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ORIGINAL ARTICLE

Phylogeography, origin and population structure of the self-fertile emerging plant pathogen *Phytophthora pseudosyringae*

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Abstract

Phytophthora pseudosyringae is a self-fertile pathogen of woody plants, particularly associated with tree species from the genera *Fagus*, *Notholithocarpus*, *Nothofagus* and *Quercus*, which is found across Europe and in parts of North America and Chile. It can behave as a soil pathogen infecting roots and the stem collar region, as well as an aerial pathogen infecting leaves, twigs and stem barks, causing particular damage in the United Kingdom and western North America. The population structure, migration and potential outcrossing of a worldwide collection of isolates were investigated using genotyping-by-sequencing. Coalescent-based migration analysis revealed that the North American population originated from Europe. Historical gene flow has occurred between the continents in both directions to some extent, yet contemporary migration is overwhelmingly from Europe to North America. Two broad population clusters dominate the global population of the pathogen, with a subgroup derived

from one of the main clusters found only in western North America. Index of association and network analyses indicate an influential level of outcrossing has occurred in this preferentially inbreeding, homothallic oomycete. Outcrossing between the two main population clusters has created distinct subgroups of admixed individuals that are, however, less common than the main population clusters. Differences in life history traits between the two main population clusters should be further investigated together with virulence and host range tests to evaluate the risk each population poses to natural environments worldwide.

KEYWORDS
forest pathogen, homothallic, invasive pathogen, migration, outcrossing, population genetics

1 | INTRODUCTION

Phytophthora is an oomycete genus of major importance with species capable of infecting a wide range of plant species, causing significant damage to an array of economically important crops and ecosystems worldwide (Erwin & Ribeiro, 1996). Notable examples of *Phytophthora* causing destructive plant diseases include *P. infestans* responsible for late blight of potato, cause of the Irish potato famine; *P. ramorum* causing sudden oak death in the United States and sudden larch death in Europe, permanently altering forest ecosystems; *P. cinnamomi* causing eucalyptus diebacks and widescale environmental damage in Australia; and *P. lateralis*, the Port Orford cedar (*Chamaecyparis lawsoniana*) pathogen (Brasier & Webber, 2010; Grünwald et al., 2012; Hansen et al., 2000; Shakya et al., 2021; Turner, 2005). These prominent examples of exotic, invasive *Phytophthora* species emphasize how important knowledge of their geographic origin, sources of potential migrants and evolutionary history are for developing and implementing proper management and control strategies.

Phytophthora pseudosyringae was described from central European and Italian broad-leaved forests in 2003, initially isolated from the rhizosphere of oak (*Quercus* spp.) and found causing necrosis of roots and collar rots of beech (*Fagus sylvatica*) and alder (*Alnus glutinosa*) (Jung et al., 2003). Soon afterwards it was reported from California, United States, causing leaf and twig necrosis of California bay laurel (*Umbellularia californica*) and occasionally stem lesions on coast live oak (*Quercus agrifolia*) and tanoak (*Notholithocarpus densiflorus*) (Martin & Tooley, 2003; Wickland et al., 2008). The pathogen has since been found along the entire western coast of North America from California to Oregon, Washington and British Columbia to Alaska (Bourret et al., 2023; Feau et al., 2022; Hansen et al., 2017; McKeever & Chastagner, 2016; Reeser et al., 2011) and in the Appalachian Mountains of North Carolina and Pennsylvania in the eastern United States (Bily et al., 2022; Hwang et al., 2007). It is widespread throughout Europe from the southern Mediterranean countries through central, eastern and northern Europe, having been found in Spain, Portugal, Italy, Slovenia, France, Germany, Ireland, the United Kingdom, the Netherlands, the Czech Republic, Poland, Bulgaria, Norway and Sweden (Beales et al., 2010; Bregant et al., 2023; Černý, 2016; Christova et al., 2019; Jankowiak et al., 2023; Jung, 2009; Jung et al., 2003; Motta et al., 2003; O'Hanlon et al., 2016; Redondo et al., 2016; Redondo & Oliva, 2016; Scanu et al., 2010; Scanu & Webber, 2016; Talgø et al., 2013) and also in Chile, South America (Fajardo et al., 2017; González et al., 2024; Jung, Durán, et al., 2018). It belongs to *Phytophthora* Clade 3, which currently contains only four other species (*P. ilicis*, *P. nemorosa*, *P. pluvialis*, *aP. psychrophila*).

Originally considered a soilborne *Phytophthora* species causing root necrosis and occasionally infecting the collar and lower stem of trees, *P. pseudosyringae* has also increasingly been found causing aerial infections of foliage, twigs and stems, a characteristic more typical of aerial *Phytophthora* species. (Beales et al., 2010; Fajardo et al., 2017; Jung et al., 2003; Scanu & Webber, 2016; Wickland et al., 2008). Such lifestyle variability is due to the partly caducous sporangia, with caducity in different isolates ranging from 10% to >80% (Jung et al., 2003; Scanu & Webber, 2016). Non-caducous persistent sporangia are not easily dislodged from the mycelium, either germinating in situ or releasing zoospores when enveloped by water; thus, they are ideally suited to a soilborne or waterborne lifestyle (Erwin & Ribeiro, 1996; Jung, Pérez-Sierra, et al., 2018). In contrast, caducous sporangia are easily dislodged and germinate, or release zoospores, after breaking off from below a basal plug and pedicel that attaches them to the underlying mycelium and are therefore suited to aerial dispersal and are accordingly typical of *Phytophthora* species that cause aerial infections (Erwin & Ribeiro, 1996; Jung, Pérez-Sierra, et al., 2018).

It is likely that the variable caducity of *P. pseudosyringae* sporangia has helped the species thrive in a range of habitats and ecosystems, cause a variety of symptoms including root necrosis, collar rot and stem, twig and foliar lesions and infect an ever-expanding range of hosts (Beales et al., 2010; Bregant et al., 2023; Denman et al., 2009; Green et al., 2020; Jung et al., 2016; Reeser et al., 2011; Scanu & Webber, 2016; Wickland et al., 2008; Yakabe et al., 2009). It has caused severe dieback of *Nothofagus* spp. in the United Kingdom and Chile (Fajardo et al., 2017; González et al., 2024; Scanu & Webber, 2016) and has recently been

implicated in widescale dieback of alpine plants in the north-eastern Alps (Bregant et al., 2023). Increasingly, *P. pseudosyringae* has been isolated during *P. ramorum* surveys in both North America and the United Kingdom, during which it has been found that the symptoms caused by the two pathogens are indistinguishable (Wickland et al., 2008; authors' unpublished data). Repeatedly, cankers and necrosis that appeared typical of *P. ramorum* were later associated with *P. pseudosyringae* based on culturing and molecular identification (Wickland et al., 2008; authors' unpublished data). Although *P. pseudosyringae* clearly shares a similar ecological niche to *P. ramorum*, the increasing number of findings suggest it could be causing more damage than previously believed (authors' unpublished data).

P. pseudosyringae is a homothallic, that is, inbreeding or self-fertile, species (Jung et al., 2003). Individuals are bisexual with no self-incompatibility and a single isolate can produce sexual oospores (Erwin & Ribeiro, 1996; Judelson, 2009; Tomura et al., 2017). Homothallic species do not require interaction with an opposing mating type in order to reproduce sexually, unlike heterothallic species (Erwin & Ribeiro, 1996; Judelson, 2009; Tomura et al., 2017). However, there is no barrier to outbreeding and if two individuals interact then outcrossing is possible and has been shown for a number of homothallic oomycete and *Phytophthora* species (Bhat et al., 1993; Förster et al., 1994; Francis & St. Clair, 1993; Whisson et al., 1994). In fact, outcrossing of homothallic *Phytophthora* species with a different species has resulted in the creation of several new hybrid species (Bertier et al., 2013; Declercq et al., 2010; May et al., 2003; Safaiefarahani et al., 2016; Van Poucke et al., 2021). Selfing reduces levels of genetic diversity and increases homozygosity compared to outcrossing populations (Charlesworth, 2003; Goodwin, 1997) and diversity in homothallic *Phytophthora* populations is generally low (Aguayo et al., 2013; Schoebel et al., 2014). However, considerable variability has been found in *P. pseudosyringae* gene sequences with numerous haplotypes being described, for example, in rDNA internal transcribed spacer (ITS), *β-tubulin*, *nadh1* and *cox1* (Hansen et al., 2017; Jung et al., 2003; Reeser et al., 2011; Scanu et al., 2014), suggesting that the species may be more variable or outcrosses more frequently than expected.

The global population structure and origins of many *Phytophthora* species, particularly homothallic species, are still poorly understood and *P. pseudosyringae* exemplifies this. The concurrent first findings of *P. pseudosyringae* in Europe and North America and subsequent reporting of the pathogen across large swathes of both continents has not offered any clues to its origins. It has been suggested that it is native to the coastal forests of California and Oregon, as it causes little mortality to its hosts there and geographically overlaps with their range (Hansen et al., 2017; Wickland et al., 2008). However, little mortality is observed on most of its hosts in Europe and an earlier genetic study based on amplified fragment length polymorphisms (AFLPs) and a limited number of isolates suggested it is native to Europe (Linzer et al., 2009).

This study aimed to investigate the genetic diversity and population structure of *P. pseudosyringae*. Genome-wide single-nucleotide polymorphisms (SNPs), produced using genotyping-by-sequencing (GBS), were obtained for isolates from Europe, North and South America. Specifically, we aimed to (1) assess the global genetic diversity and population structure of the pathogen, (2) use migration analysis to elucidate the centre of origin of the pathogen as well as more recent migration and (3) determine whether *P. pseudosyringae* is a purely inbreeding homothallic species or whether outcrossing occurs and to investigate the effect of this on its population structure.

2 | RESULTS

2.1 | Genotyping-by-sequencing

A total of 189 *P. pseudosyringae* isolates from 15 countries were included in the study (Figure 1), with an additional three isolates of *P. ilicis* included as an outgroup for the *P. pseudosyringae* phylogenetic tree. Seven additional isolates representing the remaining three species in Clade 3 as well as single isolates of *P. castaneae* and *P. heveae* as an outgroup to the clade were also included (Table S1). A total of 51,963 SNPs remained in the *P. pseudosyringae*-only dataset after removing loci with >80% missing data and indels and retaining only biallelic polymorphic SNPs, with 72,710 SNPs in the *P. pseudosyringae* and *P. ilicis* dataset and 109,610 SNPs in the complete Clade 3 dataset (including the outgroup species).

After linkage disequilibrium (LD) pruning and minor allele frequency (MAF) filtering, 9107 SNPs were retained in the final *P. pseudosyringae* dataset. Each of the 10 isolates included as technical replicates grouped closely with each other, demonstrating the repeatability and robustness of the protocol.

2.2 | Population structure

In the STRUCTURE analysis, assessment of ΔK (Figure S1) indicated two clusters best described the dataset (Figure 2). Inspection of the Bayesian information criterion (BIC) (Figure S2) from the *K*-means clustering of the discriminant analysis of principal components (DAPC) supported five groups (Figure 3), with the first 21 principal components used after cross-validation. The DAPC groups were highly congruent with the STRUCTURE clusters, yet formed two additional distinct groups of isolates that were highly admixed in the STRUCTURE results (DAPC3 and DAPC4) (Figure 2). In addition, the first STRUCTURE group (orange) was split into two groups by the DAPC (DAPC1 and DAPC2), with DAPC2 occurring only in North America (Figures 1 and 2). The maximum-likelihood tree revealed identical groupings to the STRUCTURE and DAPC results (Figure 4). Although initially three main groups seem evident in the maximum-likelihood tree, analyses (STRUCTURE and SplitsTree results, see above and below) show that DAPC4 is a hybrid group resulting from outcrossing between the main groups and thus inappropriately displayed on the tree. The placement of hybrid groups in phylogenetic trees is

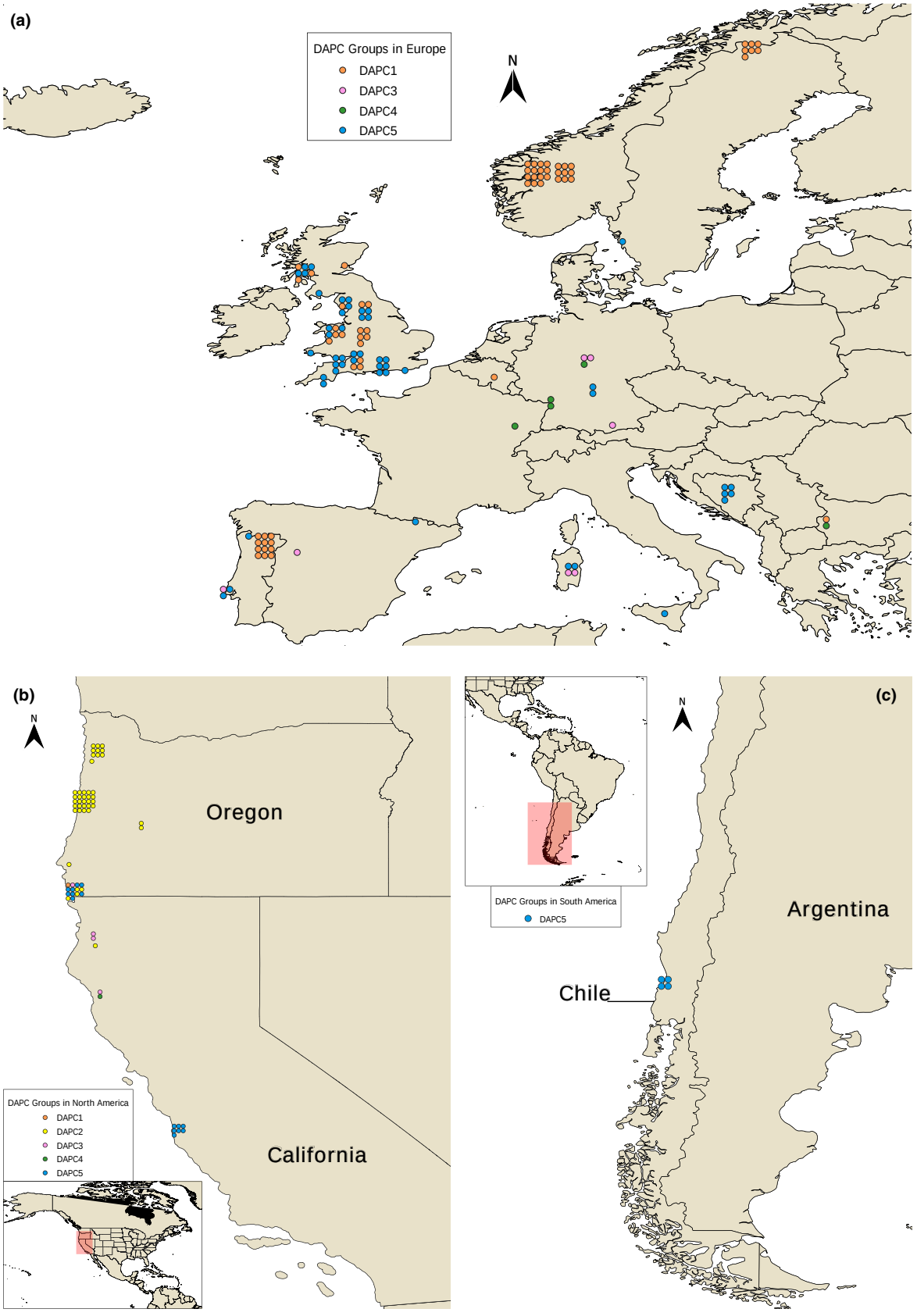


FIGURE 1 Distribution maps of *Phytophthora pseudosyringae* isolates and their discriminant analysis of principal components (DAPC) groups. Each isolate is represented by a dot coloured by its DAPC group. (a) European sampling locations. (b) North American sampling location. (c) South American sampling location. Multiple isolates from the same site are represented as a grid of dots centred on the sampling location.

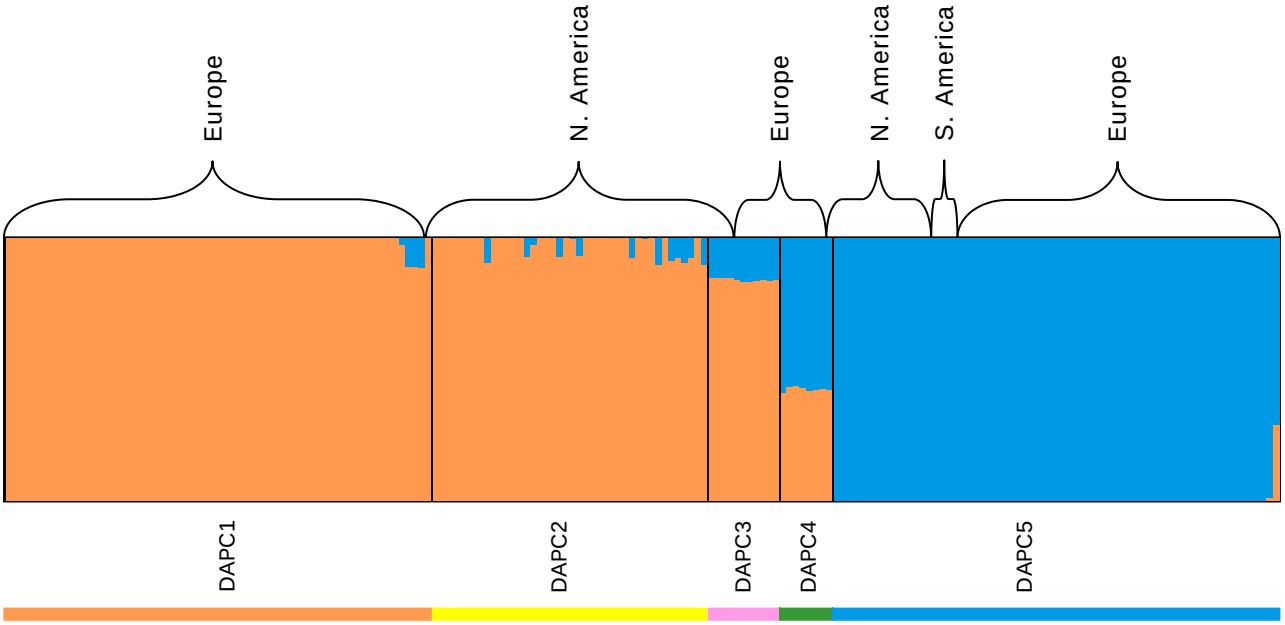
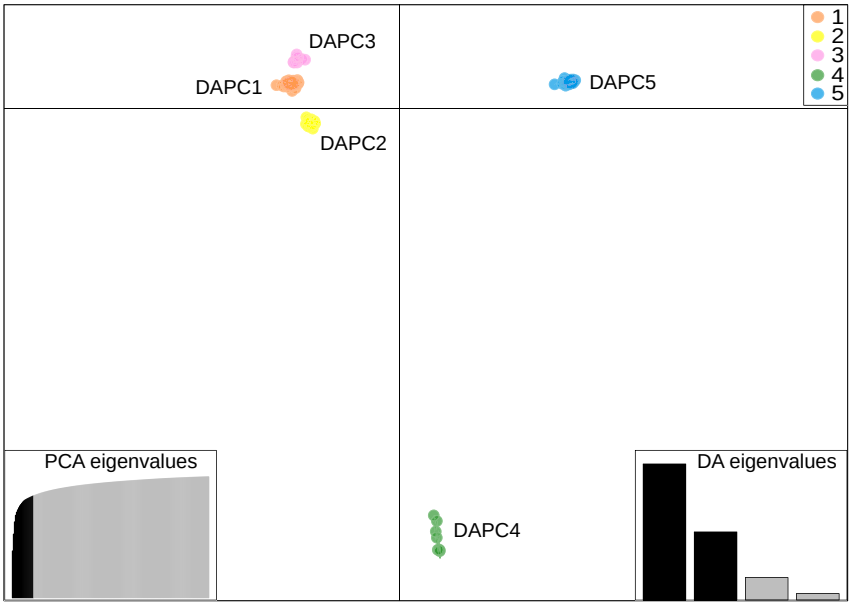


FIGURE 2 Bayesian clustering of *Phytophthora pseudosyringae* isolates using STRUCTURE at $K=2$. Each isolate is represented by a vertical line partitioned into coloured sections that represent the isolate's estimated membership fractions in each cluster. Black lines separate isolates from different discriminant analysis of principal components (DAPC) groups (see main text for details). The horizontal colour bar below the DAPC group name represents the colour used for that group in maps and other figures. The geographic distribution of the group is given above the plot.

FIGURE 3 Scatterplot of the discriminant analysis of principal components (DAPC) of *Phytophthora pseudosyringae* isolates. Individual isolates are represented by dots that are coloured by their DAPC group. At the bottom left, the PCA eigenvalues are represented, with the number of principal components used in the optimized analysis in black. At the bottom right, the Discriminant Analysis (DA) eigenvalues are displayed.



ambiguous; in some cases they are intermediate between the two parental groups while in others they are intermixed or basal to one of the parents (McDade, 1990, 1992; Posada & Crandall, 2001). Therefore, the maximum-likelihood tree displays a split between the two STRUCTURE clusters, with the additional DAPC groups visible as distinct clades in the tree. All isolates in cluster DAPC2, which occurred only in North America, grouped in a single terminal clade nested within DAPC1. As all clustering methods produced highly similar results, the names of the DAPC groups, which provided a finer level of substructuring, were adopted for reference. The phylogenetic tree of the entire clade was congruent with that of the *P. pseudosyringae* dataset and illustrated the phylogenetic relationships of the *P. pseudosyringae* populations to the other species in the clade (Figure S3).

The clusters did not correspond to geographic groups of isolates, with the exception of DAPC2, which was confined to Oregon and northern California, United States. All other clusters were found in both Europe and North America and only DAPC5 was found in South America. However, the majority of isolates from North America were of DAPC2 ($n=42$) with only a small number of isolates from the other groups (1 DAPC1, 4 DAPC3, 1 DAPC4, 15 DAPC5). In contrast, all groups (with the exception of DAPC2) were well represented and

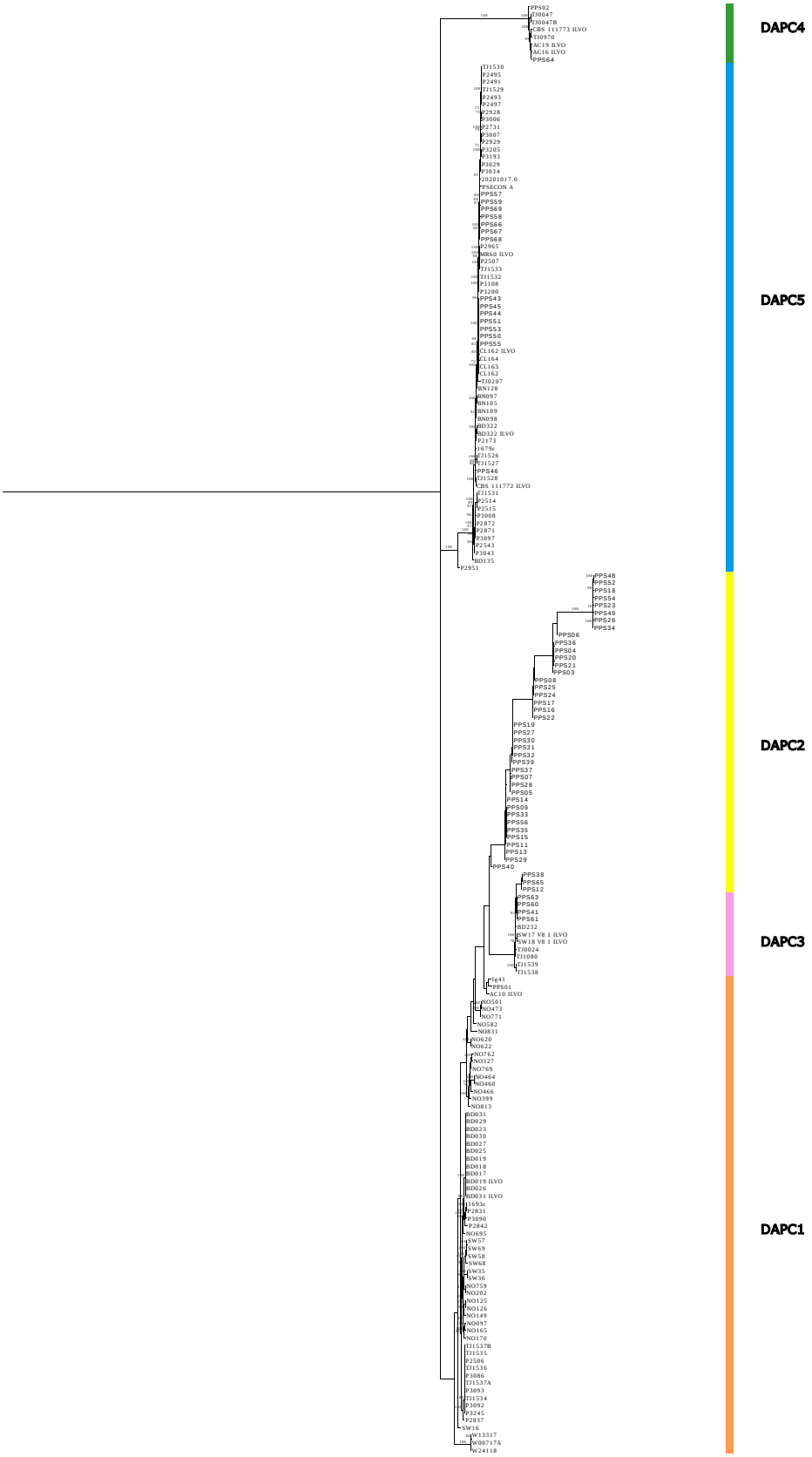


FIGURE 4 Maximum-likelihood tree of *Phytophthora pseudosyringae* isolates inferred using RAxML and 1000 bootstraps. Coloured vertical bars represent the discriminant analysis of principal components (DAPC) group colour used in other figures. Isolate codes from North America are shown in bold, those from South America in italics, and those from Europe in normal font. Only bootstrap values >70 are displayed on the tree. The tree was rooted using *Phytophthora ilicis* as an outgroup (not shown).

distributed in Europe. Only in northern Europe (above 58° latitude) were the number of groups restricted and only DAPC1 was found (Figure 1).

2.3 | Diversity and evidence of outcrossing

The European population contained 39 multilocus lineages, the North American population nine and the South American population only one. Nucleotide diversity (π) was the highest in Europe (9.24×10^{-6}), considerably lower in North America (7.13×10^{-6}) and the lowest in South America (5.63×10^{-6}). Nei's gene diversity was similar in Europe and North America (0.20 and 0.21, respectively) and far lower in South America (0.05).

Initial evidence of outcrossing in the STRUCTURE analysis, seen as groups of admixed individuals (DAPC3 and DAPC4) (Figure 2), was further investigated using network analysis in SplitsTree. The SplitsTree network showed the same groupings as the population clustering analyses, while also revealing reticulation and gene exchange, most likely due to outcrossing. This reticulation is most clearly evident in DAPC4, which is the most evenly admixed group in the STRUCTURE results, as well as DAPC3 (Figure 5).

All groupings in the index of association (I_A) were significantly different ($p<0.05$) based on the Kruskal–Wallis rank sum test. Both European and North American populations of *P. pseudosyringae* are predominantly clonal and/or selfing. However, the I_A results of these populations were significantly lower than that of a purely clonal (100% linkage) or mostly clonal (90% linkage) population (Figure 6), indicating low levels of outcrossing have taken place.

2.4 | Continental origin and migration of *P. pseudosyringae*

The evaluation of all historical divergence models in Migrate-n clearly gave most support to the model in which the North American population diverged from the European population with continued bidirectional gene flow after divergence (Model 8; Table 1). In most model pairs (three out of four) the model in which the North American population diverged from the European one had higher support than the model in which the European population diverged from the North American one. The least-supported pair of models was that with no continuing gene flow in either direction after divergence (Models 1 and 2).

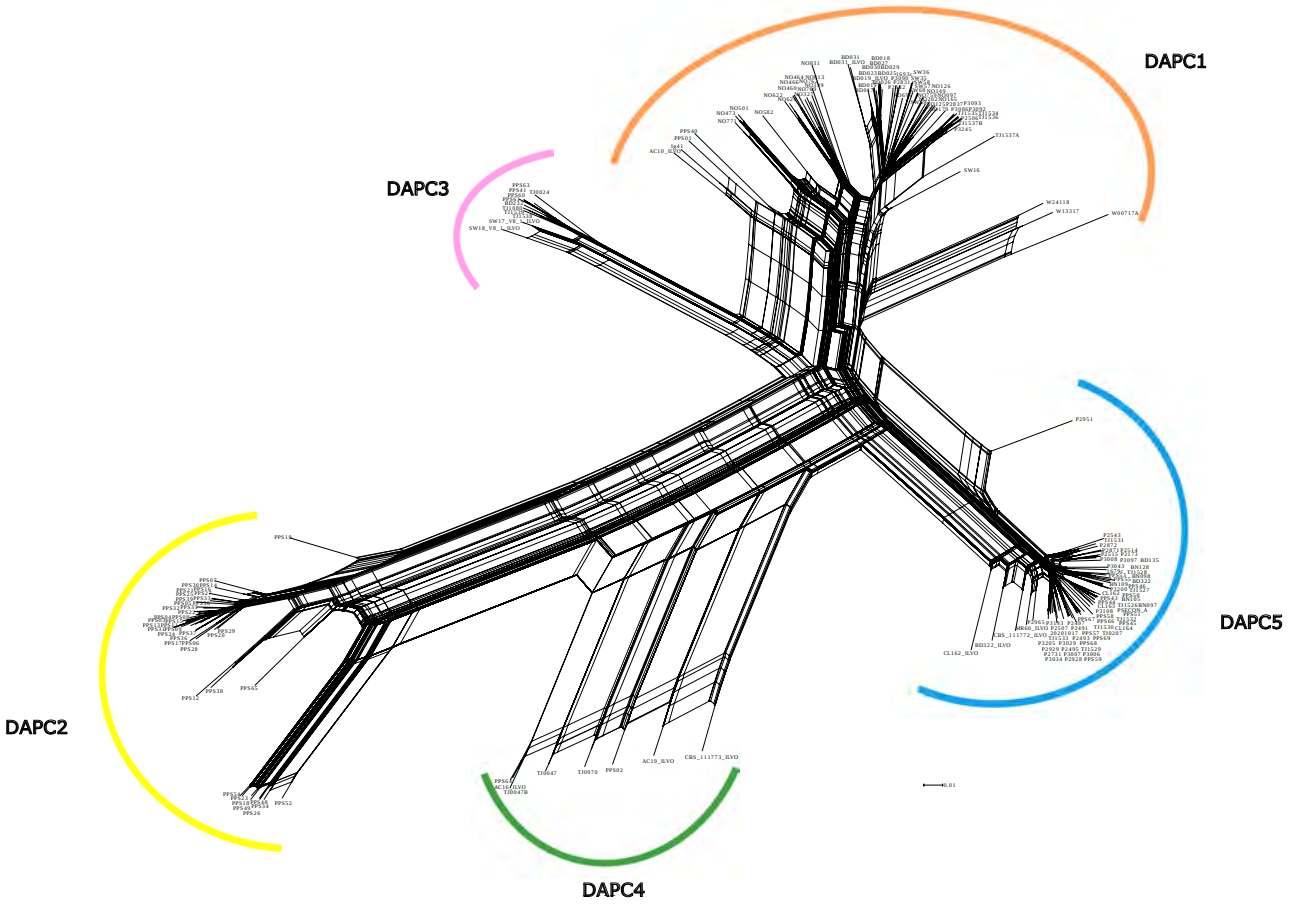


FIGURE 5 SplitsTree network of the *Phytophthora pseudosyringae* isolates constructed with the equal angle algorithm using uncorrected *p*-distances with discriminant analysis of principal components (DAPC) groups outlined and coloured.

Contemporary levels of gene flow, estimated in BayesAss, between Europe and North America were strongly asymmetric. Gene flow from Europe to North America (0.10776 ± 0.01914 *SD*) was over 10 times larger than from North America to Europe (0.00782 ± 0.00458 *SD*).

3 | DISCUSSION

This study provides insights into the population structure, breeding system and origins of *P. pseudosyringae*. Migration analyses reveal that the North American population of the pathogen diverged from the European population, congruent with the pathogen being native to Europe. Gene exchange in both directions, from Europe to North America and vice versa, has occurred and is ongoing; however, contemporary migration from North America to Europe is negligible, with that from Europe to North America being over 10 times greater.

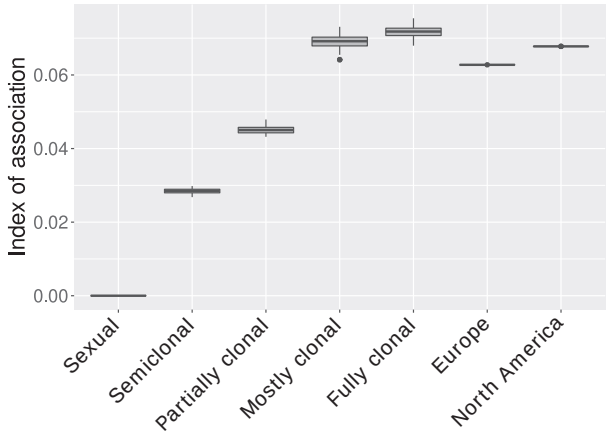


FIGURE 6 Estimation of the degree of linkage disequilibrium (LD) in *Phytophthora pseudosyringae* populations by the index of association (I_A). The first five boxplots represent the I_A for simulated populations under sexual (0% linkage), semiclonal (50% linkage), partially clonal (75% linkage), mostly clonal (90% linkage) and fully clonal (100% linkage) reproduction. All groupings were significantly different ($p < 0.05$) based on the Kruskal–Wallis rank sum test.

The presence of multiple population clusters in North America strongly suggests multiple introductions from Europe, particularly as the two main European clusters are present (DAPC1 and DAPC5). However, clusters arising from outcrossing (DAPC3 and DAPC4) also occur in North America and these may have emerged from outcrossing in situ (i.e., in North America), rather than from introduction of the hybrid clusters directly from Europe. Although not a distinct cluster in the STRUCTURE results, the DAPC revealed a group unique to North America (DAPC2) that is integrated with DAPC1 in the main STRUCTURE results and is nested within it in the phylogenetic tree. Nonetheless, the presence of a unique group in North America could be due to the pathogen being present long enough to slightly diverge genetically. Populations that colonize new habitats are exposed to strong selection pressures due to novel abiotic conditions, environmental pressures and interspecific interactions, which are exacerbated by the stresses of encountering and infecting suitable new host species, reproducing and dispersing (Hereford, 2009; Parker & Gilbert, 2004). These selection pressures may lead to rapid adaptation and accelerated evolution (Parker & Gilbert, 2004), thereby giving rise to a genetically differentiated group. Although it is unknown how *P. pseudosyringae* was introduced to North America, it seems likely that the plant trade played an important role, particularly as the species has been found in plant nurseries in both Europe and the United States (Anonymous, 2006; Jung, 2009; Jung et al., 2016; Yakabe et al., 2009). Liebhold et al. (2012) estimated that c. 70% of non-native forest pests in the United States were introduced through the plant trade and it is well established that numerous *Phytophthora* species have been, and continue to be, successfully spread via the plant trade, with *P. ramorum* perhaps the best-known example (Goss et al., 2009, 2011; Jung et al., 2016).

In contrast to the multiple introductions to North America, the South American population, although only represented by a few isolates, belongs to a single population cluster, suggesting a single introduction. The Chilean isolates all belong to a population cluster that is widespread and common in Europe, while limited in North

TABLE 1 Log Bayes factor comparison of the migration models of *Phytophthora pseudosyringae* using Migrate-n v. 5.0.4.

Model	Model schematic[a]	Log (mL)	Log Bayes factor	Model probability	Model ranking
Model 8	E ↔ N.A.	−44102.83	0.00	1.0000	1
Model 7	N.A. ↔ E	−44154.01	−51.18	0.0000	2
Model 6	E ← N.A.	−44771.04	−668.21	0.0000	3
Model 3	N.A. → E	−44782.57	−679.74	0.0000	4
Model 4	E → N.A.	−44797.54	−694.71	0.0000	5
Model 5	N.A. ← E	−44809.30	−706.47	0.0000	6
Model 9	Panmictic (E + N.A.)	−45582.01	−1479.18	0.0000	7
Model 2	E ‖ N.A.	−46910.04	−2807.21	0.0000	8
Model 1	N.A. ‖ E	−46914.71	−2811.88	0.0000	9

[a]The population on the right is derived from the population on the left. E = Europe; N.A. = North America. Arrows indicate direction of gene flow post-divergence. ‖ indicates no gene flow post-divergence.

America, supporting a European origin of the species. The exact route of introduction to South America, however, whether directly from Europe or via North America, is unknown and would require more isolates from South America for a robust analysis.

Revealing the timing of introductions can be challenging using only molecular data and is particularly problematic for a homothallic species with high levels of selfing; therefore, using historical records is often a pertinent additional method of inference. In the United States *P. pseudosyringae* was first detected in California in the early 2000s before it was formally described (Rizzo et al., 2002; Wickland et al., 2008). However, a PCR-based study of symptomatic and asymptomatic herbarium specimens of California bay laurel and tanoak, the most common hosts of *P. pseudosyringae* in California, collected between 1861 and 1984 did not detect the pathogen and therefore support a non-native origin of the pathogen (Monahan et al., 2008). Although first officially described from Europe in 2003 *P. pseudosyringae*, as its name suggests, is morphologically extremely similar to *P. syringae* (Jung et al., 2003). Many isolates previously identified as *P. syringae* have since been redesignated as *P. pseudosyringae*, including numerous isolates from beech (Jung et al., 2003). As beech has not been confirmed as a host of *P. syringae* using molecular methods it suggests older reports of *P. syringae* on beech may in fact be *P. pseudosyringae*, including those of Day (1938) (Jung et al., 2003). This implies that the first record of *P. pseudosyringae* in Europe could be over 85 years old, in agreement with its putative native origin.

The epidemic nature of the pathogen in North and South America also suggests it is non-native to these areas, as pathogens introduced into new environments with non-adapted hosts can be severely destructive (Stukenbrock & McDonald, 2008). In Chile *P. pseudosyringae* causes severe damage on native *Nothofagus* species (Fajardo et al., 2017; González et al., 2024), while in California and Oregon native bay laurel, tanoak and coast live oak are the species most often affected (Wickland et al., 2008). As symptoms are identical to those of *P. ramorum* it is difficult to disentangle the extent of the damage caused by each species in western North America (Wickland et al., 2008). Undoubtedly *P. ramorum* is the more destructive pathogen, yet damage by *P. pseudosyringae* is almost certainly under-reported. Conversely, *P. pseudosyringae* causes limited damage and is considered a relatively benign *Phytophthora* in much of Europe. Usually isolated from rivers and streams, soil and the rhizosphere of forest trees, it often causes little obvious damage on native hosts (Jung et al., 2003). Such behaviour is typical of co-evolved hosts and pathogens and supports Europe being the centre of origin of the species.

Nevertheless, *P. pseudosyringae* does cause serious damage in certain regions of Europe, most notably in the United Kingdom. This damage is, however, primarily on non-native hosts such as *Nothofagus* species, native to South America, and Japanese and hybrid larch (*Larix kaempferi* and *L.* × *eurolepis*) (Scanu & Webber, 2016; authors' unpublished data) and thus also constitutes novel host–pathogen interactions. In this case a non-native host has been introduced into the native range of the pathogen, a situation well known to be able to result in disease epidemics (Parker & Gilbert, 2004). However, it must also be considered that the United Kingdom could be outside the native range of *P. pseudosyringae* in Europe, as the United Kingdom, due to the Pleistocene glaciations, has an impoverished flora compared to the rest of Europe (Ingrouille, 2012).

P. pseudosyringae belongs to *Phytophthora* Clade 3, a small, morphologically and behaviourally cohesive clade currently containing only four other species (*P. psychrophila*, *P. ilicis*, *P. nemorosa* and *P. pluvialis*), all of which are homothallic. *P. psychrophila* and *P. ilicis* are likely to be native to Europe (Pérez-Sierra et al., 2013; Scanu et al., 2014). *P. psychrophila* is a weak pathogen widespread in *Quercus* forests, particularly around the Mediterranean (Jung et al., 2002; Pérez-Sierra et al., 2013; Seddaiu et al., 2020). *P. ilicis*, known exclusively from holly (*Ilex* spp.), has been recorded from North America but only in horticultural or park settings whereas it is widespread in Europe, especially the natural montane forests of Sardinia and Corsica (Hansen et al., 2017; Scanu et al., 2014). However, the centre of origin of the remaining two species in Clade 3, *P. nemorosa* and *P. pluvialis*, is less clear. *P. nemorosa* has only been reported from Oregon and California and Hansen et al. (2017) suggest it may be indigenous, or at least naturalized, there, yet it is genetically highly uniform and a population study by Linzer et al. (2009) suggests that it is a recent introduction to the region. Of note is that *P. nemorosa* has recently been detected once in Belgium (Kurt Heungens, personal communication), as well as in Croatia on nursery stock imported from another EU country (Zeljko Tomić, personal communication). The final species in the clade, *P. pluvialis*, was first reported from Oregon (Reeser et al., 2013), has been introduced to New Zealand (Dick et al., 2014; Tabima et al., 2021) and has recently been reported from the United Kingdom (Pérez-Sierra et al., 2022) and Belgium (Pirronitto et al., 2024). The species was believed to originate from western North America, but it is possible that its origins lie elsewhere, particularly given its destructive behaviour to North American conifer species both in North America and the United Kingdom. Evidently the centre of origin of many species in Clade 3 is still equivocal and based mainly on conjecture, with some species hypothesized to be from Europe and others from North America. Future research may clarify these origins as more isolates, and possibly species, are obtained from both continents and may reveal an ancient Laurasian origin of the clade.

Within continents, *P. pseudosyringae* populations appeared to be highly clonal and without clear geographical structure. Lack of clear geographical structure has been found in population studies of other homothallic *Phytophthora* species (Aguayo et al., 2013; Cooke et al., 2005; Schoebel et al., 2014; Tsykun et al., 2022), although only a few such studies have been conducted. This lack of geographical structure is probably linked to the high levels of selfing exemplified by these species combined with clonal reproduction via asexual zoospores. However, the diversity and traits exhibited by the *P. pseudosyringae* population cannot be explained by strict selfing. The admixed groups revealed by the STRUCTURE plot and SplitsTree network affirm the lack of complete LD and indicate an important component of outcrossing has shaped the population.

It is known that homothallic species can outcross, with outcrossing rates in the laboratory often ranging between 1% and 10% of oospore progeny, yet rates up to 76% have been recorded (Bhat & Schmitthenner, 1993; Förster et al., 1994; Francis & St. Clair, 1993, 1997; Whisson et al., 1994). The rate of outcrossing in natural settings is unknown but is also likely to be low. Highly successful laboratory methods of inducing outcrossing include mixing zoospores in liquid media (Bhat & Schmitthenner, 1993) and *Phytophthora* clades with many aquatic species have a high propensity for hybridization, that is, outcrossing between species, (e.g., Clade 6, which contains predominantly homothallic or sterile species), suggesting that an aquatic lifestyle promotes outcrossing and hybridization (Burgess, 2015; Hüberli et al., 2013; Jung et al., 2017; Jung, Durán, et al., 2018; Nagel et al., 2013; Oh et al., 2013). The high retrieval rate of *P. pseudosyringae* from rivers and streams illustrates this species is well suited to riparian habitats, which may well help explain the level of outcrossing observed. Nonetheless, the level of outcrossing is unknown for any of the homothallic Clade 3 species, and, to date, no interspecific hybridization, that is, outcrossing between species, is known to include any of its members (Van Poucke et al., 2021). Selfing and clonal reproduction are without a doubt the most common forms of reproduction for *P. pseudosyringae*, yet low levels of outcrossing have had a disproportionate effect on its population structure, creating unique groups that, if ecologically fit, are then easily and rapidly spread through clonal reproduction and selfing.

The diversity in gene regions (ITS, *β-tubulin*, *nadh1* and *cox1*) found by other authors (Hansen et al., 2017; Jung et al., 2003; Reeser et al., 2011; Scanu et al., 2014) suggested diversity in *P. pseudosyringae* was higher or that outcrossing occurred more often than expected. This has been confirmed with the GBS data in this study and the population clusters identified here correlate with the groups formed by the single gene regions, at least in the limited number of isolates included in both studies. While the detailed DAPC groups may not be discernible using sequencing of single genes, the main two STRUCTURE groups are. Affirmation of this with a larger number of isolates would allow simple identification of these populations. The two main STRUCTURE population clusters may have slightly different habitat preferences or life histories. In one population cluster (consisting of DAPC1 and DAPC2) a preponderance of isolates was obtained from rivers or streams; in DAPC1 almost half (49%) and in DAPC2 most (79%) of the isolates. Conversely, in the other main population cluster (DAPC5) less than 9% were obtained from watercourses. This is almost certainly skewed by sampling strategy but does indicate a trend to be explored further. The difference could be linked to variation in the proportion of caducous versus non-caducous sporangia produced by each group, making one group more suited to the riverine environment. Variation in other factors among the groups, particularly virulence and host range, should also be investigated to help quantify the risk each population poses to forests worldwide. While species of *Phytophthora* pose threats to plants within their native ranges, it is through invasions that *Phytophthora* has made the greatest impact on agriculture and ecosystems. Insights into the populations, biogeography and evolution of this important forest pathogen have far-ranging implications in the continuing battle against invasive species.

4 | EXPERIMENTAL PROCEDURES

4.1 | Isolate selection and DNA extraction

In total 189 isolates of *P. pseudosyringae* were selected from across the pathogen's known range in Europe and North America. Isolates from Chile, the only country in South America from which the pathogen is known, were also included, as were isolates from Belgium and Bosnia, countries that have not previously reported presence of the pathogen (Table S1). Details of how the isolates were isolated and identified are given in Supplementary File S1. Three isolates of *P. ilicis*, a relative of *P. pseudosyringae* from Clade 3, were included for use as an outgroup for the *P. pseudosyringae* phylogenetic tree. Representative isolates from each of the species in *Phytophthora* Clade 3 were incorporated to produce a phylogeny of the entire clade, using *P. castaneae* and *P. heveae* as an outgroup (Table S1).

Mycelium for DNA extraction was obtained by growing isolates in 17 mL 5% clarified V8 juice broth for 1 week at 20°C in a shake culture. Mycelium was then rinsed thoroughly with sterile distilled water and vacuum-dried on a Whatman no. 1 filter paper and subsequently homogenized using lysing matrix A (MP Biomedicals) and a Precellys Evolution homogenizer (Bertin Technologies). The Nucleospin Plant II kit (Macherey-Nagel) was used to extract DNA according to the manufacturer's instructions, using extraction buffer PL1 and eluted into 50 μL. Ten isolates were included as technical replicates to assess the reproducibility of the GBS protocol. Separate DNA extractions were carried out for these isolates and the independently prepared libraries were included in different sequencing runs.

4.2 | GBS, read processing, SNP calling and data filtering

GBS libraries were prepared according to the method described in Van Poucke et al. (2021) and Mullett et al. (2023), which followed an approach developed by Elshire et al. (2011) and Poland et al. (2012). Briefly, this consisted of digestion of genomic DNA with PstI and HpaII restriction enzymes, annealing of barcodes and adaptors and fragment amplification. Groups of 95 isolates, each isolate having a unique barcode, were pooled and paired-end sequenced (2 × 150 bp) using a NovaSeq6000 (Illumina).

The sequences were preprocessed using the custom-made pipeline of Van Poucke et al. (2021), available at https://gitlab.com/ahaegeman/GBS_Phytophthora and at Zenodo with doi: https://doi.org/10.5281/zenodo.3363287. This pipeline consisted of (1) demultiplexing of the reads using GBSX v. 1.1.5 (Herten et al., 2015), (2) trimming of adapters and the remainder of the restriction sites using Cutadapt v. 1.16 (Martin, 2011) and FastX toolkit v. 0.0.14, (3)

merging of the forward and reverse reads with PEAR v. 0.9.8 (Zhang et al., 2014) and (4) quality filtering using FastX toolkit, prinseq-lite (Schmieder & Edwards, 2011), OBITOOLS v. 1.2.5 (Boyer et al., 2016) and Pairfq v. 0.14.

The preprocessed reads were then mapped to the *P. pseudosyringae* genome (isolate SCRP734, GCA_019155715.1) (Thorpe et al., 2021) using BWA-MEM v. 0.7.15 (Li, 2013). Samtools v. 1.14 (Li et al., 2009) was used to convert the resulting sam file to bam format, sort and index it. SNPs and haplotypes were called using GATK HaplotypeCaller v. 4.2.5.0, merged into a single gvcf file using GATK CombineGVCFs and then jointly genotyped using GATK GenotypeGVCFs (McKenna et al., 2010). After visual inspection of read depths using violin plots and missing data using heat maps using VCFR v. 1.10.0 (Knaus & Grünwald, 2017) loci with a read depth of <5 and >60 and >80% missing data were removed. VCFR was also used to remove nonpolymorphic sites and indels and retain only bi-allelic SNPs.

4.3 | Analysis of the genetic structure

Alleles in LD are redundant and can adversely affect many population clustering approaches (Abdellaoui et al., 2013; Calus & Vandenplas, 2018; Malomane et al., 2018; Privé et al., 2020). LD-based SNP pruning and MAF filtering were therefore done on the dataset for population structure analyses (STRUCTURE and DAPC). This was conducted in Plink v. 1.9 (Chang et al., 2015; www.cog-genomics.org/plink/1.9/) using a 50 SNP window size, a 5 SNP step size and a variance inflation factor [$1/(1-r^2)$] of 1.5 (setting --indep 50 5 1.5) and a MAF of 1%. Three complementary population analysis methods were implemented: (1) STRUCTURE, (2) DAPC and (3) maximum-likelihood phylogenetic trees.

STRUCTURE v. 2.3.4 (Falush et al., 2003) estimates the probability of genotypes being distributed into *K* number of clusters. The program implements a Bayesian, model-based clustering algorithm that maximizes Hardy–Weinberg equilibrium and minimizes LD within the clusters (Pritchard et al., 2000). Twenty independent runs of $K = 1$–10 were carried out, each with a burn-in of 100,000 iterations followed by 500,000 data-collecting iterations. The STRUCTURE model used no priors (i.e., no information on geographical location or host was provided), correlated allele frequencies and allowed admixture among populations. STRUCTURE multi PBS Pro scripts (https://github.com/V-Z/structure-multi-pbspro) were used to parallelize the analysis. The ΔK method of Evanno et al. (2005) was used to assess the optimum value of *K*, implemented in CLUMPAK (Kopelman et al., 2015), which was also used to align all optimum *K* STRUCTURE runs to the permutation with the highest *H*-value. DISTRUCT v. 1.1 (Rosenberg, 2004) was used to visualize the CLUMPP output.

DAPC, implemented in the R package adegenet v. 2.1.3 (Jombart & Ahmed, 2011; Jombart et al., 2010), was used to complement the Bayesian approach used in STRUCTURE. DAPC identifies clusters (*K*) of genetically related individuals by minimizing variation within groups and maximizing variation between groups while making no genetic assumptions (e.g., population models or data structure) (Jombart et al., 2010). Prior to the DAPC itself a sequential *K*-means procedure followed by an assessment of the BIC is used to assess the optimal number of clusters. Determination of the optimal number of principal components to retain in the analysis was done by cross-validation (Jombart & Collins, 2015).

Phylogenetic trees are a standard approach to reveal underlying population structure, thus RAxML v. 8.2.12 (Stamatakis, 2014) was used to produce a maximum-likelihood phylogenetic tree with the full dataset (i.e., prior to LD pruning and MAF filtering), using *P. ilicis* as an outgroup. A phylogenetic tree of the entire clade was also produced using *P. castaneae* and *P. heveae* as an outgroup. Ascbias (https://github.com/btmartin721/raxml_ascbias) was used to remove all invariant SNPs from the datasets. The GTRCAT model without rate heterogeneity with a correction for ascertainment bias (ASC_GTRCAT), together with the Lewis correction for ascertainment bias (asc-corr = lewis) were used and 1000 bootstrap replicates were performed. Visualization of the output was done in Figtree v. 1.4.4 (Rambaut, 2018).

4.4 | Mode of reproduction, outcrossing and diversity

The index of association (I_A), a measure of LD, was used to infer the predominant mode of reproduction (Brown et al., 1980; Milgroom, 1996) and was calculated in poppr v. 2.9.3 (Kamvar et al., 2014). The I_A was first calculated on 1000 simulated datasets, constructed using adegenet v. 2.1.3 (Jombart & Ahmed, 2011), with 0%, 50%, 75%, 90% or 100% linkage representing sexual, semiclonal, partially clonal, mostly clonal and fully clonal populations, respectively. As a single SNP is unlikely to produce a new multilocus genotype, particularly as missing data and genotyping error are common in high-throughput sequencing data, individual genotypes were collapsed into multilocus lineages using the average neighbour algorithm (genetic distance cut-off of 0.04706011) (Kamvar et al., 2015) implemented in poppr. The I_A was calculated on the multilocus lineage dataset for the European and North American populations and compared to that of the simulated datasets (Tabima et al., 2018). The South American population was excluded due to its small sample size. After testing the data for normality using the Shapiro–Wilk's test, a Kruskal–Wallis rank sum test and a post hoc rank comparison was conducted in R (R Development Core Team, 2020).

To investigate reticulate evolutionary relationships and the possibility of outcrossing SplitsTree v. 4.16.2 (Huson & Bryant, 2006) was used to construct a phylogenetic network using the LD-pruned and MAF-filtered dataset implementing the neighbour-net and equal angle algorithms using uncorrected *p*-distances with heterozygous ambiguities averaged and normalized.

For each population (Europe, North America, South America) Nei's gene diversity (H_s) was calculated using hierfstat v.

0.5–11 (Goudet, 2005) and nucleotide diversity (π) calculated using a 100,000 window in VCFtools v. 0.1.16 (Danecek et al., 2011).

4.5 | Modelling of evolutionary history and migration

Models of historical migration to elucidate the origin of *P. pseudosyringae*, North America or Europe, were tested using the coalescent-based program Migrate-n v. 5.0.4 (Beerli and Felsenstein, 1999, 2001). VcfR2migrate, implemented in the package vcfR (Knaus and Grünwald, 2017), was used to convert the VCF file to Migrate-n hapmap format. Forty randomly sampled isolates per population (North America and Europe) were selected to make the runs computationally tractable, the same 40 isolates were selected in all runs. Preliminary runs were used to establish the priors for the mutation-scaled population size (θ), mutation-scaled migration (M) and divergence (Δ) parameters. Following the test runs the parameters were uniform, set to a maximum $\theta = 10$, maximum $M = 1000$ and maximum $\Delta = 500$. After a burn-in of 200,000 steps, 20,000 steps were recorded every 100 steps for a total sampling of 2,000,000 genealogies. Four heated chains were run with temperatures of 1.0, 1.5, 3.0 and 1,000,000. The marginal likelihood of each model was compared using thermodynamic integration following Beerli and Palczewski (2010) and Palczewski and Beerli (2014), calculated using the python script 'bf.py', from Beerli et al. (2019). This method compares and ranks the Bézier log marginal likelihood between different models and calculates their probability based on the Bayes factor.

A total of nine models were evaluated to elucidate the geographical origin of *P. pseudosyringae*, either North America or Europe. The following four scenarios were run in models with both the North American and European population as the parental population: (1) one population diverged from the other with no subsequent gene flow in either direction (Models 1 and 2); (2) one population diverged from the other with subsequent unidirectional gene flow from the parental population to the diverged population (Models 3 and 4); (3) one population diverged from the other with subsequent unidirectional gene flow from the diverged population to the parental population (Models 5 and 6); (4) one population diverged from the other with subsequent bidirectional gene flow, that is, gene flow from the parental population to the diverged population and vice versa (Models 7 and 8). In even-numbered models, the North American population diverged from the European population; in odd-numbered models, the European population diverged from the North American population. An additional model in which both populations belonged to a single panmictic population was also tested (Model 9).

Contemporary migration rates, over the last few (1–3) generations, between North America and Europe were estimated using Bayesian inference in the disequilibrium-based program BayesAss v. 3.0.4 (Mussmann et al., 2019; Wilson and Rannala, 2003). Starting mixing parameters for migration rates (−m), allele frequencies (−a) and inbreeding coefficients (−f) were obtained by first running BA3-SNPs-autotune (Mussmann et al., 2019) with 100,000 generations and a burn-in of 10,000. BayesAss was then run with the resulting mixing parameters (−m 0.1; −a 0.325, −f 0.0094) using 10 million MCMC generations, a burn-in of 1,000,000 generations and a sampling interval of 1000. Five independent runs, each with a different random seed, were performed and their convergence was examined by comparing their traces in Tracer v. 1.6 (Rambaut et al., 2018).

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DATA AVAILABILITY STATEMENT

Raw sequence reads are deposited in the NCBIs SRA at https://www.ncbi.nlm.nih.gov/sra/ with accession BioProject PRJNA962869. Custom scripts for pre-processing of the raw data were used from Van Poucke et al. (2021) and are available at https://gitlab.com/ahaegeman/GBS_Phytophthora and at Zenodo with doi: https://doi.org/10.5281/zenodo.3363287.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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