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Contrasting demographic histories revealed in two invasive populations of the dry rot fungus *Serpula lacrymans*

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Abstract

Globalization and international trade have impacted organisms around the world leading to a considerable number of species establishing in new geographic areas. Many organisms have taken advantage of human-made environments, including buildings. One such species is the dry rot fungus *Serpula lacrymans*, which is the most aggressive wood-decay fungus in indoor environments in temperate regions. Using population genomic analyses of 36 full genome sequenced isolates, we demonstrated that European and Japanese isolates are highly divergent and the populations split 3000–19,000 generations ago, probably predating human influence. Approximately 250 generations ago, the European population went through a tight bottleneck, probably corresponding to the fungus colonization of the built environment in Europe. The demographic history of these populations, probably lead to low adaptive potential. Only two loci under selection were identified using a F_{ST} outlier approach, and selective sweep analyses identified three loci with extended haplotype homozygosity. The selective sweep analyses found signals in genes possibly related to decay of various substrates in Japan and in genes involved DNA replication and protein modification in Europe. Our results suggest that the dry rot fungus independently established in indoor environments in Europe and Japan and that invasive species can potentially establish large populations in new habitats based on a few colonizing individuals.

KEYWORDS
demographic inference, dry rot, fungi, population genomics, selection

1 | INTRODUCTION

Due to globalization and climate change an increasing number of fungal species are colonizing new areas worldwide. Numerous plant pathogenic fungi have benefitted from modern agriculture practices and trade, and are recognized as growing threats to food security, conservation of biodiversity and global economy (Fisher et al., 2012; Islam et al., 2016; Rosenblum et al., 2010). These fungi often show complex population genetic structure due to multiple dispersal and back-dispersal events, varying demographic histories and hybridization events (Brasier & Kirk, 2010; Gladieux, Feurtey et al., 2014; Gladieux et al., 2018; Gladieux, Ropars et al., 2014; Stukenbrock et al.,

Martin and Kauserud Shared last authors.

2007). Modern agricultural practices involve large-scale monocultures where well-adapted fungal pathogens can colonize and spread rapidly (Croll & McDonald, 2017; Stukenbrock & McDonald, 2008).

It is less known to what degree fungi adapt to other dimensions of human-made habitats. A few fungi have colonized buildings where the environment is dry. Such species may reduce indoor air quality or decompose wooden structures, causing substantial economic losses (Schmidt, 2007). In this study, we focus on the dry rot fungus *Serpula lacrymans* (Serpulaceae, Boletales, Agaricomycetes, Basidiomycota). *Serpula lacrymans* is a primary decomposer of large substrates both in nature and in buildings (Harmsen, 1960; Kauserud et al., 2012). It has a natural distribution in conifer woodlands in high altitude and/or latitude in Asia, from which it has invaded human-made constructions in temperate regions all over the world (Kauserud et al., 2007).

Previous population genetic studies based on microsatellites showed that the genetic diversity of the European population is very low (Engh et al., 2010; Kauserud et al., 2007; Maurice et al., 2014), suggesting that a few individuals established through a founder event. Further evidence for a narrow population bottleneck in Europe stems from a limited number of mating type (MAT) and self-recognition vegetative incompatibility (*vic*) alleles present in European isolates (Engh, Skrede et al., 2010; Kauserud, 2004; Kauserud et al., 2006; Maurice et al., 2014; Skrede et al., 2013). Observations of natural Agaricomycete populations indicate high numbers of MAT and *vic* alleles are expected due to frequency-dependent selection acting on both loci (Coelho et al., 2017; Engh, Carlsen et al., 2010; Raper, 1996).

The European population of *S. lacrymans* has most probably dispersed via human vectors to North and South America, Australia and New Zealand (Kauserud et al., 2007). Population genetic analyses indicate that the Japanese dry rot population represents a separate transition from the natural habitat in mainland Asia to the built environment (Kauserud et al., 2007). In addition, the Japanese population possesses significantly higher genetic diversity compared to the European population (Kauserud et al., 2007), also manifested in a higher number of MAT and *vic* alleles (Engh, Carlsen et al., 2010). Evidence of admixture between Asian and European populations was identified in isolates from New Zealand (Kauserud et al., 2007), suggesting multiple introduction events from different source populations. However, which populations and genetic material contribute to the variation in the New Zealand population are unknown.

The indoor habitat exploited by *S. lacrymans* resembles its natural habitat in terms of the relatively dry conditions during most of the year and the scattered presence of large resource units for colonization. Nevertheless, the transition to the indoor environment probably imposed a series of novel selective regimes. Analyses of allelic variation in a few neutral microsatellite loci suggest European and Japanese indoor populations are highly genetically differentiated (Kauserud et al., 2007). Recent gene expression analyses suggested a wider niche related to competitive ability and substrate breath for a Japanese strain compared to a European strain (Hess et al., 2021). However, it is not known whether the two indoor populations possess different adaptations or physiological characteristics as a consequence of their independent evolutionary histories. Similar adaptive traits between the two independent founder populations (Europe vs. Japan) could indicate which characteristics are crucial for long-term survival in the built environment. Isolates of *S. lacrymans* possess significantly more efficient wood decay capacity on spruce compared to the sister species *S. himantioides* (Balasundaram et al., 2018; Hess et al., 2021). Further, comparative genomic and transcriptomic analyses of these sister species suggested that the extremely effective brown rot decay mechanism of *S. lacrymans* was probably due to loss of genes encoding carbohydrate active enzymes, and an increased dependency of the chelator mediated Fenton reaction (CMF). The evolution of specifically efficient CMF may be linked to the reduced enzymatic machinery compared to other brown rot fungi (Balasundaram et al., 2018; Eastwood et al., 2011; Presley & Schilling, 2017), including its sister species *S. himantioides* (Balasundaram et al., 2018). These genomic analyses suggested that adaptive changes in genes related to intracellular transport and growth were important for the colonization of large substrates.

In this study, we confirmed the presence of two divergent populations of *S. lacrymans* in Europe and Japan. We estimated the time since establishment in the built environment and the number of haplotypes founding each of these two populations using demographic inference. Previous analyses indicated that isolates from New Zealand possessed admixed genotypes between European and Japanese isolates. We investigated whether this was due to a recent admixture event or if isolates from New Zealand represent a third genetic group. Finally, we tested whether selection has affected the evolution of the European and Japanese populations, and whether wood decay efficiency has been involved in the success of these populations. Thus, we searched for genomic islands of differentiation and selective sweeps as signals of selection, and investigated the wood decay ability of some isolates as a measure of fitness across the populations.

2 | MATERIALS AND METHODS

2.1 | Isolates included

A total of 36 dikaryotic isolates were included in the analyses, 18 from Japan, 16 from Europe (France, Germany, Norway, Poland, UK) and two from New Zealand (Table 1). Southern France isolates M1 and M2 were collected from different parts of the same building. French and Japanese isolates were kindly provided by Dr G. Le Floch, University of Brest, France and Dr Sakae Horisawa, Kochi University of Technology, Japan, respectively.

2.2 | DNA extraction and sequencing procedures

For all isolated, with the exception of those from France, DNA was extracted using a phenol-chloroform protocol available at the JGI webpage (Isolation of genomic DNA from *Phytophthora*: http://jgi.

TABLE 1 Isolates of *Serpula lacrymans* included in the population genomic analyses, collector, collecting year (where this information is known), population ID (assumed population identity) and their geographic origin

Isolate number	Alternate name	Year	Collector	Population ID	Geographic origin	*N* reads	Mapping %	*F*
S7[a] reference	BAM133	1937	O. Schmidt	Europe	Germany, Berlin	–	–	–
003	LMSA1.11.003	2011	S. Maurice	Europe	France, Finistere	29652700	96.4	0.99
004	LMSA1.11.004	2011	S. Maurice	Europe	France, Finistere	32637231	96.5	0.99
008	LMSA1.11.008	2011	S. Maurice	Europe	France, Finistere	57182833	96.1	0.99
114			S. Maurice	Europe	France, Finistere	20903116	97.5	0.99
74	LMSA1.10.074	2009	S. Maurice	Europe	France, Ardeche	17487073	94.1	0.99
75	LMSA1.10.075	2009	S. Maurice	Europe	France, Finistere	29668681	94.4	0.99
96	LMSA1.10.096	2010	S. Maurice	Europe	France, Manche	44987861	94.6	0.99
M1				Europe	France, Metz, Lorraine	35854157	81.5	0.94
M2				Europe	France, Metz, Lorraine	37312297	64.4	0.96
M4				Europe	France, Metz, Lorraine	35598756	78.7	0.97
MBGT1[a]		2013	I. Skrede and L. Thorbek	Europe	Norway, Oslo	20488750	98.4	0.96
S5	Ebw.1	1935	O. Schmidt	Europe	Germany, Eberswalde	73393713	98.9	0.98
SL187[a]	S3/LU5	1967	O. Schmidt	Europe	UK, Liverpool	44782176	96.6	0.98
SL2		2001	E. Myhre	Europe	Norway, Oslo	24816500	96.1	0.99
SL200[a]	S27	1953	O. Schmidt	Europe	Poland, Warsaw	24769320	93.3	0.95
SL210	S38	1984	O. Schmidt	Europe	Germany, Krefeld	64274030	98.2	0.98
SL198[a]	S21/7801	1978	O. Schmidt	Japan	Japan, Hokkaido, Asahikawa	24816500	90.0	0.23
SL261	8607		provided by S. Doi	Japan	Japan, Hokkaido, Asahikawa	32436203	89.2	0.95
SL262	7906		provided by S. Doi	Japan	Japan, Kimobetsu	22289582	95.3	0.33
SL263	8008		provided by S. Doi	Japan	Japan, Hokkaido, Asahikawa	20817792	93.6	0.23
SL265	8105		provided by S. Doi	Japan	Japan	25951217	88.9	0.19
SL391	8104		G. Griffith	Japan	Japan, Honshu, Tokyo, Akikawa	30574942	95.6	0.32
SL392	8209		G. Griffith	Japan	Japan, Hokkaido, Sapporo	24101054	93.6	0.96
SL393[a]	8604		G. Griffith	Japan	Japan, Honshu, Nagano, Ina	44174171	93.6	0.39
SL420[a]	7806		provided by Doi	Japan	Japan, Hokkaido, Biei	14409695	94.6	0.33
SL424	7905		Provided by S. Horisawa	Japan	Japan, Hokkaido, Asahikawa	32820262	55.9	0.23
SL435[a]	8015		Provided by S. Horisawa	Japan	Japan, Hokkaido, Kushiro	33433985	94.2	0.19
SL445[a]	8013		Provided by S. Horisawa	Japan	Japan, Hokkaido, Kushiro	6109363	94.1	0.39
SL460	8601		Provided by S. Horisawa	Japan	Japan, Hokkaido, Asahikawa	19945199	93.6	0.96

(Continues)

TABLE 1 (Continued)

Isolate number	Alternate name	Year	Collector	Population ID	Geographic origin	*N* reads	Mapping %	*F*
SL462	8603		Provided by S. Horisawa	Japan	Japan, Honshu, Nagano, Saku	16653608	94.7	0.96
SL465	8701		Provided by S. Horisawa	Japan	Japan, Hokkaido, Asahikawa	75059045	93.9	0.52
SL468	8704		Provided by S. Horisawa	Japan	Japan, Honshu, Toyama	14303983	95.2	0.95
SL480	9302		Provided by S. Horisawa	Japan	Japan, Hokkaido, Tsubetsu	24520034	94.3	0.27
SL481	9401		Provided by S. Horisawa	Japan	Japan, Honshu, Tokyo, Akikawa	31709538	93.8	0.95
950		2003	R. S. Ridley	New Zealand	New Zealand, Rotorua	38216474	97.4	0.97
ICMP18202[a]		1995	P. K. Buchanan	New Zealand	New Zealand, Auckland, Massey	15778240	97.5	0.91

Note: N reads are the number of filtered reads used for the mapping analyses. Mapping % is percentage of the N reads that mapped to the reference genome *S. lacrymans* S7.3 v2 (using Bowtie2). F is the inbreeding coefficient for each individual as calculated by VCFtools

[a]Isolates included in the wood decay experiments.

doe.gov/collaborate-with-jgi/pmo-overview/protocols-sample-preparation-information/) combined with the Qiagen genomic tip protocol (Qiagen). Briefly, about 500 mg fresh mycelium, from isolates grown on Serpula Czapek Dox medium (see Eastwood et al., 2011), was flash frozen in liquid N_2 and ground to powder in a mortar. We added 60 ml extraction buffer (0.2 M Tris pH 8.5, 0.25 M NaCl, 25 mM EDTA, 0.5% SDS) to the mortar before the sample was distributed into four 50 ml tubes. Then, 15 ml 7:3 phenol:chloroform was added to each sample before they were mixed and incubated for 90 min at room temperature. The samples were centrifuged at 6,000 *g* for 15 min. The aqueous phase was added to equal volume (V) of chloroform. After mixing, the samples were centrifuged for another 5 min at 6000 g. The aqueous phase was transferred to a clean tube and 0.6 V isopropanol added. The samples were incubated on ice for 30 min before centrifugation at 4°C at 6000 *g* for 15 min. The pellet was washed with 20 ml 70% EtOH and dried for 5 min at RT. The DNA was then dissolved in 500 µl of milli-Q H_2O. The four samples were pooled, 2 mg RNase A (Invitrogen) was added, and incubated for 90 min at 37°C. Then, 8 ml of Qiagen QBT buffer was added, and the mix transferred to genomic-tip columns and processed following the Qiagen genomic-tip protocol. The three samples SL200, SL198 and SL265 were extracted without using the genomic-tip protocol, according to Balasundaram et al. (2018). DNA of the French isolates was extracted using a CTAB – Qiagen genomic tip protocol as described in Payen et al. (2015).

Genomic DNA was used to construct paired-end (2 × 125 bp) libraries using SBS v4 Sample Prep Kit. Libraries were sequenced using the Illumina HiSeq 2500 platform (Illumina, Inc.) at the GeT-PlaGe sequencing facility (Toulouse, France). For the isolates SL200, SL198 and SL265 (2 × 108 bp) libraries were sequenced on the Illumina GAII at the SNP&SEQ Technology Platform.

2.3 | Sequence alignment and variant calling

Genomic sequences were analysed in parallel using two pipelines: (i) the first pipeline trimmed the data using TrimGalore version 0.3.3, aligned using Bowtie2 (Langmead & Salzberg, 2012), and SAMtools (Li et al., 2009) to include only reads that mapped concordantly and only once to remove PCR duplicates. Variants were called for each alignment using HaplotypeCaller, combined into a common variant file with GenotypeGVCFs and further quality filtered with VariantFiltration (QD < 2.0||FS > 60.0||MQ < 40.0||MQRankSum < −12.5||ReadPosRankSum < −8.0) in the Genome Analysis Tool Kit (GATK) (McKenna et al., 2010; Van der Auwera et al., 2013). (ii) The second pipeline trimmed the sequences using Trimmomatic (Bolger et al., 2014), mapped the reads using BWAmem (Li, 2013), filtered using SAMtools, called variants using BCFtools call and filtered with BCFtools view. For both pipelines, the sequence data were mapped to the monokaryotic *S. lacrymans* isolate S7.3, version 2 (Eastwood et al., 2011). Repetitive regions of the *S. lacrymans* version 2 genome were annotated using the REPET package version 2.5 (Flutre et al., 2011), following the procedure outlined in Sipos

et al., (2017). Regions annotated as transposable element-derived were filtered from the SNP data set using BEDTOOLS (Quinlan & Hall, 2010). A combined data set using only SNPs called by both pipelines resulted in 419,196 high quality SNPs for the 36 isolates included in this analysis.

2.4 | Population structure and demographic history

To investigate the structure of the data set, we used a model-based clustering approach as implemented in ADMIXTURE (Alexander et al., 2009). For the ADMIXTURE analyses the number of populations was inferred by analysing the different number of populations (K) and the cross-validation (CV) error for each K. The CV error is used to find which K has the best predictive accuracy, but does not try to determine the absolute K. The full data set including all isolates and SNPs were analysed, in addition to reduced data sets of only European and only Japanese isolates (SNP data set reduced by minor allele count ≥1 in VCFTOOLS [Danecek et al., 2011]). All data sets were transformed from vcf format to plink format in VCFTOOLS. Furthermore, the variation and genetic distance between and within populations were visualized by a PCA plot analysed in EIGENSOFT (Price et al., 2006). The PCA analyses were run on the full SNP data set, and also on the split data sets (European and the Japanese isolates) as in the ADMIXTURE analyses. Three PC axes were produced for each of the three PCA analyses.

Coalescent simulations were used to infer the demographic history of *S. lacrymans* in Europe and Japan using the model-based approach implemented in FASTSIMCOAL2 (Excoffier et al., 2013; Excoffier & Foll, 2011). In FASTSIMCOAL2 the likelihood of predefined evolutionary models can be compared. In addition, demographic parameters, such as the effective population size, population growth rate, as well as timing of evolutionary events, can be estimated for the different evolutionary models. To test the divergence of *S. lacrymans*, we defined three realistic evolutionary models, supported by what is known from the literature. The first model represents a scenario, where *S. lacrymans* moved to an indoor environment in Japan, before migrating to the built environment in Europe. The second model represents a scenario where *S. lacrymans* has moved into the built environment, independently in Japan and Europe, from two natural populations that diverged prior to the colonization into houses. In addition to the divergence between Europe and Japan, the change in population size is important for understanding current patterns of genetic variation. The European population has been shown to be highly reduced in genetic diversity, probably resulting from a founder event when the population was established. To account for that, we included a population growth rate in Europe for both models. In the third model, we also implemented a growth rate for the Japanese population.

The likelihood of each model was inferred from the simulated site frequency spectrum (SFS) fitted to the observed minor allele frequency spectrum with the composite likelihood calculated in FASTSIMCOAL2. For each model 50 independent FASTSIMCOAL2 runs of 1,000,000 coalescence simulations and 40 cycles were analysed. Confidence intervals for the point estimates were calculated using the parametric bootstrap approach used in Excoffier et al. (2013). We analysed the data with both 10^{-7} and 10^{-8} as the mutation rate per site per year. The number of generations rather than years was calculated, as commonly used for such analyses. The generation time for *S. lacrymans* is probably highly context-dependent. For instance, under optimal growth conditions, the fungus can colonize, grow and expand extremely quickly and fruit after one year, and probably fruit successively for several years. Alternatively, under suboptimal conditions the fruiting frequency will vary extensively. It is highly plausible that fruiting in the human-made habitat will lead to a reaction from the home owner and often the death of the fungus. Compared to other taxa, all somatic mutations in a fungal individual have a chance to contribute to the next generation, explaining the different scales of mutation rates across organisms. There are also few available estimates of mutation rates for wood decay basidiomycetes. Recently, a mutation rate of 10^{-10} was estimated for a single diploid individual of the fungal pathogen and wood decay fungus *Armillaria gallica* (Anderson et al., 2018). This relatively slow mutation rate is probably not representative of a sexually reproductive population. Regarding other fungal phyla, higher mutations rates have been estimated, for example, 7.29×10^{-7} for the chytrid *B. dendrobatidis* (O'Hanlon et al., 2018), 2.4×10^{-6} to 2.6×10^{-6} for ascomycete yeast *Saccharomyces cerevisiae* (Gallone et al., 2016) and on average 1.98×10^{-8} in *Magnaporthe oryzae* (Ascomycota) using tip dating of temporally separated samples (Gladieux et al. 2018). Thus, using both mutation rates of 10^{-7} and 10^{-8} in our demographic analyses allowed us to explore the effect of mutation rates on the analyses.

2.5 | Admixture in New Zealand isolates

In founder events involving a few initial founders, the small effective population size will result in strong effect of genetic drift and increased linkage disequilibrium, often resulting in large changes in allele and haplotype frequencies. Thus, founder events complicate estimates of the relationship between populations using allele frequency-based methods, such as ADMIXTURE. However, the haplotype structure contains information that may be used to identify the relationship between populations. To utilize the haplotype structure to infer the relationship between the New Zealand population and the European and Japanese populations, we performed a local ancestry assignment using PCADMIX (Brisbin et al., 2012) with both Europe and Japan as ancestral groups and the New Zealand isolates as an admixed population. PCADMIX uses phased haplotypes derived from both reference panels and the admixed isolates to infer the ancestry of genomic windows. We used BEAGLE 4.0 (Browning & Browning, 2007) to phase the data for each population, without imputation, using default settings. The local ancestry was inferred with PCADMIX, which uses principal components analysis in windows of 10 SNPs along the genome to identify ancestry from a set of predefined potential ancestral populations. Thus, in the case of the two

isolates from New Zealand, the populations from Europe and Japan were defined as the ancestral populations.

We also wanted to specifically test admixture by analysing the allele frequencies between a target population (New Zealand) to two ancestral populations (Europe and Japan) using f3 statistics (Patterson et al., 2012). A negative f3 value indicates admixture. The f3 statistics was analysed in ADMIXTOOLS (Patterson et al., 2012). We performed two separate analyses, one where both the two isolates from New Zealand were used as a target population, and another where the individual isolates were analysed separately as targets.

2.6 | Population diversity

The two isolates comprising the New Zealand population were omitted from further population genetic analyses. As linkage disequilibrium (LD) is expected to decay rapidly with large effective population size and high recombination rate, we calculated LD within 5 kb nonoverlapping windows for the European and the Japanese populations separately using the --geno-r2 command in VCFTOOLS (Danecek et al., 2011). The mean r^2 values for each distance between loci were plotted in R to visualize LD decay. Given that the LD decay decreased rapidly for the Japanese population, a genomic window of 10 kb was chosen as a compromise between LD decay and SNP density for the analyses of genome-wide diversity within and between Japan and Europe. Nucleotide diversity π (Nei & Li, 1979) was calculated for both populations using VCFtools. Levels of genetic differentiation between populations was estimated by calculating F_{ST} (Hudson et al., 1992) and nucleotide substitution per site (D_{XY}) using the python script from Simon Martin (https://github.com/simonhmartin). VCFTOOLS was used to estimate Tajima's *D* statistics (Tajima, 1989) across the 10 kb windows, in order to detect departure from the standard neutral model. Tajima's *D* was estimated on a genome wide level and for specific genomic windows of interest. Estimated on a single locus, positive values of Tajima's *D* indicate balancing selection, while negative values indicate directional selection. By contrast, genome-wide distribution of Tajima's *D* values can give insights into demographic population events, with negative values indicating population expansion while positive values indicate population contraction. Manhattan plots were created using the R package qqman to visualize the F_{ST}, D_{XY}, π and Tajima's *D* along the whole genome and for scaffolds of interest (Turner, 2014).

2.7 | Selection pressure

We used a Bayesian approach, as incorporated in BAYESCAN (Foll & Gaggiotti, 2008) to estimate candidate loci (island of differentiation) under natural selection between the Japanese and European populations. The approach estimates a posterior probability for each locus being under selection based on the allele frequencies of the two populations being significantly more or less divergent than the total shared allele frequencies of all loci in the data set. The method incorporates uncertainties of small population sizes and varying effective population size, which is appropriate for our study. We analysed the combined SNP set of Japanese and European isolates where the two populations were compared, using default settings. The resulting files were analysed in R, after formatting with PGDSPIDER (Lischer & Excoffier, 2011).

Signatures of selective sweeps can be investigated both within population using the integrated haplotype homozygosity (IHH) or between populations applying the population extended haplotype homozygosity (XP-EHH) (Voight et al., 2006). Considering that IHH is dependent on knowledge of the ancestral state, we focused on the XP-EHH approach to detect selective sweeps in which the selected allele has approached fixation within one population. The analysis was done using the R program REHH (Gautier & Vitalis, 2012). Since calculation of XP-EHH is dependent on knowledge of haplotypes, the data was first phased using FASTPHASE v.1.4 with default settings (Scheet & Stephens, 2006).

All significant loci in predicted genes were further analysed for function by InterProScan, using version InterPro 83.0 (www.ebi.ac.uk/interpro/). InterPro and PFAM domains were used for evaluation of gene function.

2.8 | Wood decay experiments

The decay ability of five isolates from Japan, four isolates from Europe and one isolate from New Zealand was investigated by measuring wood mass loss after 60 days of growth on three different substrates, *Abies lasiocarpa* (fir), *Pinus sylvestris* (pine) and *Picea abies* (spruce) according to Balasundaram et al. (2018). The isolates included are indicated in Table 1. A total of three to 10 replicates were included for each isolate.

3 | RESULTS

For the 36 isolates of *S. lacrymans* from Europe, Japan and New Zealand, between 55.9% and 98.9% of the reads mapped to the reference genome of *S. lacrymans* S7.3 (Table 1). After quality control and filtering, 419,196 SNPs were called from the full data set and used for the subsequent analyses.

3.1 | Population divergence and demography

The admixture analyses of the population genomic data revealed that *S. lacrymans* isolates formed geographically structured groups and subgroups (Figure 1). When enforcing a two-group structure ($K = 2$), isolates from Europe and New Zealand were separated from Japanese isolates (the cross-validation error was clearly lowest for $K = 2$; Figure S1). The principal component analysis (PCA, Figure 2a)

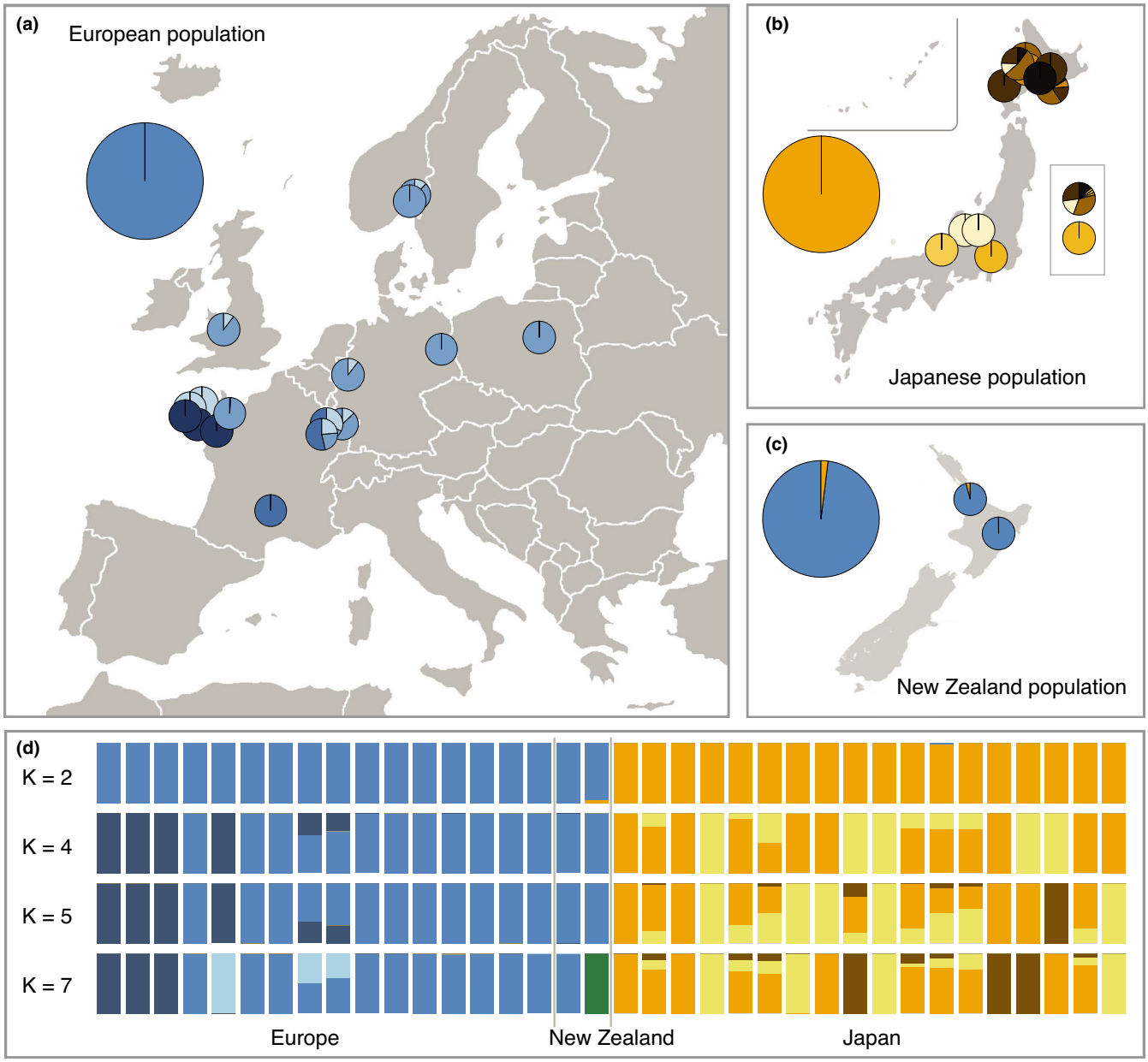

FIGURE 1 Geographic distribution of the included isolates of *Serpula lacrymans* from the built environment in Europe, Japan and New Zealand. (a–c) Show genetic assignment to groups using the software ADMIXTURE. Large pie charts indicate results from the full data set (ADMIXTUREK = 2), the smaller pie charts indicate genetic structuring when each population was analysed separately. As only two isolates were included from New Zealand, they were not analysed separately and the small pie charts are derived from the full data set. (d) Demonstrate the assignment for all 36 isolates for the full data set (each bar shows the probability of assignment to groups for one isolate) to K = 2, K = 4, K = 5, and K = 7 (i.e., those with the lowest cross validation error; see Figure S1)

likewise divided the isolates into the same two main groups (Europe/New Zealand vs Japan) along the first axis, explaining 49.8% of the variation. F_{ST} and D_{XY} estimates confirmed that the Japanese and European populations were strongly differentiated, both based on average F_{ST} of 0.572, D_{XY} of 0.524 and the genome-wide plots (Figure 3).

When the number of groups in the admixture analysis was raised to four (K = 4), both the Japanese population and the European/New Zealand group split into two (Figure 1d). Four French isolates were separated from the rest of the European/New Zealand isolates and five Japanese isolates were separated from the rest of the Japanese isolates. One isolate from New Zealand (ICMP18202) that was separated from the European samples along axis 1 in the PCA plot, was partially admixed in the K = 2 ADMIXTURE analyses and formed a separate group in K = 7 (Figure 1d).

ADMIXTURE and PCA analyses performed independently on the European and Japanese populations revealed further geographic substructuring within each population (Figures 1 and 2). For K = 4, the

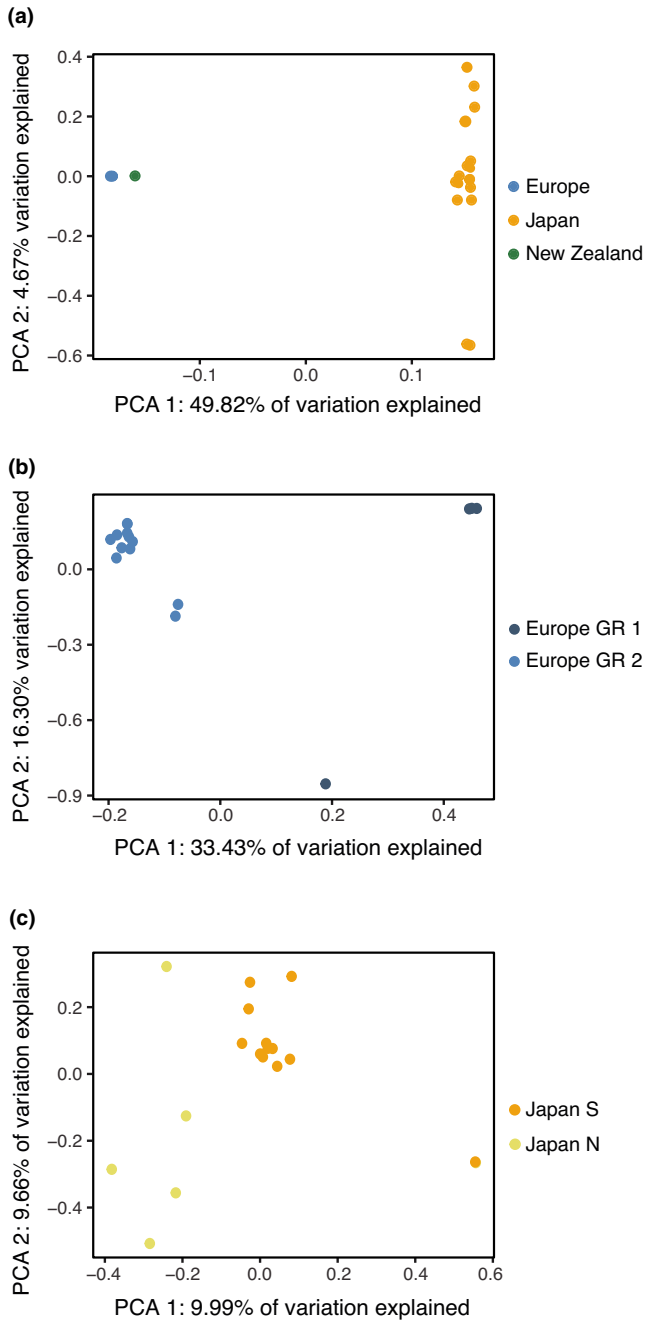

FIGURE 2 Principal component analyses (PCA) of 419,196 SNPs from 36 isolates of the dry rot fungus *Serpula lacrymans*. The x axis indicates the PCA axis 1, and the y axis indicate PCA axis 2. (a) Analyses of the full data set, coloured by geographic origin. (b) Analyses of a separate data set of only European strains, coloured by the two groups from Europe when the full data set was separated by $K = 4$ (Figure 1d). (c) Analyses of a separate data set of only Japanese strains, coloured by geographic origin from S (Honsu) or N (Hokkaido)

European population was divided into a northern European group, two groups in eastern France, and a southern French group, also visible in the PCA plot (Figure 2). When splitting the Japanese population into $K = 7$, a distinct northern group, three southern groups, and three additional admixed groups were identified. These groups were also partially recognized in the PCA (Figure 2). Demographic analyses based on a mutation rate of 10^{-7}, indicated that the historic population that gave rise to the current European population split from the Japanese population around 3,000 generations ago (confidence interval 2012–6157; Figure 4). The estimated divergence time (i.e., generations) was highly sensitive to the selected mutation rate, and increased to 18,770 generations with a mutation rate of 10^{-8}. The modelled demographic scenario in which both populations experienced a change in population size was more likely than the scenario where only the European population changed size (likelihood difference between the two models, ΔAIC =58,899). The European population went through a strong bottleneck about 250 generations ago (confidence interval 198–650), and FASTSIMCOAL2 analyses indicate that only six haplotypes were involved (confidence interval: 4.18–19.40). This could be a slight underestimate, as some of the European isolates were sampled at earlier time points (i.e., from 1935 to 2014; Table 1), which may affect the models. Nevertheless, our model indicates the Japanese population experienced a population size reduction considerably earlier than the European population, and in the same time period as the ancestral population diverged (around 3,500 generations). The reduction in the ancestral Japanese population was less severe, with an estimated effective population size of 1,337. The current effective population sizes were estimated at 1,273 individuals in Europe and 12,500 individuals in Japan (Figure 4).

3.2 | Admixture in one New Zealand isolate

The two isolates from New Zealand showed varied ancestry patterns when the level of admixture was analysed with PCADMIX (Figure 5). Isolate 950 shared close to 100% common ancestry with European isolates along the whole genome. The majority of the genome of isolate ICMP18202 shared common ancestry with the European population, but a large portion of scaffolds 1 and 3, together with other smaller regions scattered throughout the genome, showed shared ancestry with the Japanese population. The f3 analyses using both New Zealand isolates as target was significantly in favor of admixture (f3 = −0.2375, Z = −4.544). For individual analyses of the two isolates independent, admixture is indicated for ICMP18202 (f3 = −0.1205, Z = −0.758, not significant), but not for 950 (f3 = 0.0731, Z = 1.128).

3.3 | Population diversity

The European and Japanese populations had marked differences in their levels of linkage disequilibria. The European population possessed strong linkage disequilibrium, with slow LD decay, while the Japanese population demonstrated a more rapid LD decay (Figure 6). The European population's genetic diversity (π = 0.00028, number of SNPs =18,982) was lower than the Japanese population's (π = 0.00235, number of SNPs =231,952;

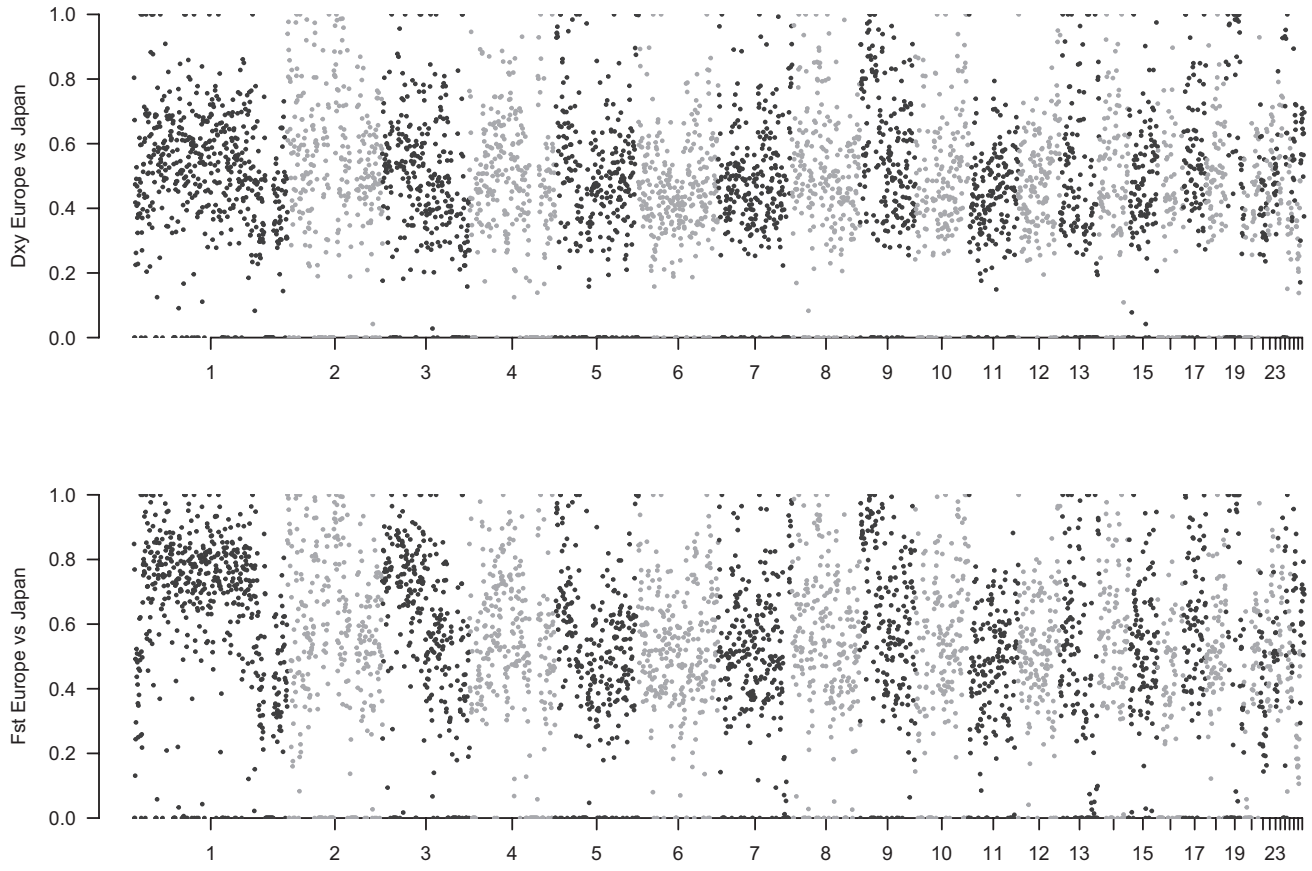

FIGURE 3 Manhattan plot of D_{XY} and F_{ST} between the European and Japanese populations of *Serpula lacrymans* using 10 kb genomic windows along the 30 largest scaffolds of the European *S. lacrymans* S7.3 genome. Black and grey dots separate the adjacent scaffolds, numbered on the x axis. (a) D_{XY}, (b) F_{ST}

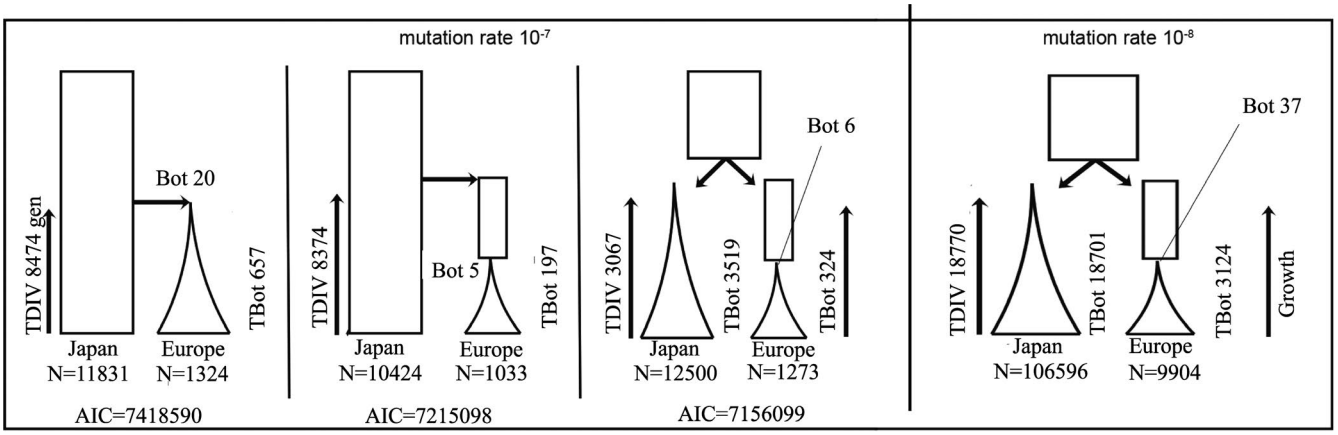

FIGURE 4 The three different models used in FASTSIMCOAL2 when modelling the demographic history of the Japanese and European populations. Two different mutation rates were used, 10^{-7} and 10^{-8}. The model with a population split followed by a bottleneck is the most probable with a lower AIC. The current effective population size is annotated with N, while Bot indicates the effective population size of the bottleneck. TBot indicates time since bottleneck, TDIV indicates time since populations diverged

Table 2). The higher level of genetic diversity in the Japanese population was observed throughout the entire genome (Figure 7). Nevertheless, the Japanese population possessed some genomic regions of lower genetic diversity, specifically in scaffolds 1 and 3 (which are the same genomic regions as where the isolate ICMP18202 from New Zealand shared ancestry to the Japanese population; Figure 5). By contrast, the European population had more narrow genomic regions with high genetic diversity

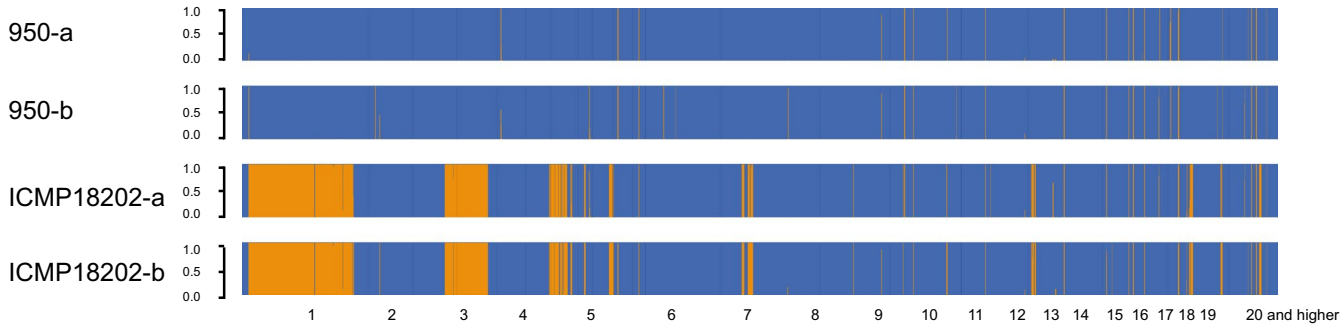

FIGURE 5 The genomic assignment of the two isolates of *Serpula lacrymans* from New Zealand (950 and ICMP18202) to the European and Japanese populations estimated with PCAdmix. The analyses are done long the genome of the European *S. lacrymans* S7.3, for genomic windows of 10 SNPs, where the numbers on the x-axis represent the scaffold numbers. Strain ID-a and -b indicate the two different haplotypes after phasing the SNPs from the dikaryotic strains using Beagle. Blue indicates genomic windows assigned to the European population, while yellow indicates genomic windows assigned to the Japanese population

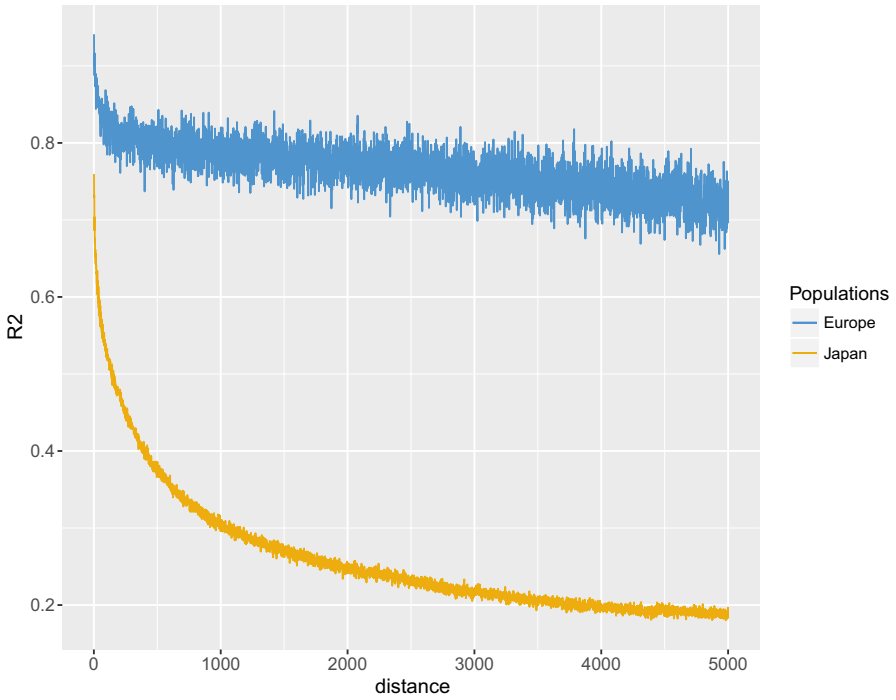

FIGURE 6 Linkage decay of the European (blue) and the Japanese population (yellow) of *Serpula lacrymans*. Distance in x-axis indicates number of base pairs, while R_2 on the y-axis indicates linkage disequilibrium

TABLE 2 Analyses of genome-wide population genetic measures using 10 kb genomic windows of the European and Japanese populations of *Serpula lacrymans*.

Genomic region	No. of SNPs Europe	No. of SNPs Japan	Tajima's *D* Europe	Tajima's *D* Japan	π Europe	π Japan	D_{XY}	F_{ST}
Full genome	18,982	23,1952	−0.079	0.724	0.00028	0.00234	0.518	0.57
Scaff 8: 2440001–2450000	163	163	−2.388	2.042	0.00025	0.00560	0.525	0.45
Scaff 27: 1–10000	101	101	0.829	−0.648	0.00186	0.00245	0.478	0.36

Note: Specific information for the two loci detected in Bayescan to significantly deviate from the expectations are included. No. of SNPs for the Full genome is the number of variable SNPs within the populations, for the specific loci it indicates the total number of SNPs in the dataset for this region.

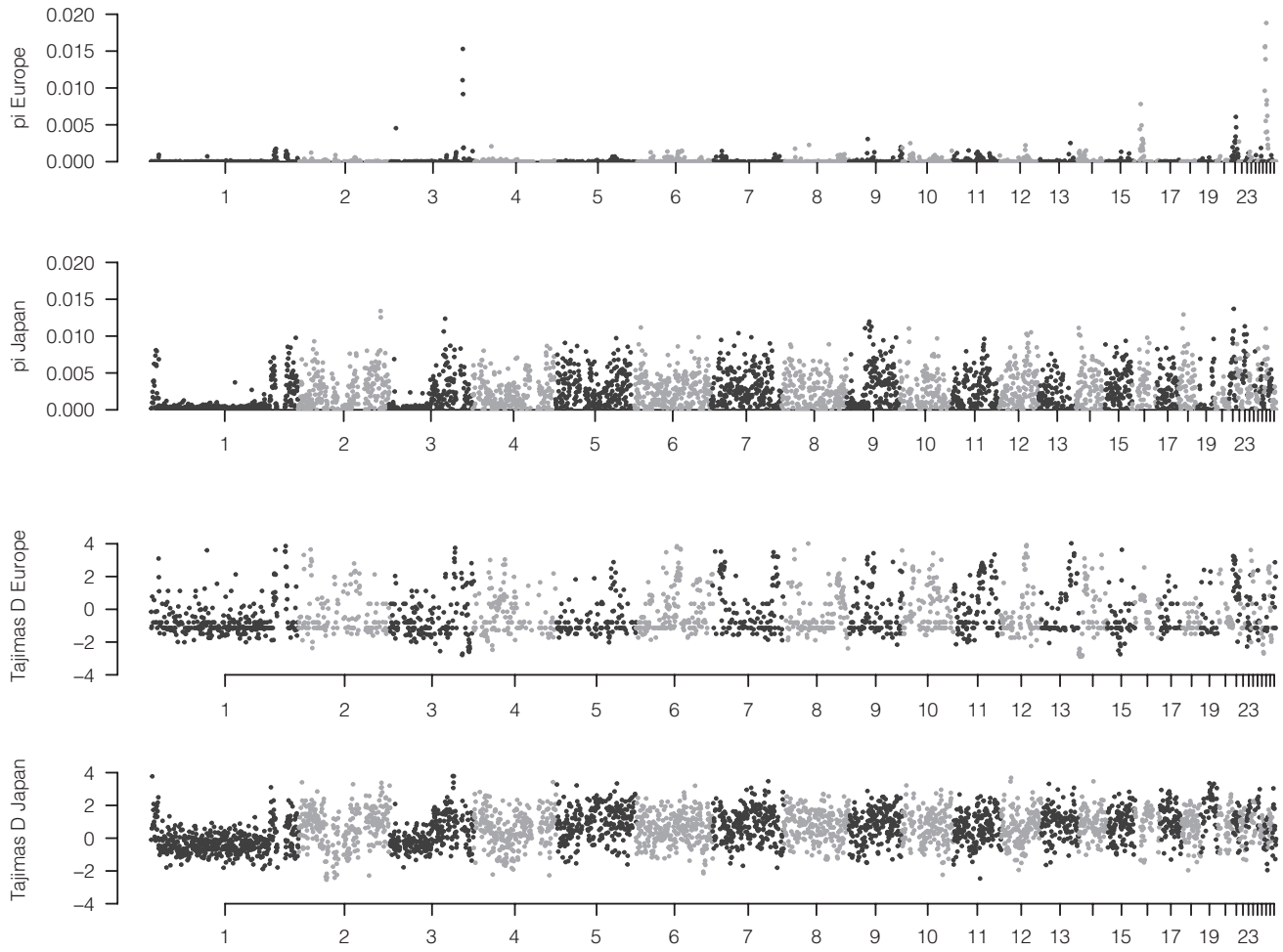

FIGURE 7 Manhattan plots of nucleotide diversity (π) and Tajima's *D* for 10 kb genomic windows along the 30 largest scaffolds of the European *S. lacrymans* S7.3 genome. (a) π of European isolates, (b) π of Japanese isolates, (c) Tajima's *D* of European isolates and (d) Tajima's *D* of Japanese isolates

TABLE 3 Functional annotation of loci with signals of selection in populations of *Serpula lacrymans* from Japan and Europe, by genomic windows of differentiation in Bayescan (GWD) or selective sweep analyses in REHH (Sweep).

Scaffold	Position	Population	Method	Function
Scaffold 8:	2,440,344	Both	GWD	In Protein ID 139103; IPR030077 SNF1 protein kinase subunit beta-2/beta-3, PF04739 AMPKBI
Scaffold 27	4748	Both	GWD	In Protein ID 79357; IPR000648 Oxysterol-binding protein, PF01237 Oxysterol_BP
Scaffold 32	27,468–27,474	Japan	Sweep	In between predicted genes: Protein ID 79617, IPR001202 WW-domain; Protein ID 79618, IPR001128 Cytochrome P450, IPR002401 Cytochrome P450, E-class group 1, PF00463 EP450 I, PF0067 Cytochrome P450; Protein ID 191157 no domains
Scaffold 8	1,313,114–1,313,303	Europe	Sweep	In Protein ID 74433, IPR010285 DNA helicase Pif1-like, PFAM05970 Pif1
Scaffold 13	484,108–484,143	Europe	Sweep	In Protein ID 77115, IPR019378 GDP-fucose protein O-fucosyltransferase, PF10250 O-FucT

(Figure 7). Both populations showed high inbreeding coefficients, with an average F_{IS} of 0.978 for the European and 0.520 for the Japanese population (Table 1).

The average Tajima's *D* values calculated using 10 kb genomic windows along the genome were higher in the Japanese population than in the European population (0.724 vs. −0.079, Table 2).

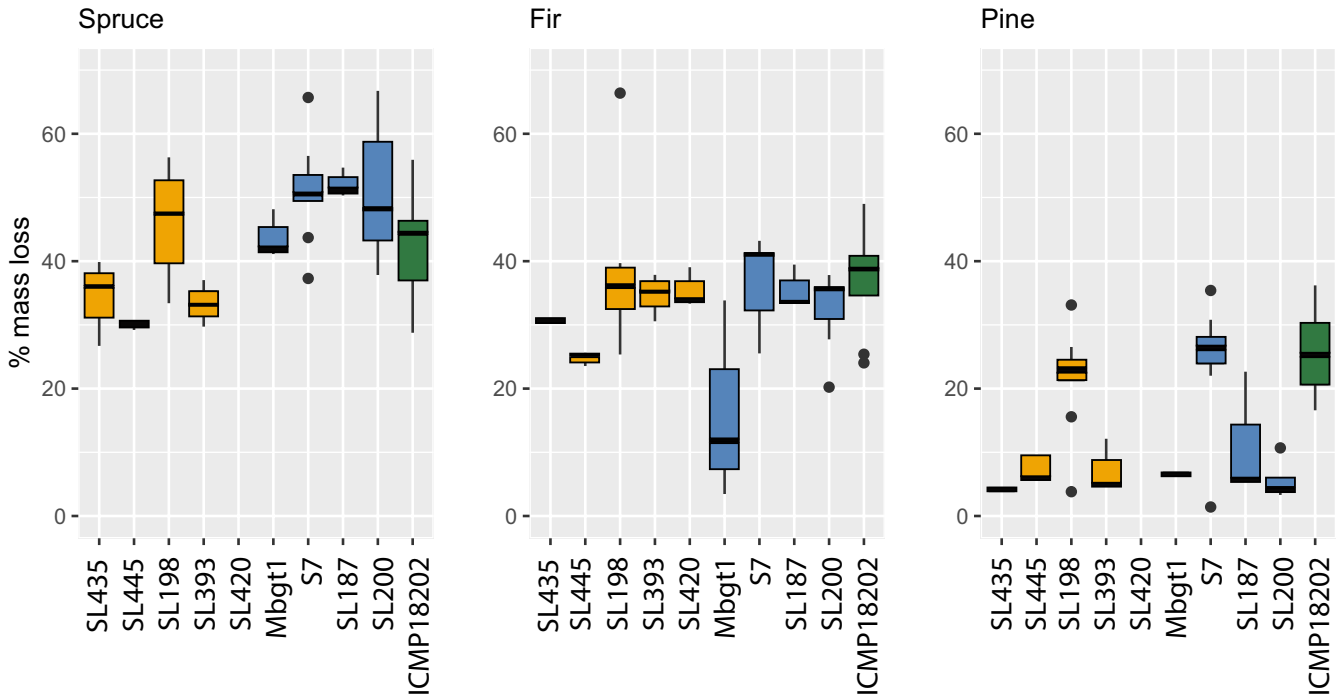

FIGURE 8 The wood decay rates of *Serpula lacrymans* on spruce, fir and pine for isolates from Europe, Japan and New Zealand. Five, four and one isolate included in the mass loss experiments from Japan (yellow), Europe (blue) and New Zealand (green), respectively. The y-axis indicates the percent mass loss of the wood blocks after 60 days of decay

3.4 | Genomic islands of differentiation and selective sweeps

BayeScan analyses were used to detect genetic loci with signatures of selection. When comparing the European and Japanese populations using a false discovery rate of $\alpha < 0.05$, two loci were detected (Figure S2; *S. lacrymans* S7.3 v. 2: scaffold 27, position 4,748 and *S. lacrymans* S7.3 v. 2: scaffold 8, position 2,440,344). Both loci had significantly lower F_{ST} than expected from the BayeScan analyses, with F_{ST} of 0.45 and 0.36 for the loci at scaffold 27 and 8, respectively, indicating purifying or balancing selection (See Figure S3 for F_{ST} and D_{XY} along these scaffolds).

The locus at scaffold 8 is in a predicted gene (protein ID 139103) with a SNF1 protein kinase subunit beta-2/beta-3 Interpro domain (Table 3). The D_{XY} of a 10 kb genomic window surrounding this locus was intermediate (0.525). The European population had low π (0.00025) and negative Tajima's *D* (–2.388), and the opposite was recorded for the Japanese population (π = 0.00560 and Tajima's *D* = 2.042) (Table 2, see Figures S3 and S4 for detailed plots of D_{XY}, F_{ST}, π and Tajima's *D* along scaffold 8). The locus at scaffold 27, was located in a predicted gene (protein ID 79357/190659) with an oxysterol-binding Interpro domain (Table 3). As opposed to the locus at scaffold 8, the locus at scaffold 27 had a lower than average D_{XY} (0.450). Further, the π for the European population was high compared to the average for this population (0.00184), while the Japanese population had an average π = 0.00245. Tajima's *D* estimate for the Japanese populations was negative (–0.648) and opposite to that described for the European population (0.829) (Table 2, Figures S3 and S5).

Extended haplotype homozygosity (EHH) indicates selective sweeps, and more recent selection than the F_{ST} outliers detected by BayeScan (Gautier & Vitalis, 2012; Vitti et al., 2013). EHH identified two selective sweeps in the European population, located in a gene in scaffold 8 (protein ID 79617) and a gene in scaffold 13 (protein ID 77115; Table S1), annotated with DNA helicase Pif1-like and a GDP-fucose protein O-fucosyltransferase Interpro domains, respectively (Table 3). For the Japanese population, the EEH analyses detected a selective sweep in a locus between predicted genes on scaffold 32. Within a 10 kb window surrounding this sweep there are three predicted genes, one with a cytochrome P450 Interpro domain (protein ID 79618), one with a WW Interpro domain (protein ID 79617), and one without any conserved domains.

3.5 | Wood decay assessment

We also assessed differences in wood decay efficiency as a measure of fitness by conducting decomposition experiments of isolates from Europe, Japan and New Zealand. All strains decayed spruce fastest, followed by fir and then pine. For pine there was higher variation in the decay rates among the strains, but the differences among populations were not significant (Figure 8).

4 | DISCUSSION

We confirmed that the two populations of *S. lacrymans* var. *lacrymans* from the built environment in Japan and Europe are highly

divergent, in concordance with Kauserud et al. (2007), and that the divergence between the two populations predated human influence. The results from the demographic modelling analyses strongly support this hypothesis, indicating that the ancestral population split more than 3,000 generations ago giving rise to the current divergent populations in Japan and Europe. The genomic similarity of the wild *S. lacrymans* var. *shastensis* and the building occupant *S. lacrymans* var. *lacrymans* suggests that this species is one of few wood-decay fungi that was already adapted to a niche with some similarities to the built environment (Balasundaram et al., 2018). As a result, it established extensive populations in temperate regions worldwide vectored by human translocation (Kauserud et al., 2007).

4.1 | The split between the two invasive populations predates human influence

The natural habitat of *S. lacrymans* is high alpine regions with scattered large conifer logs (Kauserud et al., 2012). From there, *S. lacrymans* has established independently at least twice in the indoor habitat (Kauserud et al., 2007). However, our dating of this split is influenced by the implemented mutation rate, illustrated by an increase in number of generations from 3067 to 18,770 when using 10^{-8} as alternative mutation rate (to 10^{-7}). Assuming a split approximately 3000 generations ago and a generation time of one year under optimal fungal growth conditions, human-made habitats would have been in existence at the time of the split, for example, 3000 years before present. Indeed, the earliest known wooden constructions in Europe date to circa 7000 years ago (Tegel et al., 2012). However, a generation time (for establishment, vegetative growth and fruiting) that exceeds one year is plausible and the mutation rate is uncertain, suggesting the split of the ancestral population probably predated the availability of the built environment. Central and eastern Asia, where *S. lacrymans* can be found in nature, were not covered by ice sheets during the last glaciation 115–11 K BP (Tian & Jiang, 2016). The dry and cold areas may have driven *S. lacrymans* into refugia, thus splitting *S. lacrymans* into several subpopulations. Although speculative, such a scenario also fits well with the estimated reduction in population size at almost the same time as the split. Consequently, the Himalayas, where the fungus has it westernmost natural distribution (Kauserud et al., 2012), and another north Eastern Asian population, might have functioned as separate source populations of the current indoor populations in Europe and Japan. From previous population studies of *S. lacrymans*, it is known that the European population shares genetic material with specimens from the Himalayas, and that the Japanese population is geographically and genetically closer to the natural population in East Asia (Kauserud et al., 2007, 2012).

The genome-wide SNP data confirmed that the Japanese population is genetically more variable than the European population and that more genetic variation was retained during its founder event(s). This is mirrored by the higher number of vegetative incompatibility (*vic*) alleles and diversity of mating types present in the Japanese population (Engh, Carlsen et al., 2010). The two genetic regions in scaffolds 1 and 3 with lower genetic diversity, cover two large genomic regions containing many genes with various functions. One possible interpretation is that these two genomic regions harbour inversions and therefore show lower rates of recombination in the Japanese population (and in one New Zealand isolate). However, better genome assemblies, which can be achieved with long read sequence data are required to test this. Currently, the function and effect of these possible genome rearrangements are unknown.

4.2 | The European population invaded the built environment about 250 generations ago

As noted above, genetic similarity has previously been observed between Himalayan specimens collected in forests and the European indoor (Kauserud et al., 2007; Singh et al., 1993). Our demographic modelling suggests that the colonization of Europe happened between 200 and 400 generations ago. Assuming a generation time of one year, the colonization of Europe occurred a minimum of 200 years ago, which is consistent with the description of *S. lacrymans* from a European specimen 240 years ago in 1781 (Wulfen, 1781). During this period, and also somewhat earlier, there were considerable trade activities between Europe and Asia which could easily have vectored the colonization of *S. lacrymans* to Europe, for example, through the trade and transport of timber. Human activity might have further spread *S. lacrymans*, from Europe to North America and Australia (Kauserud et al., 2007) and is also considered the main agent for dispersal of several plant pathogens, including *Microbotryum lychnidis-dioicae* and *Ophiostoma ulmi* (Brasier, 1991; Fontaine et al., 2013). To better understand the colonization event of *S. lacrymans* in Europe, the relatedness of European isolates to isolates from the natural range in the Himalayas should be further investigated.

The European population of *S. lacrymans* has low genetic diversity, and the founding members were estimated to consist of only four or five haplotypes (depending on mutation rate). Hence, it is possible that only two or three heterokaryotic isolates colonized and founded the entire European population. This assumption is strongly supported by the low number of mating (MAT) and vegetative incompatibility (*vic*) alleles detected in this population (Engh, Skrede et al., 2010; Kauserud et al., 2006; Skrede et al., 2013). Similar to *S. lacrymans*, the European population of the invasive ash dieback fungus *H. fraxineus* is genetically extremely homogenous and was established by only two haploid individuals (McMullan et al., 2018). Two different subspecies of the Dutch Elm disease parasite *Ophiostoma novo-ulmi* established as clonal parasites in Europe. Later, sexual reproduction between these populations produced a hybrid with high pathogenicity (Brasier & Kirk, 2010). Hence, there are now multiple lines of evidence that invasive fungi may establish on other continents through very tight founder events followed by extensive population growth.

The small founder event establishing the European population is also reflected in the slow LD decay and high levels of F_{IS} observed in the European population. A high degree of selfing or clonal dispersal may cause such abnormal linkage decay curves (Nieuwenhuis & James, 2016). Similar patterns of linkage disequilibrium were observed for isolated and highly biparentally inbred wolf populations in Italy and the Iberian peninsula (Pilot et al., 2014). The very low number of founder isolates in the European population of *S. lacrymans* has probably led to high levels of biparental inbreeding. The limited number of mating alleles available will necessarily lead to a reduction in mating opportunities between individuals, and the tetrapolar mating system of *S. lacrymans* still allows 25% of the spores from the same fruit body to mate. No putative clonal isolates were found in our or previous studies (Engh, Skrede et al., 2010; Kauserud et al., 2007; Maurice et al., 2014), supporting that selfing or clonal dispersal is not the main explanation of the slow linkage decay.

4.3 | Signatures of selection

We detected signs of selection at only two loci using a F_{ST} outlier approach and three loci showed significant extended haplotype homozygosity that may result from selective sweeps. Comparative genomic analyses previously suggested that *S. lacrymans* were preadapted to the indoor conditions (Balasundaram et al., 2018) and it is likely that these adaptations occurred before the split of the European and Japanese populations. The infrequent signatures of divergent selection between the European and the Japanese population may reflect a natural environment, similar to the indoor conditions. The colonization of the built environment, where few competitors exist, may not have created strong selective pressure. During the establishment of the European population, genetic drift has probably been more important for shaping the genetic diversity than selection, resulting in a genetically depauperate population with reduced potential for adaptive evolution. In the F_{ST} outlier test, we observed significantly lower F_{ST} values than expected for two loci. However, the D_{xy} values did not show values that deviated from expectations. Taken together, these results suggest that the effect of selection may be low or this observation is an artefact resulting from demographic events rather than selection.

Extended haplotype heterozygosity suggest that selective sweeps has occurred in the European population in genes related to DNA replication (a DNA helicase with a Pif1 domain) and protein modification (O-Fuct domain involved in glycosylation). In accordance with this, associations between helicases and the environment have been found in several landscape genomic studies, for example, the wood decay fungus *Phellopilus nigrolimitatus* (Sønstebø et al., *under review*), the ectomycorrhizal *Suillus brevipes* (Branco et al., 2017) and the red bread mold *Neurospora crassa* (Ellison et al., 2011). Modification of DNA replication may be the first signals of local adaptation for recently founded populations, such as for the European *S. lacrymans* population.

The selective sweep in the Japanese population was in a non-coding region. Thus, we cannot conclude about the function of this sweep. However, within a 10 kb window of this sweep there are three predicted genes, of which one is a cytochrome P450. Cytochrome P450 s are monooxygenase enzymes known to be involved in the detoxification of polyphenols and other defence molecules secreted by other organisms or encountered during wood decay (Cresnar & Petric, 2011; Ichinose, 2013; Xu et al., 2015). For fungi, cytochrome P450 s were recently suggested to be involved in heavy metal tolerance in *Suillus luteus* (Bazzicalupo et al., 2019) and during pathogenic interactions between *Heterobasidion annum* and conifer trees (Karlsson et al., 2008). Wood type dependent difference in gene expression of cytochrome P450 s have previously been found for two wood decay species (Wymelenberg et al., 2011). Further, in our recent study of *S. lacrymans* (Hess et al., 2021), a larger repertoire of differentially expressed cytochrome P450 s was associated with significantly faster decay of recalcitrant pinewood in a Japanese isolate compared to an isolate from the European population. However, in the experiments in the current study we did not detect systematic differences in the ability to decay different substrates between the Japanese and the European populations, rather that there is high strain to strain variation in this trait. More detailed functional studies are therefore required to better understand the functions of individual cytochrome P450s.

4.4 | The New Zealand population is admixed between European and Asian populations

Inclusion of two isolates from New Zealand enabled us to test whether this population has an admixed ancestry, as hypothesized in Kauserud et al. (2007). Indeed, isolate ICMP18202 possessed a combination of European and Japanese alleles and a negative (although not significant) f3 value, in support of this hypothesis. Similarly, in other invasive fungi, including *B. dendrobatidis*, *O. ulmi/novo-ulmi*, *H. fraxineus*, and *Cryphonectria parasitica*, secondary admixture between independently evolved lineages have been observed (Brasier & Kirk, 2010; Hessenauer et al., 2020; Jezic et al., 2012; McMullan et al., 2018; O'Hanlon et al., 2018). The merging of genetic lineages in founder areas may lead to novel and more aggressive genotypes, as shown for most of these species (Brasier & Kirk, 2010; Hessenauer et al., 2020; Jezic et al., 2012; McMullan et al., 2018; O'Hanlon et al., 2018; Stukenbrock & McDonald, 2008). In our wood decay experiment, the New Zealand isolate ICMP18202 decayed pine wood rapidly, though more isolates are needed to confirm whether this is a population level trait.

The observed admixture was heterogeneously distributed in the genome (mainly scaffolds 1 and 3), indicating limited cycles of recombination. However, it could also be that PCAdmix assigned genomic windows more readily to homogenous genomic regions with low diversity, and hence, more readily detects admixture in scaffolds 1 and 3 with lower diversity as compared to the rest of the genomes

of the Japanese isolates. The reasons for reduced diversity and signs of admixture in large genomic regions in the admixed isolate from New Zealand are currently unknown. This could be a consequence of genomic areas of low recombination, for example, resulting from chromosomal rearrangements. In the future, thorough analyses of genomic synteny based on assembled genomes of additional isolated from these populations may shed light on their effect on population divergence. Given that the two isolates from New Zealand showed different ancestry patterns, we cannot disregard the possibility that the strain showing signals of admixture is part of a divergent, previously unsampled population. Thus, including more isolates from the full geographic distribution of *S. lacrymans* would contribute to better understand the demographic history of isolates from New Zealand.

4.5 | Concluding remarks

Our study confirms that invasive species can establish through founder events involving a few individuals, and that limited genetic diversity does not restrict further expansion. A similar pattern has been observed for many invasive plant and animal pathogens (e.g., Fontaine et al., 2013; McMullan et al., 2018; O'Hanlon et al., 2018; Stauber et al., 2021; Wuest et al., 2017), as well as for the invasive ectomycorrhizal species *Amanita phalloides* (Pringle et al., 2009). Our results confirm that this also applies to invasive wood decay fungi, such as *S. lacrymans*.

Due to their demographic histories, the adaptive potential of both European and Japanese isolates has probably been low, particularly for European isolates influenced by the recent founder event. Low genetic diversity will often result in reduced adaptive potential as genetic drift will be a stronger evolutionary force (Willi et al., 2006). Thus, even if rapid adaptation in invasive pathogenic fungi has been observed (reviewed in Gladieux, Feurtey et al., 2014), this has probably not been the case for *S. lacrymans*. Accordingly, we identified only a few loci under selection.

The introduction of novel genetic material should be avoided as it may enhance the aggressiveness of invasive species (Brasier & Kirk, 2010; Jezic et al., 2012; McMullan et al., 2018; O'Hanlon et al., 2018; Stukenbrock & McDonald, 2008). Admixture between different invasive lineages may promote further adaptation due to novel allele combinations (Prentis et al., 2008). This was recently shown for the Dutch elm disease, where repeated introgressions have increased the fungus temperature tolerance and pathogenicity (Hessenauer et al., 2020). Unfortunately, the limited number of *S. lacrymans* isolates from New Zealand analysed here do not allow us to test whether admixture has enhanced the decay abilities of this population.

Due to globalization processes, invasive species is an increasing problem and involves all types of organisms. Further population genomic studies will be important to obtain more information about evolutionary and ecological drivers of adaptation in invasive species, information that may be used in the management of invasive species.

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AUTHOR CONTRIBUTIONS

Inger Skrede, Claude Murat, Jaqueline Hess, Sundy Maurice, Jørn Henrik Sønstebø, Nils Högberg, Dan Eastwood, Francis Martin and Håvard Kauserud designed the study. Inger Skrede cultured and extracted DNA from all non-French samples. Inger Skrede, Claude Murat, Jaqueline Hess, Annegret Kohler and Jørn Henrik Sønstebø organized sequencing and analysed the data. Inger Skrede, Sundy Maurice, Dominique Barry-Etienne contributed samples. Inger Skrede, Jaqueline Hess, Sundy Maurice, Jørn Henrik Sønstebø, Dan Eastwood and Håvard Kauserud interpreted results and wrote the manuscript. All authors read, commented and approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

The raw sequence reads of SL200 have been made available on NCBI SRA at Bioproject PRJNA412961. The raw sequence reads of SL198 are available on NCBI SRA at Bioproject PRJNA655420. All other raw sequence reads are available on NCBI SRA at Bioproject PRJNA685018. The final SNP data set (vcf file) was deposited in the Dryad repository under accession https://doi.org/10.5061/dryad.ttdz08kxx.

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REFERENCES

Alexander, D. H., Novembre, J., & Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, *19*, 1655–1664.

Anderson, J. B., Bruhn, J. N., Kasimer, D., Wang, H., Rodrigue, N., & Smith, M. L. (2018). Clonal evolution and genome stability in a 2500-year-old fungal individual. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20182233.

Balasundaram, S. V., Hess, J., Durling, M. B., Moody, S. C., Thorbek, L., Progida, C., LaButti, K., Aerts, A., Barry, K., Grigoriev, I. V., Boddy, L., Högberg, N., Kauserud, H., Eastwood, D. C., & Skrede, I. (2018). The fungus that came in from the cold: Dry rot's pre-adapted ability to invade buildings. *The ISME Journal*, *12*, 791–801.

Bazzicalupo, A. L., Ruytinx, J., Ke, Y.-H., Coninx, L., Colpaert, J., Nguyen, N. H., Vilgalys, R., & Branco, S. (2019). Incipient local adaptation in a fungus: evolution of heavy metal tolerance through allelic and copy number variation. *bioRxiv*. https://doi.org/10.1101/832089

Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*, *30*, 2114–2120.

Branco, S., Bi, K., Liao, H.-L., Gladieux, P., Badouin, H., Ellison, C. E., Nguyen, N. H., Vilgalys, R., Peay, K. G., Taylor, J. W., & Bruns, T. D. (2017). Continental-level population differentiation and environmental adaptation in the mushroom *Suillus brevipes*. *Molecular Ecology*, *26*, 2063–2076.

Brasier, C. M. (1991). *Ophioistoma novo-ulmi* sp. Nov., causative agent of current Dutch elm disease pandemics. *Mycopathologia*, *115*, 151–161.

Brasier, C. M., & Kirk, S. A. (2010). Rapid emergence of hybrids between the two subspecies of *Ophiostoma novo-ulmi* with a high level of pathogenic fitness. *Plant Pathology*, *59*, 186–199.

Brisbin, A., Bryc, K., Byrnes, J., Zakharia, F., Omberg, L., Degenhardt, J., Reynolds, A., Ostrer, H., Mezey, J. G., & Bustamante, C. D. (2012). PCAdmix: principal components-based assignment of ancestry along each chromosome in individuals with admixed ancestry from two or more populations. *Human Biology*, *84*, 343–364.

Browning, S. R., & Browning, B. L. (2007). Rapid and accurate haplotype phasing and missing-data inference for whole-genome association studies by use of localized haplotype clustering. *The American Journal of Human Genetics*, *81*, 1084–1097.

Coelho, M. A., Bakkeren, G., Sun, S., Hood, M. E., & Giraud, T. (2017). Fungal Sex: The Basidiomycota. *Microbiology. Spectrum*, *5*, 1–23.

Cresnar, B., & Petric, S. (2011). Cytochrome P450 enzymes in the fungal kingdom. *Biochimica Et Biophysica Acta, Protein and Proteomics*, *1814*, 29–35.

Croll, D., & McDonald, B. A. (2017). The genetic basis of local adaptation for pathogenic fungi in agricultural ecosystems. *Molecular Ecology*, *26*, 2027–2040.

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., Handsaker, R. E., Lunter, G., Marth, G. T., Sherry, S. T., McVean, G., & Durbin, R. (2011). The variant call format and VCFtools. *Bioinformatics*, *27*, 2156–2158.

Eastwood, D. C., Floudas, D., Binder, M., Majcherczyk, A., Schneider, P., Aerts, A., Asiegbu, F. O., Baker, S. E., Barry, K., Bendiksby, M., Blumentritt, M., Coutinho, P. M., Cullen, D., de Vries, R. P., Gathman, A., Goodell, B., Henrissat, B., Ihrmark, K., Kauserud, H., … Watkinson, S. C. (2011). The plant cell wall-decomposing machinery underlies the functional diversity of forest fungi. *Science*, *333*, 762–765.

Ellison, C. E., Hall, C., Kowbel, D., Welch, J., Brem, R. B., Glass, N. L., & Taylor, J. W. (2011). Population genomics and local adaptation in wild isolates of a model microbial eukaryote. *Proceedings of the National Academy of Sciences of the USA*, *108*, 2831–2836.

Engh, I. B., Carlsen, T., Saetre, G.-P., Högberg, N., Doi, S., & Kauserud, H. (2010). Two invasive populations of the dry rot fungus *Serpula lacrymans* show divergent population genetic structures. *Molecular Ecology*, *19*, 706–715.

Engh, I. B., Skrede, I., Saetre, G.-P., & Kauserud, H. (2010). High variability in a mating type linked region in the dry rot fungus *Serpula lacrymans* caused by frequency-dependent selection? *BMC Genetics*, *11*, 64.

Excoffier, L., Dupanloup, I., Huerta-Sanchez, E., Sousa, V. C., & Foll, M. (2013). Robust demographic inference from genomic and SNP data. *PloS Genetics*, *9*, e1003905.

Excoffier, L., & Foll, M. (2011). fastsimcoal: A continuous-time coalescent simulator of genomic diversity under arbitrarily complex evolutionary scenarios. *Bioinformatics*, *27*, 1332–1334.

Fisher, M. C., Henk, D. A., Briggs, C. J., Brownstein, J. S., Madoff, L. C., McCraw, S. L., & Gurr, S. J. (2012). Emerging fungal threats to animal, plant and ecosystem health. *Nature*, *484*, 186–194.

Flutre, T., Duprat, E., Feuillet, C., & Quesneville, H. (2011). Considering transposable element diversification in *de novo* annotation approaches. *PLoS One*, *6*, e16526.

Foll, M., & Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics*, *180*, 977–993.

Fontaine, M. C., Gladieux, P., Hood, M. E., & Giraud, T. (2013). History of the invasion of the anther smut pathogen on *Silene latifolia* in North America. *The New Phytologist*, *198*, 946–956.

Gallone, B., Steensels, J., Prahl, T., Soriaga, L., Saels, V., Herrera-Malaver, B., Merlevede, A., Roncoroni, M., Voordeckers, K., Miraglia, L., Teiling, C., Steffy, B., Taylor, M., Schwartz, A., Richardson, T., White, C., Baele, G., Maere, S., & Verstrepen, K. J. (2016). Domestication and divergence of *Saccharomyces cerevisiae* beer yeasts. *Cell*, *166*, 1397–1410.

Gautier, M., & Vitalis, R. (2012). rehh: an R package to detect footprints of selection in genome-wide SNP data from haplotype structure. *Bioinformatics*, *28*, 1176–1177.

Gladieux, P., Feurtey, A., Hood, M. E., Snirc, A., Clavel, J., Dutech, C., Roy, M., & Giraud, T. (2014). The population biology of fungal invasions. *Molecular Ecology*, *24*, 1969–1986.

Gladieux, P., Ravel, S., Rieux, A., Cros-Arteil, S., Adreit, H., Milazzo, J., Thierry, M., Fournier, E., Terauchi, R., & Tharreau, D. (2018). Coexistence of multiple endemic and pandemic lineages of the rice blast pathogen. *MBio*, *9*, e01806–e1817.

Gladieux, P., Ropars, J., Badouin, H., Branca, A., Aguileta, G., Vienne, D. M., Rodríguez de la Vega, R. C., Branco, S., & Giraud, T. (2014). Fungal evolutionary genomics provides insight into the mechanisms of adaptive divergence in eukaryotes. *Molecular Ecology*, *23*, 753–773.

Harmsen, L. (1960). Taxonomic and cultural studies on brown spored species of the genus *Merulius*. *Friesia*, *6*, 233–277.

Hess, J., Balasundaram, S. V., Bakkemo, R. I., Drula, E., Henrissat, B., Högberg, N., Eastwood, D., & Skrede, I. (2021). Niche differentiation and evolution of the wood decay machinery in the invasive fungus *Serpula lacrymans*. *The ISME Journal*, *15*, 592–604.

Hessenauer, P., Fijarczyk, A., Martin, H., Prunier, J., Charron, G., Chapuis, J., Bernier, L., Tanguay, P., Hamelin, R. C., & Landry, C. R. (2020). Hybridization and introgression drive genome evolution of Dutch elm disease pathogens. *Nature Ecology and Evolution*, *4*, 626–638.

Hudson, R. R., Boos, D. D., & Kaplan, N. L. (1992). A statistical test for detecting geographic subdivision. *Molecular Biology and Evolution*, *9*, 138–151.

Ichinose, H. (2013). Cytochrome P450 of wood-rotting basidiomycetes and biotechnological applications. *Biotechnology and Applied Biochemistry*, *60*, 71–81.

Islam, M. T., Croll, D., Gladieux, P., Soanes, D. M., Persoons, A., Bhattacharjee, P., Hossain, M. S., Gupta, D. R., Rahman, M. M., Mahboob, M. G., Cook, N., Salam, M. U., Surovy, M. Z., Sancho, V. B., Maciel, J. L. N., NhaniJúnior, A., Castroagudín, V. L., Reges, J. T. D. A., Ceresini, P. C., … Kamoun, S. (2016). Emergence of wheat

blast in Bangladesh was caused by a South American lineage of *Magnaporthe oryzae*. *BMC Biology*, *14*, 84.

Jezic, M., Krstin, L., Rigling, D., & Curkovic-Perica, M. (2012). High diversity in populations of the introduced plant pathogen, *Cryphonectria parasitica*, due to encounters between genetically divergent genotypes. *Molecular Ecology*, *21*, 87–99.

Karlsson, M., Elfstrand, M., Stenlid, J., & Olson, Å. (2008). A fungal cytochrome P450 is expressed during the interaction between the fungal pathogen *Heterobasidion annosum sensu lato* and conifer trees. *DNA Sequence*, *19*, 115–120.

Kauserud, H. (2004). Widespread vegetative compatibility groups in the dry-rot fungus *Serpula lacrymans*. *Mycologia*, *96*, 232–239.

Kauserud, H., Knudsen, H., Hogberg, N., & Skrede, I. (2012). Evolutionary origin, worldwide dispersal, and population genetics of the dry rot fungus *Serpula lacrymans*. *Fungal Biology Reviews*, *26*, 84–93.

Kauserud, H., Saetre, G.-P., Schmidt, O., Decock, C., & Schumacher, T. (2006). Genetics of self/nonself recognition in *Serpula lacrymans*. *Fungal Genetics and Biology*, *43*, 503–510.

Kauserud, H., Svegården, I. B., Sætre, G.-P., Knudsen, H., Stensrud, Ø., Schmidt, O., Doi, S., Sugiyama, T., & Högberg, N. (2007). Asian origin and rapid global spread of the destructive dry rot fungus *Serpula lacrymans*. *Molecular Ecology*, *16*, 3350–3360.

Langmead, B., & Salzberg, S. L. (2012). Fast gapped-read alignment with Bowtie 2. *Nature Methods*, *9*, 357–359.

Li, H. (2013). Aligning sequence reads, clone sequences and assembly contigs with BWA-MEM. *BioRxiv*, arXiv.1303.3997.

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., & Durbin, R. (2009). The Sequence Alignment/Map format and SAMtools. *Bioinformatics*, *25*, 2078–2079.

Lischer, H. E. L., & Excoffier, L. (2011). PGDSpider: an automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics*, *28*, 298–299.

Maurice, S., Skrede, I., LeFloch, G., Barbier, G., & Kauserud, H. (2014). Population structure of *Serpula lacrymans* in Europe with an outlook to the French population. *Mycologia*, *106*, 889–895.

McKenna, A., Hanna, M., Banks, E., Sivachenko, A., Cibulskis, K., Kernytsky, A., Garimella, K., Altshuler, D., Gabriel, S., Daly, M., & DePristo, M. A. (2010). The Genome Analysis Toolkit: A MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Research*, *20*, 1297–1303.

McMullan, M., Rafiqi, M., Kaithakottil, G., Clavijo, B. J., Bilham, L., Orton, E., Percival-Alwyn, L., Ward, B. J., Edwards, A., Saunders, D. G. O., Garcia Accinelli, G., Wright, J., Verweij, W., Koutsovoulos, G., Yoshida, K., Hosoya, T., Williamson, L., Jennings, P., Ioos, R., … Clark, M. D. (2018). The ash dieback invasion of Europe was founded by two genetically divergent individuals. *Nature Ecology & Evolution*, *2*, 1000–1008.

Nei, M., & Li, W. H. (1979). Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences*, *76*, 5269–5273.

Nieuwenhuis, B. P. S., & James, T. Y. (2016). The frequency of sex in fungi. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *371*, 20150540.

O'Hanlon, S. J., Rieux, A., Farrer, R. A., Rosa, G. M., Waldman, B., Bataille, A., Kosch, T. A., Murray, K. A., Brankovics, B., Fumagalli, M., Martin, M. D., Wales, N., Alvarado-Rybak, M., Bates, K. A., Berger, L., Böll, S., Brookes, L., Clare, F., Courtois, E. A., … Fisher, M. C. (2018). Recent Asian origin of chytrid fungi causing global amphibian declines. *Science*, *360*, 621–627.

Patterson, N., Moorjani, P., Luo, Y., Mallick, S., Rohland, N., Zhan, Y., Genschoreck, T., Webster, T., & Reich, D. (2012). Ancient admixture in human history. *Genetics*, *192*, 1065–1093.

Payen, T., Murat, C., Gigant, A., Morin, E., De Mita, S., & Martin, F. (2015). A survey of genome-wide single nucleotide polymorphisms through genome resequencing in the Perigord black truffle (*Tuber melanosporum* Vittad.). *Molecular Ecology Resources*, *15*, 1243–1255.

Pilot, M., Greco, C., vonHoldt, B. M., Jędrzejewska, B., Randi, E., Jędrzejewski, W., Sidorovich, V. E., Ostrander, E. A., & Wayne, R. K. (2014). Genome-wide signatures of population bottlenecks and diversifying selection in European wolves. *Heredity*, *112*, 428–442.

Prentis, P. J., Wilson, J. R. U., Dormontt, E. E., Richardson, D. M., & Lowe, A. J. (2008). Adaptive evolution in invasive species. *Trends in Plant Science*, *13*, 288–294.

Presley, G. N., & Schilling, J. S. (2017). Distinct growth and secretome strategies for two taxonomically divergent brown rot fungi. *Applied and Environmental Microbiology*, *83*, e02987–e03016.

Price, A. L., Patterson, N. J., Plenge, R. M., Weinblatt, M. E., Shadick, N. A., & Reich, D. (2006). Principal components analysis corrects for stratification in genome-wide association studies. *Nature Genetics*, *38*, 904–909.

Pringle, A., Adams, R. I., Cross, H. B., & Bruns, T. D. (2009). The ectomycorrhizal fungus *Amanita phalloides* was introduced and is expanding its range on the west coast of North America. *Molecular Ecology*, *18*, 817–833.

Quinlan, A. R., & Hall, I. M. (2010). BEDTools: a flexible suite of utilities for comparing genomic features. *Bioinformatics*, *26*, 841–842.

Raper, J. R. (1996). *Genetics of Sexuality in Higher Fungi*. Ronald Press Company.

Rosenblum, E. B., Voyles, J., Poorten, T. J., & Stajich, J. E. (2010). The deadly chytrid fungus: a story of an emerging pathogen. *PLoS Path*, *6*, e1000550.

Scheet, P., & Stephens, M. (2006). A fast and flexible statistical model for large-scale population genom type data: applications to inferring missing genotypes and haplotypic phase. *American Journal of Human Genetics*, *78*, 629–644.

Schmidt, O. (2007). Indoor wood-decay basidiomycetes: damage, causal fungi, physiology, identification and characterization, prevention and control. *Mycological Progress*, *6*, 281.

Singh, J., Bech-Andersen, J., Elborne, S. A., Singh, S., Walker, B., & Goldie, F. (1993). The search for wild dry rot fungus (*Serpula lacrymans*) in the Himalayas. *Mycologist*, *7*, 124–130.

Sipos, G., Prasanna, A. N., Walter, M. C., O'Connor, E., Bálint, B., Krizsán, K., Kiss, B., Hess, J., Varga, T., Slot, J., Riley, R., Bóka, B., Rigling, D., Barry, K., Lee, J., Mihaltcheva, S., LaButti, K., Lipzen, A., Waldron, R., … Nagy, L. G. (2017). Genome expansion and lineage-specific genetic innovations in the forest pathogenic fungi *Armillaria*. *Nature Ecology & Evolution*, *1*, 1931–1941.

Skrede, I., Maurice, S., & Kauserud, H. (2013). Molecular characterization of sexual diversity in a population of *Serpula lacrymans*, a tetrapolar basidiomycete. *G3: Genes. Genomes, Genetics*, *3*, 145–152.

Stauber, L., Bader, T., Feurtey, A., Prospero, S., & Croll, D. (2021). Emergence and diversification of a highly invasive chestnut pathogen lineage across southeastern Europe, *eLife*, *10*, e56279.

Stukenbrock, E., Banke, S., Javan-Nikkhah, M., & McDonald, B. A. (2007). Origin and domestication of the fungal wheat pathogen *Mycosphaerella graminicola* via sympatric speciation. *Molecular Biology and Evolution*, *24*, 398–411.

Stukenbrock, E. H., & McDonald, B. A. (2008). The origins of plant pathogens in agro-ecosystems. *Annual Review of Phytopathology*, *46*, 75–100.

Tajima, F. (1989). The effect of change in population size on DNA polymorphism. *Genetics*, *123*, 597–601.

Tegel, W., Elburg, R., Hakelberg, D., Stäuble, H., & Büntgen, U. (2012). Early neolithic water wells reveal the World's oldest wood architecture. *PLoS One*, *7*, e51374.

Tian, Z., & Jiang, D. (2016). Revisiting last glacial maximum climate over China and East Asian monsoon using PMIP3 simulations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *453*, 115–126.

Turner, S. D. (2014). qqman: an R package for visualizing GWAS results using Q-Q and manhattan plots. *BioRxiv*. https://doi.org/10.1101/005165

Van der Auwera, G. A., Carneiro, M. O., Hartl, C., Poplin, R., del Angel, G., Levy-Moonshine, A., Jordan, T., Shakir, K., Roazen, D., Thibault,

J., Banks, E., Garimella, K.V., Altshuler, D., Gabriel, S., & DePristo, M.A. (2013). From FastQ data to high confidence variant calls: the Genome Analysis Toolkit best practices pipeline. *Current Protocols in Bioinformatics*, *43*, 11.10.1–33.

Vitti, J. J., Grossman, S. R., & Sabeti, P. C. (2013). Detecting natural selection in genomic data. *Annual Reviews in Genetics*, *47*, 97–120.

Voight, B. F., Kudravalli, S., Wen, X., & Pritchard, J. K. (2006). A map of recent positive selection in the human genome. *PLoS Biology*, *4*, e72.

Willi, Y., van Buskirk, J., & Hoffman, A. A. (2006). Limits to the adaptive potential in small populations. *Annual Review of Ecology, Evolution and Systematics*, *37*, 433–458.

Wuest, C. E., Harrington, T. C., Fraedrich, S. W., Yun, H. Y., & Lu, S. S. (2017). Genetic variation in native populations of the laurel wilt pathogen, *Raffaelea lauricola*, in Taiwan and Japan and the introduced population in the United States. *Plant Disease*, *101*, 619–628.

Wulfen, C. (1781). *Jacquin, Miscell. Austriac*, *2*, 111.

Wymelenberg, A. V., Gaskell, J., Mozuch, M., BonDurant, S. S., Sabat, G., Ralph, J., Skyba, O., Mansfield, S. D., Blanchette, R. A., Grigoriev, I. V., Kersten, P. J., & Cullen, D. (2011). Significant alteration of gene expression in wood decay fungi *Postia placenta* and *Phanerochaete chrysosporium* by plant species. *Applied and Environmental Microbiology*, *77*, 4499–4507.

Xu, J., Wang, X.-Y., & Guo, W.-Z. (2015). The cytochrome P450 superfamily: Key players in plant development and defense. *Journal of Integrative Agriculture*, *14*, 1673–1686.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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