *Phytophthora*-selective agar media (Arentz & Simpson, 1986; Dobrowolski, Tommerup, Shearer, & O'Brien, 2003; T. Jung, Blaschke, & Neumann, 1996; T. Jung et al., 2017, 2013; T. Jung & Dobler, 2002; T. Jung, Durán, et al., 2018; Celeste Linde et al., 1997; Scanu et al., 2014). *P. cinnamomi* isolates from the US were primarily sampled from *Rhododendron* in ornamental nurseries in Oregon (Parke, Knaus, Fieland, Lewis, & Grünwald, 2014; Weiland et al., 2020). Isolates were identified to species based on sequence analysis of the internal transcribed spacer (ITS1-5.8S-ITS2) region of the ribosomal DNA using the forward primers ITS1 or ITS6 and the reverse primer ITS4 (Cooke, Drenth, Duncan, Wagels, & Brasier, 2000; Grünwald et al., 2010; T. Jung et al., 2017; White et al., 1990). The *P. cinnamomi* isolates were collected in compliance with the Nagoya protocol (Table S1) and samples were not used for any commercial purposes.

2.2 Genome sequencing, SNP calling and filtering

DNA extraction, library preparation and sequencing were performed by the Center for Genome Research Biocomputing (CGRB) at Oregon State University. DNA was extracted using the Qiagen (Germantown, MD) DNEasy plant kit following manufacturer's instructions. Digestion of genomic DNA was done using the two restriction enzymes *Pst*I and *Msp*I followed by sequencing on the Illumina Hiseq 3000 (San Diego, CA) with 100 bp single end (SE) reads in three different runs. Raw fastq reads were demultiplexed using sabre (https://github.com/najoshi/sabre). The *P. cinnamomi* reference genome v.1.0 was downloaded from the Joint Genome Institute (https://genome.jgi.doe.gov/Phyci1/Phyci1.home.html). Reads were mapped against the reference using bowtie2 v2.3.2 (Langmead & Salzberg, 2012). The resulting Sequence Alignment Map (SAM) file was converted to bam format, sorted and indexed using samtools v1.3 (Li et al., 2009). Genomic variant call files (GVCF) were produced for each sample and variants were called using GATK HaplotypeCaller v3.7 (McKenna et al., 2010). GVCFs were combined to produce a VCF file. Variants were filtered based on the sites that were consistently scored in technical replicates (W1733-NSW, PH162-France and CIN-9-Dominican Republic) with no missing value and at least 10x coverage. The upper and lower five per cent read depth quantiles were removed for each sample. Indels, non-biallelic loci and non-genotyped loci were removed. *Phytophthora sojae* (P7076) from phylogenetic Clade 7b was used as an outgroup in the analysis and *P. sojae* raw reads (GenBank accession: SRX389724) were mapped to the *P. cinnamomi* reference genome using the procedure to call variants as described above. Only the variants that were scored in *P. sojae* and *P. cinnamomi* isolates were retained for the final analysis. A total of 299 high quality single nucleotide polymorphisms (SNPs) were retained for further data analysis.

2.3 Mating types (A1:A2) ratio

All *P. cinnamomi* isolates, except 19 isolates from Oregon nurseries, were paired on clarified V8-juice agar with A1 and A2 tester strains of *P. cinnamomi* (Jung et al., 2017). After 4 weeks, the paired cultures were examined under the microscope at 80x for the presence of oospores to identify the mating type. We tested the hypothesis of a 1:1 mating type ratio for each population using the two sided binom.test function in R (Table 1).

2.4 Genetic diversity and population structure

Populations were defined by regions as follows: Africa, Australia, Europe, North America, South America, Taiwan and Vietnam. Note that for certain continents sampling was limited: Africa (Algeria, Tunisia and South Africa), North America (USA and Dominican Republic), South America (Chile). Vietnam and Taiwan were of particular interest and these populations were thus not merged into an Asian sample to allow study of differentiation and migration among these populations. Genotypic diversity was assessed by calculating the number of multilocus genotypes (MLGs). A MLG was defined as a unique combination of SNPs. We assessed the number of MLGs using the R package *poppr* v.2.5.0 (Kamvar, Tabima, & Grünwald, 2014). MLGs were merged into larger groups called multilocus lineages using the average neighbor algorithm (Kamvar, Brooks, & Grünwald, 2015). A greater number of MLGs, private MLGs, and higher genetic diversity among MLGs are expected for a sexually reproducing population compared to a clonally reproducing population. Rarefaction was used to visualize MLG diversity and to correct for uneven sample sizes using the R package *vegan* v.2.4-2 (Oksanen et al., 2016).

Population structure was inferred using ADMIXTURE v.1.3 (Alexander, Novembre, & Lange, 2009). ADMIXTURE models the probability of genotypes for different ancestor groups similar to the software STRUCTURE (Pritchard, Stephens, & Donnelly, 2000). VCF data was first converted to the plink format to allow for use in ADMIXTURE (Purcell et al., 2007). A total of 2 to 10 clusters (K) were evaluated. Cross validation errors were calculated to infer the optimal number of clusters. ADMIXTURE was also run for each population individually following the above method.

2.5 Phylogenetic analyses and ancestral area reconstruction

A maximum likelihood (ML) phylogenetic tree was generated using RAxML v.8.2.11 (Stamatakis, 2006, 2014) to determine relationships among samples. Genotypes were extracted from the VCF Data using *vcfR* v.1.6.0 (Knaus & Grünwald, 2017) and coded as 3-character multistate diploid SNPs (0/0 = 0; 0/1 or 1/0 = 1 and 1/1=2). Therefore, the ASC-MULTIGAMMA model with "Lewis correction" was used to correct for ascertainment bias resulting due to exclusion of invariable positions (Lewis, 2001). *P. sojae* was used as outgroup to root the tree. A total of 1,000 bootstrap

replicates were performed and a tree was plotted using the R package *ape* v.5.0 (Paradis, Claude, & Strimmer, 2004). The ML tree inferred, after removing the *P. sojae* root, was used to estimate the ancestral area (or range) probabilities using the ace (ancestral character estimation) function implemented in the R package *ape*. Geographic locations were mapped onto nodes. The probabilities supporting an ancestral geographic region were overlain on the nodes of ML trees using the R package *phytools* v.0.6-44 (Revell, 2012).

2.6 Inferring the mode of reproduction

The index of association (I_A) is a measure of linkage disequilibrium and can be used to infer the mode of reproduction in a population. I_A was calculated on clone corrected data for Australian, Taiwanese and Vietnamese populations using the R package *poppr* (Kamvar et al., 2015, 2014). First we simulated the distribution of I_A under clonal (90 % linked SNPs), partially-clonal (50 % linked SNPs) and sexual (10 % linked SNPs) modes of reproduction with *adegenet* v.2.1.1 (Jombart & Ahmed, 2011) and compared our observed I_A with simulated I_A (Tabima, Coffey, Zazada, & Grünwald, 2018). I_A was calculated on 100 randomly sampled SNPs with 100 replicates. Means of I_A were compared for significance using the Tukey's HSD test in R.

2.7 Migration analyses

Migration analysis was performed using coalescent approaches in the software Migrate-n v.4.2.14 (P. Beerli & Felsenstein, 2001; Peter Beerli, 1998, 2009). We determined the likely migration pathways among the four populations that had moderate to high genetic diversity: Africa, Australia, Taiwan and Vietnam (Fig. S1). Various models of divergence and migration were tested using randomly selected sets of 50, 100 and 299 SNPs for these four populations. We evaluated 14 models with for example Taiwan or Vietnam as the most recent common ancestor and various patterns of descent as well as no migration, directional or bidirectional migration between Africa and Australia (Fig. S1). Two independent runs were performed with 5 and 10 randomly sampled isolates per population to allow for balanced sample sizes. The VCF file was converted to the Migrate-n hapmap format file using the function vcfR2migrate implemented in the package *vcfR* (Knaus & Grünwald, 2017). Migrate-n was run for 10,000, 20,000, 50,000, and 100,000 generations with a step size of 100.

The first 10% of the analyses were discarded as burn-in. Heating was applied using four chains set to 1, 1.2, 3, and 1,000,000. The models were evaluated using the Bayes factor (Kass & Raftery, 1995).

3. RESULTS

3.1 Presence of two panglobal lineages, intermediate diversity in Australia and South Africa, and highest diversity in Asia

We obtained 165 unique genotypes based on 299 high quality SNP variants from a total of 201 *P. cinnamomi* isolates sampled worldwide (as well as 3 additional strains from Papua New Guinea not included in the main analysis because of low sample numbers). Given that a single SNP is unlikely to result in a new multilocus genotype, we collapsed closely related genotypes based on the technical replicates and a genetic distance cutoff of 0.06 into clonal lineages (referred to hereafter as Multilocus Lineages, MLL) which resulted in a final set of 28 MLLs. This approach removes technical error (e.g., variation observed within technical replications due to PCR and sequencing error) and groups variation at a threshold level of a clone. Isolates from Asia (Taiwan and Vietnam) had the highest number of MLLs followed by Australia and Africa (Fig. 2A, 3). Private MLLs were observed predominantly for the Asian samples with the exception of one private MLL observed in South Africa. Rarefaction curves showed highest diversity for the Asian samples and lowest diversity for the South American (Chile) samples (Fig. 3B). None of the other populations had private MLLs. The South Africa and Australia populations were similar in intermediate diversity (Fig. 3B).

Population structure inferred by ADMIXTURE analysis at K = 5 clusters (based on cross-validation errors) supported the presence of two dominant panglobal, clonal lineages (black and dark pink) and admixed populations in Taiwan and Vietnam (Fig. 2B). The Australian and African populations were intermediate, and each were assigned predominantly to 3 clusters (black, pink, and red; Fig. 2B).

3.2 Phylogenetic analyses and ancestral area reconstruction suggest Taiwan as a candidate center of origin

To infer the ancestral relationships among *P. cinnamomi* populations we constructed a maximum likelihood (ML) tree with 1,000 bootstrap replicates and "Lewis" correction to correct for ascertainment bias using RAxML. Note, that *P. sojae*, was used as an outgroup to determine ancestral state, but removed from the tree for visualization. Our ML tree corroborates the observation of the existence of two panglobal clonal lineages and high diversity in Taiwanese and Vietnamese populations (Fig. 4). Taiwanese isolates were observed at the root of the tree. Isolates from Australia and South Africa clustered together in one genetically diverse clade, but were also found in the two dominant clonal lineages. The ML tree was used to infer the likelihood of the probability of geographic origin for each node. Ancestral area reconstruction for geographic origin of populations supports Taiwan as the ancestral population given the current sample (Fig. 5).

3.3 Mating type and mode of reproduction

We observed both A1 and A2 mating types in Asia, Australia and South Africa. However, only populations from Asia (Taiwan and Vietnam) met our expectation of a 1:1 mating type ratio based on an exact binomial test consistent with the expectation of sexual reproduction at a candidate center of origin (*P* value = 0.9 that the population was clonally reproducing). Occurrence of the A1 mating type outside of Asia was rare (Table 1). Based on simulations of linkage evaluated using the index of association, populations from Taiwan and Vietnam indicated a partially clonal mode of reproduction whereas the Australian and African populations most likely result from clonal reproduction (Fig. 6). This is based on testing the observed index of association with simulated distributions under a clonal (90 % linkage), partially-clonal (50 % linkage) and mostly sexual (10 % linkage) mode of reproduction.

3.4 Phylogeographic analysis suggests Taiwan as the ancestral population in our sample

We simulated scenarios for multiple models of population divergence and migration using coalescent approaches as implemented in migrate-n. The model with the highest probability varied between two different models (referred as model A and model B) depending on the number of individuals, number of SNPs and number of MCMC runs (Fig. 7, Table S2). When using all 299 SNPs, 100,000 MCMC runs and five random samples each from Taiwan, Vietnam, Australia and the

Africa populations resulted in model B as the best model with a Bayes factor value of 1 (Table S2, S3). However, increasing the sample size to 10 per population with 299 SNPs and 100,000 MCMC runs resulted in model A as the most supported model with a Bayes factor value of 1 (Table S2, S3). The only difference between these two models is in the first emergence of either the African or Australian population outside of Asia. The first model suggests Australia as the first population emerging from Asia whereas the other model suggests Africa. Regardless of which population first emerged from Asia, both models suggest Taiwan as an ancestral population (given the sample) and evidence of bidirectional gene flow between Africa and Australia

4. DISCUSSION

Based on the fact that the native vegetation in Southeast Asia was resistant to *P. cinnamomi*, Crandall & Gravatt (1967) first proposed Southeast Asia as the center of origin for this aggressive, highly invasive wide-host range pathogen. Our analyses on global populations of *P. cinnamomi* strongly support this hypothesis. Of the locations sampled in our study, Taiwan and Vietnam showed the highest genetic diversity and presence of both mating types at approximately equal frequencies, clearly indicating that both regions lie within or near the center of origin of *P. cinnamomi*. Populations outside of Asia are genetically less diverse and reproduce clonally, confirming previous reports regarding a lack of genetic diversity and clonality (Beaulieu et al., 2017; Eggers et al., 2012; Engelbrecht et al., 2017; Socorro Serrano et al., 2019). These results are consistent with the hypothesis of *P. cinnamomi* migrating from Asia to the rest of the world. Ancestral area reconstruction suggests Taiwan as the likely center of origin for the pathogen, but further sampling in adjacent regions is required to ascertain the center of highest diversity. As further regions in Southeast Asia, in particular the vast Indonesian and Malaysian archipelago, are sampled in future studies, Taiwan may not necessarily be the area of highest diversity; however, it is clear that Taiwan is at or near the center of origin of *P. cinnamomi*. Previously, Papua New Guinea was described to have a diverse population of *P. cinnamomi* and was also hypothesized to be a candidate center of diversity (Arentz & Simpson, 1986; Socorro Serrano et al., 2019). In our phylogenetic analysis we were only able to study a modest sample from Papua New Guinea, consisting of two isolates belonging to the

A1 mating type and one to the A2 mating type. The two A1 mating type samples were placed within the diverse main cluster of Taiwanese isolates and the Australian-African cluster, respectively (Fig. 4). The A2 isolate from PNG clusters with one of the panglobal A2 genotypes (Fig. 4). This supports the hypothesis of Arentz (2017) that the A1 mating type was introduced from Taiwan to Papua New Guinea during the first human colonization more than 40,000 years ago whereas the A2 mating type arrived much later during European colonization. Further sampling in Papua New Guinea is needed to determine if this region could be a center of diversity.

One of the recurring themes in multiple earlier studies of *P. cinnamomi* populations from Australia, South Africa and the United States was the emergence of two A2 mating type lineages and the rare presence or absence of the A1 mating type (Beaulieu et al., 2017; Dobrowolski et al., 2003; Eggers et al., 2012; Engelbrecht et al., 2017; Celeste Linde et al., 1997, 1999; Pagliaccia, Pond, McKee, & Douhan, 2013; Socorro Serrano et al., 2019). A major insight from our work, which included a larger and more representative global population of *P. cinnamomi* than previous studies, is the confirmation of the existence of two panglobally distributed, clonal lineages from the A2 mating type. To allow consistent nomenclature we are naming the two panglobal clonal lineages PcG1-A2 and PcG2-A2 (Fig. 4, 5). Consistent naming of clonal lineages is instrumental in allowing communication with regulatory agencies and managers as exemplified by the nomenclature developed for clonal lineages of the sudden oak death pathogen *P. ramorum* (Grünwald et al., 2009).

We found both mating types of *P. cinnamomi* in a balanced near 1:1 ratio in natural forests of Taiwan and Vietnam. Comparison between the simulated I_A and the observed I_A suggests a partially sexual, semi-clonal mode of reproduction for the Taiwan and Vietnam regions. This is consistent with a native population of a heterothallic *Phytophthora* species which spreads and reproduces regularly with asexual zoospores and chlamydospores and shows occasional outcrossing via mating between A1 and A2 individuals. Previous studies demonstrated that both mating types also co-occur in *P. cinnamomi* populations of South Africa and Australia which provides an opportunity for sexual reproduction; however, population genetic studies using isozymes and microsatellites showed no evidences for sexual reproduction of both mating types in these regions (Dobrowolski et al., 2003; Engelbrecht et al., 2017; Celeste Linde et al., 1997). As possible explanations for this lack of sexual reproduction, Dobrowolski et al. (2003) argued that under the harsh environmental conditions of

Western Australia oospores might not germinate or progenies might fail to survive. However, frequent occurrence of oospores produced via selfing by the A2 mating type of *P. cinnamomi* in infected fine roots of various native host plants in Western Australia suggests they play a major role for the survival of this pathogen (T. Jung et al., 2013). Alternatively, the A1 and A2 populations of *P. cinnamomi* in both South Africa and Western Australia might have originated from different source populations in Asia which were geographically isolated from each other for considerable periods of time, hence building up partial reproductive barriers. This is supported by the high genetic distance between A1 and A2 isolates from South Africa (Linde et al., 1997). Although hybrid progeny were produced between A1 and A2 mating type isolates from South Africa they showed a lower level of aggressiveness than the parental isolates (C. Linde, Soo, & Drenth, 2001).

In heterothallic *Phytophthora* species, both mating types can be introduced singly or in combination as expected by chance. In Europe, following the introduction of the A2 mating type of *P. infestans* from Mexico in the late 1970s, almost 150 years after the first introduction of the A1 mating type, sexual populations became established in some environments (A. Drenth, Turkensteen, & Govers, 1993). However, since *Phytophthora* pathogens are usually clonally introduced with very small founder populations (Goodwin, 1997) most heterothallic *Phytophthora* species occur in their introduced areas either as a single mating type or in highly unbalanced mating type ratios. In Vietnam, highly unbalanced A1:A2 ratios ranging from 1:3 to 1:5 of the introduced pathogen *P. capsici* were found in four provinces (Truong, Liew, & Burgess, 2010). In China' s Henan province all isolates of the introduced *P. nicotianae* recovered from tobacco plantations belonged to the A2 mating type (Cui, Gao, Guo, Kang, & Hu, 2018) whereas all isolates of the Asian pathogen *P. colocasiae* obtained from taro fields in Hawaii were of the A1 mating type (Ko, 1979). An extensively studied pathogen is *P. ramorum* with two A2 lineages and one A1 lineage introduced into North America and two A1 lineages introduced into Europe (Grünwald et al., 2012; Van Poucke et al., 2012). Interestingly, in Vietnam and Japan both mating types were shown to co-occur in natural ecosystems (Jung et al., 2021). Co-occurrence of both mating types and a balanced mating type ratio are expected for native situations but not a necessary condition.

The predominance of only one mating type (A2) of *P. cinnamomi* globally might be explained by stochastic sampling from the populations of origin and/or by population bottlenecks that occurred

during the global migration. In particular, if the A2 matin type was introduced first it would have a higher likelihood of spreading and establishing broadly (André Drenth, McTaggart, & Wingfield, 2019).

Our data and analyses are consistent with South Africa and Australia being stepping-stone populations for the migration of *P. cinnamomi* to the rest of the world (Fig. 8). South Africa and Australia share very similar MLLs but have intermediate levels of diversity compared to Asia and the rest of the world. High genetic similarity between the South African and Australian populations have also been reported previously using RFLP markers (Celeste Linde et al., 1999). This similarity could possibly be due to the introduction from the same potential source population or migration between these two regions. Our migration analyses provide support for the bidirectional gene flow between the South African and Australian populations.

One of the downsides of the GBS technique is the large proportion of missing data (Wickland, Battu, Hudson, Diers, & Hudson, 2017). In our work we were able to generate 299 high quality SNPs after filtering for low coverage SNPs. Going forward, the use of whole genome sequences could provide a better approach for understanding the genome wide variation within and between *P. cinnamomi* populations. Recently, a few more genomes of *P. cinnamomi* were sequenced and made available which could be used to perform a comparative analysis to identify large indels, structural variations, and presence/absence polymorphism of genes to understand the emergence of distinct lineages and to find candidate regions undergoing a selective sweep or selection (Longmuir, Beech, & Richardson, 2017; Studholme et al., 2015).

Our results and those from previous studies on *P. cinnamomi* (Dobrowolski et al., 2003; Hardham & Blackman, 2018; Jung, Durán, et al., 2018, 2018; Shearer & Tippett, 1989; Socorro Serrano et al., 2019), *P. infestans* (Goss et al., 2014, p. 21014; Grünwald & Flier, 2005), *P. ramorum* (Goss et al., 2009; Grünwald et al., 2012; Van Poucke et al., 2012), *P. lateralis* (Clive M. Brasier et al., 2012; Hansen et al., 2000), *P. pinifolia* (Durán et al., 2008) and fungal tree pathogens like *C. parasitica* (Rigling & Prospero, 2018), *H. fraxineus* (Gross et al., 2014; McMullan et al., 2018) and *C. ribicola* (Brar et al., 2015) emphasize the threat posed by the introduction of invasive pathogens, often as clonal lineages. As demonstrated by near ubiquitous infestations of European and US nurseries with more than 50 exotic *Phytophthora* species including *P. cinnamomi*, *P. lateralis* and *P. ramorum*

(Bienapfl & Balci, 2014; Goss et al., 2009; Jung et al., 2016; Parke et al., 2014), the continuously growing volume and complexity of the international nursery trade provide support for the introduction and spread of *Phytophthora* pathogens with live plants (Drew, Anderson, & Andow, 2010; Jung et al., 2016; Liebhold et al., 2012; Santini et al., 2013).

In conclusion, we show that *P. cinnamomi* populations in Taiwan and Vietnam, based on their high standing genetic diversity and presence of both mating types in equal frequency, are endemic to these locations, and that Taiwan is a candidate center of origin of *P. cinnamomi* given our sample. Further surveys in other regions of Southeast Asia, in particular Indonesia and Malaysia, are needed to finally pin down the center of origin of this notorious invasive pathogen. In the rest of the world two dominant, panglobal clonal lineages of the A2 mating type were identified and designated as PcG1-A2 and PcG2-A2. The A1 mating type is rare in most parts of the world except for Asia and its presence in Taiwan and Vietnam provides an opportunity for sexual reproduction thus providing a source of genetically diverse populations with high adaptive potential.

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AUTHOR CONTRIBUTIONS

NJG and TJ conceived and designed the study. TJ, JEW, CM, MHJ, AnD, DIG, ECYL, AlD, ESS, CC, TTC, CHF, NMC, PQT and BS conducted field sampling and isolate identification. SKS, VJF, and NJG sequenced samples. SKS, BJK, and NJG conducted bioinformatic and population genomic analyses. NJG and TJ obtained funding. All authors edited and approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

GVCF data and associated scripts used in this work are deposited on GitHub (https://github.com/grunwaldlab/GBS-Pcinnamomi). Sequence data in fastq format that resulted from the GBS analysis are deposited in the NCBI SRA (BioProject: PRJNA608031).

COMPETING INTERESTS

The authors declare no competing interests.

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Figures

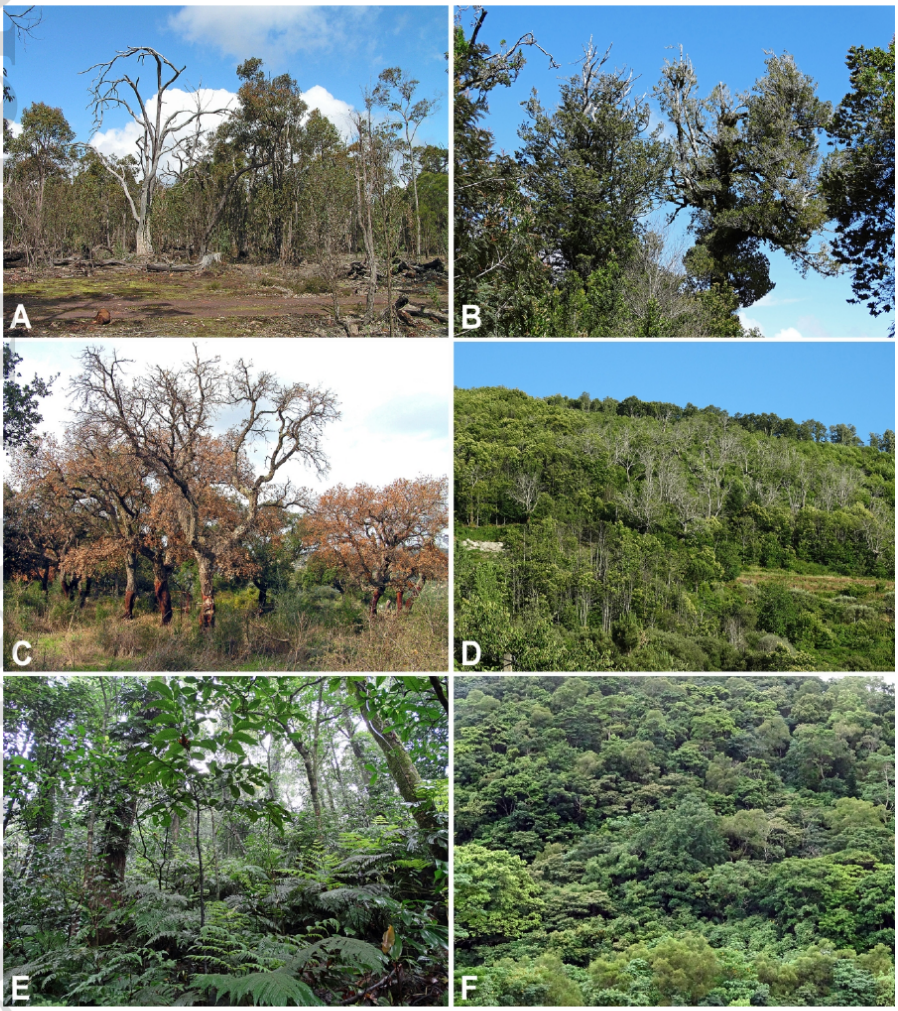

Fig. 1. Ecosystem impacts of *Phytophthora cinnamomi* as an invasive (A-D) and native (E-F) soilborne root pathogen. (A-D) Forest diebacks caused by the invasive, globally distributed, clonal A2 lineages. **(A)** dieback of a jarrah (*Eucalyptus marginata*) forest in the southwest of Western

Australia. **(B)** Dieback of the endangered conifer *Saxegothaea conspicua* in a Valdivian rainforest in Chile. **(C)** Acute mortality of a cork oak (*Quercus suber*) stand in Sardinia, Italy. **(D)** Severe dieback and mortality of a chestnut (*Castanea sativa*) forest in Portugal. **(E-F)** Healthy, diverse subtropical monsoon forests with co-occurrence of both mating types of *P. cinnamomi* in **(E)** northern Vietnam and **(F)** Taiwan.

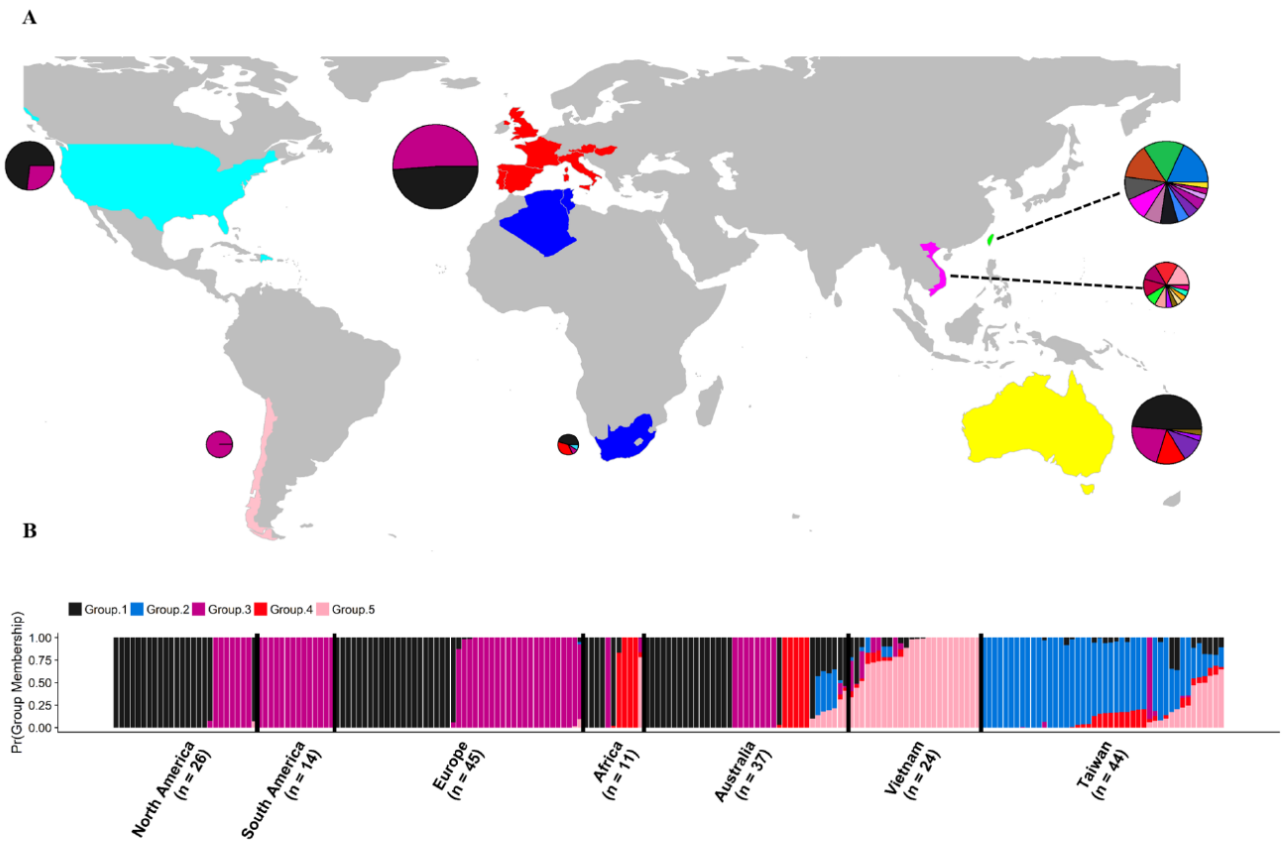

Fig. 2. Global distribution and admixture population structure of *P. cinnamomi*. **(A)** Distribution of *P. cinnamomi* multilocus lineages (MLL) where pie charts show each MLL in a different color. Countries sampled are colored on the world map. **(B)** ADMIXTURE plot of *P. cinnamomi* isolates by populations at K = 5. Each bar represents an isolate with proportional ancestry assigned to one of each K populations. The two panglobal lineages are shown in black and dark pink.

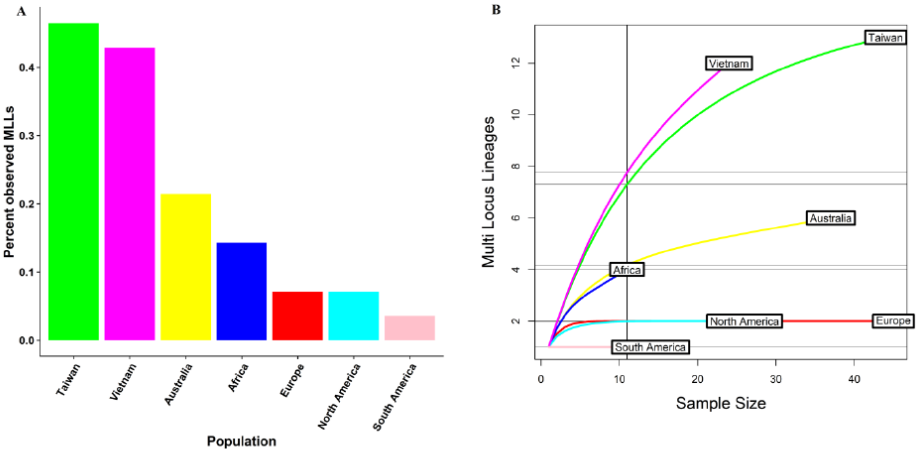

Fig. 3. Global genetic diversity observed in *P. cinnamomi* by population. (A) Proportion of observed multilocus lineages (MLL) by population using a bitwise cutoff distance of 0.06. **(B)** Rarefaction curves for each regional population sampled.

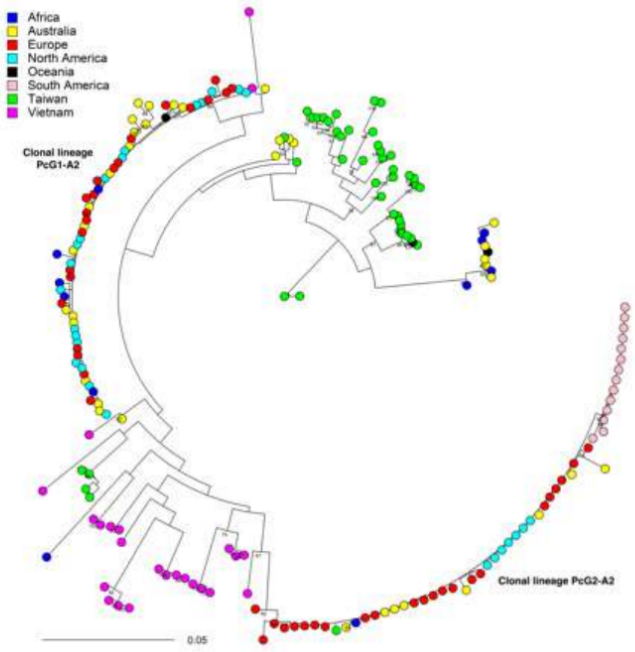

Fig. 4. Maximum likelihood tree of *P. cinnamomi* samples. The tree was inferred using 299 concatenated single nucleotide polymorphism (SNP) with 1,000 bootstrap replicates using RAxML version 8.2.11. ASC-MULTIGAMMA substitution model with "Lewis correction" was used to correct for ascertainment bias. The numbers at a node indicate bootstrap support greater than 80%. The tree was rooted using *P. sojae* as an outgroup. The two panglobal lineages are named PcG1-A2 and PcG2-A2, respectively.

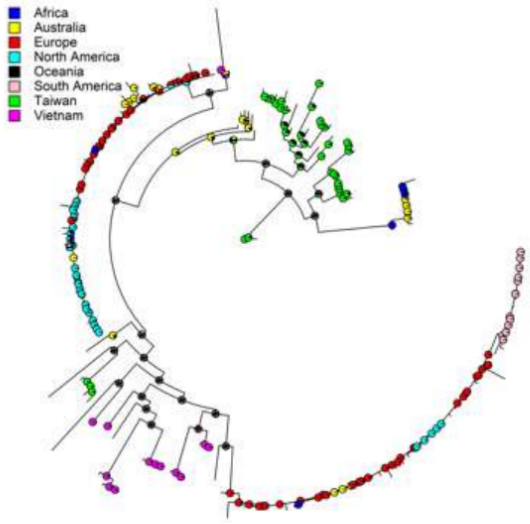

Fig. 5. Ancestral area reconstruction based on maximum likelihoods for nodes by geographic origin. The pie chart represents the likelihood of the node being assigned to each geographic region sampled in this study.

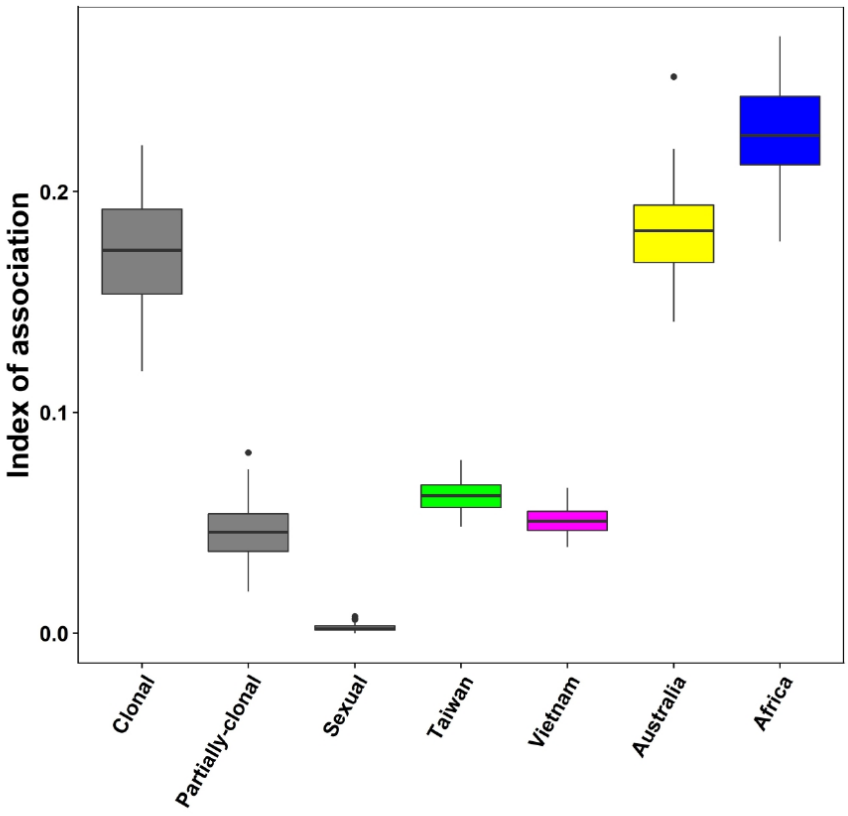

Fig. 6. Determination of linkage among markers using the index of association (I_A). The first three box plots (in grey) represent the simulated I_A under clonal, partially clonal and sexual reproduction scenarios. Comparison between the simulated I_A and the observed I_A suggests for the Taiwanese and Vietnamese populations a partially clonal mode of reproduction, whereas the Australian and African populations most likely result from clonal reproduction.

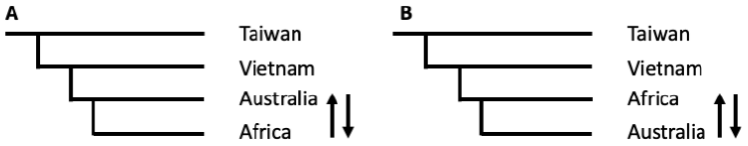

Fig. 7. Migration scenarios with the highest likelihood based on coalescent analysis using migrate-n. Various combinations of divergence and migration models were tested using migrate-n. The two scenarios obtained the highest likelihood based on Bayes factor. In both models, Taiwan is inferred as the ancestral population, given our sample, and bi-directional migration between Australia and Africa which might have led to the genetic similarity between these regions.

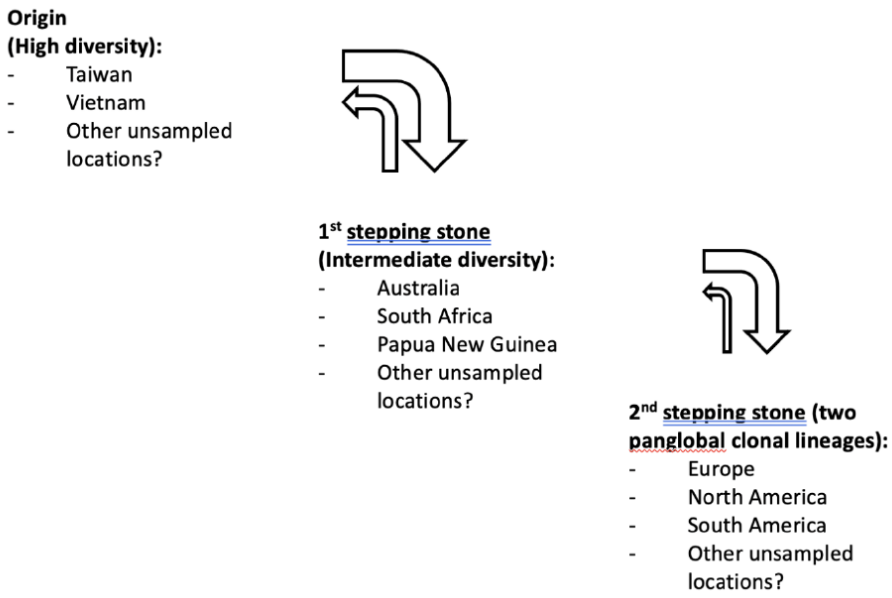

Fig. 8. Model of the stepwise emergence of *Phytophthora cinnamomi* from Asia in a stepping-stone model via Australia and South Africa to the rest of the world as two dominant A2 mating type panglobal lineages PcG1-A2 and PcG2-A2. The model depicts putative bidirectional migration with differing rates, indicating larger migration rates with larger arrows.

TABLES

Table 1. A1 and A2 mating type ratios of *Phytophthora cinnamomi* isolates in different geographical populations (i.e., regions). Departures from the expected mating type ratio of A1/A2 = 1 were statistically evaluated using a binomial distribution.

Population	Number of isolates	A1	A2	A1/A2	*P*-value
Taiwan	44	23	21	1.09	0.88
Vietnam	24	10	14	0.71	0.54
Australia[1]	37	5	30	0.17	< 0.05
Africa[2]	11	5	6	0.83	1.00
Europe	45	0	45	0	< 0.05
North America[3]	26	0	7	0	0.01
South America	14	0	14	0	< 0.05

[1] Two isolates were sterile.

[2] In Algeria and Tunisia only the A2 mating type found.

[3] Mating type was only identified for 7 of the 26 isolates.