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Modeling disease expression of *Phytophthora ramorum* to estimate potential economic impacts in European forests

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ABSTRACT

Phytophthora ramorum is an invasive generalist plant pathogen introduced to North America and Europe in the mid-1990s and is now established in forests and the nursery industry. It causes sudden oak death in the western US and sudden larch death in Western Europe, leading to extensive forest decline and mortality. While well studied in California and Oregon, no quantitative assessment exists for its potential economic impact on European forestry. We assessed the potential direct economic impact of *P. ramorum* on larch and beech in Europe under a "no-control" scenario. Climatically optimal areas for disease expression were derived using the CLIMEX niche model with refined parameter values, updated climate data, and *P. ramorum* occurrence records from symptomatic forest trees. These areas were overlaid with host distribution data to identify assets at risk. We then applied a radial range expansion model and a partial budgeting method to quantify annualized average damage costs. Our results indicate that 10 % of the study area is climatically optimal for disease expression. Within that area, 4 223 km^2 of larch and 2 577 km^2 of beech are at risk. Under worst-case spread and mortality assumptions, annual direct damage costs could exceed €117 million for larch and €130 million for beech. Countries such as the UK, Italy, Austria, and Germany face the highest risks, while potential impacts in Southern Europe are negligible. This study provides an updated risk assessment of the current post-invasion state of *P. ramorum* in Europe, facilitating informed decision-making and the development of appropriate management strategies.

1. Introduction

Phytophthora ramorum Werres, de Cock & Man in't Veld (PhR) is a generalist, airborne plant pathogen native to Japan, Vietnam, and most likely other regions of East Asia (Jung et al., 2021, 2020; Werres et al., 2001), which has been introduced to North America and Europe in the mid-1990s. Currently, 12 behaviorally diverse phylogenetic lineages are known from Europe (EU1, EU2), North America (NA1, NA2), Japan (NP1–3), and Vietnam (IC1–5) (Jung et al., 2021; Franceschini et al., 2014; Van Poucke et al., 2012). In Europe and North America, PhR has become established in both forest ecosystems and the nursery industry, affecting over 170 host plant species (EPPO, 2025; APHIS, 2024; Harris et al., 2021; Defra, 2015; Webber, 2007; Rizzo et al., 2005). Along the Pacific coast of the United States, it causes sudden oak death (SOD), a lethal canker disease responsible for the mortality of millions of oak (*Quercus* spp.) and tanoak (*Notholithocarpus densiflorus*) trees (Frankel and Palmieri, 2014; Rizzo et al., 2007; Goheen et al., 2002). In Europe, PhR is the causal agent of sudden larch death, leading to extensive dieback of larch plantations (*Larix kaempferi*, *L. decidua*, *L.* × *marchinsii*) in the UK, Ireland, and France (Beltran et al., 2024; Brasier and Webber, 2010; Jung et al., 2018; O'Hanlon et al., 2018; Ministère de l'Agriculture et de la Souveraineté alimentaire, 2017). Other important hosts include rhododendrons, various woody ornamentals, and European beech (*Fagus sylvatica*) (Jung et al., 2018; Brasier and Webber, 2010; Grünwald et al., 2008; Ivors et al., 2004). The latter species is affected in forests and parks across Europe by root losses and bark cankers caused by a range of *Phytophthora* species, including PhR (only in the UK), leading to decline and mortality (Corcobado et al., 2020; Jung et al., 2018; Telfer et al., 2015; Jung, 2009; Brown and Brasier, 2007).

The expression of symptoms caused by PhR varies depending on the

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host species and the part of the host affected (Grünwald et al., 2008). On foliar hosts, such as bay laurel (*Umbellularia californica*) and *Rhododendron* species and hybrids, the pathogen typically causes non-lethal leaf blight and shoot dieback, known as ramorum leaf blight and ramorum shoot dieback, respectively (Pintos et al., 2023; Parke and Peterson, 2019; Beales et al., 2004). In contrast, on canker hosts, such as oaks and European beech, PhR induces bleeding bark cankers on stems and branches, resulting in impaired sap flow and stem hydraulic conductivity, crown decline, and ultimately tree mortality (Collins et al., 2009; Brown and Brasier, 2007). Notably, both tanoak and larch species are unique in exhibiting both foliar and canker symptoms (Jung et al., 2018; Harris and Webber, 2016; Grünwald et al., 2012). Although infestations in commercial nurseries and landscaped settings can often be contained through conventional control methods, the scale and intensity of outbreaks in natural ecosystems render management efforts largely infeasible (Cunniffe et al., 2016; Tjosvold et al., 2005).

Despite recognition of PhR as a serious threat to forest health in both North America and Europe, economic impact assessments have largely been limited to the US and remain scarce for Europe. In Oregon, Hall and Albers (2009) estimated that PhR could cost the state's forest industry between US$21 million and US$1.24 billion over 20 years, depending on the pathogen's spread rate, potential increases in harvest costs, and the control policy scenario. Similarly, Kliejunas (2010) reported that, if eradication failed and PhR spread into southwestern Oregon, annual harvest losses could reach US$100 million. An assessment in Coos County projected that SOD could lead to US$58 million in losses of wages per year and 1 182 lost jobs in the forest sector for the period 2028–2038 (Highland Economics, 2019). In neighboring Curry County, ENTRIX (2008) estimated economic losses range from US$64.93 million to US$652.3 million over 2009–2028 under a no-control scenario. In California, Kovacs et al. (2011) estimated discounted costs associated with SOD of US$7.5 million for treatment, tree removal, and reforestation, and US$135 million property value losses over 2010–2020. In the UK, Eschen et al. (2023) reported that PhR imposed annual costs of approximately £ 4.2 million, and, based on Forestry Commission data, estimated cumulative losses of £ 91.5 million for the period 2010–2017. Impacts on the nursery sector have also been substantial. In Washington State, a survey of 32 nurseries found mean losses exceeding US$11,000 per nursery in both 2004 and 2005 (Dart et al., 2007).

PhR has been the subject of sustained regulatory attention in Europe due to its potential impact on plant health. In 2002, the European Commission adopted Decision 2002/757/EC, introducing provisional emergency phytosanitary measures to prevent its introduction into and spread within the Union (European Commission, 2002). This included mandatory annual surveys in nurseries and natural environments across Member States. This Decision was amended several times (2004/426/EC, 2007/201/EC, 2013/782/EU, and (EU) 2016/1967) (European Commission, 2016, 2013, 2007, 2004), before being repealed and replaced by Regulation (EU) 2021/2285 (European Commission, 2021). In parallel, PhR was added to the European and Mediterranean Plant Protection Organization (EPPO) A2 List of pests recommended for regulation as quarantine pests in 2013, indicating its presence in the EPPO region and the need for official control (EPPO, 2025). Under the current EU framework, Regulation (EU) 2021/2285, a distinction is made between non-EU isolates, classified as Union Quarantine pests (Annex II A, Regulation (EU) 2019/2072), and EU isolates, categorized as Regulated Non-Quarantine Pests (RNQP, Annex IV) (European Commission, 2021, 2019). This classification reflects the current situation in which only the EU1 lineage is established within the EU, while all other lineages remain regulated in an attempt to prevent their introduction. The regulation sets specific requirements and prohibitions regarding the introduction and movement of plants, plant products, and other objects within the EU, along with emergency measures targeting certain species, including PhR.

Although PhR has been present in Europe since its initial detection in Germany and the Netherlands in 1993 (Werres et al., 2001), two important knowledge gaps remain regarding its potential impact on European forestry. Firstly, no quantitative assessment has been conducted to estimate the pathogen's potential economic impact on either the nursery or forestry sectors. The only available analysis is a qualitative risk assessment conducted as part of the EU RAPRA project, which suggested that PhR could have a moderate impact on the European nursery industry and a moderate to major impact on Northern and Southern European tree host systems, respectively (Sansford et al., 2009; Kehlenbeck, 2008; Anonymous, 2007). Secondly, no study has yet mapped which regions the pathogen is likely to induce symptom expression and tree mortality, particularly in forest ecosystems. Previous research has employed bioclimatic models, such as the process-based semi-mechanistic CLIMEX model and the correlative MaxEnt model, to explore the potential distribution of PhR based on climatic suitability for establishment (Shamoun et al., 2018; Ireland et al., 2013; Sansford et al., 2009; Venette and Cohen, 2006). These studies addressed the important research question of where the pathogen could survive. Building on these works, our study focuses on identifying areas where climatic conditions may support disease expression and tree mortality; an essential input for estimating potential economic impacts (Tassone et al., 2008). Notably, earlier studies relied on occurrence data without distinguishing between nursery and forest settings, which was suitable for their objective. However, for economic impact assessment, such a distinction is critical. As Frankel et al. (2025) emphasize, failing to distinguish differences between infections in nurseries and forests can lead to biologically misleading conclusions. Presence alone does not equate to direct economic impact, and meaningful impact assessments require identifying where disease expression and host mortality are likely to occur.

This study focuses on the potential direct economic impact of PhR on European forestry, specifically on forests of larch (*Larix* spp.) and beech (mainly *F. sylvatica*), two ecologically and economically important tree genera. Larch species are fast-growing conifers valued for their adaptability and their durable tannin- and resin-rich wood, which is widely used for carpentry, naval construction, traditional alpine houses, furniture, flooring, and in other weatherproof structures (da Ronch et al., 2016; Praciak, 2013). Larch needles have been demonstrated to support higher sporulation rates of the EU1 lineage than *Rhododendron* (Harris and Webber, 2016). European beech, often described as one of the most "successful Central European plant species", forms pure stands in many regions and is associated with more than 250 documented uses (Houston et al., 2016; Leuschner et al., 2006). Its timber is valued for its strength, hardness, flexibility, and water resistance, rendering it suitable for diverse applications, such as boatbuilding, furniture, musical instruments, and plywood (Houston et al., 2016).

Larch species and European beech are both highly susceptible to PhR[1], but their disease etiology differs considerably. Larch species are highly susceptible to leaf blight and bark cankers, and support abundant sporulation on needles, thereby serving as a competent transmissive host, enabling pathogen spread. European beech, in contrast, functions primarily as a bark host and does not support foliar sporulation (=dead-end host). Consequently, for stem canker development, the proximity of transmissive leaf hosts that produce high levels of sporangial inoculum, which is splash-dispersed by rain onto beech stems, is required (Anonymous, 2007; Brasier et al., 2004). Two larch species (*L. kaempferi*, *L. decidua*) and their hybrid (*L.* × *eurolepis*) are classified as both "highly" vulnerable to PhR disease development and competent for sporangia production and pathogen spread. Beech also appears "highly"

[1] The concept of the susceptibility of a host species to a pest or pathogen consists of two components: vulnerability and competence. Vulnerability refers to a host species' ability to develop symptoms and damage after infection, while competence describes its ability to multiply and transmit the pathogen after infection by allowing sporulation (ANSES opinion Collective expert appraisal report, 2018; Johnson et al., 2013).

vulnerable but with "low or insignificant" competence, which means that it might not contribute to disease spread, but could be infected if there is a dense understory of sporulating foliar hosts around it (Harris et al., 2021; ANSES opinion collective expert appraisal report, 2018). Examples of highly competent foliar hosts that allow the production and dispersal of sporangia are common ash (*Fraxinus excelsior*), Douglas fir (*Pseudotsuga menziesii*), sweet chestnut (*Castanea sativa*), *Rhododendron ponticum*, holm oak (*Quercus ilex*), as well as larch (Harris et al., 2021; ANSES opinion collective expert appraisal report, 2018; Sansford et al., 2009; Anonymous, 2007). Notably, *R. ponticum* has been identified as a principal foliar host contributing to the production of sporangia that subsequently infect the bark of nearby trees, including beech (Defra, 2008). In this study, we apply a climate niche model to identify areas at risk of disease expression and investigate the potential direct damage costs of PhR in European forests.

2. Materials and methods

To investigate the potential direct damage costs of PhR in European forests, we employed a multi-step approach combining bioclimatic modeling, host distribution data, and economic analysis. These components are essential for conducting a quantitative economic impact assessment as outlined by Soliman et al. (2015); Kriticos et al. (2013). Firstly, we utilized the CLIMEX niche model (Kriticos et al., 2015) to identify areas in Europe that are climatically suitable for PhR sporulation, infection, and symptom expression. We used updated parameter values on PhR climate-related symptom expression requirements and occurrence data that explicitly represent PhR records from symptomatic forest trees. Then, we overlaid these areas with spatial data on primary PhR tree hosts (larch and beech), and key sporulating foliar hosts that are essential for natural infection of beech stems, namely *Pseudotsuga menziesii*, *Fraxinus excelsior*, *Castanea sativa*, *Larix* spp., and *Rhododendron ponticum.* These host layers were combined to generate composite maps of host areas at risk, explicitly accounting for host co-occurrence, a key prerequisite for bark infection and canker development in beech. Finally, we used the resulting estimates of areas at risk as input to quantify the potential direct damage costs under a "no-control" scenario, using a partial budgeting approach (Soliman et al., 2015; Wesseler and Fall, 2010). Partial budgeting is an appropriate method to evaluate the economic consequences of a shock, such as a pathogen invasion, by accounting for potential economic benefits and losses through changes in gross margins (Soliman et al., 2015). In the case of PhR, the direct impacts are solely negative, consisting of losses in standing timber stock.

2.1. Data collection and cleaning

2.1.1. Phytophthora ramorum occurrence records

We compiled a dataset of geo-referenced PhR occurrence records, explicitly associated with symptomatic tree infections. The dataset integrates records from several sources, including EPPO (EPPO, 2025), the Global Biodiversity Information Facility (GBIF.org, 2025), the United States Department of Agriculture (USDA), and literature (e.g., Beltran et al., 2024; Dun et al., 2024; Carleson et al., 2021; O'Hanlon et al., 2018; Lione et al., 2017; Franceschini et al., 2014; Ireland et al., 2013).

GBIF records were initially filtered based on specific selection criteria, retaining only those entries labeled as "present", dated after 1990, and accompanied by photographic material of the symptoms or host from which the pathogen was isolated (172 initial records). Subsequently, these records underwent manual verification to confirm that the photographs depicted symptomatic tree infections. Entries lacking photographic verification, precise coordinates, or explicit symptom descriptions were excluded, resulting in 80 verified records. Furthermore, we supplemented the GBIF records with data from the EPPO Global Database. For the occurrence records in the literature, we used the keywords "*Phytophthora ramorum* + [country name]" in Google Scholar for each country where PhR presence has been confirmed by EPPO (last update: May 2025). Only records from symptomatic tree infections in outdoor settings were included, excluding nursery or asymptomatic detections. Finally, unpublished data were kindly provided by the USDA (*personal communication with Sarah Navarro, Forest Service, USDA*), comprising PhR isolations from symptomatic tanoak trees collected in Oregon from 2001 to 2023.[2] All occurrence records were compiled into a single composite dataset, where duplicates were removed. The final dataset comprised a total of 515 unique occurrence records, representing infected trees around the globe (**Appendix**), plus 3 569 records for Oregon.

2.1.2. Climate data

We used the "CliMond CM_TC10: World" climate dataset (C. Duffy, *unpublished data*) to model the current climatic suitability for PhR. This dataset consists of global climate variables interpolated at 10-arc-minute resolution, based on 30-year averages centered on 1995 (1981–2010). In particular, it includes daily minimum and maximum temperatures (°C), monthly precipitation (mm), and relative humidity (%) recorded at 09:00 and 15:00 h. Earlier studies on the potential distribution of PhR, such as those by Ireland et al. (2013) and Venette and Cohen (2006), used older datasets centered on 1945 (1931–1960) and 1975 (1961–1990), respectively. In the context of ongoing climate change, using an updated climate dataset representing the current climatic conditions could mean increased accuracy of the model outcomes.

2.1.3. Host availability

To identify the area at risk by PhR, we used spatial data on the distribution of two primary forest hosts – larch and beech – obtained from the European Forest Institute (EFI) (Brus et al., 2012). These maps provide predicted proportions of species presence at 1 km^2 resolution across Europe, with values ranging from 0 to 100, representing the percentage of the cell occupied by the species.

The total land covered by each host species was calculated using the following equation:

$$Land\ covered\ by\ host\ trees\ (km^2) = \sum_{i=1}^{n} \left(\frac{Predicted\ proportion}{100} \right) \quad (1)$$

where n is the number of grid cells. Each value was divided by 100 to convert percentages into fractional areas. For example, a grid cell with a predicted proportion of 45 % was counted as 0.45 km^2. Country-level host areas were calculated using the "Zonal Statistics" function in QGIS version 3.40.2.

As depicted in Fig. 1, larch forests are primarily distributed across Central Europe and the United Kingdom, whereas beech forests occur more commonly across Central, Western, Southern, and Southeastern Europe.[3]

To identify areas where PhR-induced beech mortality is plausible, we constructed a composite binary map representing the distribution of five key sporulating hosts: *P. menziesii*, *F. excelsior*, *C. sativa*, *R. ponticum,* and *Larix* spp. Spatial data for the first three species were obtained from the Joint Research Centre of the European Commission (de Rigo et al., 2016a, 2016b, 2016c). These data provide the relative probability of a species' presence (RPP) per 1 km^2 grid cell (Fig. S1). We converted these maps to binary presence/absence (1 = presence, 0 = absence) layers by applying an RPP threshold of ≥ 0.5, representing "medium-high"

[2] Due to private concerns associated with exact coordinates, these data are not included in the supplementary material. However, a publicly accessible version of these data at a coarser spatial resolution is available online (USDA Oregon SOD Program, 2024).

[3] Predicted proportions are not normalized to 100 %. The values represent the proportion of each 1 km^2 grid cell occupied by the host tree. A 100 % value would indicate full occupancy, which does not occur for the host trees considered.

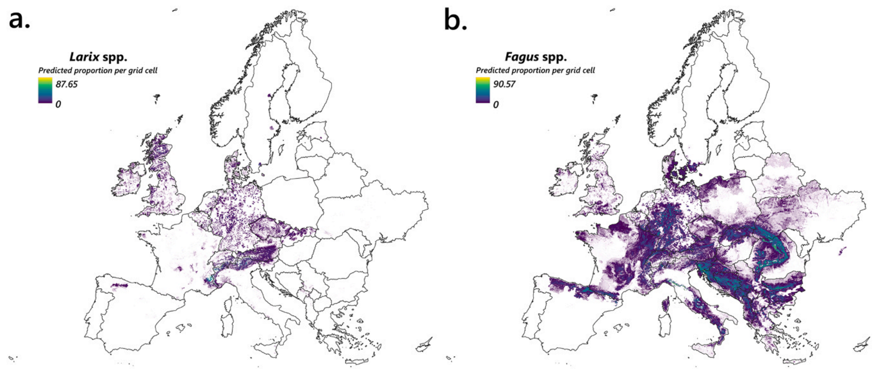

Fig. 1. Distribution and proportion of two primary forest hosts of Phytophthora ramorum in Europe (Brus et al., 2012). **(a.)** *Larix* spp. and **(b.)** *Fagus* spp. (almost exclusively *F. sylvatica*; *F. orientalis* only occurs in the southeastern Balkans). Each grid cell has a resolution of 1 km^2, with 0 representing absence and higher values reflecting increasing canopy coverage.

species presence and beyond (Beck et al., 2023). Further, occurrence records[4] for *R. ponticum* were retrieved from GBIF (Fig. S2). The R code used for the acquisition and cleaning of the GBIF data is provided in the **Appendix.** Lastly, the *Larix* spp. raster was also converted to a binary layer using a predicted proportion threshold of > 0.

All resulting binary layers were combined to generate the final composite layer, indicating the likely substantive presence of at least one competent sporulating host. This composite layer was then overlaid with the *Fagus* spp. raster, showing the areas where beech presence and potential inoculum sources (leaf host presence) coincide.

2.2. Modeling disease expression in Europe

To delineate regions where PhR could lead to forest damage, we modeled the climatic suitability not only for pathogen persistence but also for sporangia production, which is a prerequisite for infection and disease expression, requiring more stringent conditions. While various biotic and abiotic factors influence the potential distribution of species, climate remains a key determinant and is widely used in ecological niche models due to its quantitative nature (Kriticos et al., 2015; Woodward, 1996; Andrewartha and Birch, 1954).

We used the CLIMEX niche model to estimate the climatic suitability of PhR, focusing on its capacity to produce sporangia, infect, and cause disease symptoms under current climatic conditions. CLIMEX simulates species responses to climate by integrating a series of growth and stress indices with meteorological data into a single annual composite index of climatic suitability, the Ecoclimatic Index (EI) (Kriticos et al., 2015). The EI ranges from 0 (unsuitable conditions) to a theoretical maximum of 100 (optimal conditions). Previous CLIMEX applications for PhR (Ireland et al., 2013; Venette and Cohen, 2006) have modeled the potential climate suitability for the presence of the pathogen, but they did not distinguish between simple survival of the pathogen and spread, infection, and symptom expression needed to identify the areas where considerable economic impact is likely to occur. However, symptom expression and bark canker development in trees require not just pathogen persistence but sustained aerial inoculum pressure and conducive environmental conditions that enable sporulation and infection (ANSES opinion Collective expert appraisal report, 2018).

To address this, we refined the parameter values used in earlier CLIMEX studies for PhR (Ireland et al., 2013; Venette and Cohen, 2006), aiming to capture the areas where the climatic conditions may support sporangia production and spread, and, hence, cause the expression of disease symptoms and tree mortality. A comparison of the parameter

Table 1
CLIMEX parameter values used for *Phytophthora ramorum* in the literature and the current study. Parameter values without units are dimensionless indices of plant available soil moisture.

Parameters	Description	Unit	Venette and Cohen (2006)	Ireland et al. (2013)	Current study
DV0	Limiting low temperature	°C	2	0	7
DV1	Lower optimal temperature	°C	17	18	14
DV2	Upper optimal temperature	°C	25	22	17
DV3	Limiting high temperature	°C	30	30	24
SM0	Limiting soil moisture		0.4	0.2	0.6
SM1	Lower optimal moisture		0.7	0.7	0.8
SM2	Upper optimal moisture		1.3	1.3	1.3
SM3	Limiting high moisture		3	2	2
TTCS	Cold stress temperature threshold	°C		−8	−8
THCS	Cold stress temperature rate	week^{-1}		−0.02	−0.02
DTCS	Cold stress day-degree temperature threshold	°C	15		
DHCS	Cold stress day-degree rate	week^{-1}	−0.0001		
TTHS	Heat stress temperature threshold	°C	30	31	25
THHS	Heat stress rate	week^{-1}	0.005	0.03	0.005
SMDS	Dry stress threshold		0.2	0.2	0.2
HDS	Dry stress rate	week^{-1}	−0.005	−0.005	−0.005
SMWS	Wet stress threshold		2.5	2	2
HWS	Wet stress rate	week^{-1}	0.002	0.002	0.002

[4] A distribution map with sufficient resolution was not available, so GBIF occurrence records were rasterized to a 1 km^2 grid cell and then overlayed with the other relevant data layers, as described in the text.

Table 2
Information sources used to set the CLIMEX parameter values for *Phytophthora ramorum* in this study.

Index	Information for parameter values	Source
Temperature Index	DV0 was set to 7 °C because in laboratory tests, most EU1, NA1, and NA2 lineage isolates of PhR tested failed to produce sporangia at 6 °C, and chlamydospore germination rate was nil at 5 °C and very low at 10 °C.	Englander et al. (2006); Tooley et al. (2014)
	DV1 and DV2 were set to 14 and 17 °C, respectively, because: (i) In lab tests for all tested EU1 isolates, numbers of sporangia produced were at 14 °C reasonably high and at 18 °C almost as high as at 22 °C;	Englander et al. (2006)
	(ii) The optimum temperature for sporangia production and zoospore release in *Phytophthora* species is usually lower than the optimum temperature for hyphal growth; therefore, the optimum temperature for sporangia formation in PhR should be < 20 °C;	Erwin and Ribeiro (1996); Ribeiro (1983)
	(iii) Sporangia production of *P. ramorum* on infected *Rhododendron* leaf discs under wet conditions was higher at 14 and 6.7 °C than at 20 °C;	Peterson et al. (2025)
	(iv) Chlamydospore germination rate of EU1, NA1 and NA2 was optimal at 20 °C and higher at 15 °C than at 25 °C; germination of chlamydospores is necessary for sporangia production after dormancy;	Tooley et al. (2014)
	(v) The sporulation period of *P. ramorum* on larch needles occurs during needle senescence in autumn, in SW-Scotland from mid to late September to mid-October, and in Cornwall, UK, from early October to late November.	Dun (2021); Dun et al. (2024); (Forest Research, 2010); Frederickson-Matika et al. (2019); Green et al. (2019)
	(vi) Observations over three consecutive years (2017–2019) in SW-Scotland showed that the greatest increase in new *P. ramorum* infections occurred between September and May, not during the summer.	Dun (2021); Dun et al. (2024)
	DV3 was set to 24 °C because: (i) In lab tests, most EU1 isolates tested failed to produce sporangia at 26 °C;	Englander et al. (2006)
	(ii) In other lab tests, *P. ramorum* failed to produce sporangia at 28 °C.	Peterson et al. (2025)
Moisture Index	With 0.6 and 0.8, respectively, SM0 and SM1 were set slightly higher than in Ireland et al. (2013), with 0.2 and 0.7, respectively, to better reflect the requirement of PhR for continuous rain and high relative humidity to build up sufficient sporangial inoculum to be spread via rain splash onto neighboring uninfected tissues and trees and cause epidemic disease levels.	
	The long-term average annual precipitation in the geographic origins of PhR in Sapa (Vietnam), Kagoshima (Kyushu, Japan), and Kochi (Shikoku, Japan) is 2 363, 2 336, and 2 030 mm, respectively, and, hence, comparable to the Galloway Forest area in SW-Scotland with ca 2 000 mm.	Dun (2021); Jung et al. (2021); Klimadaten (n.d)
	The summers and autumns of 2012 and 2017, which preceded the 2013 and 2018 SLD epidemic outbreaks in Galloway, Scotland, had higher than average rainfall, providing the surface moisture required for successful needle infections.	Dun (2021); Dun et al. (2024)
	The values of SM2 and SM3 were retained from Ireland et al. (2013).	Ireland et al. (2013)
Cold stress	The values for TTCS and THCS were retained from Ireland et al. (2013)	Ireland et al. (2013)
Heat stress	TTHS was set to 25 °C because in lab tests, most EU1 isolates tested failed to produce sporangia at 26 °C. Venette and Cohen (2006) and Ireland et al. (2013) used 30 and 31 °C, respectively, because they modelled persistence instead of spread and infection.	Englander et al. (2006); Ireland et al. (2013); Venette and Cohen (2006)
Dry stress	The values of SMDS and HDS were retained from Ireland et al. (2013) and Venette and Cohen (2006)	Ireland et al. (2013); Venette and Cohen (2006)
Wet stress	The value of SMWS was retained from Ireland et al. (2013) and is consistent with the same value of SM3 (=2). HWS was set to 0.002 week^{-1}, in accordance with both previous CLIMEX studies for PhR.	Ireland et al. (2013); Venette and Cohen (2006)

values used in prior CLIMEX models for PhR and those used in the current study is presented in Table 1. The resulting CLIMEX outputs are shown for Europe and the Pacific coast of the US in Fig. S3 and Fig. S4, respectively. All parameter values were constrained to remain biologically plausible, and their rationale is provided in Table 2.

A parameter sensitivity table and an uncertainty map are provided in the **Appendix** (Table S1 and Fig. S6, respectively).[5] The sensitivity

[5] Parametric sensitivity and overall model uncertainty were revealed using the "Compare Locations + SA (one species)" function in CLIMEX (Kriticos et al. 2015). The sensitivity analysis evaluates how each state variable responds to a simple increase and decrease perturbation for each parameter. The uncertainty analysis applies a Latin hypercube sampling framework to vary parameters within plausible ranges, generating a set of uncertainty maps. In this study, we extracted the variance in the EI values, as this most directly affects the economic analyses.

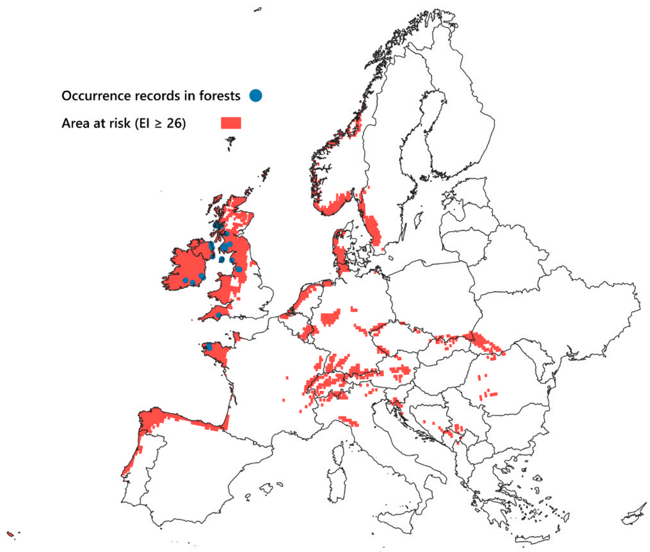

Fig. 2. Binary climatic suitability map for *Phytophthora ramorum* in Europe based on refined CLIMEX parameter values and an Ecoclimatic Index threshold of EI $\geq$ 26. This threshold highlights areas with optimal conditions for pathogen spread, infection, and disease expression, where symptomatic infections and tree mortality are expected to occur. Blue points indicate confirmed *P. ramorum* occurrences from symptomatic trees.

analysis reveals that three parameters (DV1, TTCS, and TTHS) have a sensitivity greater than 2 % for the EI. Each of these parameters was set with a fair degree of confidence (Table 2). The variance map of EI shows that the model uncertainty is very low across our focus area (EI≥26) (cf. Fig. 2 with Fig. S6).

2.3. Model fitting

We used the "Compare Locations (one species)" module in CLIMEX (v4.1.1.0) to project the climatic suitability of PhR under current climatic conditions (Kriticos et al., 2015). As a starting point, we adopted the parameter values from the most recent published CLIMEX model for PhR (Ireland et al., 2013), which focused on exploring the areas where the climatic conditions are favorable for the pathogen's establishment. However, favorable climatic conditions supporting establishment or persistence do not necessarily imply disease expression or tree mortality. Consequently, we refined these parameter values to better reflect conditions conducive to sporangia production, spread and symptom expression in trees, by considering (i) recent literature not used in earlier CLIMEX studies, (ii) the two available published CLIMEX models for PhR, (iii) data and expert knowledge on PhR biology and epidemiology, and (iv) PhR occurrence records explicitly linked to symptomatic tree infections. The model fitting was conducted iteratively, with particular attention given to Europe – our primary study area – and Oregon, where the EU1 lineage is also known to occur (Grünwald et al., 2016). Oregon was particularly valuable as a reference area due to the high number of occurrence record data from symptomatic tanoak trees (3 569 records).

To delineate areas most relevant for tree mortality and potential economic losses in Europe, we converted the continuous EI output of CLIMEX into a binary raster layer. More specifically, we retained only grid cells with EI $\geq$ 26, as EI values above this threshold have been interpreted in previous CLIMEX studies on PhR as indicative of optimal conditions for persistent establishment, while lower values reflect marginal or suboptimal suitability (Ireland et al., 2013; Venette and Cohen, 2006). All grid cells with EI $\geq$ 26 were assigned a value of 1, and the rest were set to 0. The resulting binary suitability layer was used to proceed to the economic assessment. The unrestricted model output is presented in Fig. S5.

2.4. Spread

The rate of spread of PhR is a key factor affecting the potential direct damage costs (Wesseler and Fall, 2010). Grünwald et al. (2012) identified four primary dispersal pathways for PhR: (i) rain and wind, (ii) rivers and streams, (iii) human activities, and (iv) animals. Specifically, the pathogen spreads via sporangia and releases zoospores to neighboring host plants through water splash, typically over distances of 5–10 m (Davidson et al., 2007). Longer distance dispersal, ranging up to a few kilometers, occurs via wind, rain, rivers, and streams, as observed in Oregon, where infections across the landscape reached up to 4 km from the inoculum source (Hansen et al., 2008). Stream monitoring has documented downstream dispersal distances between 1 and 20 km, although this pathway is considered a rare event (Grünwald et al., 2012; Sutton et al., 2009). Human-mediated spread, particularly the trade of infected plant material or the movement of infested soil, has played a substantial role in PhR spread within and between Western countries (Jung et al., 2016; Cushman and Meentemeyer, 2008). Additionally, recreational activities in affected areas can further contribute to dispersal via infested soil adhering to vehicles, bicycle tires, and footwear (Davidson et al., 2007). Lastly, wildlife, including vertebrates like deer, squirrels, and birds, as well as some invertebrates, such as snails, may serve as vectors by transporting infested soil and infected plant material (Grünwald et al., 2012).

Previous studies provide estimates of PhR spread rates in outdoor settings. For example, Meentemeyer et al. (2011) modeled SOD spread in Californian wildlands from 1990 to 2030, noting short-distance dispersal typically up to 1 km, and rare long-distance dispersal events extending up to 100 km. The dispersal kernel was parameterized by a short-distance scale parameter of 20.57 m and a long-distance one of 9.5 km (Cunniffe et al., 2016). Similarly, Hall and Albers (2009) examined the potential spread of SOD in Oregon under a no-control policy scenario, considering rates of 19, 37.5, and 75 km yr^{-1}, and documented an observed average disease spread rate of approximately 3.7 km yr^{-1} over eight years.

For this analysis, we employed a radial range expansion spread model (Schneider et al., 2020; Robinet et al., 2012; Wesseler and Fall, 2010). To parameterize the model, we adopted observed PhR dispersal distances from Peterson et al. (2015), which documented historical spread patterns of SOD in Oregon's tanoak forests in North Chetco (2001–2011) and Borax (2006–2011). More specifically, we selected three representative spread rates: slow (0.25 km yr^{-1}), moderate (2.01 km yr^{-1}), and fast (4.26 km yr^{-1}). The affected area IA_t (km^2) after t years was computed as:

$$IA_t = \begin{cases} (rr \bullet t)^2 \bullet \pi, \text{ if } IA_t < SA \\ SA, \ otherwise \end{cases} \tag{2}$$

Where rr is the radial range expansion rate (km yr^{-1}), π is the mathematical constant, and SA (km^2) is the total susceptible area identified by our CLIMEX model (EI $\geq$ 26). Consequently, Eq. 2 ensures that IA_t does not exceed the total susceptible area SA (km^2).

As the radius grows over time, the affected area expands quadratically, as per the geometric relation of the area of a circle. The model inherently assumes a uniform distribution of susceptible hosts and a constant annual spread rate, focusing explicitly on natural dispersal mechanisms and excluding human-mediated spread. Given that PhR may spread beyond the modelled susceptible area (EI $\geq$ 26), only the fraction of hosts occurring within this area was considered. In particular, the host area affected for each year ($IA_{t,h}$) for each host h was derived by scaling IA_t with an average host proportion across the study area: 0.43 % for larch and 3.19 % for beech. Likewise, for country-level calculations, we used the host proportion of each country relative to its susceptible area (SA_i) to obtain the host area affected in year t and country i ($IA_{t,h,i}$) (Table S4).

2.5. Host tree mortality

The impact of PhR on tree mortality has been well documented, particularly in California and Oregon. For instance, SOD resulted in approximately 80 % mortality of tanoaks across roughly 3 200 ha of Californian forest (Everhart et al., 2014; Rizzo et al., 2005). Further research in these regions reported mortality rates of above-ground biomass reaching up to 90 %, while root systems generally remained unaffected (Cobb et al., 2020, 2012).

Mortality rates associated with PhR infection vary substantially among host tree species. For larch trees, mortality rates across Western, Japanese, and European larch have been reported to range from 33.3 % to 55.5 %, with no significant differences between the NA1, NA2, and EU1 PhR lineages (Chastagner et al., 2013). Field observations reveal a rapid progression of disease symptoms such as branch dieback, ultimately leading to high mortality (>95 %) within approximately four years post-infestation (Dun et al., 2024; Dun, 2021). Similarly, in the Saint-Cadou Forest of France, the proportion of mature larch trees infested with PhR increased from 27 % in May to 42 % by September 2017, with symptomatic trees showing wilting, discolored needles, and branch mortality (Schenck et al., 2018).

Due to limited mortality data for European beech (*F. sylvatica*), our assumptions were based on qualitative assessments. *Fagus sylvatica* was described as highly susceptible to PhR, based on wound inoculation trials (Sansford et al., 2009). Similarly, it has been classified as "moderate to high" vulnerability to PhR[6] (ANSES opinion Collective expert appraisal report, 2018). Consequently, we assume beech trees are somewhat less susceptible than larch trees.

Based on the information above, we assume a linear delay in tree mortality between the initial year of PhR infestation and subsequent tree mortality, which is host tree-specific:

$$m_t = \begin{cases} m, \ if\ t \geq d_h \\ m \bullet \dfrac{t}{d_h}, \ if\ t < d_h \end{cases} \tag{3}$$

where, m_t is the mortality rate (%) at year t after infestation, m is the maximum mortality rate, and d_h is the delay (years) for each host h until m is reached. We set $d_h = 4$ for larch (Dun et al., 2024; Dun, 2021) and $d_h = 6$ for beech, reflecting the latter's comparatively lower susceptibility to PhR. For example, under a $m = 50\%$ scenario for larch ($d_h = 4$), then m_t increases linearly from 12.5 % in the first year after infestation to the full 50 % when $t = d_h = 4$.

To ensure comparability among the outcomes, for the "EU as a single unit" analysis, we simulated five mortality scenarios (10 %, 30 %, 50 %, 70 %, and 90 %) for both hosts, while for the country-level analysis, we used three mortality scenarios (10 %, 50 %, and 90 %).

2.6. Direct economic impact

The potential direct economic impact of PhR infestation in the EU was computed using a partial budgeting approach under a "no-control" scenario (Soliman et al., 2015; Kriticos et al., 2013; Wesseler and Fall, 2010). The "no-control" scenario assumes persistent and unmanaged PhR infestation and uniform spread in all directions until the suitable area is fully occupied, while the impact continues perpetually, reflecting a worst-case scenario. We quantified the direct economic impact in terms of the total loss in timber production volume, assuming both the standing timber stock and timber prices remain constant over time.

We report the results for the EU27, plus Norway, Switzerland, and the United Kingdom, using two alternative aggregation approaches, similar to those by Wesseler and Fall (2010). In the first case, the EU was treated as a single spatial unit, using the total susceptible area for the EU (SA) and the total host area at risk within it. Infestation was simulated once for the EU, and damages were calculated. In the second case, infestation was simulated separately for each country, using its susceptible area (SA_i) and the corresponding affected host area $IA_{t,i,h}$. Then, the EU total was obtained for each scenario by summing across all countries.

The potential direct economic damage costs $DD_{h,t}$ (in €) for host h, at year t are calculated as:

$$DD_{h,t} = IA_{t,h} \bullet VT_h \bullet m_t \bullet p_h \tag{4}$$

Where, $IA_{t,h}$ is the affected host area (km^2) at year t, VT_h is the average timber volume (m^3/km^2) for each host h (23 830 m^3/km^2 for larch; 23 047 m^3/km^2 for beech),[7] m_t is the mortality rate (%) at year t, and p_h is the average timber market price (€59.6/m^3 for larch[8]; €74.3/m^3 for beech[9]):

Future economic losses were discounted to their present values. Thus, $DD_{h,t}$ is expressed in terms of present value PVD_h based on the following equation:

$$PVD_h = \frac{DD_{h,t}}{(1+r)^t}, \quad t = 1, 2, 3\ldots \tag{5}$$

where, PVD_h stands for the present value of direct damage costs for host h. The denominator is the discount factor, where $r = 4.49\%$[10]. Finally, the total discounted economic impact calculated over an infinite time horizon was translated into Average Annual Costs (AAC_h) as follows:

$$AAC_h = r \bullet \sum_{t=1}^{\infty} PVD_h \tag{6}$$

The AAC_h provides a tangible annualized economic metric under the defined "no-control" scenario (Wesseler and Fall, 2010). Eq. 6 incorporates an infinite planning horizon and the transversality condition, ensuring that the present value of damage costs converges to zero as the planning horizon recedes toward infinity. This condition facilitates the economic feasibility of the analysis and reflects the practical assumption of the negligible contribution of distant future costs.

The same procedure was also applied at the country level, where (SA_i) corresponds to each country's susceptible area. Country-level results were then aggregated to obtain an EU total, allowing comparison with the EU-wide approach.

3. Results

3.1. Model fit and disease expression

The restricted CLIMEX model output (EI ≥ 26), representing areas

[6] In the same report, three larch species are classified as "highly" vulnerable.

[7] Derived from the EFISCEN Inventory Database. These averages were computed first at the national level and subsequently aggregated across countries (Table S2).

[8] Converted from the average softwood sawlog price of £ 50.7/m^3 in Great Britain (2012–2024) (Forest Research, 2025) (Table S3), based on an average exchange rate of GBP 1 = EUR 1.1755 (for the period 24/01/2015 – 25/01/2025) (European Central Bank).

[9] Derived as an average from roundwood log prices for Austria (1973–2021), the Czech Republic (2005–2019), Slovenia (2006–2022), and Switzerland (2000–2014) (UNECE, 2023). These average prices were €70.3/m^3, CZK 1626.3/m^3 (~€63.1/m^3), €62.6/m^3, and CHF 107.3/m^3 (~€101.2/m^3), respectively. For the conversion to €, we used an average exchange rate of CHF 1 = EUR 0.9429 (for the period 24/01/2015 – 25/01/2025) (European Central Bank) and an average exchange rate of CZK 1 = EUR 0.03882 (for the period 24/01/2015 – 25/01/2025) (European Central Bank).

[10] We use 4.49 % as it is the average discount rate for most EU Member States (Austria, Belgium, Cyprus, Germany, Estonia, Greece, Spain, Finland, France, Croatia, Ireland, Italy, Lithuania, Luxembourg, Latvia, Malta, the Netherlands, Portugal, Slovenia, and Slovakia) over the period 2023–2024. Source: Reference and discount rates (in %) since 01.08.1997, European Commission

where PhR symptom expression and tree mortality are likely, aligns with the known current distribution of symptomatic trees, especially within our primary focus areas of Europe (Fig. 2) and Oregon. Following the Köppen-Geiger climate classification (Beck et al., 2018), the model highlights extensive areas of temperate oceanic climates (Cfb), characterized by mild temperatures, abundant precipitation, and high relative humidity. In Europe, such climates predominate in western coastal regions, including Ireland, the United Kingdom, northern Spain, Brittany and the Saint Cadou Forest of France, coastal Belgium and the Netherlands, western and coastal Germany and Denmark, and the southwestern coasts of Norway and Finland.

Furthermore, suitability was also projected across substantial areas of warm-summer, humid continental climates (hemiboreal) climates (Dfb), particularly in central and eastern Europe, including parts of eastern and southern Germany, northern Italy, Switzerland, the Czech Republic, Slovakia, Austria, Romania, and Ukraine. Lastly, smaller discontinuous patches of Mediterranean climates, primarily warm-summer (Csb), and less frequently hot-summer (Csa), such as the northwestern Portuguese coast, Galicia (Spain), Liguria (Italy), and coastal Croatia, may also support sporulation and symptom expression during favorable years.

3.2. Area at risk

In total, approximately 0.5 million km^2 (10 % of land area of Europe) is climatically suitable for PhR disease expression across the countries considered (Table 3). These risk areas are strongly clustered along the Atlantic façade, including the British Isles, coastal France, the Netherlands, Belgium, and northwestern Spain, as well as in parts of the Alps and southern Scandinavia. The United Kingdom (139 577 km^2; ~57 % of territory) and Ireland (69 985 km^2; 100 %) together account for more than 42 % of the climatically optimal zone, followed by Germany (43 100 km^2; ~12 %), France (39 007 km^2; ~6 %), Norway (38 592 km^2; 10 %), and Spain (35 888 km^2; ~7 %). Notably, when considered relative to total land area, particularly high levels of risk are evident in smaller western countries such as Switzerland (~51 %), Denmark (~32 %), and the Netherlands (30 %). In contrast, several eastern and northern countries, such as Bulgaria, Estonia, Finland, Greece, Hungary, Latvia, Lithuania, and Luxembourg, exhibit negligible or no suitability for PhR disease expression, reflecting their less favorable climatic conditions.

Across Europe, host availability introduces further constraints (Table 4). Larch distribution is relatively limited in extent, concentrated mainly in central and northwestern countries. The largest larch areas are in Germany (3 021 km^2), Italy (2 795 km^2), and the United Kingdom (2 285 km^2). In contrast, beech (*Fagus* spp., predominantly *F. sylvatica*) is far more widespread, forming extensive stands in central, western, and parts of southern Europe. The most extensive beech areas are found in Romania (17 130 km^2), Germany (16 224 km^2), and France (13 482 km^2).

Spatially intersecting host distributions with the EI ≥ 26 layer markedly narrows the potential host area at risk. For larch, 4 223 km^2 (28 % of the European total larch area) falls within zones climatically optimal to disease expression. Most of this risk area is concentrated in the United Kingdom (1 745 km^2), followed by Austria (652 km^2), Italy

Table 3
Total land area of each country, area at risk (susceptible area) of *Phytophthora ramorum* symptom expression (km^2), based on the CLIMEX model output (restricted to EI ≥ 26), and proportion of area at risk relative to the total country area (%).

Country	Country total area (km^2)	Area at risk (km^2)	Proportion of area at risk (%)
Austria	83 878	14 254	17
Belgium	30 667	7 758	25
Bulgaria	110 996	0	0
Croatia	56 594	1 847	3
Cyprus	9 253	0	0
Czech Republic	78 871	5 347	7
Denmark	42 925	13 611	32
Estonia	45 336	0	0
Finland	338 411	0	0
France	638 475	39 007	6
Germany	357 569	43 100	12
Greece	131 694	0	0
Hungary	93 012	0	0
Ireland	69 947	69 985	100
Italy	302 079	10 859	4
Latvia	64 586	0	0
Lithuania	65 284	0	0
Luxembourg	2 595	72	3
Malta	316	0	0
Netherlands	37 378	11 220	30
Norway	385 207	38 592	10
Poland	311 928	5 838	2
Portugal	92 227	12 651	14
Romania	238 398	4 740	2
Slovakia	49 035	3 757	8
Slovenia	20 273	1 293	6
Spain	505 983	35 888	7
Sweden	447 424	15 380	3
Switzerland	41 285	20 996	51
United Kingdom	243 610	139 577	57
Total	4 895 236	495 772	10

Table 4
Country-level distribution of *Larix* spp. and *Fagus* spp. in Europe, and their extent within climatically suitable zones for *Phytophthora ramorum* symptom expression (EI ≥ 26). For *Fagus* spp., the last column (*Fagus* spp. area with foliar host co-occurrence within EI ≥ 26) represents the subset where beech co-occurs with at least one sporulating foliar host (*Pseudotsuga menziesii*, *Fraxinus excelsior*, *Castanea sativa*, *Larix* spp., and *Rhododendron ponticum*). The Relative Probability of Presence threshold for the first three host species was set to ≥ 0.5.

Country	Total *Larix* spp. area (km^2)	*Larix* spp. area within EI ≥ 26 (km^2)	Total *Fagus* spp. area (km^2)	*Fagus* spp. area with foliar host co-occurrence within EI ≥ 26 (km^2)
Austria	2 027	652	3 748	336
Belgium	162	77	765	98
Bulgaria	9		7 487	
Croatia	0		4 415	
Cyprus[k]				
Czech Republic	1 009	134	1 583	133
Denmark	278	42	1 148	8
Estonia	8		0	
Finland	0		0	
France	1 239	38	13 482	44
Germany	3 021	384	16 224	665
Greece	3		1 714	
Hungary	18		1 055	
Ireland	304	304	154	71
Italy	2 795	502	8 003	499
Latvia	7		2	
Lithuania	0		2	
Luxembourg	1		203	0
Malta				
Netherlands	187	3	131	3
Norway	0		10	0
Poland	21	6	3 369	18
Portugal	0		0	
Romania	3		17 130	
Slovakia	410	55	4 091	207
Slovenia	119		4 043	
Spain	150		4 085	2
Sweden	151		638	0
Switzerland	717	281	2 108	188
United Kingdom	2 285	1 745	1 011	304
Total	14 926	4 223	96 599	2 577

[k] The EFI dataset does not provide coverage Cyprus and Malta

(502 km^2), Germany (384 km^2), and Ireland (304 km^2). Smaller patches are located in Switzerland, the Czech Republic, Belgium, Slovakia, Denmark, and France, while larch stands in countries such as Spain, Slovenia, and Sweden fall entirely outside the risk zones. For beech, the ecological requirement of co-occurrence with sporulating foliar hosts (*Pseudotsuga menziesii*, *Fraxinus excelsior*, *Castanea sativa*, *Larix* spp., and *Rhododendron ponticum*) further constrains the host area at risk. More specifically, out of approximately 96 600 km^2 of beech in Europe, only 2 577 km^2 (2.7 %) meet both EI $\geq$ 26 and foliar host co-occurrence criteria. The beech area at risk is concentrated in Germany (665 km^2), Italy (~500 km^2), Austria (336 km^2), the United Kingdom (~300 km^2), and Slovakia (~200 km^2). Evidently, several countries with extensive beech cover, such as Romania, France, Spain, and Slovenia, have little to no at-risk beech forests.

3.3. Direct economic impact

The potential direct damage costs induced by PhR infestation vary substantially depending on host species, spread rate, and mortality. When the EU is treated as a single spatial unit (EU-wide aggregation using average host proportion on total land), annual losses for larch range from €0.15 million yr^{-1} (10 % mortality, 0.25 km yr^{-1} spread) to over €117.5 million yr^{-1} under the worst-case scenario (90 % mortality, 4.26 km yr^{-1} spread) (Table 5). Under the 50 % mortality and 2.01 km yr^{-1} scenario, average annual damage costs are approximately €33 million. For beech, EU-wide losses are consistently higher, ranging from €1.31 million yr^{-1} in the best-case scenario to over €130 million yr^{-1} in the worst-case scenario. The 50 % mortality and 2.01 km yr^{-1} spread scenario results in average annual damage costs of approximately €62 million, about twice the larch total in the same scenario.

To capture country heterogeneity, we also applied the simulated damages separately for each country using country-specific susceptible areas and susceptible host areas and then summed them to the EU total. This method highlights strong regional variation in potential direct damage costs between countries (Fig. 3), reflecting differences in climatic suitability for PhR, host distribution, and, for beech, the co-occurrence of competent transmissive foliar hosts. Using the (moderate) spread rate scenario (2.01 km yr^{-1}) as a reference, annual losses for larch at 50 % mortality are concentrated in Austria (€8.1 million yr^{-1}), Italy (€6.9 million yr^{-1}), the United Kingdom (€4.8 million yr^{-1}), and Switzerland (€2.9 million yr^{-1}) (Table S5). In the case of beech, potential losses are greater than those of larch. More specifically, in the same scenario, the largest annual impacts are projected for Italy (€8.3 million yr^{-1}), Germany (€5.5 million yr^{-1}), Austria (€5 million yr^{-1}), Slovakia (€4.7 million yr^{-1}), and the Czech Republic (€2.8 million yr^{-1}) (Table S6). At low mortality rates (10 %, 2.01 km yr^{-1}), country-level damage costs for larch remain $\leq$ €1.6 million yr^{-1} (Austria), and for beech $\leq$ €1.7 million yr^{-1} (Italy). In contrast, at high mortality (90 %, 2.01 km yr^{-1}), annual losses exceed €14 million yr^{-1} in Austria and Italy, for larch and beech, respectively.

At the scenario extremes, losses range from negligible values (<€0.6 million yr^{-1} per country) under the best-case scenario (10 % mortality, 0.25 km yr^{-1}) to substantial impacts exceeding €26 million for larch in the United Kingdom and €22 million for beech in Italy under the worst-case scenario (90 % mortality, 4.26 km yr^{-1}). Summed across countries, totals range from €0.8–107 million yr^{-1} for larch, and €2.6–96 million yr^{-1} for beech. While these extreme scenarios represent the outer bounds of our assumptions and are therefore less probable, they illustrate the potential bandwidth of direct damage costs under a no-control scenario.

Notably, several countries with extensive beech stands, such as Romania and France, exhibit negligible or zero losses in all scenarios due to the absence of co-occurring competent foliar hosts within climatically suitable zones (EI $\geq$ 26). Likewise, 14 countries (Bulgaria, Croatia, Estonia, Finland, Greece, Hungary, Latvia, Lithuania, Luxembourg, Norway, Portugal, Romania, Slovenia, and Sweden) experience no losses for either host in any scenario, explaining their absence from Fig. 3.

Table 5
Average annual direct damage costs (€ million yr^{-1}) due to *Phytophthora ramorum* for *Larix* spp. and *Fagus* spp. in Europe under a no-control scenario, for different mortality and spread rate scenarios. Host proportions for the EU as a single unit aggregation equal 0.43 % for larch and 3.19 % for beech (on the total land area). Similarly, we used an average timber price of €59.6/m^3 for larch (softwood sawlog) and of €74.3/m^3 for beech (roundwood logs).

Mortality rate (%)	Spread rate (km yr^{-1})	Larch (€ million yr^{-1})	Beech (€ million yr^{-1})
10	**0.25**	0.2	1.3
	2.01	6.6	12.4
	4.26	13.1	14.5
30	**0.25**	0.5	3.9
	2.01	19.8	37.1
	4.26	39.2	43.6
50	**0.25**	0.8	6.6
	2.01	33.1	61.8
	4.26	65.3	72.7
70	**0.25**	1.1	9.2
	2.01	46.3	86.5
	4.26	91.4	101.8
90	**0.25**	1.4	11.8
	2.01	59.5	111.2
	4.26	117.5	130.9

4. Discussion

This study aimed to identify areas in Europe where climatic conditions are conducive to disease expression and damage caused by *Phytophthora ramorum* (PhR), and to quantify the pathogen's potential direct economic impacts under a "no-control" scenario on larch and beech. We refined the more recently published CLIMEX model for PhR using updated climate data and parameter values to capture conditions suitable for sporangia production and spread, infection, and disease expression rather than mere survival or presence, and we fitted the model considering exclusively PhR occurrence records from symptomatic trees in outdoor settings. The resulting climate suitability projections were intersected with spatial data on host distributions, and, by employing a partial budgeting approach, estimates of the potential economic damages were obtained. The analysis yielded four main findings: (i) more than 10 % (~500 000 km^2) of the European land area is climatically suitable for disease expression (EI $\geq$ 26); (ii) within that zone, 4 233 km^2 of larch and 2 577 km^2 of beech are at risk; (iii) under worst-case spread and mortality assumptions, annual direct damage costs could reach €106–117 million for larch and €96–130 million for beech; and (iv) the risk is mostly concentrated in a subset of countries, such as the UK, Italy, Austria, and Germany, whereas projected impacts are negligible across most southern and eastern European countries.

Our CLIMEX model closely reflects the risk areas where climatic conditions are suitable for PhR disease expression in natural forest settings in Europe. Suitable areas are mainly clustered along the Atlantic façade, parts of the Swiss, German, Austrian, and Italian Alps and their foothills, and southern Scandinavia. The UK and Ireland together account for more than 42 % of the climatically suitable zone, while countries such as Bulgaria, Estonia, Greece, Hungary, Latvia, Lithuania, and Finland are deemed unsuitable under recent historical climate. This pattern corresponds well with reported PhR occurrences in Europe, which are predominantly concentrated in the UK, Ireland, and Brittany (Beltran et al., 2024; Brasier and Webber, 2010; O'Hanlon et al., 2018; Ministère de l'Agriculture et de la Souveraineté alimentaire, 2017). Countries identified as unsuitable have never reported PhR in their territory, except for Finland, where the pathogen is classified as "transient" and was only found in nurseries and garden centers (EPPO, 2025). Interestingly, elsewhere in Europe, most detections remain confined to nurseries, although our model indicates that natural and semi-natural ecosystems may still be at risk and that the pathogen has not yet reached its climatic limits.

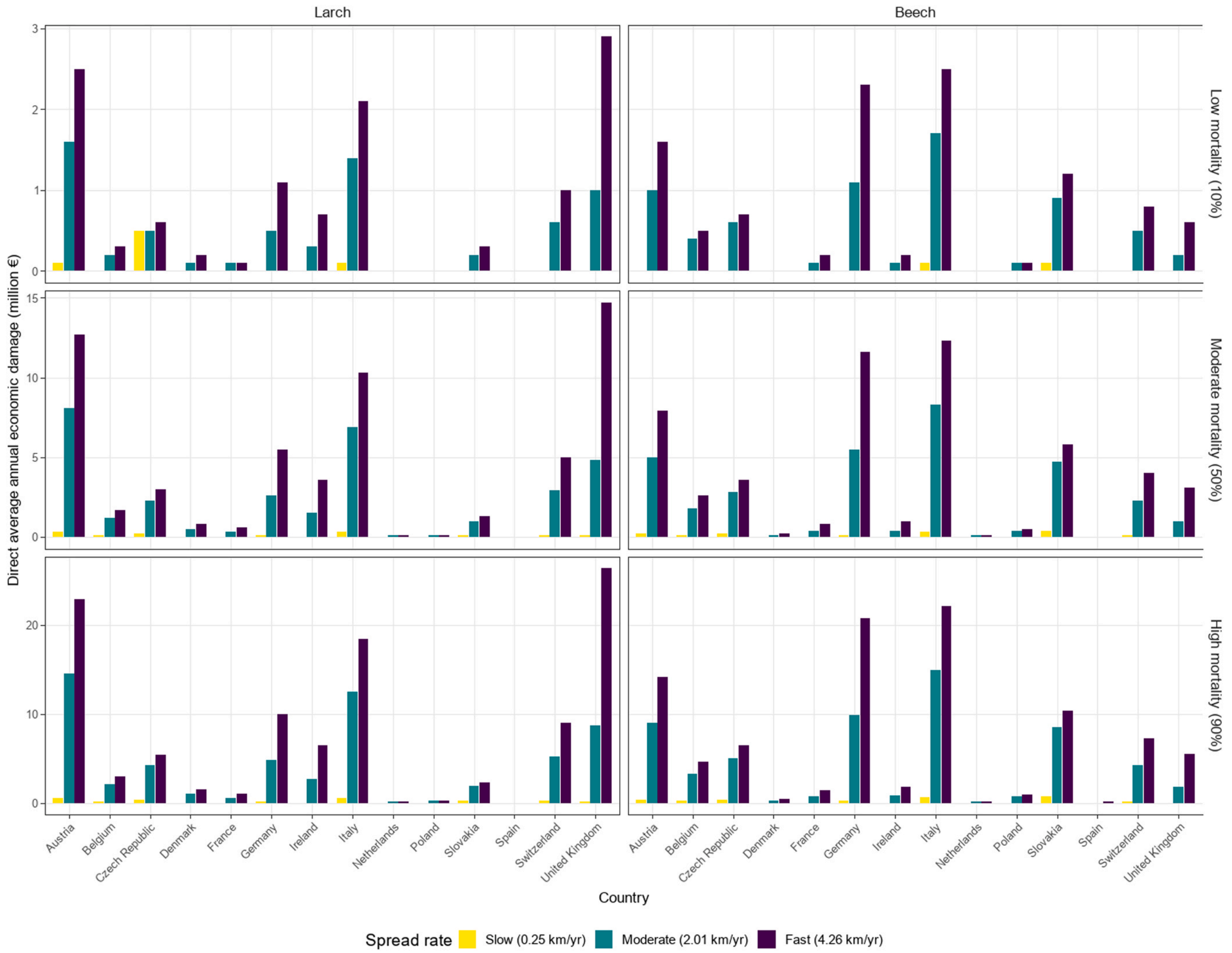

Fig. 3. Average annual direct damage costs (€ million yr^{-1}) due to *Phytophthora ramorum* for *Larix* spp. (left panels) and *Fagus* spp. (right panels) by country, under a no-control scenario, for three spread rates (Slow: 0.25 km yr^{-1}; Moderate: 2.01 km yr^{-1}; Fast: 4.26 km yr^{-1}) and three mortality rates (Low: 10 %; Moderate: 50 %; High: 90 %). Timber prices used: €59.6/m^3 for larch (softwood sawlog) and €74.31/m^3 for beech (roundwood logs). Countries with zero estimated losses across all scenarios and for both hosts – Bulgaria, Croatia, Estonia, Finland, Greece, Latvia, Lithuania, Luxembourg, Norway, Portugal, Romania, Slovenia, and Sweden – do not appear in this figure. Exact values are provided in Table S5 and Table S6. Note that the y-axis scales differ among mortality scenarios.

The CLIMEX model also accords with PhR occurrence records in Oregon, another global hotspot, where SOD is prevalent in the southwestern region (USDA Oregon SOD Program, 2024; Sutton et al., 2009; Hansen et al., 2008; Goheen et al., 2007). Moreover, our risk map accords with the climatic suitability map for PhR infection in the UK for the period 2007–2011 (Purse et al., 2015). This attests to the accuracy of our CLIMEX model when projected into regions where PhR has not yet been detected, at least with respect to conditions for disease expression in natural settings. In contrast, attempts to fit our model to inland Californian PhR occurrence records resulted in an overestimation of optimal suitability projections across Europe, inconsistent with the current PhR distribution. Likewise, Shamoun et al. (2018), used the correlative maximum entropy MaxEnt model to estimate the climatic suitability of PhR. The results varied substantially depending on the origin of the occurrence data. When calibrated with European occurrence records, the model projected suitability primarily in the UK, Ireland, and the west coast of Canada, whereas calibration with North American records shifted suitability to areas predominantly along the Mediterranean coast. This discrepancy may be attributed to the transferability of the model across regions, but also to underlying genotypic and phenotypic differences between North American and European PhR populations (Jung et al., 2021; Franceschini et al., 2014; Ivors et al., 2006). California, a SOD hotspot, reflects a very particular ecological and climatic context rather than a model for Europe (*personal communication with Richard C. Cobb*). The Mediterranean-type climate along the Pacific coast is atypical and characterized by recurring foggy conditions favorable for sporangia production, spread, and infection of PhR. Similar challenges have been encountered in modeling studies of other *Phytophthora* species. For instance, Burgess et al. (2017) developed two distinct CLIMEX parameter sets for *Phytophthora cinnamomi* to adequately fit the pathogen's distribution data in North America and Tasmania. Such considerations support our decision to focus model fitting on Europe and Oregon by explicitly aiming to capture conditions for disease expression in forests. Both regions also share PhR lineages (EU1 in Europe and Oregon, EU2 in Europe) (Grünwald et al., 2016), suggesting comparable climatic requirements.

An important consideration for model fitting is the type of PhR occurrence records used. Frankel et al. (2025) caution that failing to differentiate between PhR records in anthropogenic settings like nurseries or garden centers and in wildlands can lead to biologically misleading conclusions, because the epidemiology of the pathogen differs fundamentally between these environments. In nurseries, disease dynamics are strongly influenced by irrigation and trade of infected plants, in contrast to forests, where they are governed by ambient climatic conditions and natural dispersal. Consequently, in order to avoid those pitfalls, we fitted our CLIMEX model considering exclusively records from symptomatic trees in natural and semi-natural ecosystems.

Our results indicate that further spread of PhR could impose substantial economic losses on European forestry, especially if left uncontrolled. These losses are not evenly distributed across the European continent but are concentrated in a handful of countries. For larch, the greatest losses could occur in the UK, Italy, Austria, and Germany, which together account for approximately 72 % of the projected total losses in the study area. Under a moderate mortality and fast spread scenario (50 % mortality, 4.26 km yr^{-1}), these four countries could face average annual losses of approximately €43 million yr^{-1}, rising to €78 million yr^{-1} under a high mortality scenario with the same spread rate (90 % mortality, 4.26 km yr^{-1}). On the other hand, for beech, Italy, Germany, Austria, and Slovakia bear the highest risks, jointly contributing 70 % of the projected total European losses. Under 50 % mortality and 4.26 km yr^{-1} spread rate assumptions, their combined annual economic losses could reach €37.6 million yr^{-1}, increasing to €67.6 million yr^{-1} under high mortality (90 %) at the same spread rate. These projected costs for European forestry are comparable to those calculated for Oregon's forest industry, ranging from US$1 million to US$62 million yr^{-1} under different pathogen spread rates, harvest costs, and control policy (Hall and Albers, 2009). Annual harvest losses in Oregon could reach US$100 million in case eradication efforts fail to cease PhR spread (Kliejunas, 2010).

Prior to this study, economic assessments of PhR damage and management costs in Europe have been scarce. Eschen et al. (2023) estimated that the pathogen incurred average annual costs of £ 4.2 million (~€4.9 million) in the UK between 2010 and 2017, including management expenses and timber losses. Of this total, timber losses accounted for £ 1.5 million (~€1.7 million) per year. In the moderate scenario of our study (50 % mortality, 2.01 km yr^{-1} spread rate), slightly higher timber losses were projected, amounting to €4.8 million yr^{-1} for larch and €1 million yr^{-1} for beech in the UK. This difference likely reflects our approach of full occupation of the susceptible area to obtain annualized estimates, while Eschen et al. (2023) reported realized averages from 2010 to 2017 (ongoing PhR spread). At the European scale, the only prior forward-looking assessment was conducted under the RAPRA project (Sansford et al., 2009; Kehlenbeck, 2008; Anonymous, 2007), which concluded that PhR impacts were minimal to moderate in northern tree host systems and minimal but potentially major in the southern tree host system. Our results accord with the former statement; however, they are not directly comparable to the southern projection since our analysis focuses on larch and beech (not Mediterranean laurel or *Quercus ilex*) and applies an EI ≥ 26 threshold that yields only limited climatically suitable pockets in southern Europe. Hence, we do not project any "major" impacts in this region, regardless of host presence.

Our findings highlight the damage potential of PhR to forestry in Europe, but they are subject to specific assumptions and limitations. Firstly, we only accounted for natural dispersal, whereas in reality, long-distance spread occurs via the nursery trade and movement of infected plant material (Grünwald et al., 2012; Cushman and Meentemeyer, 2008). An extensive study demonstrated widespread occurrence of PhR in nurseries across Europe (Jung et al., 2016), providing ample opportunities for PhR introductions to previously non-infested areas. However, modeling these processes at the European scale is challenging and potentially highly uncertain. Nonetheless, local or regional studies could benefit from incorporating more detailed epidemiological models. Secondly, we restricted our analysis to forestry hosts, although a broader range of economically important hosts are susceptible to PhR, such as rhododendron, *Viburnum, Pieris,* and *Camellia* (EPPO, 2025; Thomsen et al., 2023; Anonymous, 2007). Thirdly, our estimates were derived under a "no-control" scenario, which provides an upper bound on potential damages but does not necessarily reflect the reality of ongoing management interventions, particularly in the UK, Ireland, and France, which may slow the spread of PhR. Fourthly, occurrence data for PhR remain difficult to access, as they are often not publicly available. Finally, our economic analysis considers only direct timber losses, excluding indirect impacts, non-market values, forest growth, and reforestation.

Since the 12 known lineages of PhR show considerable genotypic and phenotypic variability, such as in growth rates and cardinal temperatures (Jung et al., 2021; Franceschini et al., 2014), efforts to prevent the introduction of the 10 known lineages not yet present in Europe, as well as any unknown lineages, should probably remain a priority for European biosecurity. Achieving this requires moving beyond the species-by-species regulatory approach, which relies heavily on visual inspections and falls short in tackling latent infections or unknown pests and pathogens. Integrating pathway risk analysis, risk-based inspection regimes, and molecular high-throughput tools could decrease the risk of new introductions (Favaro et al., 2024; Jung et al., 2018, 2016; Eschen et al., 2015a, b; Brasier, 2008; Santini et al., 2013; Liebhold et al., 2012). Furthermore, the high potential annual losses projected for a "no-control" scenario underline the necessity of targeted and effective eradication actions in infested larch and beech stands, as is already implemented in the UK and France (Beltran et al., 2024; O'Hanlon et al., 2018). Moreover, the ubiquitous infestations of European nurseries with more than 100 *Phytophthora* species, including PhR (Green et al., 2025; Horta Jung et al., 2025; Bačova et al., 2024; Mora-Sala et al., 2022; Jung et al., 2016), make an EU-wide nursery certification and accreditation scheme indispensable, given the upcoming large-scale afforestation under the nature restoration Regulation (EU) 2024/1991 (European Commission, 2024). Such schemes already exist, including the Nursery Industry Accreditation Scheme Australia (NIASA), the Avocado Nursery Voluntary Accreditation Scheme (ANVAS) in Australia, the California Nursery Stock Registration & Certification Program, the Accreditation to Improve Restoration (AIR) in California, and the Plant Healthy Certification Scheme in the UK. All these schemes implement an array of science-based and field-validated biosecurity measures to reduce the introduction and spread of harmful plant pests and pathogens via the nursery trade, and can be used as a blueprint (Pérez-Sierra and Jung, 2013; Parke and Grünwald, 2012). They also facilitate the recognition of producers and organizations that operate following high biosecurity standards.

5. Conclusion

PhR is already widespread in nurseries across the European continent (EPPO, 2025; Jung et al., 2016), but its establishment in forests has so far been largely confined to the UK, Ireland, and France. As the pathogen spreads via nursery trade, the likelihood of spillover infestations into natural parks, gardens, and forest stands increases, where eradication becomes more challenging. Strengthening risk-based inspections, enhancing monitoring efforts, and implementing Best Management Practices in nurseries remain key strategies against further pathogen introductions. In addition, areas where disease expression is most likely to occur due to optimal climatic conditions for PhR sporulation, along with high densities of vulnerable tree hosts, should be prioritized for surveillance and monitoring activities, enabling more efficient allocation of resources to regions most conducive to disease establishment and spread.

After three decades of PhR presence in Europe, a large-scale invasion of Mediterranean forests appears unlikely, consistent with their suboptimal climatic conditions. In contrast, in the temperate regions of Europe, extensive larch and beech stands remain vulnerable, and the costs related to further spread of the disease can be substantial. Nurseries often serve as a foci for the spread of the disease. An EU-wide nursery registration and accreditation system for controlling the spread, based on the potential costs avoided, may be economically justified.

CRediT authorship contribution statement

Stelios Kartakis: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Justus Wesseler:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Thomas Jung:** Writing – review & editing, Validation, Methodology, Data curation, Conceptualization. **Darren J. Kriticos:** Writing – review & editing, Validation, Software, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123367.

Data availability

The occurrence records used in this study are available as Supplementary Data, except for the records in Oregon, which were provided by the USDA and are not publicly accessible.

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