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Molecular phylogenomics and population structure of

Phytophthora pluvialis

Javier F. Tabima^{1,2}, Lilah Gonen¹, Mireia Gómez-Gallego^{3,4,5}, Preeti Panda^{3,6}, Niklaus J.

Grünwald⁷, Everett M. Hansen¹, Rebecca McDougal³, Jared M. LeBoldus^{1,8*}, Nari M.

Williams^{3,6*}

¹ Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis OR 97331, USA.

² Department of Biology, Clark University, The Lasry Center for Bioscience, Worcester, MA 01610, USA.

³ New Zealand Forest Research Institute (Scion), 49 Sala Street, Te Papa Tipu Innovation Park, Private Bag 3020, Rotorua 3046, New Zealand.

⁴ Department of Forest Mycology and Plant Pathology, Swedish University of Agricultural Sciences, Box 7026, 750 07 Uppsala, Sweden.

⁵ UMR IAM – Interactions Arbres-Microorganismes, Université de Lorraine, INRAE, Nancy 54000, France

⁶ Department of Pathogen Ecology and Control, Plant and Food Research, Private Bag 1401, Havelock North 4130, New Zealand

⁷ USDA Agricultural Research Service, Horticultural Research Unit, 3420 NW Orchard Ave, Corvallis, OR 97331, USA.

⁸ Department of Forest Engineering, Resources and Management, Oregon State University, Peavy Forest Science Center, Corvallis OR 97331, USA.

*** Corresponding author:** Jared M. LeBoldus and Nari M. Williams share the role of corresponding author.

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ABSTRACT

Phytophthora pluvialis is an oomycete that was first isolated from soil, water, and tree foliage in mixed Douglas-fir - tanoak forests of the US Pacific Northwest (PNW). It was then identified as the causal agent of red needle cast (RNC) of radiata pine (*Pinus radiata*) in New Zealand (NZ). Genotyping-by-sequencing (GBS) was used to obtain 1,543 single nucleotide polymorphisms (SNPs) across 145 *P. pluvialis* isolates to characterize the population structure in the PNW and NZ. We tested the hypothesis that *P. pluvialis* was introduced to NZ from the PNW using genetic distance measurements and population structure analyzes among locations between countries, . The low genetic distance, population heterozygosity, and lack of geographic structure in NZ, suggest a single colonization event from the US followed by clonal expansion in NZ. The PNW Coast Range was proposed as a presumptive center of origin of the currently known distribution of *P. pluvialis* based on its geographic range and position as the central cluster in a minimum spanning network. The Coastal cluster of isolates were located at the root of every US cluster, and emerged earlier than all NZ clusters. The Coastal cluster had the highest degree of heterozygosity ($H_s = 0.254$) and median pairwise genetic distance (0.093) relative to any other cluster. Finally, the rapid host diversification between closely related isolates of *P. pluvialis* in New Zealand, indicate that this pathogen has the potential to infect a broader range of hosts than is currently recognized.

INTRODUCTION

The introduction of exotic plant pathogens poses risks to agroecosystems, natural environments, and human health (Fisher et al. 2012, Wingfield et al. 2015, Corredor-Moreno and Saunders 2019, Scott et al. 2019). For example, the introduction of *Phytophthora infestans* (Montagne) de Bary to Europe from Mexico in the nineteenth century, caused the Irish Potato Famine. This famine was a result of the near-total failure of Ireland's primary food staple, the potato, following an outbreak of *P. infestans*. The loss of potatoes led to widespread starvation and the Irish diaspora (Goss et al. 2012). Recently, introduced plant pathogens such *Phytophthora ramorum* Werres, De Cock & Man in 't Veld, the cause of sudden oak death (Cobb et al. 2012), and *Cronartium ribicola* J.C. Fisch, the cause of white pine blister rust (Kinloch 2003), have had devastating impacts to natural ecosystems. These and other reported introductions of plant pathogens have been linked to human-mediated movement of infected plants and infested soil (Kamvar et al. 2015; Wingfield et al. 2015; Tabima et al. 2020). Understanding the source-sink dynamics of these introductions informs policy, prevents future introductions, and can be used to mitigate disease impacts.

Microorganisms coevolve with sympatric plant species, and can cause little to no disease in their hosts within their native range (Stukenbrock and McDonald 2008). When their geographic distribution shifts, they come into contact with naïve plant species, potentially leading to new disease outbreaks (Grünwald and Flier 2005, Stukenbrock and McDonald 2008). The source of exotic pathogens can provide important information about the genetic diversity of the microbe, its native hosts, and potential sources of resistance. For example, the establishment of the center of origin of *P. infestans* in Mexico led to the identification of wild *Solanaceae* spp. with co-evolved resistance to the pathogen. These species have been used to identify resistance genes that have been integrated into commercial potato varieties (Grünwald and Flier 2005). In

the case of forest ecosystems, *Bretziella fagacearum* (T. W. Bretz) J. Hunt, the causal agent of oak wilt, is another example. The current range of *B. fagacearum* is restricted to the US, but population genetic analyses indicate that the genetic diversity of the species is very limited in the US and likely a result of a single clonal introduction. It has therefore been hypothesized to have been introduced from either Mexico, Central America, or northern South America despite the lack of reports from these regions (Juzwik et al. 2008).

A similar example of long-distance movement of a plant-associated microbe is *Phytophthora pluvialis* Reeser, Sutton, & Hansen. This oomycete was first isolated from baited streams, soil, and canopy drip in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirbel] Franco)/tanoak (*Notholithocarpus densiflorus* [Hook. & Arn.] Manos, Cannon, & Oh) forests in southwestern Oregon (OR) (Reeser et al. 2013, Hansen et al. 2017). In 2014, *P. pluvialis* was confirmed as the cause of red needle cast (RNC), a disease of radiata pine (*Pinus radiata* [D. Don]) that was first identified on the North Island of New Zealand (NZ) in 2008 (Dick et al. 2014). Radiata pine is a tree species native to coastal California (CA) and was introduced to NZ in the nineteenth century for use in plantation forestry (Burdon et al. 2017). Symptoms of RNC start as discrete olive-colored lesions and black resinous bands on needles. As the disease progresses the lesions change color from yellow to red brown. Needles on affected trees eventually turn a reddish color and senesce. Premature defoliation of the lower crown and occasionally the entire tree is observed. In addition, *Phytophthora pluvialis* has been isolated from olive-colored Douglas-fir needles growing near radiata pine plantations in NZ (Gómez-Gallego et al. 2019).

On the west coast of the United States (US) *P. pluvialis* has been isolated from scattered regions in Washington (WA), Oregon (OR), and CA (Hansen et al. 2015; Gómez-Gallego et al.

2019; Brar et al. 2018). A variety of approaches have been used to collect isolates including canopy drip, symptomatic needle tissue, soil baiting, and stream baiting (Gómez-Gallego et al. 2019; Reeser et al. 2013, Hansen et al. 2017). In NZ, collections have been made from Douglas-fir plantations across both islands (Gómez-Gallego et al. 2019). The symptoms on Douglas-fir are more cryptic than those found on radiata pine. Isolations can frequently be made from olive-colored and asymptomatic needles. Since its initial description, *P. pluvialis* has been isolated from symptomatic Douglas-fir and tanoak in the US and radiata pine, Douglas-fir, patula pine (*Pinus patula* Schiede ex Schltdl. & Cham.), and Eastern white pine (*Pinus strobus* L.) in NZ.

The discovery of *P. pluvialis* in both OR and NZ suggests human-mediated migration across the Pacific Ocean. Like other Clade 3 *Phytophthora* spp., *P. pluvialis* disperses aerially over relatively short distances, via rain splash and wind-driven rain (Dick et al. 2014, Hansen et al. 2017). Recent efforts to identify the pathway of introduction of *P. pluvialis* used 28 single nucleotide polymorphisms (SNPs). The analysis suggested two introductions of *P. pluvialis* from OR to NZ (Brar et al. 2018). The authors hypothesized that the introduction was likely due to movement of soil, water, or asymptomatic plant material (Brar et al. 2018). Similar mechanisms of anthropogenic-mediated spread have been suggested for *P. ramorum* and other plant pathogens (Davidson et al. 2008, Grünwald et al. 2012). In order to test the hypothesis of multiple introductions the authors suggested that increasing the number of SNP and the geographic range of the sampling would be necessary.

Building on Brar et al. (2018), the sampling in the forests of the US PNW was expanded and additional samples from NZ were added. These samples were collected from various hosts across the current distribution of the pathogen. Our overarching goal was to develop a better understanding of the population dynamics of *P. pluvialis* in NZ and the US. The specific

objectives were to: 1) characterize the population structure of *P. pluvialis* in the US and NZ; 2) study the genetic diversity of *P. pluvialis* at the state/location level within these geographic regions; and 3) examine the interaction between genetic structure and host range. To meet these objectives 157 isolates of *P. pluvialis* were genotyped using genotyping-by-sequencing (GBS) and a population genomics framework was used to address the objectives.

MATERIALS AND METHODS

Isolate collection. A total of 157 curated isolates of *P. pluvialis* from NZ (n=91) and the US (n=66) were selected for genotyping. Selections were made in order to maximize the temporal (2008-2018) and geographic range of sampling (Supp. Table 1). In NZ samples were collected from across the North and South Island from 14 regions as defined by Crosby (1976): Northland (ND; n = 5), Gisborne (GB; n = 36), Bay of Plenty (BP; n = 11), Waiarapa (WA-NZ; n = 5), Rangitikei (RI; n = 3), Taupo (TO; n = 7), Taranaki (TK; n = 1), Auckland (AK; n = 1), Coromandel (CL; n = 2), Hawkes Bay (HB; n = 4), Nelson (NN; n = 11), Wellington (WN; n = 3), Waikato (WO; n = 1), and Wanganui (WI; n = 1). The US isolates were collected from 14 regions in Brookings (n = 6), Cascades (n = 4), Central OR (n = 10), Del Norte Co. (n = 3), Florence (n = 1), Humboldt (n = 5), Little Lobster (n = 2), Medocino (n = 9), North CA (n = 4), Port-Orford (n = 14), Redwood national trail (n = 1), South OR (n = 1), South WA (n = 1), Washington (n = 3), Wheeler (n = 1). These regions were spread across three states. WA (n = 5), OR (n = 39) and CA (n = 22). All isolates of *P. pluvialis* were grown in clarified carrot broth for 4-5 days in the dark at 17°C. Mycelia were harvested, washed twice, transferred to 96-well collection tubes (Qiagen, USA) and sent to the Center for Genome Research and Biocomputing (CGRB) at Oregon State University (Corvallis, USA) for genomic DNA extraction and GBS.

Genotyping-by-sequencing, read mapping, and quality filtering. To reduce the complexity of the genome, a double restriction enzyme digestion was performed with the endonucleases PstI and MstI (New England Biolabs, Ipswich, MA). All samples were sequenced on the Illumina HiSeq 3000 platform using 150 base pair (bp) single end reads following the Illumina protocol (San Diego, CA). Sequenced libraries were demultiplexed using the program *sabre* (<https://github.com/najoshi/sabre>). All reads are available at the NCBI SRA repository (accession number: PRJNA638875).

The reads from the sequenced isolates were aligned to the reference genome of *P. pluvialis* type strain LC-9 (Studholme et al. 2015). Alignments were made using bowtie 2, with the “–very careful” option as the sole parameter added to the program (Langmead and Salzberg 2012). In order to identify which of the genetic variants represent the ancestral state, reads from the genome of *Phytophthora agathidicida* B.S. Weir, Beever, Pennycook & Bellgard strain NZFS 3770 were also mapped to the *P. pluvialis* reference (Studholme et al. 2015). The resulting SAM file was converted into a BAM file, sorted, and indexed using SAMTools V. 2.1.2 (Li et al. 2009). *P. agathidicida* is a sister species found in *Phytophthora* Clade 5 and is the most closely related *Phytophthora* species with a reference genome. This polarization approach will allow more accurate prediction of the earliest emerging populations of *P. pluvialis* (US or NZ).

Genomic variants were predicted using GATK V. 4.0 (McKenna et al. 2010). Initially, each sample was independently genotyped with GATK’s HaplotypeCaller and the GVCF option. All samples were pooled, and common variants identified in the CombineGVCFs program. Finally, the likelihood of each variant was estimated using the GenotypeGVCFs program for all samples. The final variant files were filtered for quality using the *vcfR* package (Knaus and Grünwald 2016) in R (R Core Team 2019). Two variant files were created for subsequent

analysis: (i) *P. pluvialis* and *P. agathidicida* reads (combined-species dataset); and (ii) *P. pluvialis* reads only (single-species dataset).

Variants were filtered in a three-stage process. In stage one, for the combined-species dataset variant positions missing in *P. agathidicida* were removed. In stage two, for both the combined-species and single-species datasets, filtering was performed to remove individual variants with a minimum read depth (DP) of $< 4x$ and greater than the 95th percentile of each sample DP distribution. In stage three, variants were filtered by mapping quality (MQ = 44), minimum allele frequency (MAF < 0.05), and missing data. All variant positions with any missing data were removed and finally samples with more than 70% missing data were eliminated. The final single-species and combined-species files were used in all subsequent analysis.

Population differentiation of *P. pluvialis* between countries. To characterize the population dynamics between the US and NZ and identify a presumptive center of origin, we measured the degree of genetic differentiation across *P. pluvialis* samples in a hierarchical manner. Initially, comparisons between countries were made among geographic regions within countries. To identify the earliest emerging population of *P. pluvialis* from our sampled populations, a phylogenetic tree using maximum likelihood was reconstructed in RAxML (Stamatakis et al. 2007) on both the combined-species dataset and single-species dataset. In both cases, *P. agathidicida* was the outgroup used to polarize the tree. The MULTIGAMMAI model of substitution with 1,000 bootstraps was used. The degree of genetic connectivity among populations was evaluated using a minimum spanning network (MSN) constructed in the R package poppr 2.1.5 (Kamvar et al. 2014; 2015b). Finally, population differentiation was evaluated at the different hierarchies with Nei's G_{ST} , an F_{ST} analog estimated in the mmod 1.13

package (Winter, 2012). Population heterozygosity was estimated and statistically contrasted for each population using the `Hs.test` function with 499 replicates using the same package (Winter, 2012). Population differentiation and population heterozygosity were measured in the single-species dataset

Population dynamics in the US. For the single-species dataset the number of genetic clusters (K) of *P. phuvialis* was estimated using the `find.clusters` function of the `adegenet` package in R (Jombart 2008). The optimal number of clusters was automatically determined by goodness of fit with Bayesian Inference Criterion (BIC) across all values of $K = 2 - 10$. A discriminant analysis of principal components (DAPC; Jombart et al. 2010) was performed for each sample using the predicted genetic clusters as a population index.

For each genetic cluster, heterozygosity was calculated using the `Hs` function in the `mmod` package (Winter 2012). The distribution and median estimates of pairwise genetic distance within each population were calculated using the `bitwise.distance` function in `poppr` (Kamvar et al. 2014). The index of association (I_A) was calculated for each genetic cluster to identify the degree of linkage within populations. I_A was calculated with the `RbarD` index implemented in `poppr` (Kamvar et al. 2014). A total of 999 `RbarD` permutations were performed.

To identify the degree of genetic differentiation across the predicted genetic clusters, Nei's G_{ST} was estimated for each pairwise combination of genetic clusters as described above (Winter 2012). To evaluate the relatedness of the predicted genetic clusters, the maximum likelihood phylogenetic reconstruction from the previous step was colored by genetic cluster in `ggtree` (Yu et al. 2017). Similarly, the MSN was colored by genetic cluster and geographic regions in order to observe how different geographic regions were grouped within each predicted genetic cluster. To identify if the predicted genetic clusters were grouped geographically, a map

of the samples colored by genetic cluster was constructed using the ggmap package in R (Khale and Wickham 2013).

Population structure and host specificity of *P. pluvialis*. To test the relatedness of *P. pluvialis* samples from different hosts in NZ, the host information was superimposed on the MSN and phylogenetic reconstruction of the single species dataset. The overlay was performed by creating a stratified data frame of hosts in the genind object of the single species SNP dataset in poppr (Kamvar et al. 2014) nodes were colored by host. The ML tree was colored by host using the strata host table in ggtree (Yu et al. 2017).

RESULTS

Summary statistics from genotyping-by-sequencing. A total of 1,543 SNPs were obtained from 145 isolates of *P. pluvialis* after variant filtering by DP, MQ, MAF and missing data. Eight samples were removed from the single species dataset. The combined species dataset had considerably fewer variants and isolates: 156 SNPs across 78 samples after variant filtering.

Genetic differentiation between US and NZ populations of *P. pluvialis*. Differences between the US and the NZ populations were observed across all analyses performed. The phylogenetic reconstruction with *P. agathidicida* as a root reveals that all samples from the US are clustered in two early emerging clades, while the NZ samples were grouped in a single terminal clade (Supp. Fig. 1A), with the exception of pluv-3635. The US clades have a longer average branch length than the NZ clade, indicating a higher average number of substitutions per site. The MSN also separated the US samples from the NZ samples (Supp. Fig. 1B). Pairwise genetic distances from the MSN showed that the US samples had an overall greater genetic distance among samples than those collected in NZ. Population heterozygosity metrics indicated significantly higher heterozygosity in the US (0.285) compared to NZ (0.239) (Hs.test, $p = 0.002$). The NZ sample

pluv-3635 is clustered in a different clade than the other NZ samples. It is more closely related to MG-AND1 and MG-YUK-4, two samples from the Cascades cluster in OR. This placement is consistent in both the phylogenetic reconstruction and the MSN.

Genetic differentiation among regions in the US and NZ. Stratification of isolates by region within countries revealed low pairwise differences in genetic diversity between regions (Supp. Figs. 3 and 4). In most cases, the closer the regions the less genetic differentiation. However, there were several exceptions (Supp. Figs. 2 and 3). Across the US, the Central OR, South WA, Florence OR and WA-state regions were all similar ($G_{st} < 0.05$), compared to the other geographic regions in the US. Additionally, samples from the Port-Orford region had the highest genetic differentiation ($G_{st} > 0.12$) when compared to all US regions, with the exception of South OR and Florence OR. In the case of NZ, the only geographic area with strong evidence for genetic differentiation was ND. Pairwise comparisons of genetic differentiation between ND and GB, BP, WA-NZ, RI, and TO regions had an $G_{st} > 0.12$ (Crosby, 1976). The pairwise genetic differentiation indicates low differentiation between regions within countries. Two regions from NZ, TK and WI, were weakly differentiated ($G_{st} < 0.1$) when compared with all the US regions with the exception of Central OR and Port-Orford.

Population dynamics of *P. pluvialis* between its US center of origin and NZ. Five genetic clusters were identified across the US ($n=3$) and NZ ($n=2$) (Figure 1A; Fig 2A and 2B). The Coastal, Central, and Port-Orford genetic clusters grouped most US samples. The remaining samples were from the Cascades region, and clustered within NZ1. The Coastal cluster grouped all southern OR and northern CA coastal samples. The Central cluster grouped all northern OR and WA samples. Port-Orford samples grouped in their own cluster with a single sample from the Cascades. NZ1 grouped all samples from the regions of ND, AK, TK, three from NN, two

from HB, one from WN in NZ, and three samples from the OR Cascades region in the US. NZ2 was exclusive to NZ and grouped all samples from GB, BP, WA, RI, four samples from TO, eight from NN, two from HB, two from WN, and one from CL.

The Coastal genetic cluster is the most diverse of the genetic clusters, both in terms of heterozygosity and pairwise genetic distance, while the Port-Orford and NZ2 clusters are the least diverse (Table 1, Supp. Fig. 4). The Coastal genetic cluster had the lowest genetic differentiation when compared to any other genetic cluster ($G_{ST} < 0.15$, Table 2). All other pairwise comparisons had similar levels of genetic differentiation ($G_{ST} > 0.18$). The I_A simulations indicate that the NZ2 and Port-Orford clusters have the largest simulated values of R_{barD} compared to the other clusters. This indicates a higher degree of genetic linkage within these populations and a higher degree of clonal reproduction compared to the other populations (Supp. Fig. 5).

The Coastal genetic cluster had more connections to other genetic clusters in the MSN. Phylogenetic reconstruction revealed that the Coastal cluster was always positioned with the earliest emerging clade, suggesting the Coastal cluster is the center of origin of *P. pluvialis*. All population clustering metrics indicated that MG-YUK-4, MG-CASC-5, and MG-AND-1, isolated from Douglas-fir in the Cascades region of OR, are the most closely related to the NZ samples clustered within NZ1.

Genetic structure and host associations in New Zealand *P. pluvialis* samples. Host overlay on the MSN indicates no correlation between the genetic cluster, phylogenetic clade, or geographic region of the isolate with host specificity (Figure 3). All samples from the US were exclusively isolated from Douglas-fir and as a result not included in this analysis. The phylogenetic tree indicates no host specificity or directional selection to date.

DISCUSSION

The hypothesis of a single colonization of *P. pluvialis* giving rise to the NZ RNC epidemic is supported by the analysis and results described above. A demographic analysis of the 147 isolates indicates that unidirectional migration from the US to NZ is the most parsimonious explanation for the observed genetic patterns (Supp. Fig. 2). The source of this colonization event was likely the Cascades region in OR. Weak genetic differentiation among isolates from the Cascades region in the US and the Northland and Nelson regions in NZ resulted in their grouping into a single genetic cluster. In addition, all measures of genetic diversity from US samples were greater than the samples from NZ, regardless of the metric used for comparison (Supp. Figure 3).

The increased number of molecular markers, as a result of the GBS, improved the characterization of the US and NZ source-sink dynamics. This can best be seen when comparing the single-species versus combined-species datasets. The analysis with the combined-species dataset groups one NZ isolate within the US samples (Supp. Fig. 1A). In this reduced dataset the sample labelled pluv-3635 is more closely related to the US samples than to NZ samples. When the same analysis is conducted with the larger single-species dataset (1,543 SNP) this isolate is repositioned within the NZ1 genetic cluster. The likely explanation for this change is the small number of molecular markers retained ($n = 156$) when using the distantly related *P. agathidicida* to polarize the ML tree (Supp. Fig. 1A). Furthermore, a similar pattern was noted by Brar et al. (2018) who suggested that the NZ outbreak was a result of two separate introductions. Their analysis used 27 SNP rather than the 1,543 SNPs identified in the single-species dataset described herein. The combination of the number of markers in this analysis and the population

genetics metrics (Figs. 1B, 2A and 2B) strongly support the hypothesis of a single introduction of *P. pluvialis* into NZ.

The pattern of introduction followed by clonal expansion observed between the US and NZ can be seen at a smaller spatial scale within the US. The samples from the US have high levels of genetic association over small geographic distances. This pattern resembles small, local epidemic events following initial migration of a small number of individuals into a new region. A good example of this is the regional outbreak of *P. pluvialis* reported for the Coast Range of Oregon in 2015 (Hansen et al. 2017). The Central genetic cluster appears to have originated from the Coastal genetic cluster followed by clonal expansion within the central region. This hypothesis is supported by the low genetic diversity, high population differentiation, and strong population structure found in the Central genetic cluster (Table 1). The Port-Orford genetic cluster exhibits similar characteristics. This cluster appears to have emerged in a manner similar to what was described above, movement from the Coastal cluster followed by local clonal expansion (Figs. 1 and 2). Both of these examples, occurring at different times (Port-Orford in 2013-2014 and Central in 2017) suggest that local environmental conditions may be driving clonal expansion and outbreak development. Similar scenarios have been proposed for local dispersal of the invasive oomycete *P. ramorum* in the western US (Peterson et al. 2014). Continued sampling both within and beyond the regions sampled in this study, and implementation of a demographic analysis would be required to detect the putative origin of *P. pluvialis*.

The question remains as to how and when *P. pluvialis* was introduced to NZ. The ubiquitous presence of *P. pluvialis* in the Coast Range of Oregon suggests many possible modes of introduction from Douglas-fir needles to infested soil. Increased biosecurity restrictions in NZ

since the late 1990's and early 2000's have significantly curtailed the risk of pathogen movement from overseas, suggesting an introduction which occurred prior to these restrictions. However, once established in NZ, few measures are in place to minimize the spread of pathogens among forested areas (Froud 2018; Hood 2019).

Reports of *P. pluvialis* in the US are limited to the forests of the PNW (Hansen et al. 2015; Gómez-Gallego et al. 2020; Brar et al. 2018). All of the US samples were collected from a single conifer species, Douglas-fir; whereas the isolates collected in NZ came from four different conifer species. In NZ, isolates were collected from Douglas-fir (n=9), radiata pine (n=79), Eastern white pine (n=1), and patula pine (n=1) (Supp. Table 1). However, there was no correlation between genetic or geographic cluster and host specificity. Although the isolates predominantly came from the most abundant host, *P. radiata*, multiple shifts between Douglas-fir and radiata pine were observed within the same genetic cluster and phylogenetic clade (Fig. 3) suggesting a broader host range than originally described (Hansen et al. 2017). The historic range of radiata pine spans from the northern San Francisco Bay Area in CA to northern Baja in Mexico (Millar 1999). This overlaps with the southern range of Douglas-fir. However, *P. pluvialis* has not been recovered from radiata pine in CA as either a pathogen or endophyte. Although RNC has never been reported in radiata pine's native range. Further sampling efforts to determine if *P. pluvialis* can be found in alternate coniferous hosts throughout North America is warranted. Finally, it is also important to note that *P. pluvialis* is less noticeable when infecting Douglas-fir compared to radiata pine where it causes RNC. However, infected Douglas-fir needles are cast prematurely and severe defoliation in the lower canopy has been noted on occasion in both the US and NZ (Hansen et al. 2015). This may suggest a coevolutionary history between the two species whereby *P. pluvialis* plays a role in the suppression of understory

species, a pattern that is characteristic of Douglas-fir stands (Gómez-Gallego et al. 2020). This potential coevolution and mutualistic ecological interactions between both species requires further exploration.

The population structure approach presented here suggests that *P. pluvialis* could have originated in the coastal Douglas-fir forests of the PNW where the population exhibits some characteristics of a center of origin. From this region, *P. pluvialis* was introduced at least once to NZ. Following the introduction, the pathogen was able to infect a wider range of host species than described in the PNW. These rapid host shifts may have been a contributing factor in its establishment and impact on the exotic radiata pine plantations grown throughout temperate regions of NZ. However, more evidence should be presented to support this hypothesis. The recent discovery of *P. pluvialis* has not permitted extensive sampling in areas of North America and NZ. As a result, the potential exists for undiscovered populations of *P. pluvialis* outside of these locations. In order to establish where *P. pluvialis* may have originated, more extensive sampling over a wide geographic area is required. This may reveal both the center of origin of this pathogen and other possible routes of migration.

Future work should focus on increased sample size, in terms of both geographic area and hosts sampled, in North America and NZ. A focus on whole genome resequencing with a higher depth of coverage would further increase the number of alleles that can be detected and provide a clearer view of the genetic diversity of this pathogen. Finally, demographic modeling of migration scenarios and history to test different routes of introduction and migration would be valuable. This work highlights the importance of phylogenomics to identify sources of forest pathogens that can potentially endanger naïve hosts.

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Figures and Tables.

Figure 1. Population structure of *P. pluvialis* in the US and NZ using the genetic variants extracted from the reads mapped to the *P. pluvialis* reference genome A). Bar plot result of the discriminant analysis of principal components. Each color represents the posterior probability membership value per sample to one of the five predicted genetic clusters B). Maximum likelihood phylogenetic reconstruction. Bootstrap support values over 70 are shown in the nodes. Tip color represent genetic cluster assignment per sample. Region abbreviations for NZ: Northland (ND), Gisborne (GB), Bay of Plenty (BP), Wairarapa (WA-NZ), Rangitikei (RI), Taupo (TO), Taranaki (TK), Auckland (AK), Coromandel (CL), Hawkes Bay (HB), Nelson (NN), Wellington (WN), Waikato (WO), and Wanganui (WI).

Figure 2. Population dynamics of *P. pluvialis*. A). Minimum spanning network reconstructed using pairwise distances between samples. Node color represents geographic regions of each sample. Edge thickness represents genetic distance between samples. Overlaying polygons represent each predicted genetic cluster. B). Geographic distribution of samples used in this study. Colors represent sample membership to each predicted genetic cluster. Region abbreviations for NZ: Northland (ND), Gisborne (GB), Bay of Plenty (BP), Wairarapa (WA-NZ), Rangitikei (RI), Taupo (TO), Taranaki (TK), Auckland (AK), Coromandel (CL), Hawkes Bay (HB), Nelson (NN), Wellington (WN), Waikato (WO), and Wanganui (WI).

Figure 3. Host shifts in NZ samples of *P. pluvialis*. Each color represents the host where each sample was isolated from. A). Subset of the minimum spanning network reconstructed in figure

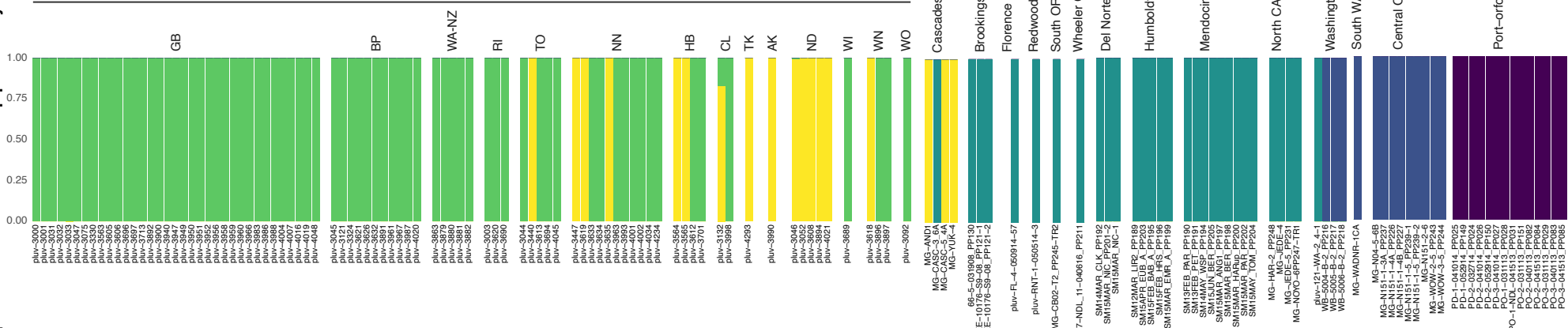
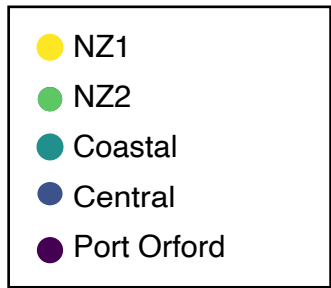
2 representing samples on NZ. B). Subset of the phylogenetic reconstruction in figure 1 representing samples of NZ.

Table 1. Summary statistic for genetic diversity and linkage measurements for *P. phuvialis* genetic clusters.

| Genetic cluster | Heterozygosity | Median pairwise genetic distance | Index of association (RbarD) |
|-----------------|----------------|----------------------------------|------------------------------|
| Coastal | 0.254 | 0.093 | 0.037 |
| Central | 0.228 | 0.054 | 0.034 |
| Port-Orford | 0.201 | 0.032 | 0.047 |
| NZ1 | 0.213 | 0.044 | 0.032 |
| NZ2 | 0.207 | 0.040 | 0.135 |

Table 2. Population differentiation via Nei's G_{ST} for all pairwise comparisons of genetic clusters predicted for *P. pluvialis*

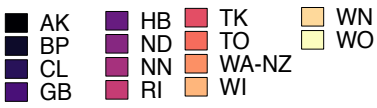
| | Coastal | NZ2 | Central | Port-Orford |
|--------------------|----------------|------------|----------------|--------------------|
| NZ2 | 0.144 | - | - | - |
| Central | 0.155 | 0.258 | - | - |
| Port-Orford | 0.086 | 0.223 | 0.235 | - |
| NZ1 | 0.153 | 0.184 | 0.231 | 0.230 |



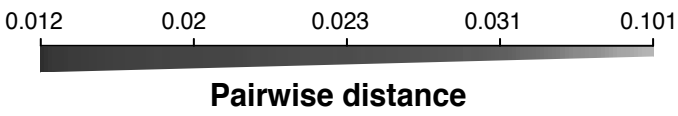
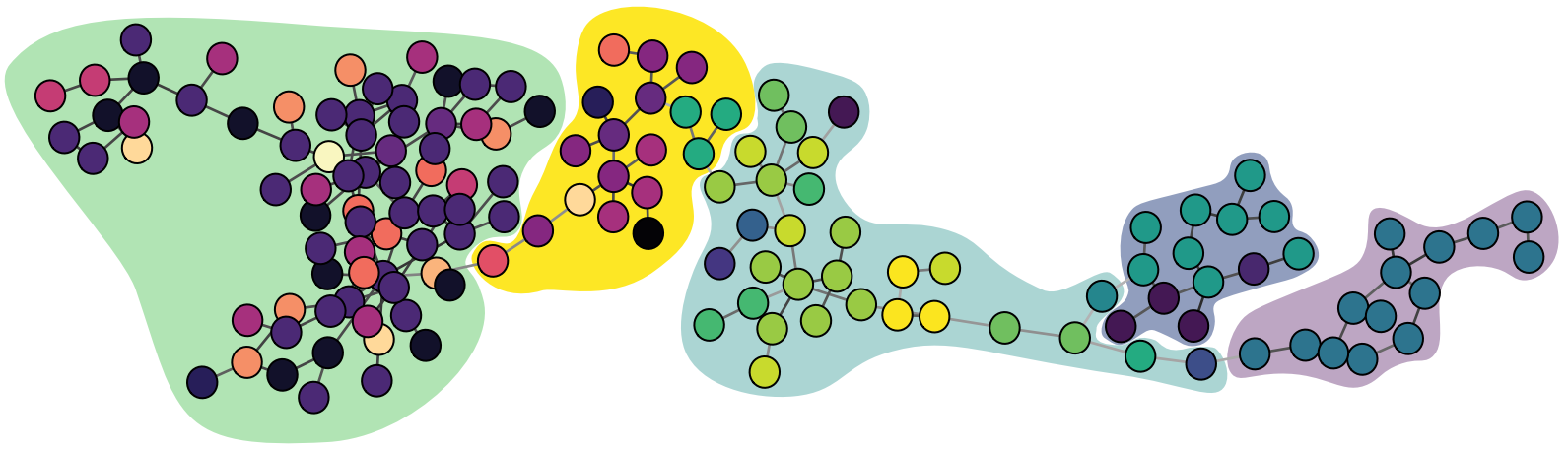
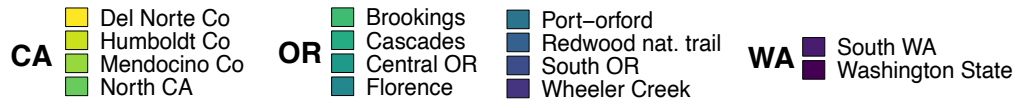
A.

Site of collection (Circles)

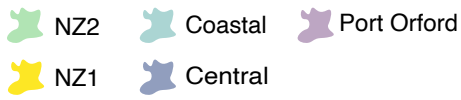
New Zealand



USA

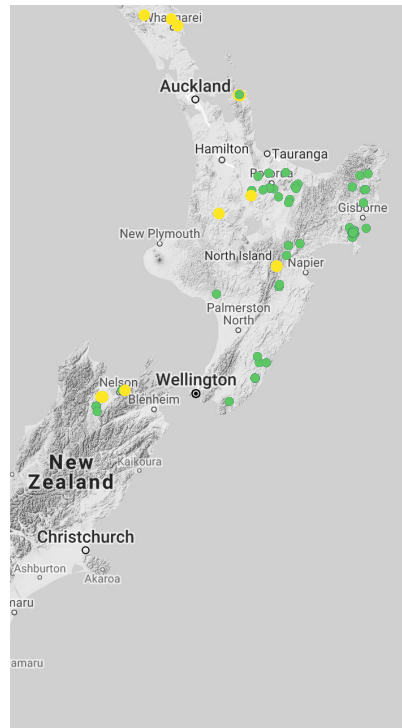


Genetic cluster

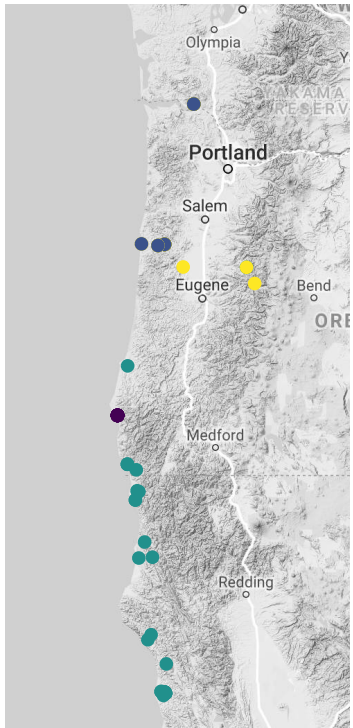


B.

New Zealand

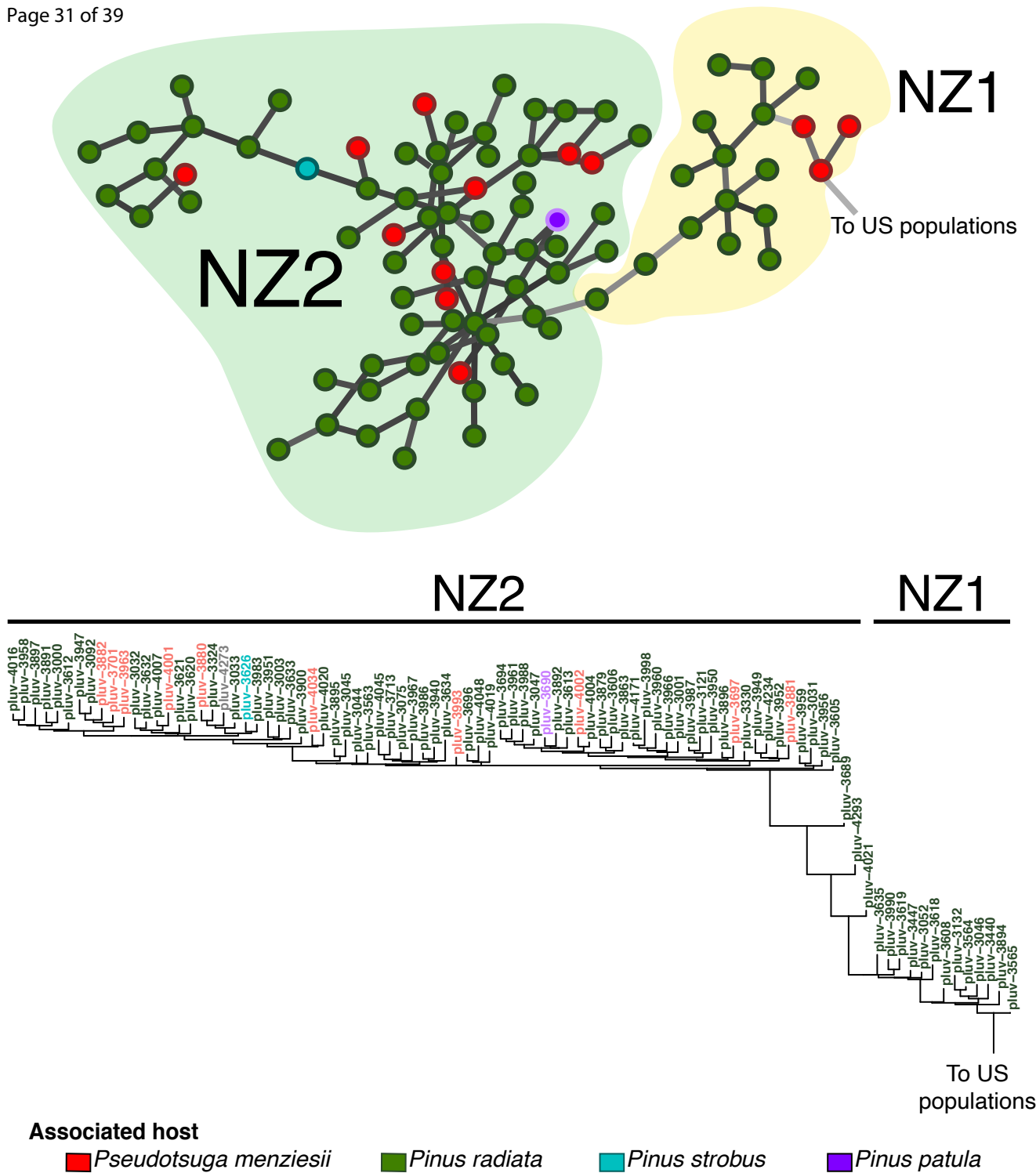


U.S.A P.N.W

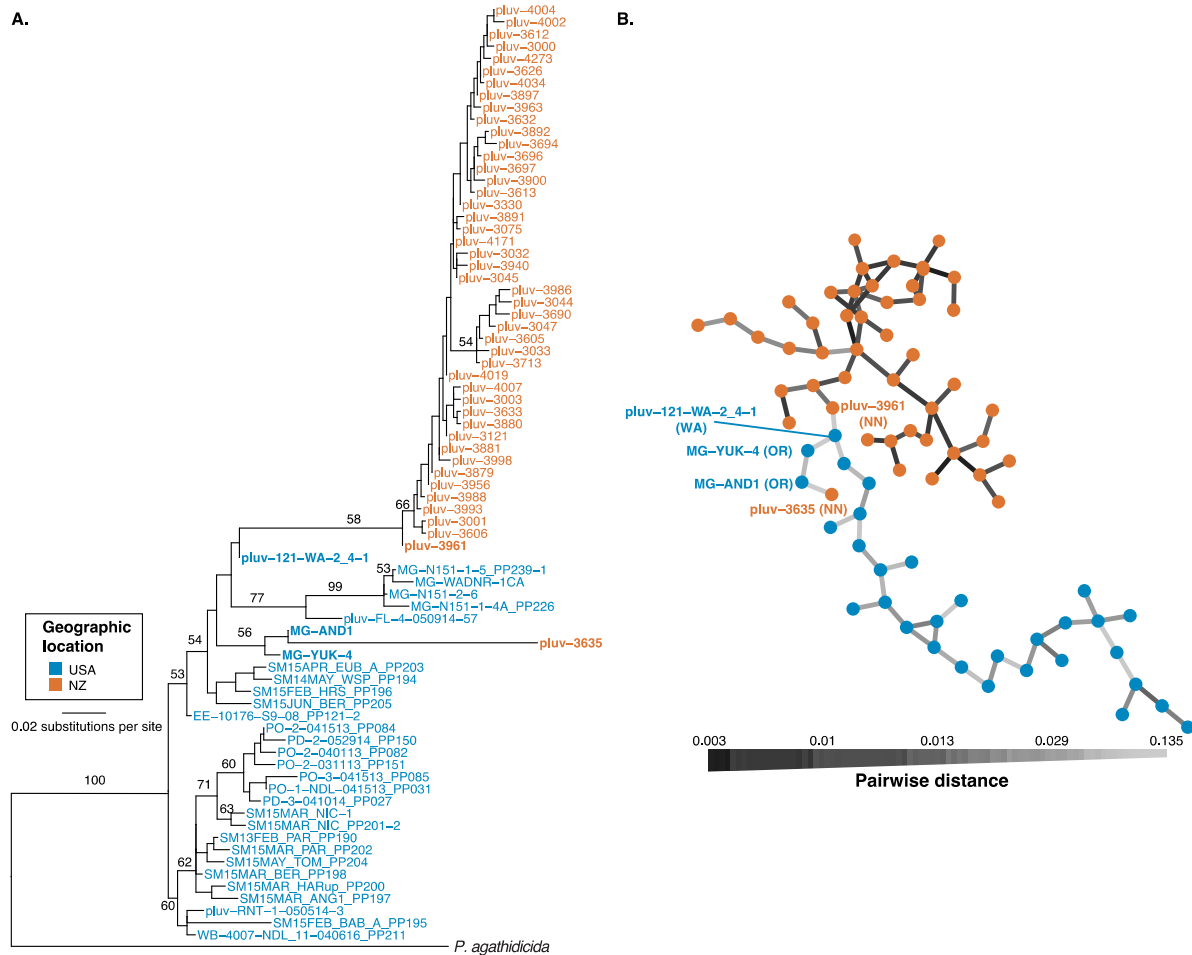


Genetic cluster

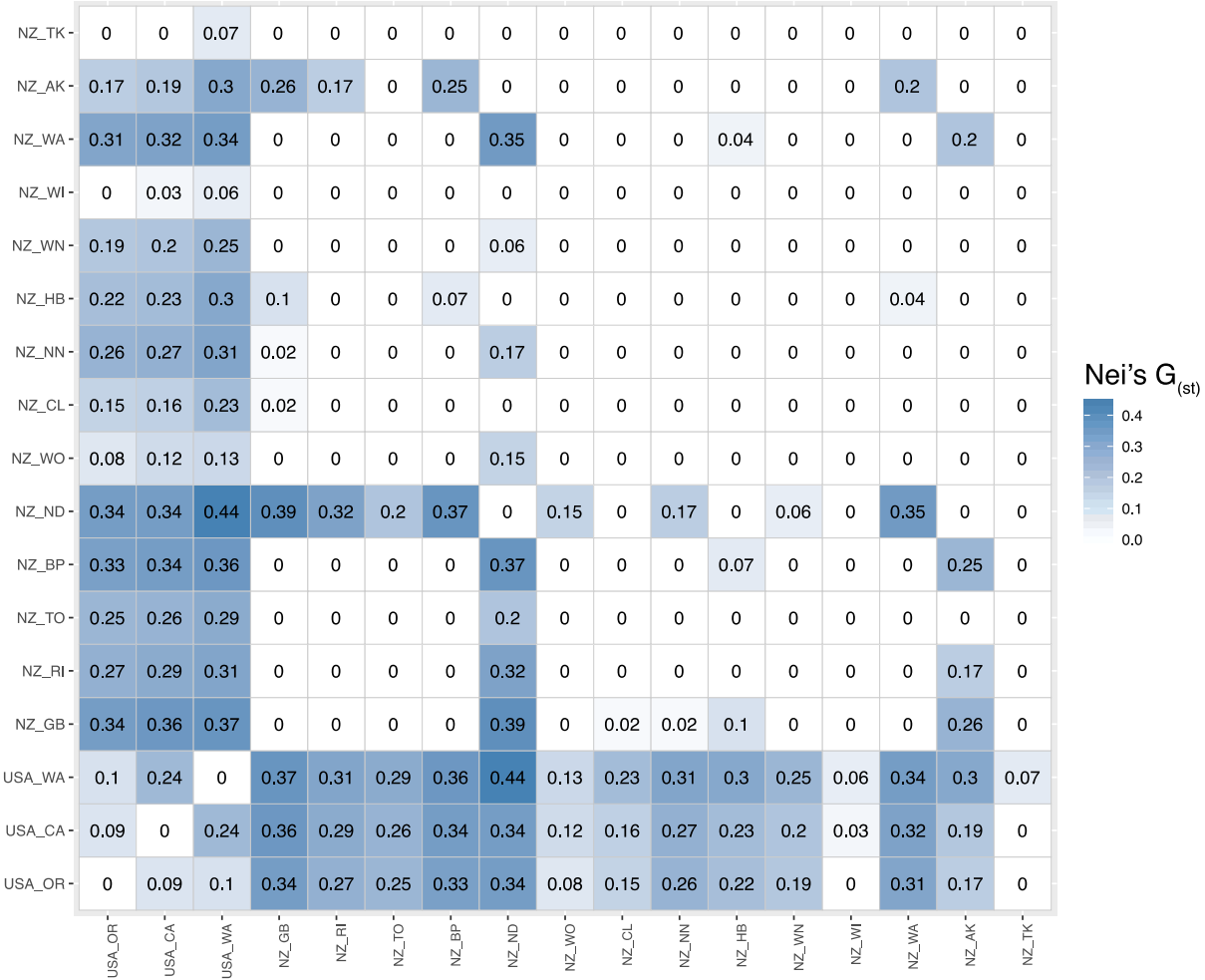




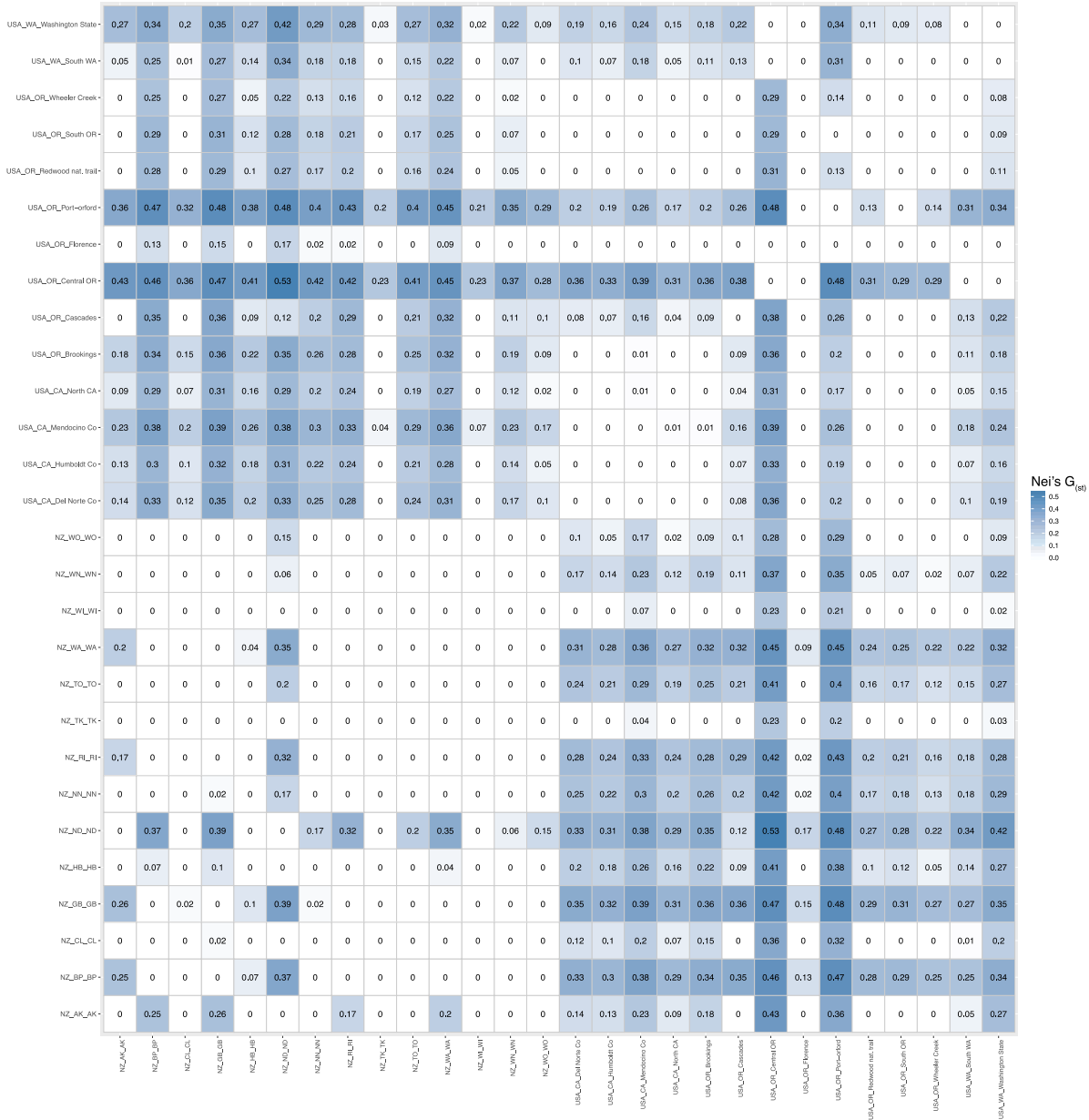
Supplementary Figures and Tables. (Tabima et al. 2020).



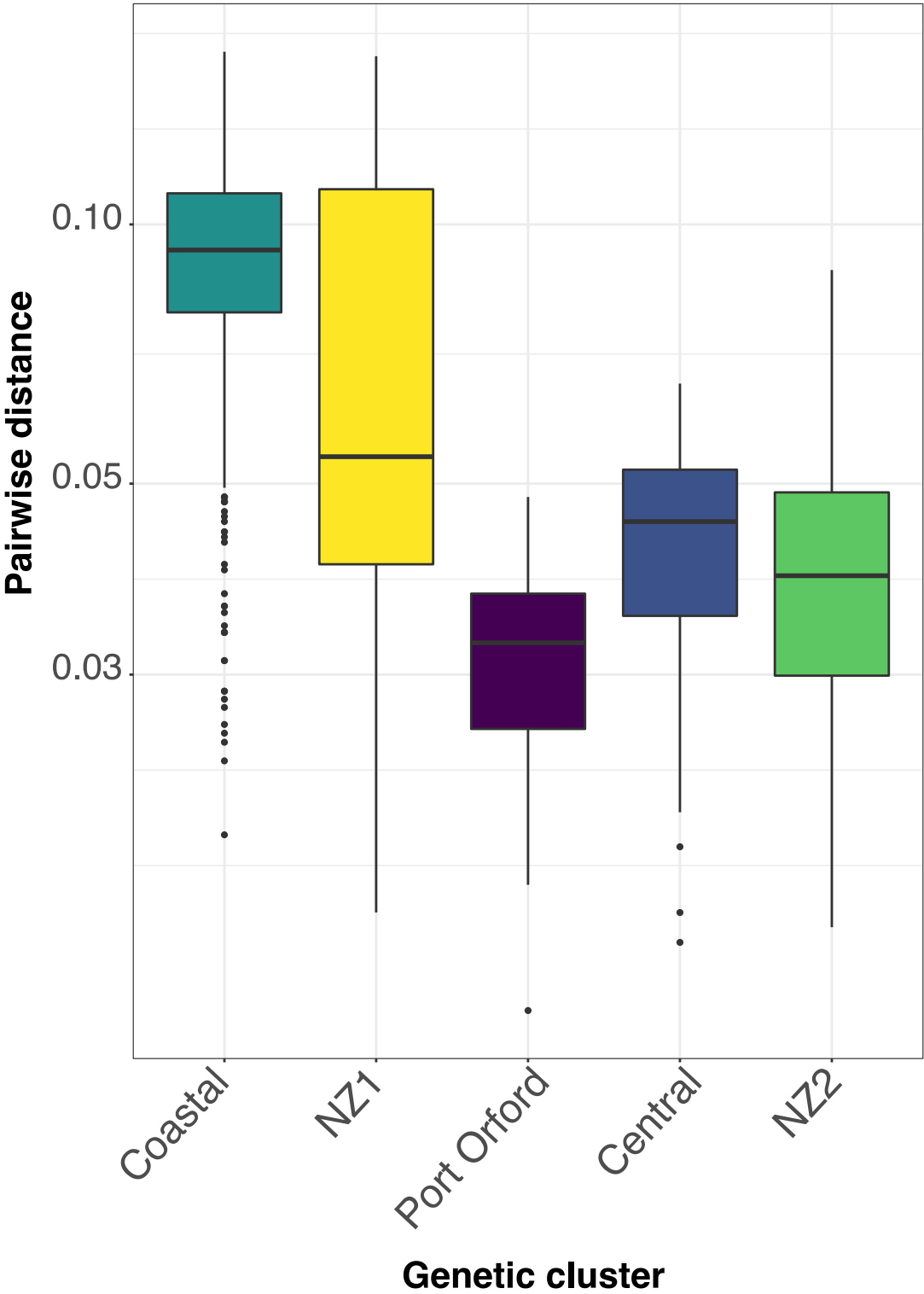
Supplementary Figure 1. Population structure of *P. pluvialis* in the US and NZ using the genetic variants extracted from the reads mapped to the *P. agathidicida* reference genome A). Maximum likelihood phylogenetic reconstruction. Bootstrap support values over 70 are shown in the nodes. Tip color represent country of origin. B). Minimum spanning network reconstructed using pairwise distances between samples (*P. agathidicida* was removed from the analysis). Node color represents country of origin of each sample. Edge thickness represents genetic distance between samples.



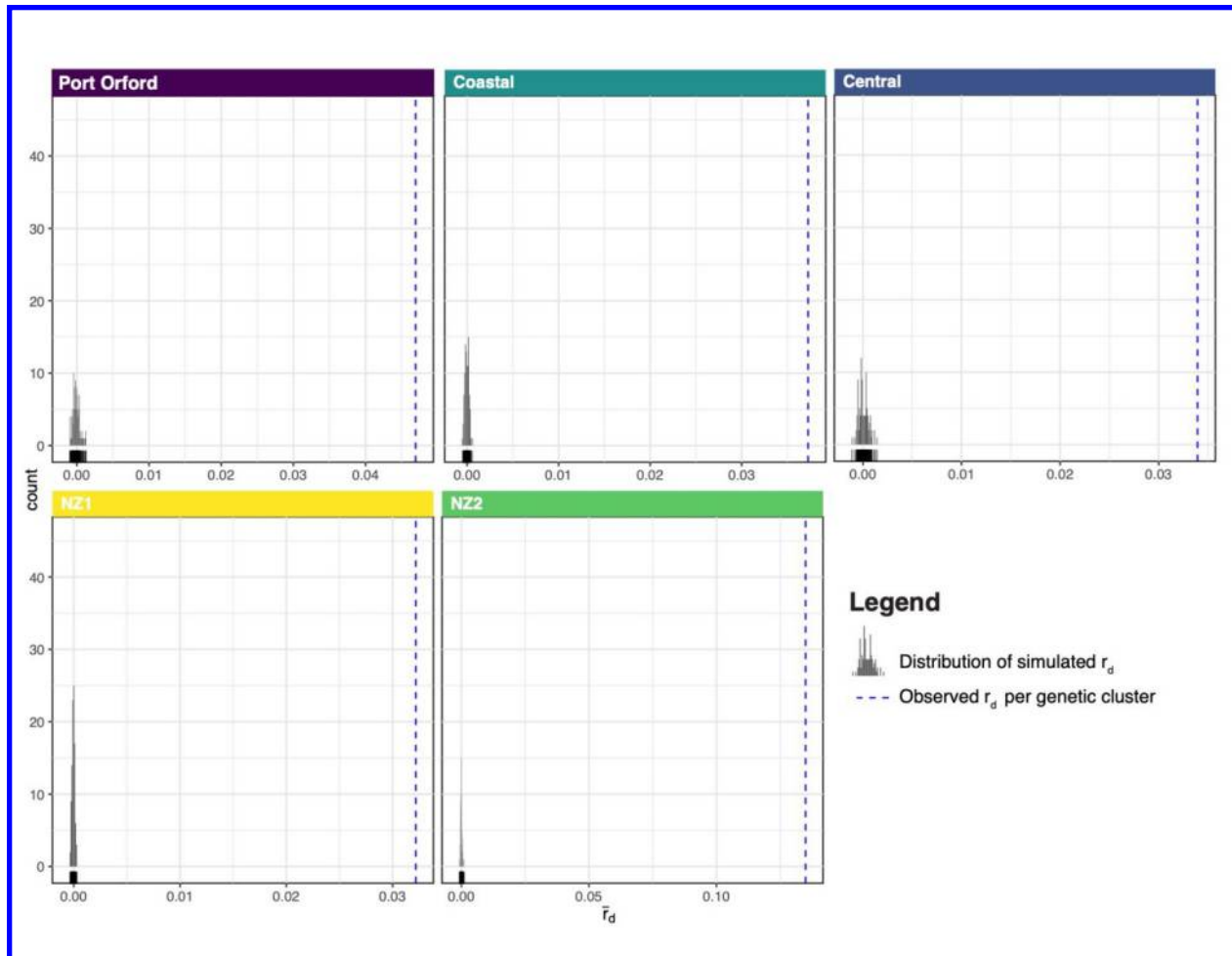
Supplementary Figure 2. Genetic differentiation based on pairwise G_{st} estimation at the hierarchical level of US states/NZ geographic locations. Colors represent G_{st} values, where darker colors represent higher genetic differentiation between locations.



Supplementary Figure 3. Genetic differentiation based on pairwise G_{ST} estimation at the hierarchical level of location within each state and country. Colors represent G_{ST} values, where darker colors represent higher genetic differentiation between states.



Supplementary Figure 4. Distribution of pairwise genetic distance measured by bitwise.distance function of the poppr package across the predicted genetic clusters of *P. phuvialis*.



Supplementary Figure 5. Index of Association (RbarD) estimation the predicted genetic clusters of *P. pluvialis*. Distributions represent 999 permutations of RbarD simulations, and vertical line represents the estimated values of RbarD per genetic cluster.

Supp Table 1. Samples used in this study

| Sample ^a | Country | State | Region | Latitude | Longitude | Isolation source |
|---------------------|---------|-------|--------------------|------------|------------|------------------------------|
| pluv-4171 | NZ | NZ | Taupo (TO) | -38.67539 | 176.44520 | <i>Pinus radiata</i> |
| pluv-4273 | NZ | NZ | Taupo (TO) | -38.259982 | 175.8606 | <i>Pinus radiata</i> |
| pluv-3990 | NZ | NZ | Auckland (AK) | -36.804268 | 175.651518 | <i>Pinus radiata</i> |
| pluv-3045 | NZ | NZ | Bay of Plenty (BP) | -38.168896 | 176.779757 | <i>Pinus radiata</i> |
| pluv-3121 | NZ | NZ | Bay of Plenty (BP) | -37.993311 | 176.53988 | <i>Pinus radiata</i> |
| pluv-3324 | NZ | NZ | Bay of Plenty (BP) | -38.001729 | 176.209895 | <i>Pinus radiata</i> |
| pluv-3621 | NZ | NZ | Bay of Plenty (BP) | -38.404855 | 176.618723 | <i>Pinus radiata</i> |
| pluv-3626 | NZ | NZ | Bay of Plenty (BP) | -38.242728 | 176.306942 | <i>Pinus strobus</i> |
| pluv-3632 | NZ | NZ | Bay of Plenty (BP) | -38.205504 | 176.718861 | <i>Pinus radiata</i> |
| pluv-3891 | NZ | NZ | Bay of Plenty (BP) | -38.050239 | 176.001762 | <i>Pinus radiata</i> |
| pluv-3961 | NZ | NZ | Bay of Plenty (BP) | -38.228751 | 176.221057 | <i>Pinus radiata</i> |
| pluv-3967 | NZ | NZ | Bay of Plenty (BP) | -38.228751 | 176.221057 | <i>Pinus radiata</i> |
| pluv-3987 | NZ | NZ | Bay of Plenty (BP) | -38.256896 | 176.09933 | <i>Pinus radiata</i> |
| pluv-4020 | NZ | NZ | Bay of Plenty (BP) | -38.235523 | 176.739133 | <i>Pinus radiata</i> |
| pluv-3132 | NZ | NZ | Coromandel (CL) | -36.796902 | 175.623673 | <i>Pinus radiata</i> |
| pluv-3998 | NZ | NZ | Coromandel (CL) | -36.790311 | 175.637221 | <i>Pinus radiata</i> |
| pluv-3000 | NZ | NZ | Gisborne (GB) | -38.869783 | 177.819637 | <i>Pinus radiata</i> |
| pluv-3001 | NZ | NZ | Gisborne (GB) | -38.869783 | 177.819637 | <i>Pinus radiata</i> |
| pluv-3031 | NZ | NZ | Gisborne (GB) | -38.842413 | 178.104533 | <i>Pinus radiata</i> |
| pluv-3032 | NZ | NZ | Gisborne (GB) | -38.881695 | 177.855329 | <i>Pinus radiata</i> |
| pluv-3033 | NZ | NZ | Gisborne (GB) | -38.880972 | 177.872417 | <i>Pinus radiata</i> |
| pluv-3047 | NZ | NZ | Gisborne (GB) | -38.255539 | 178.070845 | <i>Pinus radiata</i> |
| pluv-3075 | NZ | NZ | Gisborne (GB) | -38.21425 | 177.83473 | <i>Pinus radiata</i> |
| pluv-3330 | NZ | NZ | Gisborne (GB) | -38.458015 | 178.051855 | <i>Pinus radiata</i> |
| pluv-3563 | NZ | NZ | Gisborne (GB) | -38.254348 | 178.088993 | <i>Pinus radiata</i> |
| pluv-3605 | NZ | NZ | Gisborne (GB) | -38.037182 | 177.982285 | <i>Pinus radiata</i> |
| pluv-3606 | NZ | NZ | Gisborne (GB) | -38.833167 | 177.779304 | <i>Pinus radiata</i> |
| pluv-3696 | NZ | NZ | Gisborne (GB) | -38.977135 | 177.835688 | <i>Pinus radiata</i> |
| pluv-3697 | NZ | NZ | Gisborne (GB) | -38.012511 | 178.138193 | <i>Pseudotsuga menziesii</i> |
| pluv-3713 | NZ | NZ | Gisborne (GB) | -38.922781 | 177.883422 | <i>Pinus radiata</i> |
| pluv-3892 | NZ | NZ | Gisborne (GB) | -38.896755 | 177.875965 | <i>Pinus radiata</i> |
| pluv-3895 | NZ | NZ | Gisborne (GB) | -38.912777 | 177.833036 | <i>Pinus radiata</i> |
| pluv-3900 | NZ | NZ | Gisborne (GB) | -38.911281 | 177.831563 | <i>Pinus radiata</i> |
| pluv-3940 | NZ | NZ | Gisborne (GB) | -38.90359 | 177.835519 | <i>Pinus radiata</i> |
| pluv-3947 | NZ | NZ | Gisborne (GB) | -38.912777 | 177.833036 | <i>Pinus radiata</i> |
| pluv-3949 | NZ | NZ | Gisborne (GB) | -38.889205 | 177.874822 | <i>Pinus radiata</i> |
| pluv-3950 | NZ | NZ | Gisborne (GB) | -38.889205 | 177.874822 | <i>Pinus radiata</i> |
| pluv-3951 | NZ | NZ | Gisborne (GB) | -38.904708 | 177.839344 | <i>Pinus radiata</i> |
| pluv-3952 | NZ | NZ | Gisborne (GB) | -38.889205 | 177.874822 | <i>Pinus radiata</i> |
| pluv-3956 | NZ | NZ | Gisborne (GB) | -38.905794 | 177.83792 | <i>Pinus radiata</i> |
| pluv-3958 | NZ | NZ | Gisborne (GB) | -38.912777 | 177.833036 | <i>Pinus radiata</i> |
| pluv-3959 | NZ | NZ | Gisborne (GB) | -38.904708 | 177.839344 | <i>Pinus radiata</i> |
| pluv-3960 | NZ | NZ | Gisborne (GB) | -38.909245 | 177.835481 | <i>Pinus radiata</i> |
| pluv-3966 | NZ | NZ | Gisborne (GB) | -38.909907 | 177.834281 | <i>Pinus radiata</i> |
| pluv-3983 | NZ | NZ | Gisborne (GB) | -38.907074 | 177.837684 | <i>Pinus radiata</i> |
| pluv-3986 | NZ | NZ | Gisborne (GB) | -38.871645 | 177.857277 | <i>Pinus radiata</i> |
| pluv-3988 | NZ | NZ | Gisborne (GB) | -38.889205 | 177.874822 | <i>Pinus radiata</i> |
| pluv-4004 | NZ | NZ | Gisborne (GB) | -38.889205 | 177.874822 | <i>Pinus radiata</i> |
| pluv-4007 | NZ | NZ | Gisborne (GB) | -38.889205 | 177.874822 | <i>Pinus radiata</i> |
| pluv-4016 | NZ | NZ | Gisborne (GB) | -38.909287 | 177.835417 | <i>Pinus radiata</i> |
| pluv-4019 | NZ | NZ | Gisborne (GB) | -38.907063 | 177.837677 | <i>Pinus radiata</i> |
| pluv-4048 | NZ | NZ | Gisborne (GB) | -38.909062 | 177.846542 | <i>Pinus radiata</i> |
| pluv-3564 | NZ | NZ | Hawkes Bay (HB) | -39.413303 | 176.364163 | <i>Pinus radiata</i> |
| pluv-3565 | NZ | NZ | Hawkes Bay (HB) | -39.413302 | 176.364163 | <i>Pinus radiata</i> |
| pluv-3612 | NZ | NZ | Hawkes Bay (HB) | -39.076077 | 176.817507 | <i>Pinus radiata</i> |
| pluv-3701 | NZ | NZ | Hawkes Bay (HB) | -39.252954 | 176.556203 | <i>Pseudotsuga menziesii</i> |
| pluv-3046 | NZ | NZ | Northland (ND) | -35.2812 | 173.830536 | <i>Pinus radiata</i> |
| pluv-3052 | NZ | NZ | Northland (ND) | -35.219206 | 173.798511 | <i>Pinus radiata</i> |
| pluv-3608 | NZ | NZ | Northland (ND) | -35.604258 | 174.31654 | <i>Pinus radiata</i> |
| pluv-3894 | NZ | NZ | Northland (ND) | -35.709001 | 174.437952 | <i>Pinus radiata</i> |
| pluv-4021 | NZ | NZ | Northland (ND) | -35.542232 | 173.789672 | <i>Pinus radiata</i> |

| | | | | | | |
|-------------------------|----|----|-----------------|------------|------------|------------------------------|
| pluv-3447 | NZ | NZ | Nelson (NN) | -41.348279 | 172.947959 | <i>Pinus radiata</i> |
| pluv-3619 | NZ | NZ | Nelson (NN) | -41.350218 | 172.978392 | <i>Pinus radiata</i> |
| pluv-3633 | NZ | NZ | Nelson (NN) | -41.247197 | 173.352377 | <i>Pinus radiata</i> |
| pluv-3634 | NZ | NZ | Nelson (NN) | -41.253842 | 173.364333 | <i>Pinus radiata</i> |
| pluv-3635 | NZ | NZ | Nelson (NN) | -41.252332 | 173.414333 | <i>Pinus radiata</i> |
| pluv-3963 | NZ | NZ | Nelson (NN) | -41.486022 | 172.855989 | <i>Pseudotsuga menziesii</i> |
| pluv-3993 | NZ | NZ | Nelson (NN) | -41.486022 | 172.855989 | <i>Pseudotsuga menziesii</i> |
| pluv-4001 | NZ | NZ | Nelson (NN) | -41.486022 | 172.855989 | <i>Pseudotsuga menziesii</i> |
| pluv-4002 | NZ | NZ | Nelson (NN) | -41.486022 | 172.855989 | <i>Pseudotsuga menziesii</i> |
| pluv-4034 | NZ | NZ | Nelson (NN) | Unknown | Unknown | <i>Pinus radiata</i> |
| pluv-4234 | NZ | NZ | Nelson (NN) | -41.561909 | 172.8738 | <i>Pinus radiata</i> |
| pluv-3003 | NZ | NZ | Rangitikei (RI) | -39.719075 | 176.40844 | <i>Pinus radiata</i> |
| pluv-3620 | NZ | NZ | Rangitikei (RI) | -39.718903 | 176.41004 | <i>Pinus radiata</i> |
| pluv-3690 | NZ | NZ | Rangitikei (RI) | -39.687564 | 176.41991 | <i>Pinus patula</i> |
| pluv-4293 | NZ | NZ | Taranaki (TK) | -38.61826 | 175.24105 | <i>Pinus radiata</i> |
| pluv-3044 | NZ | NZ | Taupo (TO) | -38.880972 | 177.872417 | <i>Pinus radiata</i> |
| pluv-3440 | NZ | NZ | Taupo (TO) | -38.346272 | 175.867125 | <i>Pinus radiata</i> |
| pluv-3613 | NZ | NZ | Taupo (TO) | -39.102989 | 176.595443 | <i>Pinus radiata</i> |
| pluv-3694 | NZ | NZ | Taupo (TO) | -38.365217 | 176.400563 | <i>Pinus radiata</i> |
| pluv-4045 | NZ | NZ | Taupo (TO) | -38.452007 | 176.595888 | <i>Pinus radiata</i> |
| pluv-3863 | NZ | NZ | Waiarapa (WA) | -40.845812 | 176.023596 | <i>Pinus radiata</i> |
| pluv-3879 | NZ | NZ | Waiarapa (WA) | -40.848207 | 176.163234 | <i>Pinus radiata</i> |
| pluv-3880 | NZ | NZ | Waiarapa (WA) | -41.073545 | 175.943922 | <i>Pseudotsuga menziesii</i> |
| pluv-3881 | NZ | NZ | Waiarapa (WA) | -41.073545 | 175.943922 | <i>Pseudotsuga menziesii</i> |
| pluv-3882 | NZ | NZ | Waiarapa (WA) | -41.073545 | 175.943922 | <i>Pseudotsuga menziesii</i> |
| pluv-3689 | NZ | NZ | Wanganui (WI) | -39.831458 | 175.193992 | <i>Pinus radiata</i> |
| pluv-3618 | NZ | NZ | Wellington (WN) | -41.350218 | 172.978392 | <i>Pinus radiata</i> |
| pluv-3896 | NZ | NZ | Wellington (WN) | -41.414553 | 175.442424 | <i>Pinus radiata</i> |
| pluv-3897 | NZ | NZ | Wellington (WN) | -40.757033 | 175.990807 | <i>Pinus radiata</i> |
| pluv-3092 | NZ | NZ | Waikato (WO) | -38.267747 | 175.8793 | <i>Pinus radiata</i> |
| PP192 | US | CA | Del Norte Co | 41.810119 | -124.11201 | Stream-bait |
| PP201-2 | US | CA | Del Norte Co | 41.700806 | -124.13839 | Stream-bait |
| SM15MAR_NIC-1 | US | CA | Del Norte Co | 41.700806 | -124.13839 | Stream-bait |
| PP189 | US | CA | Humboldt | 41.009763 | -124.08422 | Stream-bait |
| PP195 | US | CA | Humboldt | 41.019489 | -123.86756 | Stream-bait |
| PP196 | US | CA | Humboldt | 40.023522 | -123.94099 | Stream-bait |
| PP199 | US | CA | Humboldt | 41.200914 | -123.99177 | Stream-bait |
| PP203 | US | CA | Humboldt | 40.08443 | -123.88914 | Stream-bait |
| PP190 | US | CA | Mendocino | 39.369521 | -123.65879 | Stream-bait |
| PP191 | US | CA | Mendocino | 39.387762 | -123.6816 | Stream-bait |
| PP194 | US | CA | Mendocino | 39.368769 | -123.65947 | Stream-bait |
| PP197 | US | CA | Mendocino | 39.728773 | -123.6477 | Stream-bait |
| PP198 | US | CA | Mendocino | 39.384445 | -123.67399 | Stream-bait |
| PP200 | US | CA | Mendocino | 39.387333 | -123.73155 | Stream-bait |
| PP202 | US | CA | Mendocino | 39.369521 | -123.65879 | Stream-bait |
| PP204 | US | CA | Mendocino | 39.342091 | -123.69312 | Stream-bait |
| PP205 | US | CA | Mendocino | 39.384445 | -123.67399 | Stream-bait |
| MG-JEDE-4 | US | CA | North CA | 41.80034 | -124.08604 | <i>Pseudotsuga menziesii</i> |
| MG-NOYO-6PP247-TR1 | US | CA | North CA | 39.38177 | -123.6703 | <i>Pseudotsuga menziesii</i> |
| PP231 | US | CA | North CA | 41.80045 | -124.08614 | <i>Pseudotsuga menziesii</i> |
| PP248 | US | CA | North CA | 39.39314 | -123.72926 | <i>Pseudotsuga menziesii</i> |
| pluv-RNT-1-050514-3 | US | CA | Brookings | Unknown | Unknown | Unknown |
| pluv-66-2-022068-129 | US | OR | Brookings | 42.12326 | -124.26535 | Soil-bait |
| pluv-EE-10253-58-09-126 | US | OR | Brookings | 42.12326 | -124.26535 | Soil-bait |
| pluv-EE-2559-513-09-122 | US | OR | Brookings | 42.12326 | -124.26535 | Soil-bait |
| PP121-1 | US | OR | Brookings | 42.12326 | -124.26535 | Soil-bait |
| PP121-2 | US | OR | Brookings | 42.12326 | -124.26535 | Soil-bait |
| PP130 | US | OR | Brookings | 42.12346 | -124.2654 | Raintrap-bait |
| MG-AND1 | US | OR | Cascades | 44.216388 | -122.24417 | <i>Pseudotsuga menziesii</i> |
| MG-CASC-3_6A | US | OR | Cascades | 44.39989 | -122.3734 | <i>Pseudotsuga menziesii</i> |
| MG-CASC-5_4A | US | OR | Cascades | 44.40004 | -122.37352 | <i>Pseudotsuga menziesii</i> |
| MG-YUK-4 | US | OR | Cascades | 44.403889 | -123.38 | <i>Pseudotsuga menziesii</i> |
| MG-N04-5-6B | US | OR | Central OR | 44.66537 | -124.04219 | <i>Pseudotsuga menziesii</i> |
| MG-N04-506A | US | OR | Central OR | 44.66537 | 124.04219 | <i>Pseudotsuga menziesii</i> |
| MG-N151-2-6 | US | OR | Central OR | 44.65978 | -123.67484 | <i>Pseudotsuga menziesii</i> |
| PP226 | US | OR | Central OR | 44.65983 | -123.67525 | <i>Pseudotsuga menziesii</i> |

| | | | | | | |
|------------------------|----|----|----------------|-----------|------------|------------------------------|
| PP227 | US | OR | Central OR | 44.65983 | -123.67525 | <i>Pseudotsuga menziesii</i> |
| PP237 | US | OR | Central OR | 44.65983 | -123.67525 | <i>Pseudotsuga menziesii</i> |
| PP239-1 | US | OR | Central OR | 44.65983 | -123.67525 | <i>Pseudotsuga menziesii</i> |
| PP239-2 | US | OR | Central OR | 44.65983 | -123.67525 | <i>Pseudotsuga menziesii</i> |
| PP243 | US | OR | Central OR | 44.646944 | -123.78038 | <i>Pseudotsuga menziesii</i> |
| PP244 | US | OR | Central OR | 44.646944 | -123.78038 | <i>Pseudotsuga menziesii</i> |
| pluv-FL-4-050914-57 | US | OR | Florence | Unknown | Unknown | Unknown |
| pluv-LL-5-051213-58 | US | OR | Little Lobster | Unknown | Unknown | <i>Pseudotsuga menziesii</i> |
| pluv-LL-5-NDL-042713-2 | US | OR | Little Lobster | Unknown | Unknown | <i>Pseudotsuga menziesii</i> |
| PP024 | US | OR | Port-Orford | 42.69623 | -124.42282 | Raintrap-bait |
| PP025 | US | OR | Port-Orford | 42.69623 | -124.42282 | Raintrap-bait |
| PP026 | US | OR | Port-Orford | 42.69623 | -124.42282 | Raintrap-bait |
| PP027 | US | OR | Port-Orford | 42.69623 | -124.42282 | Raintrap-bait |
| PP028 | US | OR | Port-Orford | 42.69614 | -124.42296 | Raintrap-bait |
| PP029 | US | OR | Port-Orford | 42.69614 | -124.42296 | Raintrap-bait |
| PP031 | US | OR | Port-Orford | 42.69614 | -124.42296 | <i>Pseudotsuga menziesii</i> |
| PP082 | US | OR | Port-Orford | 42.69614 | -124.42296 | Raintrap-bait |
| PP083 | US | OR | Port-Orford | 42.69614 | -124.42296 | Raintrap-bait |
| PP084 | US | OR | Port-Orford | 42.69614 | -124.42296 | Raintrap-bait |
| PP085 | US | OR | Port-Orford | 42.69614 | -124.42296 | Raintrap-bait |
| PP149 | US | OR | Port-Orford | 42.69623 | -124.42282 | Raintrap-bait |
| PP150 | US | OR | Port-Orford | 42.69623 | -124.42282 | Raintrap-bait |
| PP151 | US | OR | Port-Orford | 42.69614 | -124.42296 | Raintrap-bait |
| PP245-TR2 | US | OR | Brookings | 43.27168 | -124.26174 | <i>Pseudotsuga menziesii</i> |
| PP211 | US | OR | Brookings | 42.05785 | -124.12458 | Raintrap-bait |
| pluv-121-WA-2_4-1 | US | WA | Brookings | Unknown | Unknown | Unknown |
| MG-WADNR-1CA | US | WA | Washington | 46.22242 | -123.21182 | <i>Pseudotsuga menziesii</i> |
| PP216 | US | WA | Washington | 46.22248 | -123.21191 | Unknown |
| PP217 | US | WA | Washington | 46.22242 | -123.21182 | Bait screen |
| PP218 | US | WA | Washington | 46.22248 | -123.21197 | Bait screen |

^a All New Zealand *P. pluvialis* isolate numbers refer to those from the New Zealand Forest Health culture collection (NZFS) held at Scion (NZFRI, Ltd.), Rotorua, New Zealand.