The increasing threat to European forests from the invasive foliar pine pathogen, *Lecanosticta acicola*

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ABSTRACT

European forests are threatened by increasing numbers of invasive pests and pathogens. Over the past century, *Lecanosticta acicola,* a foliar pathogen predominantly of *Pinus* spp., has expanded its range globally, and is increasing in impact. *Lecanosticta acicola* causes brown spot needle blight, resulting in premature defoliation, reduced growth, and mortality in some hosts. Originating from southern regions of North American, it devastated forests in the USA's southern states in the early twentieth century, and in 1942 was discovered in Spain.

Derived from Euphresco project 'Brownspotrisk,' this study aimed to establish the current distribution of *Lecanosticta* species, and assess the risks of *L. acicola* to European forests. Pathogen reports from the literature, and new/ unpublished survey data were combined into an open-access geo-database (http://www.portaloff orestpathology.com), and used to visualise the pathogen's range, infer its climatic tolerance, and update its host range. *Lecanosticta* species have now been recorded in 44 countries, mostly in the northern hemisphere. The type species, *L. acicola*, has increased its range in recent years, and is present in 24 out of the 26 European countries where data were available. Other species of *Lecanosticta* are largely restricted to Mexico and Central America, and recently Colombia.

The geo-database records demonstrate that *L. acicola* tolerates a wide range of climates across the northern hemisphere, and indicate its potential to colonise *Pinus* spp. forests across large swathes of the Europe. Preliminary analyses suggest *L. acicola* could affect 62% of global *Pinus* species area by the end of this century, under climate change predictions.

Although its host range appears slightly narrower than the similar *Dothistroma* species, *Lecanosticta* species were recorded on 70 host taxa, mostly *Pinus* spp., but including, *Cedrus* and *Picea* spp. Twenty-three, including species of critical ecological, environmental and economic significance in Europe, are highly susceptible to *L. acicola*, suffering heavy defoliation and sometimes mortality. Variation in apparent susceptibility between reports could reflect variation between regions in the hosts' genetic make-up, but could also reflect the significant variation in *L. acicola* populations and lineages found across Europe. This study served to highlight significant gaps in our understanding of the pathogen's behaviour.

Lecanosticta acicola has recently been downgraded from an A1 quarantine pest to a regulated non quarantine pathogen, and is now widely distributed across Europe. With a need to consider disease management, this study also explored global BSNB strategies, and used Case Studies to summarise the tactics employed to date in Europe.

1. Introduction

European forests face increasing threats from native pests and pathogens such as *Ips typographus* L. and *Dothistroma septosporum* (Dorogin) M. Morelet, (Bulman et al., 2016; Drenkhan et al.,; Abdullah et al., 2018) and non-native organisms including *Ceratocystis platani* (J.M. Walter) Engelbr. and T. C. Harr., *Cryphonectria parasitica* (Murr.) Barr., *Fusarium circinatum* Nirenberg and O'Donnell, *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz and Hosoya*,* and *Phytophthora cinnamomi* Rands (Brasier, 1996, 2008; Drenkhan et al., 2016b; Rigling & Prospero, 2018; Drenkhan et al., 2020; Tsopelas et al., 2017). An upsurge in the numbers of invasive pathogens entering Europe is due in large part to the global trade in plants for planting (Santini et al., 2013) and in many cases the negative impacts of native and non-native organisms on forest health is being exacerbated by climate change which affects the behaviour of both the hosts and the pathogen (Hanso and Drenkhan 2009, 2013; Tubby and Webber, 2010; Brodde et al., 2019). Since the 1990s, *Lecanosticta acicola* (Thümen) Sydow, a foliar pathogen found predominantly on *Pinus* spp., has been expanding its range globally and increasing in impact. In the past ten years the area of forest affected by this pathogen within Europe and neighbouring countries has increased markedly (Adamson et al., 2018; Mullett et al., 2018; van der Nest et al., 2019a; Oskay et al., 2020; Laas et al., 2022). There are concerns that the pathogen could become severely damaging, both economically and environmentally, following a similar pattern to *Dothistroma* spp. which are now considered the most destructive foliar pathogens of pine (Drenkhan et al., 2016a).

Lecanosticta acicola is the causal agent of brown spot needle blight (BSNB) (Fig. 1a). Infection results in chlorotic flecking of the needle tissue and small lesions which develop into orange/yellow, sometimes resin-soaked spots on needles, superficially similar to the early stages of infection by *Dothistroma* species. *Lecanosticta acicola* lesions darken to shades of brown, sometimes with a prominent yellowish-orange border (Siggers, 1944). Acervuli develop, releasing olivaceous, cylindrical, conidia that are 0–6 septate (Kais, 1989; Jurc and Jurc, 2010), usually curved but sometimes straight and often with oil droplets (e.g. Jurc and Jurc, 2010; Hintsteiner et al., 2012; Fig. 1b and 1c). Needles typically die back from the point of infection, turning yellow and then orange/ red, with heavy infection resembling fire damage (Siggers, 1944). Eventually the whole needle turns brown and falls prematurely in late autumn to early winter (e.g. Kais and Peterson, 1986). On many hosts infection is more prevalent on the previous years' foliage e.g. *P. halepensis* Miller (Glavaš, 1979), *P. nigra* J.F. Arnold*, P. mugo* Turra and its subspecies (Holdenrieder and Sieber, 1995; La Porta and Capretti, 2000; Hintsteiner et al., 2012), *P. palustris* (Verrall, 1934; Snow, 1961), *P. taeda* L. (Parris, 1967; Boyce, 1952) and *P. strobus* L. (Boyce 1959; Stanosz et al., 1991), but can also be seen on current year's growth e.g. *P. banksiana* Lamb.*, P. clausa* (Chapman ex Engelmann) Vasey ex Sargent and *P. resinosa* Aiton (Kais, 1977), *P. palustris* (Wolf and Barbour, 1941; Siggers, 1944), *P. strobus* and *P. sylvestris* L. (Kais, 1977; Adamson et al., 2018), particularly under conditions of high inoculum pressure (Skilling and Nicholls, 1974).

Lecanosticta acicola can be highly damaging to many *Pinus* species where infection causes severe defoliation (Fig. 1a). Repeated infection cycles cause needle shortening (Parris, 1969; Glavaš, 1979), further reducing available photosynthetic area (e.g. *P. banksiana*, Kais, 1975a,b; *P. nigra,* Sadiković et al., 2019a; *P. palustris*, Siggers, 1944; *P. strobus*, Wyka et al., 2018; *P. sylvestris*, Skilling and Nicholls, 1974). In young trees infection can reduce or delay establishment, which increases their exposure to herbivores while the plants are at a vulnerable stage of development (Boyer, 1990; Enebak and Carey, 2002). Significant mortality has been observed in young *P. densiflora, P. merkusii* (Magán and de Ana, 1997), *P. palustris* (Chapman 1926; Cordell et al., 1990) and even mature trees of some species can be killed after repeated infections

(e.g. *P.* × *attenuradiata* Stockwell and Righter Lévy and Lafaurie 1994; *P. strobus*, Munck et al., 2012; Wyka et al., 2017, 2018). Repeated *L. acicola* infection reduces tree growth (*P. palustris*, Chapman, 1926; Bruce, 1956; Kais and Griggs, 1986; *P. strobus*, Wyka et al., 2018; *P. taeda*, Edgerton and Moreland, 1923) but to date, only one study on *P. palustris* has quantified the relationship between BSNB disease induced defoliation and growth finding increasing levels of infection corresponding to decreased growth (Siggers, 1944).

In the southern states of the USA, timber losses caused by BSNB on *P. palustris* and other 'southern' pine species in the 1980s exceeded 453,000 cubic metres p.a. (Cordell et al., 1990). In the north-central states, the foliar discolouration rendered millions of Christmas trees unmarketable in the 1960s to 1980s (Prey and Morse, 1971; Alexander and Skelly, 1977; Phelps et al., 1978), and the value of amenity or specimen trees has also been significantly affected (Nicholls et al., 1973; Kais and Peterson, 1986; Heimann et al., 1997).

Fig. 1. Symptoms and morphology of *Lecanosticta acicola* (a) Rapid defoliation of *P. nigra* caused by *L. acicola* over a six-month period in Slovenia (Photo by D. Jurc, Slovenian Forestry Institute) (b) acervuli of *L. acicola* on *P. mugo* (Photo by Thomas Cech, BFW) (c) *L. acicola* conidia × 400 (Photo by H. Bragança, Instituto Nacional de Investigação Agrária e Veterinária).

Fig. 1. (*continued*).

Overlapping and similar symptomology to Dothistroma needle blight (DNB), together with superficial morphological similarity of fruiting structures and conidia to *Dothistroma* species (Barnes et al., 2016) has led to taxonomic uncertainty and frequent misdiagnosis over the past 100 years. The older literature originates from North America where *L. acicola* was first isolated in South Carolina on *Pinus variabilis* Lamb (later identified as *P. caribaea* Morelet, see Wolf and Barbour, 1941) as *Cryptosporium aciculum* Thüm in 1876 (De Thümen, 1878). The asexual states (anamorphs) have been reclassified as *Cryptosporium acicolum* Thüm. (Siggers, 1944), *Septoria acicola* (Thüm) (Siggers, 1932, 1944), *Actinothyrium marginatum* Sacc., *L. acicola*, *Dothistroma acicola* (Thüm.) Shishkina and Tsanava (Shishkina and Tsanava, 1967), *Lecanosticta pini* H. Syd., *Lecanosticta decipiens* Petr., *Sphaerella acicola* Cke. and Harkn. and sexual states (teleomorphs) as *Scirrhia acicola* (Dearn.) Siggers (Siggers, 1939), *Systremma acicola* (Dearn.) Wolf and Barbour, *Dothidea acicola* (Dearn.), *Oligostroma acicola* Dearn. (Siggers, 1939), *Eruptio acicola* (Dearn.) M.E. Barr. (Barr, 1996), *Mycosphaerella acicola* (Cke. and Harkn.) Lindau, Engl. and Prantl, and *Mycosphaerella dearnessii* M.E. Barr (Saccardo, 1884; Martin, 1887; Sydow and Petrak, 1924; Siggers, 1939; Wolf and Barbour, 1941; Offord, 1964; Bonar, 1965; Barr, 1972). At least some of these specimens were probably *Dothistroma* spp. (Siggers, 1944). A full review of the taxonomy of *L. acicola* is given in van der Nest et al., (2019a).

The complications in distinguishing between *Dothistroma* and *Lecanosticta* species have led to confusion in the literature, incorrect categorisation of at least some herbarium specimens, and consequent difficulty establishing the true extent of the pathogen's range. For example, the earliest apparent report of *L. acicola* from Japan (Yoshii and Sogawa, 1955) cannot be categorically confirmed. The earliest records of *L. acicola* from Austria (von Petrak, 1961), Bulgaria (Kovačevski, 1938), Georgia (Shishkina and Tsanava, 1966a,b, 1967) and Greece (Sarejanni et al., 1954, 1955) have now been re-assigned to *Dothistroma* species following critical review (Barnes et al., 2016). However, the earliest European record of the pathogen still stands, and *L. acicola* is believed to have been introduced to Spain at least 80 years ago (Martínez, 1942).

The risk *L. acicola* poses to Europe's extensive natural and planted *Pinus* forests is concerning. Globally, *Pinus* forests have been severely impacted by *D. septosporum* throughout the last century (Bulman et al., 2016), and more recently *L. acicola* has been expanding its range from the first findings in Spain and Croatia prior to the 1980s. To this effect, a Euphresco partnership entitled 'Brownspotrisk' was established to coordinate a transnational programme of research. Members consisted of specialists and forest practitioners from ten European countries and the USA - countries experiencing local or widespread outbreaks of BSNB, together with those at risk from pathogen introduction. One of the objectives of this partnership, was to compile this review with the aims of i) raising awareness of BSNB and its potential impact ii) clarifying origins and population structure of *Lecanosticta* species iii) establishing an up-to-date distribution of *Lecanosticta* species, iv) comprehensively listing all known hosts of *L. acicola* and ranking their susceptibility through field observations and critical examination of historical literature v)

assessing the risk BSNB poses to European forests given the current state of knowledge and predicted changes in climate vi) exploring global BSNB management strategies, using Case Studies to summarise tactics employed to date in European countries and vii) identifying and highlighting knowledge gaps to focus future scientific collaborative research efforts.

2. *Lecanosticta* origins and population structure

The global increase in BSNB reports and the discovery of further *Lecanosticta* species has been facilitated by the recent development of rapid and effective molecular diagnostic techniques. Nine species of *Lecanosticta* have been described to date: the most well-known, and type species for the genus, *L. acicola*, as well as *L. brevispora* Quaedvl. and Crous, *L. gloeospora* H. C. Evans, *L. guatemalensis* Quaedvl. and Crous, *L. jani* van der Nest, M.J. Wingf. and I. Barnes, *L. longispora* Marm., *L. pharomachri* van der Nest, M.J. Wingf. and I. Barnes, *L. tecunumanii* van der Nest, M.J. Wingf. and I. Barnes, and *L. variabilis* van der Nest, M. J. Wingf. and I. Barnes (Evans, 1984; Marmolejo, 2000; Quaedvlieg et al., 2012; van der Nest et al., 2019b).

All *Lecanosticta* species, excluding *L. acicola*, are found in Central America (Marmolejo, 2000; van der Nest et al., 2019a,b). A region encompassing the southern part of North America and Central America is currently hypothesised to be the centre of diversity of the genus (Evans, 1984; van der Nest et al., 2019b). Until 2022, BSNB only caused notable disease in the Northern USA, Europe and Colombia, predominantly on *Pinus* species, and all disease was caused by *L. acicola* (Janoušek et al., 2016). However, recent reports of severe disease caused by *L. pharomachri* on plantations of exotic *Pinus* species in Colombia are concerning (Theron et al., 2022).

Lecanosticta acicola is the most widely studied species to date, and three lineages have been described based on the Translation Elongation 1-α gene region (TEF1), microsatellite and RAPD markers, together with observations of cultural morphology (Huang et al., 1995; Janoušek et al., 2016; van der Nest et al., 2019b). The northern lineage occurs in northern USA, Canada and Europe, the southern lineage is dominant in southern USA and has spread to Europe, and a third lineage occurs in Mexico and to date, appears not to have spread from this region (van der Nest et al., 2019b; Laas et al., 2022). The third lineage is the most diverse, probably constituting one or more distinct cryptic species, and Mexico may be the centre of origin of *L. acicola* (Huang et al., 1995; Janoušek et al., 2016; van der Nest et al., 2019b).

Population studies illustrate the wide dissemination of the northern and southern lineages from North America into Europe (Janoušek et al., 2014, 2016; Sadiković et al., 2019a; Laas et al., 2022) and Asia (Huang et al., 1995; Laas et al., 2022). Microsatellite and TEF1 markers demonstrate the southern USA lineage is present in southwest France, Portugal and Spain, close to the first finding of the pathogen in Europe (Janoušek et al., 2016; Laas et al., 2022). It is also present in Colombia in South America, where it may have been introduced on exotic *Pinus* seedlings used for timber plantations (Janoušek et al., 2016). RAPD (Huang et al., 1995;) and microsatellite markers (Laas et al., 2022) suggest *L. acicola* from the southern lineage is present in East Asia where disease outbreaks first occurred on *P. thunbergii* Parlatore in Jiangsu province in south western China in the 1950s, followed by more extensive outbreaks in the 1970s in plantations of imported pines including *P. elliottii* Engelmann (Ye and Wu 2011). Whether it was introduced directly from North America, or via Europe is unknown. More recent analyses show that China, Japan and Korea harbour a unique elongation factor haplotype (Janoušek et al., 2016). China and Japan share an identical microsatellite multilocus haplotype (MLH) (Laas et al., 2022), and strong trading links could have facilitated anthropogenic movement of the pathogen between these countries. Again, it is not yet clear if *L. acicola* was initially introduced to Japan and Korea through China, or from North America or Europe.

The northern lineage of *L. acicola* has been introduced from the USA to Central Europe (Janoušek et al., 2016), and is now widespread across the continent. Several separate introductions of this lineage have occurred in Europe, and distinct populations are now discernible (Adamčíková et al., 2021). One population of the northern lineage was introduced to Croatia, where the second oldest report of *L. acicola* in Europe originates (Milatović, 1976), and a second into Central Europe (Laas et al 2022). The Croatian population has not spread north to neighbouring Slovenia (Sadiković et al., 2019a), but the population appears to share common origin in North America with the populations in western Asia (Turkey, Georgia, South Russia) (Laas et al., 2022). Northern European populations originate from North America via the Central European population (Laas et al., 2022).

These recent analyses defined northern and southern lineages of *L. acicola* using molecular methods, but differences in cultural morphology and behaviour *in vitro*, and pathogenicity *in planta* between isolates from southern and northern states of the USA had been apparent from the 1970s. Isolates from Mississippi had consistently higher growth rates and higher optimum temperatures for growth (25 °C) compared to isolates from northern States (20 °C) (Kais, 1972). The pathogenicity of northern isolates was greatest on *P. sylvestris, P. banksiana* and *P. clausa* and lowest on *P. taeda* and *P. palustris*. Except for *P. sylvestris*, the southern isolates were, overall, more pathogenic than the northern isolates, and particularly damaging to *P. palustris, P. clausa* and *P. banksiana*. Population variation within these larger groupings was also apparent, as isolates from the same geographic area, therefore likely to be from the same lineage, exhibited differences in behavioural characteristics (Phelps et al., 1978; Huang et al., 1995).

To date, there has been little consideration of how the *L. acicola* lineages might behave under local European conditions. Both southern and northern lineages co-occur in France, and both mating types are found in Estonia, Lithuania, Poland, Germany, France, Ireland, Switzerland, Austria, Slovenia and Spain (Laas et al., 2022). Molecular analysis also suggested ongoing sexual recombination in Europe (Janoušek et al., 2016; Laas et al., 2022), even before it was confirmed in 2020 with the discovery of the sexual stage of *L. acicola* on *P. radiata* D. Don in Spain (Mesanza et al., 2021a). Like *Dothistroma* species, the sexual ascospores have far greater potential for long distance wind-driven dissemination than the splash-dispersed asexual conidia. Therefore, sexual recombination within and between lineages has serious implications for dispersal capability, and might explain the recent expansion of the pathogen across Europe and further afield (Laas et al., 2022). Sexual reproduction not only increases dissemination, but novel gene combinations increase the pathogen's ability to adapt to changing climate, new hosts and different management approaches between regions.

3. Current geographic distribution of *Lecanosticta* species

The occurrence of *Lecanosticta* species in some countries is well documented, with high confidence in the diagnosis, whilst in other areas, identification of the pathogen has been less reliable. For this review, information from published and grey literature was re-examined, considering advances in morphological and molecular diagnostic tools. These data have been incorporated with new, previously unpublished records to produce a contemporary, global dataset of *Lecanosticta* species. The approaches used to generate this geo-database for *Lecanosticta* follow those used by Drenkhan et al., (2016a) for *Dothistroma* species and *Fusarium circinatum* (Drenkhan et al., 2020) where a global map of records is available (https://www.portalofforestpathology.com), and users can navigate between pathogens by clicking on the 'layer' tab. Researchers from across the world, particularly from countries where the distribution of *Lecanosticta* appears to be less well established, were approached and strongly encouraged to participate in data collection. The objective of the resulting geo-database was to collate records and locations of known *Lecanosticta* species (including *L. acicola*), worldwide and with a particular focus on Europe. Certain data entry fields were

compulsory, including pathogen presence/absence, host species and forest type (urban versus natural versus plantation). Voluntary fields allowed entry of more detailed data on disease intensity, presence of other pathogens, local climate, soil type and management practices such as thinning, pruning and chemical interventions.

A dedicated web site hosts contact details, the data collection template (in Excel) and an instruction manual for the *Lecanosticta* geo-database. All data were compiled and uploaded to an interactive internet-based map hosted by Mendel University in Brno, Czechia (See https://www.portalofforestpathology.com) and further technical information on mapping and analysis is included in Supplementary material (Table S1).

Fig. 2 shows a time series illustrating when *Lecanosticta* species were first recorded in each country. (Supplementary Figure S1 presents a global overview of *L. acicola* and other *Lecanosticta* species presence/absence). The database currently incorporates geographic coordinates from 3205 records, including both positive (947) and negative (2258) reports of *Lecanosticta* species. Data cover 91 host taxa, and 44 countries, including Asia (4 countries including the Asian part of the Russian Federation), Europe (26 countries including the European part of the Russian Federation, the European part of Turkey, and Georgia) North, Central and South America (13 countries), New Zealand and South Africa. *Lecanosticta* species were considered absent in Africa (1 country) and Oceania (1 country). Countries, such as India, for which no data on presence or absence were available, were not considered to be positive or negative. A summary of pathogen distribution by continent is presented in Supplementary information Table S2 where all records relate to *L. acicola* unless specified otherwise.

3.1. Europe

The first reliable European record of *L. acicola* originates from plantations of non-native *P. radiata* in Spain in the 1940s (Martínez, 1942), probably deriving from plants imported from North America (Janoušek et al., 2016). Until the 1990s, the known European distribution was limited to Austria, France, Germany, Italy, Spain, Switzerland, and former Yugoslavia (Croatia) (Milatović, 1976; Chandelier et al., 1994 Holdenrieder and Sieber, 1995; Pehl, 1995; Cech, 1997; La Porta and Capretti 2000). The pathogen's known geographic range has increased significantly in the past ten to twenty years (Lévy and Lafaurie 1994; Drenkhan and Hanso, 2009; Jankovský et al., 2009a; Markovskaja et al., 2011; Mullett et al., 2018; van der Nest et al., 2019a; Oskay et al., 2020; Raitelaitytė et al., 2020, 2022; Laas et al., 2022).

In the current study, 2721 observations were collected from 26 European countries (see: https://www.portalofforestpathology.com) and *L. acicola* was recorded in 24 countries (Fig. 2). These data include the first report of the pathogen in Ukraine. Molecular methods were used to confirm the identification of the pathogen in 22 countries, and visual inspection of symptoms in the field and morphological diagnosis in the laboratory confirmed the pathogen in the remaining two countries (Romania and Ukraine). The pathogen was not detected in Britain and Finland despite ongoing surveillance efforts. The distribution of *L. acicola* spans the European Continent from Portugal and Ireland in the west to the Black Sea coast of Russia in the east (Laas et al., 2022), and from Estonia in the north to Turkey in the south (Drenkhan and Hanso 2009; Oskay et al., 2020). There is currently no evidence to suggest the presence of any *Lecanosticta* species other than *L. acicola* in Europe.

3.2. North, Central and South America

Lecanosticta acicola was first recorded on pines in South-Carolina, United States of America in 1876 (De Thümen, 1878). As impacts on *Pinus* spp. in this region have been significant since the beginning of the 20th century, there is extensive information on the pathogen in the North American literature (e.g. Chapman, 1926; Wolf and Barbour, 1941; Siggers, 1944). The pathogen ranges from predominantly eastern

States of the USA, to southern Canada (Chapman, 1926; Hedgecock, 1929, Siggers, 1944; Laut et al., 1966; Skilling and Nicholls, 1974; Wyka et al 2017). It appears absent from western states of the USA, although early reports from Idaho (Hedgecock, 1929; Shaw and Leaphart, 1960), Californian records of 'Sphaerella acicola' Cke. and Harkn on *P. radiata*, *Mycosphaerella acicola* (Cke. and Harn.) Lindau, Engl. and Prantl on *P. ponderosa* Douglas ex Lawson (Offord, 1964; Bonar, 1965) and a *Lecanosticta* sp. on *P. monticola* Douglas ex. D. Don. (Cobb and Miller, 1968), together with reports of a single specimen of *Scirrhia acicola* (Dearness) Siggers on *P. attenuata* from Oregon (Siggers, 1944), need clarification and confirmation.

Most geo-database records from Canada, Cuba, Jamaica, Mexico and USA are based predominantly on morphological methods. Molecular confirmation has also been used in Canada (in 1 province), Mexico and USA (7 out of the 28 states with *L. acicola* recorded present). In Central America, morphological examination confirmed *Lecanosticta* spp. causing minor foliar browning in Belize, Costa Rica, Guatemala, Honduras, and Nicaragua on native pine species including *P. caribaea*, *P. maximinoi* H. E. Moore, *P. oocarpa* Schiede ex Schlectendahl, *P. patula* Schiede *ex* Schlectendahl *et* Chamisso, *P. pseudostrobus* Lindley and *P. tecunumanii* Eguiluz et J.P. Perry. Although *L. acicola* was reported in many of these countries, none of the more recent molecular analyses have detected *L. acicola* in any Central American country (Janoušek et al., 2016; van der Nest et al., 2019b), whilst other *Lecanosticta* species have been discovered in Guatemala, Honduras, Nicaragua, and Mexico (Evans, 1984; Marmolejo, 2000; Quaedvlieg et al., 2012; van der Nest et al., 2019b). Therefore, Central American records reliant solely on morphologically diagnosis should be re-analysed by molecular methods to confirm species identity.

In South America, *L. acicola* was identified in non-native plantations of *P. elliottii*, *P. patula* and *P. radiata* in the altiplano region of Colombia through morphological (Gibson, 1980; Evans, 1984) and molecular methods (Janoušek et al., 2016; van der Nest et al., 2019b). Theron et al., (2022) also recently discovered *L. pharomachri* on *P. maximinoi*, *P. patula* and *P. tecunumanii*, representing the first record of this species outside Central America. A single record of *L. acicola* in exotic *P. patula* plantations in Ecuador (Evans and Oleas, 1983) relied solely on observations of macroscopic, foliar symptoms in a forest stand known to be infected with *Dothistroma* species. Although Ecuador is included in global records of *Lecanosticta*, samples from this region should be re-analysed using molecular methods to confirm species identity.

3.3. Asia

The earliest records of *Lecanosticta* in Asia originate from southern and eastern China (Fujian and Jiangsu provinces), Japan, and South Korea (Suto and Ougi 1998; Ye and Wu, 2011; Seo et al., 2012; Table S2) where diagnosis was confirmed using species-specific conventional PCR and sequencing, together with morphological methods. Zhukov et al. (2013) identified the pathogen in Asian Russia (Sakhalin Island, less than 100 km north of the Japanese island of Hokkaido) on *P. pumila* (Pall.) Regel via morphological methods. A 'type' of *Mycosphaerella gibsonii* was identified in the Republic of the Philippines by Ivory (1994) as having 'similarities' with *L. acicola* but there have been no confirmed records of *L. acicola* from this region. Although *Dothistroma* species are present in India's large *Pinus* plantations (Drenkhan et al., 2016a), there have been no confirmed reports of *Lecanosticta* spp. from the Indian sub-continent to date.

3.4. Africa and Oceania

Lecanosticta species were considered absent in African countries and Oceania, based on morphological and molecular diagnosis of samples (see: https://www.portalofforestpathology.com for further details).
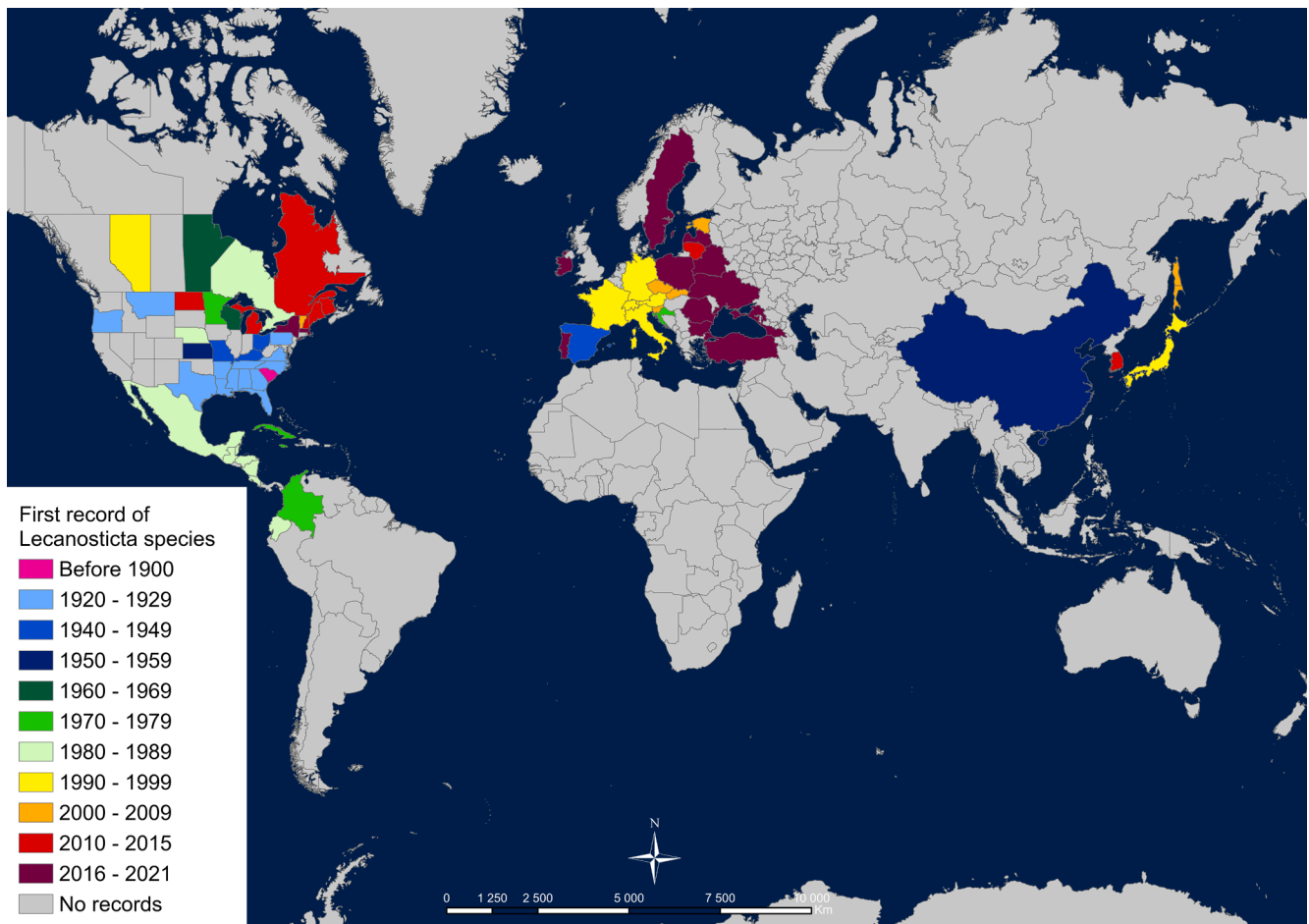
Fig. 2. Global first reports of *Lecanosticta* species compiled using information from published and previously unpublished survey data (See interactive map for further details. http://www.portalofforestpathology.com).

4. Susceptibility of Pinaceae to *Lecanosticta* species

Fifty-three host taxa were recorded for *L. acicola* by van der Nest et al., (2019a), mostly within the genus, *Pinus*, but including *Picea glauca* (Moench) Voss. Reports from 91 taxa were examined during the construction of the current *Lecanosticta* geo-database and 70 listed as susceptible to *Lecanosticta* species.

4.1. Newly recorded hosts

Matching the taxonomy in van der Nest et al (2019a) to follow Farjon (2010), nine host taxa for *L. acicola* were recorded prior to, but not reported in van der Nest et al., (2019a), including *P. brutia* Ten. var. *pityusa* (Stevens) Silba, (Zhukov and Zhukov, 2008), *P. contorta* Douglas *ex* Loudon (Evans, 1984), *P. massoniana* Lamb. (Gong and Liang, 1988; Kehui et al., 1996), *P. merkusii* Junghuhn & de Vriese ex Vriese (Magán and de Ana, 1997), *P. roxburghii* Sargent (Magán and de Ana, 1997), *P. thunbergii* Parl. aff. cv. Aurea (Mullett et al., 2018), and the hybrids *P. palustris* Miller × *P. elliottii* and *P. palustris* × *P. taeda* (Derr, 1966; Lott et al, 1996). Evans (1984) reported *L. acicola* on *P. caribaea* Morelet var. *hondurensis* (Sénécl.) W.H. Barrett et Golfari. However, given that recent molecular analyses have only proven the presence of *Lecanosticta* species other than *L. acicola* in Belize, this record is uncertain.

Pinus brutia (Mesanza et al., 2021b), *P. nigra* subsp. *pallasiana* (Lamb.) Holmboe, *P. nigra* subsp. *pallasiana* var. *fastigiata* Businský and *P. nigra* subsp. *pallasiana* var. *pallasiana* f. şeneriana (Saatçioğlu) Kandemir and Mataracı (Oskay et al., 2020) have been identified as hosts subsequent to van der Nest et al., (2019a). In addition, two further non-

pine species are now known to be susceptible to *L. acicola*: *Cedrus atlantica* (Endl.) Manetti ex Carrière (Schenck et al., 2022) and *Cedrus libani* A. Rich., although the severity of symptoms on the latter was far lower than on nearby infected pines in the arboretum (Oskay et al., 2020). Although not included in the 70 susceptible taxa noted above, Sinclair and Lyon (2005) also included *Pinus longaeva* D. K. Bailey in a list of hosts whilst providing no details for that record, and Cobb and Miller (1968) gave a preliminary diagnosis of *Lecanosticta* species on *P. monticola*. In both cases, these host records need to be re-evaluated and the presence of *Lecanosticta* spp. preferably validated with molecular methods.

Some of the more recent host reports are hybrids or subspecies of species already known to be susceptible to infection by *L. acicola*. It is thus possible that *L. acicola* has been observed on these taxa before, but that the host subspecies/variety was not reported. The likelihood is that most *Pinus* species, and many non-*Pinus* species in the Pinaceae (e.g. *Abies, Larix, Pseudotsuga* and other *Picea* and *Cedrus* species) will prove to be susceptible, particularly under conditions of high inoculum pressure (Pehl et al., 2015). It is noteworthy however, that *Picea abies* (L.) H. Karst. has remained uninfected under conditions of heavy inoculum pressure in certain European forests (Beenken et al., 2018), and following artificial inoculation (Cech, Pers. Comm. 2022, Supplementary Table S2).

Collectively, *Lecanosticta brevispora, L. gloeospora, L. guatemalensis, L. jani, L. longispora, L. pharomachri, L. tecunumanii* and *L. variabilis* have, so far, been recorded only on *P. caribaea, P. culminicola* Andresen et Beaman, *P. maximinoi, P. oocarpa, P. pseudostrobus* and *P. tecunumanii*; all *Pinus* species native to southern regions of North America and Central America.

4.2. Host susceptibility ranking

A novel overview of host susceptibility to *L. acicola* is presented in Table 1. Eight host species were categorised as resistant, meaning despite investigation, no traces of infection have been reported. Thirty-one are tentatively categorised as having low susceptibility where trace levels of foliar infection occurred, 19 are of moderate susceptibility where infection was clearly visible, but growth not seriously affected and 23 are apparently highly susceptible to infection by *L. acicola* as high levels of defoliation and in some cases, mortality were observed. In the nine cases where *Lecanosticta* species have been recorded on host taxa, but no details of disease impact are given, susceptibility is described as 'unknown', pending further investigation.

Susceptibility ratings were based on both field observations and experimental trials using natural and artificial inoculation. Data collated from reports in peer-reviewed and 'grey' literature and previously unpublished surveillance records were entered into the geo-database disease impact fields. Most reports are derived from trees growing in natural forests, plantations, botanic gardens, arboreta and field trials. Where susceptibility ratings for some hosts are based on one region only, they should be considered preliminary.

Fifteen host taxa with more than one susceptibility 'rating' are marked accordingly in Table 1. Susceptibility may vary between reports written at different time periods throughout the twentieth to twenty-first century as silvicultural practices, inoculum pressure, and climate, are all likely to have changed. Observations have also been made on host species growing within and outside their native ranges, where physiological stress may have affected resilience to infection. Host provenance could also influence susceptibility, although not specified in many records. Spanish and French provenances of *P. sylvestris* grown as Christmas trees in the USA for example, are known to be more susceptible than German and Austrian provenances (Skilling and Nicholls, 1974; Phelps, et al., 1978;). Cleary et al (2019) recorded infection only on *P. mugo* var. *Hesse* out of a range of other *P. mugo* varieties in Alnarp Botanic Garden Sweden. Cech (Pers. Comm. 2022) noted that heavily infected *P. mugo* are often surrounded by other specimens with very little foliar damage in urban settings in Austria and others have found no infection on either *P. sylvestris* or *P. mugo* individuals immediately adjacent to heavily infected pine species (Jankovský et al., 2009b; Oskay et al., 2020).

Relatively few observations entered into the geo-database contained quantitative information on the extent to which individual trees or forest stands were affected by the pathogen. The majority of positive records (3 2 4) were recorded on *P. mugo* and its variants, and infection ranged from trees with less than 1 % needle infection (Switzerland - Dubach et al., 2018) to 51 – 75 % needle infection (again Switzerland - Dubach et al., 2018; Austria - Cech, unpublished data). Sixty-nine % of the *P. mugo* observations recorded crown infection greater than 25 %. Similarly, needle infection of *P. nigra* (and its subspecies) ranged from 5 to 10 % (Bulgaria - Georgieva, 2020) to over 75 % (Turkey - Oskay et al., unpublished data), and over 86 % of records illustrated greater than 25 % needle infection. Only nine *P. sylvestris* records from Austria, Bulgaria and Spain included information on the extent of infection, but of these, seven observations recorded crown infection of over 25 %. Thirty-six % of *P. radiata* suffered greater than 25 % needle infection, all of these records originating from Spain.

There is currently insufficient information to evaluate the susceptibility of nine host taxa reported to be infected by *L. acicola* and all inferences on the susceptibility of hosts relevant to European forestry will benefit from further field data from across Europe.

5. Influence of climate on *L. acicola*

Climate is a critical driver in the lifecycle of fungal pathogens, influencing their distribution and impact (Hanso and Drenkhan, 2012, 2013; Woods et al., 2016). Extensive study of *L. acicola* in North America throughout the twentieth century has illustrated the influence of climate

on BSNB disease intensity (Chapman, 1926; Siggers, 1932; Broders et al., 2015; Wyka et al., 2017). Typically, warmer regions in the southern States of the USA have multiple disease cycles *per annum*, and foliar symptoms, conidia and ascospores can be seen throughout the year (Wolf and Barbour, 1941; Siggers, 1944; Henry, 1954a,b; Kais, 1971, 1975b). In cooler mid-western and northern regions *L. acicola* tends to have an annual life cycle, driven by mist and rain-disseminated conidia, with peaks of infection between June and September (Verrall, 1936; Kais, 1971, Nicholls et al., 1973; Kais and Peterson, 1986; Wyka et al., 2017).

Recent changes in climate appear to have caused marked increases in disease intensity in the northern USA and Canada (Kais and Peterson, 1986; Broders et al., 2015; Wyka et al., 2017) where *P. strobus* is a significant component of the local native, mixed forest biome and an important timber crop (Siggers, 1944; Kais 1989; Enebak and Starkey, 2012; Munck et al., 2012; Broders et al., 2015; Wyka et al., 2017, 2018). Until 20 years ago it was considered moderately to highly resistant to *L. acicola*, suffering only sporadic damage from North Carolina to Pennsylvania and west into Wisconsin (Boyce, 1959; Alexander and Skelly, 1977; Stanosz, 1990). Recently however, White Pine Needle Damage (WPND) caused by a combination of foliar pathogens including *L. acicola*, *Bifusella linearis* (Peck) Höhn., *Lophophacidium dooksii* Corlett and Shoemaker *(syn. Canavirgella banfieldii),* and *Septorioides strobi* Wyka and Broders (Broders et al., 2015; Wyka and Broders, 2016) has become increasingly damaging. Heavy defoliation, loss of increment and increasing levels of mortality (Siggers, 1944; Kais 1989; Enebak and Starkey, 2012; Munck et al., 2012; Broders et al., 2015; McIntire, 2018; Wyka et al., 2017, 2018) are thought to be caused by increased early summer rainfall (Skilling and Nicholls 1974; Kais, 1975b), similar to the climatic triggers associated with outbreaks of *D. septosporum* in British Columbia (Woods et al., 2005) and Britain (Archibald and Brown, 2007).

Disease modelling is used to examine the factors most strongly influencing pathogen distribution and disease intensity, allowing predictions to be made of areas likely to be worst affected. Temperature and moisture availability (precipitation and/or humidity) are often the most influential factors driving fungal foliar diseases. Although evidence suggests BSNB is strongly influenced by temperature and precipitation, to date, species distribution modelling has not been carried out specifically for *L. acicola* at a global or European scale. One regional model suggested summer precipitation and solar radiation were good predictors of disease caused by *Mycosphaerella* spp. on *P. radiata* in the Basque country, northern Spain (Iturritxa et al., 2015). However, *Mycosphaerella* needle blight diseases were considered as one entity although in this region they can be caused by three distinct species, *Dothistroma septosporum, D. pini* Hulbary*,* and *L. acicola*. Although the impacts of climate and climate change on *Dothistroma* spp. are informative (Watt et al., 2011; Woods et al., 2016), our understanding of future behaviour of *L. acicola* is currently limited.

A geo-database was therefore developed to facilitate and promote future disease modelling efforts by providing a global synthesis of available data via an easily accessible platform. Global records of *L. acicola* were analysed alongside fine scale climatic and topographical variables at 1 km spatial resolution (https://www.portaloffor-estpathology.com; Fick and Hijmans, 2017). Only data points from confirmed reports of *L. acicola* in the wider environment were used, nursery records were omitted and, given the presence of multiple *Lecanosticta* species in Mexico and Central America, only molecularly confirmed reports of *L. acicola* were included from these two regions.

The maximum temperature of the warmest month in locations where *L.* acicola was present was 35 °C (Table 2. Texas, USA). Although 35 °C is apparently lethal to *L. acicola* when grown *in vitro* (Suto and Ougi, 1998), the current analysis demonstrates the value of field data, clearly demonstrating this species can survive such temperatures *in planta*. The minimum temperature of the coldest month was −24 °C, in north-central Alberta, Canada, (Table 2). Whilst c. 5 °C is the lower limit for

growth of *L. acicola in vitro* (Suto and Ougi 1998), release of conidia can occur at temperatures as low as 2 °C in the field (Kais, 1971), and *L. acicola* can survive temperatures far lower than this *in planta*. *Lecanosticta* spp. can also be isolated from infected needles stored at −80 °C (Barnes, Pers. Comm. 2022). Ascospores of *L. acicola* have also been trapped in the field at temperatures as low as 4 °C (Kais, 1971), but as they have yet to be recorded north of Ashland, Missouri (*P. ponderosa*, Luttrell 1949), it is probable that temperature is a significant, limiting factor in their production (Kais, 1971).

The distribution of *L. acicola* geo-database records in relation to maximum monthly temperature was bimodal, with a peak in numbers of record between 22 and 23 °C, and a second between 32 and 33 °C (Fig. 3). Records from locations with Alpine and Subalpine climates and the Baltic countries, as well as the northern USA and southern Canada form the majority of data points in the first peak. A second peak includes *L. acicola* records from Mediterranean and east Asian countries and states surrounding the Gulf of Mexico. The bimodal distribution of records may partly be an artefact arising from limited data availability from some geographic regions, but could equally reflect true differences between the two groups in *L. acicola* lineage - southern, northern, and perhaps other, new populations. Equally the groupings could indicate geographic variation in susceptible host species range.

Lecanosticta acicola was recorded in regions with wide variation in annual precipitation, from a minimum 407 mm p.a. recorded in Alberta, Canada to a maximum annual precipitation of 3157 mm p.a. recorded in Colombia (Table 2). While ascospore release is not reliant on rainfall, conidial discharge is positively correlated with precipitation, and rain fall has been recorded as a significant driver of population expansion, particularly in colder regions where temperature might be limiting sexual recombination (Kais, 1971; Skilling and Nicholls, 1974). Supplementary Figures S2 to S6 illustrate the distribution of *L. acicola* records according to precipitation values in the driest and wettest months, annual precipitation, the minimum temperature of the coldest month, and annual mean temperatures. Although the *L. acicola* records span a wide range within each of these climatic variables, there was no further evidence of bimodal responses, as described above.

The geodatabase records clearly demonstrate the wide variation in temperature and precipitation tolerated by *L. acicola*. One ongoing study arising from this collaboration is utilising the geo-database resource to develop a model predicting the potential global distribution of *L. acicola*. Preliminary results utilising different climate change scenarios (five Global Climate Models (GCM), three combined pathways of shared Socioeconomic Pathway and Representation Concentration Pathway (SSP-RCP) models) illustrate a positive trend in expansion of *L. acicola* range for the period 1971–2100. Although the current distribution of *L. acicola* covers 5.9 % of *Pinus* species area, globally, the models indicate environmental conditions are suitable for proliferation of the pathogen across 58.2 % of *Pinus* species cover (period 1971–2000). The average model predictions towards the end of the century (2071–2100) showed the potential distribution of *L. acicola* rising to 62.2 %, 61.9 %, 60.3 % of global *Pinus* species area for SSP1-RCP2.6, SSP2-RCP4.5, SSP5-RCP8.5, respectively. On the other hand, the potential distribution ranged from 33.6 to 85.8 % in the period 2071–2100, indicating the influence of GCMs on the results. The relative change in potential distribution of *L. acicola* in Europe is predicted to be + 12.2 %, Asia + 10 % and North America + 3.1 % of continental pine area, assuming average predictions using scenario SSP2-RCP 4.5 (Ogris et al., in prep.). Watt et al. (2011) obtained similar results when climate change predictions were incorporated into disease models for *Dothistroma* species leading to a decrease in global forest area at risk, but an increased risk to Europe and New Zealand.

Other than the molecular studies which described the species diversity within the forests of South and Central America and Mexico, very little is known about the behaviour of the more recently discovered *Lecanosticta* species. Given their presumed, predominantly Central American origin, these species are likely to be adapted to sub-tropical and temperature climatic conditions, but it is not possible without further behavioural studies to assess their potential for range expansion.

6. Management of BSNB

6.1. Surveillance and control

The endemic nature of the disease in North America gives little reason for surveillance and no hope of eradication, but the current situation in Europe is considerably different, and surveillance, management and eradication efforts can have a major role in minimising future spread and impact.

Currently, European plant health legislation (Regulation (EU) 2016/2031) exists to help prevent entry or detect invasions of non-native pests and pathogens at an early stage, to maximise probability of effective eradication. Whilst such legislation somewhat reduces the risks of disseminating pest and pathogens, it is by no means infallible, as demonstrated by the widespread movement of *Dothistroma* species (Bednářová et al., 2006; EFSA, 2013; Barnes et al., 2014), *Fusarium circinatum* (Drenkhan et al., 2020), *Hymenoscyphus fraxineus*, (Drenkhan et al., 2014; Agan et al., 2022) and many other organisms (Brasier, 2008; Santini et al., 2013). Until 2019 *L. acicola* was an Annex I/AI quarantine organism under EU Directive 2000/29/ES, with requirements for surveillance, exclusion, containment and eradication through phytosanitary measures in all EU countries. Man-mediated dissemination of *L. acicola* primarily occurs through plant movement, with seeds not considered a primary pathway (Ye and Li, 1988). Although phytosanitary methods differ in scale and intensity between countries, traded planting stock usually undergo mandatory inspections, including sampling visibly symptomatic tissue in seed beds or in potted specimens, followed by molecular diagnosis using traditional or quantitative PCR, which distinguishes between a range of similar looking pathogens (e.g. Ioos et al., 2010; EPPO, 2015). As with *Dothistroma* spp. (Gadgil, 1977), the significant lag between infection and symptom expression can hinder detection of the pathogen.

Such phytosanitary inspections of imported planting stock resulted in the first findings of *L. acicola* in the Czechia and Belarus (Golovchenko et al., 2020). In other parts of Europe, early reports were on exotic species established in Botanic Gardens (Estonia - Drenkhan and Hanso, 2009; Latvia - EPPO, 2012; Ireland – Mullett et al., 2018) or in street trees and gardens (Austria - Cech, 1997; Brandstetter and Cech, 1999; Italy - La Porta and Capretti 2000; Slovenia - Jurc and Jurc, 2010), but in other countries the first findings occurred in the wider environment following forest surveillance activities for a range of quarantine pathogens (Lithuania – Markovskaja et al., 2011; Bulgaria - Stamenova et al., 2018; Georgieva, 2020).

Eradication measures employed in, for example Croatia (Glavaš, 1979; Glavaš and Margaletić, 2001), Cuba (López Castilla et al., 2002), France (Lévy and Lafaurie, 1994; Lévy 1996), Switzerland (Dubach et al., 2018) and the USA (Kais, 1989) have relied on various sanitation measures. These have included felling and burning or burying of infected plants and plant litter as residues of these could harbour acervuli and ascostromata which could cause further infections (Siggers, 1944; Kais 1971, 1989; Jewell, 1983; EPPO, 2008). Burning, burying, composting of material at high temperatures, soil- and bio-fumigation and steam sterilization are methods commonly used to eradicate a range of pests and pathogens, although not always successfully (Sosnowski et al., 2009).

The use of various sanitation measures have had mixed success against *L. acicola* outbreaks. The interception and destruction of the infected planting stock found in Czechia was rapid and effective, and it was seven more years before the first official record of *L. acicola* was made, but in a different part of the country (Jankovský et al., 2008). The success of eradication efforts following the similar, but more recent detection on planting stock in Belarus will take time to evaluate. In contrast, there have been further reports of infection on *P. sylvestris* and

Table 1

Susceptibility of Pinaceae species to *Lecanosticta* species (species names and native ranges as assigned by Farjon (2010).

Degree of susceptibility of host	Reference	Country of observation	Grown as native or exotic	Additional comments
Resistant (no traces of infection have been reported where hosts located close to infected trees, or in artificial inoculation studies)				
Abies concolor. (Gordon et Glendinning) Hildebrand	Adamson et al. 2015	Estonia	Exotic	Inferred: uninfected despite inoculum present within the Botanic garden
Picea abies (L.) H. Karst.	Beenken et al., 2018	Switzerland	Native	Inferred: uninfected despite inoculum present locally
	Cech (unpublished data)	Austria	Native	uninfected following artificial inoculation
Picea koyamae Shiras.	Adamson et al. 2015	Estonia	Exotic	Inferred: uninfected despite inoculum present within the Botanic garden
Pinus fenzeliana Hand.-Mazz.	Li et al., 1986	China	Native	, Inferred: forests and plantations uninfected despite inoculum present locally
P. heldreichii var. *leucodermis* (Antoine) Markgraf ex Fitschen	Adamson et al. 2015	Estonia	Exotic	Inferred: uninfected despite inoculum present within the Botanic garden
P. massoniana Lambert[‡]	Li et al., 1986	China	Native	Plantations
P. sibirica Du Tour	Adamson et al. 2015	Estonia	Exotic	Inferred: uninfected despite inoculum present within the Botanic garden
P. taiwanensis Hayata	Li et al., 1986	China	Exotic	Plantations
Low (trace levels of foliar infection)				
Cedrus libani A. Rich.	Oskay et al., 2020	Turkey	Native	Observation in Botanic garden
Picea glauca (Moench) Voss	Skilling and Nicholls, 1974	USA	Exotic to most of USA (native to Canada, Alaska, Montana, Idaho, Washington, Wyoming)	Trace infection only when exposed to high levels of inoculum
P. attenuata Lemmon	Chandelier et al., 1994	France	Exotic	Plantations
P. banksiana Lamb.[‡]	Laut et al., 1966	Canada	Native (to eastern Canada)	Plantations
	Skilling and Nicholls, 1974	USA	Native (to northern USA)	Field inoculations in Christmas tree plantations
	Adamson et al. 2015	Estonia	Exotic	Botanic garden
P. caribaea Morelet	Lin and Liang, 1988	China	Exotic	Plantations
	Evans, 1984	Belize	Native	Natural forests
				Although diagnosed as *L. acicola* on the basis of morphological examination, subsequent phylogenetic analysis suggests *L. acicola* is not present in Central America
	van der Nest et al., 2019a, b	Guatemala, Honduras	Native	Natural forests
				Phylogenetic analysis detected *L. variabilis*, *L. pharomachri*, *L. jani*, and *L. guatemalensis* but not *L. acicola*
P. contorta Douglas ex Loudon[‡]	Evans, 1984	Canada	Native	Infection recorded in forests, no details given
	Adamson et al. 2015	Estonia	Exotic	Botanic garden
P. densiflora Siebold et Zuccarini	Suto and Ougi, 1998	Japan	Native	Artificial inoculation studies. Decreasing susceptibility with age
P. elliottii Engelmann[‡]	Gibson, 1980	Colombia	Exotic	Infection present in plantations, but causing little damage
	Cao, 2008	China	Exotic	Plantations
				Tree breeding research used to produce less susceptible *P. elliottii* clones.
	Mesanza et al., 2021b	Spain	Exotic	Plantations
P. massoniana	Gong and Liang, 1988Kehui, et al., 1996	China	Native	Plantations and young trees adjacent to heavily infected *P. taeda*
P. maximinoi H. E. Moore	van der Nest et al., 2019a, b	Guatemala, Honduras, Nicaragua	Native	Natural forests
				Phylogenetic analysis detected *L. variabilis* and *L. jani*, but no *L. acicola*
P. mugo Turra	Geodatabase (this paper)	Switzerland, Austria	Native	Natural regeneration in bogs
P. nigra J.F. Arnold[‡]	Sadiković et al., 2019a[‡‡]	Slovenia	Native	Forests
	Adamson et al. 2015	Estonia	Exotic	Botanic garden
P. nigra J. F. Arnold var. *nigra*	Hintsteiner et al., 2012	Austria	Native	Mature trees in gardens
P. oocarpa Schiede ex Schlectendahl	Evans, 1984	Costa Rica,	Native	Natural forests
				Although diagnosed as *L. acicola*, subsequent phylogenetic analyses suggest *L. acicola* not present in Central America
	van der Nest et al., 2019a, b	Guatemala, Honduras, Nicaragua	Native	Phylogenetic analysis detected *L. variabilis*, *L. pharomachri*, *L. jani*, and *L. guatemalensis* but not *L. acicola*
P. palustris Miller[‡]	Webster, 1930Skilling and Nicholls, 1974	USA	Native	Plantations and field inoculations in Christmas tree plantations

Table 1 (*continued*)

Degree of susceptibility of host	Reference	Country of observation	Grown as native or exotic	Additional comments
				Impacts vary across this host's natural range, but breeding programmes have led to development of less susceptible varieties
	Huang et al., 1995	China	Exotic	Plantations
P. palustris × *elliottii*	Derr, 1966 Lott et al., 1966	USA	Native	Plantations – experimental trials of *P. palustris* hybrids
P. palustris × *taeda*	Lott et al., 1966	USA	Native	Plantations – experimental trials of *P. palustris* hybrids
P. patula Schiede *ex* Schlectendahl *et* Chamisso	Gibson, 1980	Colombia	Exotic	Plantations
P. pinaster Aiton	Siggers, 1944	USA	Exotic	Infection recorded. No details given
	Martínez and Juan, 1965	Spain	Native	Infection rare and insignificant. Location 'type' not specified
	Mesanza et al., 2021b	Spain	Native	Arboretum
P. pinea L.	Siggers, 1944	USA	Exotic	Infection recorded. No details given
	Mesanza et al., 2021b	Spain	Native	Arboretum
P. pseudostrobus Lindley	Evans, 1984 Marmolejo, 2000 van der Nest et al., 2019a,b	Mexico	Native	Natural Forests Phylogenetic analysis detected *L. gloeospora* but not *L. acicola*
	van der Nest et al., 2019a, b	Guatemala, Honduras	Native	Natural forests Phylogenetic analysis detected *L. brevispora* but not *L. acicola*
P. radiata[‡] D. Don	Chandelier et al., 1994 Lévy, 1996	France	Exotic	Plantations
P. × *rhaetica* (natural hybrid of *P. mugo* and *P. sylvestris*)	Adamson et al. 2015, 2018	Estonia	Exotic	Botanic garden and plantations where slight infection recorded in naturally regenerated trees in mixed stand of *P. mugo* and *P. sylvestris*
	Raitelatytė et al., 2022	Lithuania	Exotic	In forest plantations where slight infections were recorded in naturally regenerated trees in mixed stands of *P. mugo* and *P. sylvestris*
P. resinosa[‡] Aiton	Nicholls and Hudler, 1972	USA (Wisconsin)	Native to eastern USA	Low levels of infection in trees adjacent to heavily infected *P. sylvestris* in Christmas tree plantations
P. rigida Miller	Hedgecock, 1929 Siggers, 1944	USA	Native to SE USA	Infection recorded. No details given
	Adamson et al. 2015	Estonia	exotic	Botanic garden
Pinus roxburghii Sargent	Magán and de Ana, 1997	Spain	Exotic	Chlorosis of nursery seedlings, low levels of mortality observed
P. strobus L.[‡]	Skilling and Nicholls, 1974	USA	Native	Field inoculations in Christmas tree plantations
P. sylvestris L.[‡]	Skilling and Nicholls, 1974	USA	Exotic but considered naturalised	Christmas tree plantations - 'German' long needled provenance lowest susceptibility of four *P. sylvestris* provenances tested
	Adamson et al., 2018	Estonia	Native	Naturally regenerated trees in mixed stand of *P. mugo* and *P. sylvestris*
	Dubach et al., 2018	Switzerland	Native	Low levels of infection found during national monitoring exercises
	Sadiković et al., 2019a	Slovenia	Native	Relatively uninfected despite close proximity to heavily infected *P. mugo*
	Mesanza et al., 2021b	Spain	Native	Arboretum
	Raitelaitytė et al., 2022	Lithuania	Native	Naturally regenerated trees in mixed stand of *P. mugo* and *P. sylvestris*
	Raitelaitytė et al., 2020	Poland	Native	Naturally regenerated trees in mixed stand of *P. mugo* and *P. sylvestris*
P. taeda L.[‡]	Webster, 1930 Phelps et al., 1978	USA	Native (to southern and eastern States)	Christmas tree plantations
	Chandelier et al., 1994	France	Exotic	Plantations
	Mesanza et al., 2021b	Spain	Exotic	Arboretum
P. tecunumanii Eguiluz et J.P. Perry	van der Nest et al., 2019a, b	Guatemala Nicaragua	Native	Natural forests Phylogenetic analysis detected *L. guatemalensis, L. jani, L. pharomachri* and *L. tecunumanii* but not *L. acicola*
P. thunbergii Parlatore[‡]	Seo et al., 2012	South Korea	Native	Coastal windbreaks
	Ye and Wu, 2011	China, Jiangsu Province	exotic	Unspecified
Medium (infection clearly visible, but growth not seriously affected)				
Cedrus atlantica (Endl.) Manetti ex Carrière[‡‡]	Schenck et al., 2022	France	Native	Plantations
P. ayacahuite Ehrenberg ex Schlechtendahl	Marmolejo, 2000	Mexico	Native	Natural forests
P. brutia Tenore	Mesanza et al., 2021b	Spain	Exotic	Arboretum
P. brutia var. *pityusa* (Steven) Silba	Zhukov and Zhukov, 2008	Russia (Black Sea)	Native	Native forests and plantations

Table 1 (*continued*)

Degree of susceptibility of host	Reference	Country of observation	Grown as native or exotic	Additional comments
P. caribaea[‡]	Hedgecock, 1929	USA	Exotic	Artificial inoculation
	Li et al., 1986	China	Exotic	Plantations
P. cembroides Zuccarini	Marmolejo, 2000	Mexico	Native	Unspecified
P. clausa (Chapman ex Engelmann) Vasey ex Sargent	Li et al., 1986a	China	Exotic	Plantations
P. echinata Miller	Li et al., 1986	China	Exotic	Plantations
P. maximinoi	Theron et al., 2022	Colombia	Exotic	Young plantations infected by *L. pharomachri*
P. nigra[‡]	Georgieva, 2020	Bulgaria	Native	Plantations and natural forest
	Mesanza et al., 2021b	Spain	Native	Arboretum
P. nigra subsp. *laricio* (Poir.) Maire	Alvère et al., 2010	France	Native	Plantations
P. palustris[‡]	Li et al., 1986	China	Exotic	Plantations
P. patula	Theron et al., 2022	Colombia	Exotic	Young plantations infected by *L. pharomachri*
P. ponderosa Douglas ex Lawson[‡]	Mesanza et al., 2021b	Spain	Exotic	Arboretum
P. pumila (Pall.) Regel	Zhukov et al., 2013	Russia (Sakhalin)	Native	Natural forests
P. resinosa[‡]	Skilling and Nicholls, 1974	USA	Native (north eastern states)	Field inoculation in Christmas tree plantations
P. sylvestris[‡]	Skilling and Nicholls, 1974	USA	Exotic but considered naturalised	In Christmas tree plantations NB. 'Austrian Hills' provenance moderately susceptible in a test of four provenances
	Alvère et al., 2010	France	Native	Plantations
	Jurc and Jurc, 2010; Sadiković et al., 2019a	Slovenia	Native	Forests, urban areas
P. taeda[‡]	Hedgecock, 1929Toole, 1939Boyce, 1952	USA	Native (to southern and eastern states) Exotic	Plantations Artificial inoculations
	Ye and Li, 1996	China	Exotic	Plantations
P. tecunumanii (low elevation provenance)	Theron et al., 2022	Colombia	Exotic	Young plantations infected by *L. pharomachri*
High (high levels of defoliation and in some cases, mortality observed)				
P. × *attenuradiata* Stockwell & Righter	Chandelier et al., 1994Lévy, 1996	France	Exotic	Plantations. High mortality observed
P. caribaea[‡]	López Castilla et al., 2002	Cuba	Native	High seedling mortality in nurseries
P. cubensis Grisebach / *P. maestrensis* Bisse	López Castilla et al., 2002	Cuba	Native	High seedling mortality in nurseries
P. contorta subsp. *latifolia* (Engelm.) Critchfield[‡]	Laut et al., 1966	Canada	Native	Plantations. High mortality observed
P. densiflora[‡]	Magán and de Ana, 1997	Spain	Exotic	High seedling mortality in nurseries
P. elliottii[‡]	Li et al., 1986Ye and Li, 1996	China	Exotic	Plantations. High mortality observed prior to development of more resistant clones in China
P. halepensis Miller	Milatović, 1976Glavaš and Margaletić, 2001	Croatia	Native	Plantations and natural forests. Mortality observed
	Marmolejo, 2000	Mexico	Exotic	Research forest
P. merkusii Junghuhn & de Vriese ex Vriese	Magán and de Ana, 1997	Spain	Exotic	High seedling mortality in nurseries
P. mugo	Evans et al., 1981	Canada	Exotic	Ornamental specimens
	La Porta and Capretti, 2000 Ghelardini et al., 2019	Italy	Native	Botanic Garden, Urban and parkland trees
	Brandstetter and Cech, 2003 Hinsteiner et al., 2012	Austria	Native	Urban trees and gardens
	Markovskaja et al., 2011Raitelaitytė, et al., 2022	Lithuania	Exotic	Plantations, Botanic gardens, urban trees, Arboretum
	Adamson et al., 2015	Estonia	Exotic	Urban or parkland trees
	Raitelaitytė et al., 2020	Poland	Native	Urban trees, plantations
	Geodatabase (this paper)	Slovakia	Native	Arboretum
	Jurc and Jurc, 2010; Sadiković et al., 2019a	Slovenia	Native	Arboretum, urban areas, cemeteries Forests
	Geodatabase (this paper)	Switzerland, pol	Native	Natural regeneration in bogs
P. mugo subsp. *mugo*	Mullett et al., 2018	Russia (Black Sea)	Exotic	Botanic Garden, arboretum
P. mugo var. *Hesse*	Cleary et al., 2019	Sweden	Exotic	Arboretum
P. mugo Turra subsp. *rotundata* (Link) Janch. Et H. Neumayer	Jankovský et al., 2008, 2009b	Czech Republic	Native	Natural regeneration in bogs
P. muricata D. Don	Lévy et al., 1996	France	Exotic	Plantations
P. nigra[‡]	Skilling and Nicholls, 1974	USA	Exotic but considered naturalised	Field inoculation in Christmas tree plantations
	Evans et al., 1981	Canada	Naturalised	Plantations
	Ye and Li, 1996	China	Exotic	Plantations
	Sadiković et al., 2019a[‡]	Slovenia	Native	Forests

Table 1 (*continued*)

Degree of susceptibility of host	Reference	Country of observation	Grown as native or exotic	Additional comments
P. nigra subsp. *pallasiana* (Lamb.) Holmboe *P. nigra* subsp. *pallasiana* var. *fastigiata* Businský *P. nigra* subsp. *pallasiana* var. *pallasiana* f. şeneriana (Saatçioğlu) Kandemir and Mataracı)	Oskay et al., 2020	Turkey	Native	Arboretum
P. palustris[‡]	Chapman, 1926 Hedgecock, 1929 Siggers, 1944 Wakeley, 1970	USA	Native	Plantations. Impacts vary across this host's natural range, but mortality observed in young trees. Less susceptible varieties now available from breeding programmes
P. ponderosa[‡]	Luttrell, 1949 Peterson, 1981	USA	Native (to mid-west and western states)	Plantations and parkland trees. Mortality observed in plantations outside natural host range of western USA
P. radiata D. Don[‡]	Gibson, 1980	Colombia	Exotic	Plantations
	Ortíz de Urbina et al., 2017	Spain	Exotic	Plantations
P. resinosa[‡]	Nicholls and Hudler, 1972	USA	Native (north eastern states)	Artificial inoculation trials
P. strobus[‡]	Broders et al., 2015 Wyka et al., 2017, 2018	USA	Native	Plantations. Mortality observed
P. sylvestris[‡]	Skilling and Nicholls, 1974 Peterson, 1981	USA	Exotic but considered naturalised	In Christmas tree plantations, and landscape planting. Short-needled 'Spanish' and 'French Green' were the most susceptible of four provenances tested in Christmas tree plantations
	Zhukov and Zhukov, 2008	Russia (Black Sea)	Native	Native forests and plantations
	Oskay et al., 2020	Turkey	Native	Arboretum
	Georgieva, 2020	Bulgaria	Native	Native forests and plantations
P. taeda[‡]	Toole, 1939 Boyce, 1952	USA	Native (to southern and eastern states)	In plantations
	Li et al., 1986 Ye and Qi, 1999	China	Exotic	In plantations
P. thunbergii[‡]	Li et al., 1986	China	Exotic	In plantations
	Mullett et al., 2018	Russia (Black Sea)	Exotic	Botanic garden, arboretum
	Suto and Ougi, 1998	Japan	Native	On ornamental planting stock
Unknown				
P. coulteri D. Don	Siggers, 1944	USA	Native	Infection recorded. No details given
P. culminicola Andresen et Beaman	Marmolejo, 2000 Quaedvlieg et al., 2012	Mexico	Native	*L. longispora* detected using morphological and molecular methods, no information on host condition given
P. glabra Walter	Hedgecock, 1929, Siggers, 1944	USA	Native	Infection recorded. No details given
P. jeffreyi Greville et Balfour in A. Murray	Siggers, 1944	USA	Native	Infection recorded. No details given
P. sabiniana Douglas ex D.Don	Siggers, 1944	USA	Native to western USA	Infection recorded. No details given
P. serotina Michaux	Siggers, 1944	USA	Native to south east USA	Infection recorded. No details given
Pinus × *sondereggeri* (natural hybrid of *Pinus palustris* and *P. taeda*)	Hedgecock, 1929	USA	Native to south east USA	Infection recorded. No details given
P. uncinata Raymond *ex* DC.	Cech, unpublished data	Austria	Native	*L. acicola* detected using molecular methods, no information on host condition given
P. virginiana Miller	Hedgecock, 1929	USA	Native to east USA	Infection recorded. No details given

[‡] Denotes host species whose susceptibility has been rated differently by multiple authors and appear in more than one resistance category.

[‡‡] Sadiković et al., 2019a report varying impacts of the pathogen on *P. nigra* in Slovenia, attributing the differences to possible differences in aggressiveness of *L. acicola* populations between the regions of Tolmin (heavily affected) and Trenta (less affected).

[‡‡‡] The authors of this most recent record (Schenke et al. 2022) described considerable variation in disease severity of 15–25 year old *Cedrus atlantica* grown in plantations. Light to severe defoliation was recorded but further observations will be needed to assess susceptibility.

P. nigra up to 25 km from the original forest site in south-eastern Bulgaria despite apparently felling and removing all affected trees (Georgieva, 2020). Similarly, *L. acicola* was reported four years after the initial detection and eradication effort in the Botanic Garden in Latvia (EPPO, 2012; Mullett et al., 2018). Eradication measures in Lithuania including incineration of infected plants and prohibiting movement of host plants out of the demarcated areas for one year were also unsuccessful (Markovskaja et al., 2011). This was made apparent when, after

the first detection and eradication attempt of *L. acicola* in *P. mugo* plantations in 2009, the pathogen was then subsequently found in other locations along the Baltic Sea coast on native *P. sylvestris* and *P.* × *rhaetica* Brügger, and later in botanic gardens, arboreta, urban plantations, and most recently, a nursery (EPPO, 2020; Raitelaitytė et al, 2022).

Although *L. acicola* retains A1 quarantine status in Russia, Turkey, Ukraine and Britain (post Brexit), the pathogen became a Regulated

Table 2

Temperature, precipitation and topographical variables in locations where *L. acicola* records have been confirmed using morphological and/or molecular diagnostic methods*. (High resolution climatic variables interpolated from Fick and Hijmans 2017).

Climatic/topographical variable	Minimum	Mean	Maximum
Altitude (m a.s.L.**)	1.3	306	2459
Annual mean temperature (°C)	−1.4	10.9	26.3
Maximum temperature of the warmest month (°C)	18.4	25.5	34.9
Minimum temperature of the coldest month (°C)	−24.1	−2.6	20.7
Annual precipitation sum (mm)	407	1127	3157
Precipitation sum of the wettest month (mm)	54	137	543
Precipitation sum of the driest month (mm)	6	58	145

*Includes all global records of *L. acicola* confirmed using morphological and molecular means, except records from Mexico and Central America, where due to the presence of other species of Lecanosticta, ONLY records confirmed using molecular diagnostic methods are included.

**a.s.L – above sea level.

Non-Quarantine Pest (RNQP) in the EU in 2019 according to Commission implementing regulation (EU) 2021/2285; https://gd.eppo.int/taxon/SCIRAC/categorization). The transmission pathway is still identified primarily as specific plants for planting, with management focussing on statutory inspections of all plants for planting (ornamental and forest plants for planting) to ensure they are not infected with *L. acicola* prior to sale. However, the change in status means surveillance and management in the wider environment (forests, urban areas etc.) is no longer a statutory requirement in the EU, although regionally, surveillance requirements do differ. It remains to be seen if this change from quarantine to RNQP status will facilitate the spread of *L. acicola* throughout Europe.

6.2. Management of BSNB

Despite phytosanitary guidance and actions, *L. acicola* has managed to gain a strong foothold in Europe, and forest managers should begin to consider control measures. Due to its long history with the disease, the North American forest industry has devoted considerable resources to disease management, and some techniques could inform European forest management strategies:

6.2.1. Chemical management: Fungicides and fertilisation

Most early research on *L. acicola* was conducted on *P. palustris,* originally widely planted in southern states of the USA due to its general
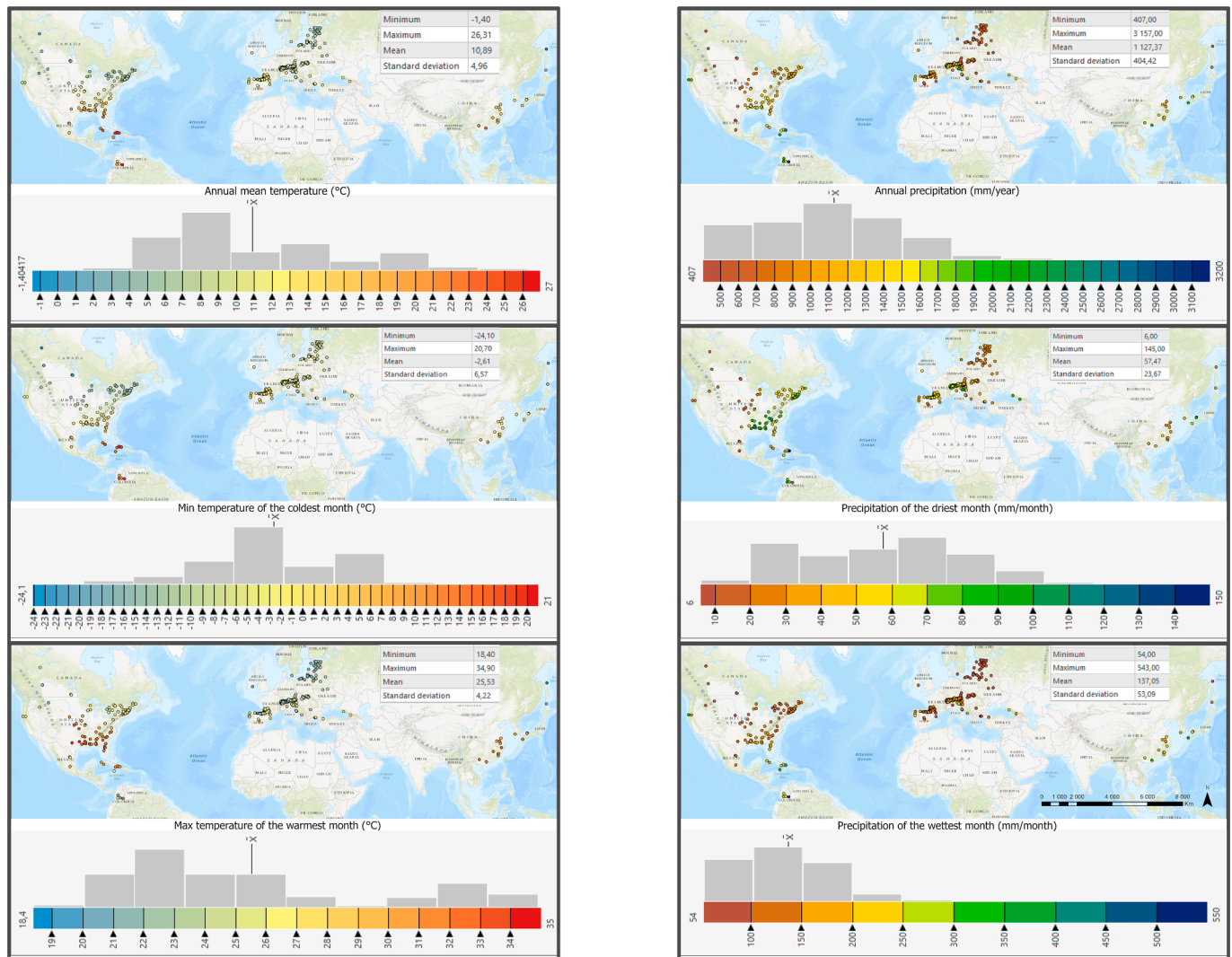

Fig. 3. Distribution of *L. acicola* records in relation to a. the maximum temperature reached in the warmest month, showing an initial peak in numbers of records between 22 and 23 °C and a second peak between 32 and 33 °C b. the minimum temperature of the coldest month c. the annual mean temperature d. the mean precipitation of the driest month e. the mean precipitation of the wettest month and f. the annual precipitation.

tolerance to pests and diseases (Siggers, 1944; Campbell and Copeland, 1954; Walkinshaw, 1978; Moser et al., 2003). From the 1920s on however, this species became increasingly affected by *L. acicola*, to which it can be highly susceptible. During this time there was heavy investment in chemical control in tree nurseries and young crops, where the toxicity or alkalinity of active ingredients such as sulphur 'hydrated lime', calcium hydroxide, and calcium caseinate impeded spore germination (Hedgecock, 1929; Webster, 1930; Siggers, 1932, 1944). Later, chlorothalonil and mancozeb were used (Kais, 1989), increasing shoot length by 10–25 % and needle length by 20 % (*P. taeda* - Parris, 1969).

Copper containing products, used widely against *Dothistroma* species (Bulman et al., 2016) also have a long history of use against *L. acicola*, with good efficacy demonstrated in the USA (Hedgecock, 1929; Siggers, 1932; Derr, 1957; Kais, 1989; Barnett et al., 2011), Colombia (CONIF, 1987), and Cuba (López Castilla et al., 2002). In nurseries, root dipping transplants with the systemic fungicide benomyl also reduced infection of *P. palustris* and *P. elliottii* seedlings by 30 %, improving establishment and growth (Cordell et al., 1984, 1990; Kais et al., 1986; Barnett and Brissett, 1987), but with some phytotoxicity (Stumpff and South; 1991). In a Chinese study, treatment of bare root seedlings of *P. taeda* and *P. elliottii* with carbendazim or thiophanate-methyl was also effective against natural and artificial inoculation with *L. acicola* (Hang et al., 1992).

Mycorrhizal (*Pisolithus tinctorius*) inoculations of seedlings or seedbeds can be used to improve establishment of seedlings and have proved most effective when combined with fungicides including benomyl (*P. palustris*, USA - Kais et al., 1981) and copper oxychloride (*P. maestrensis* seedlings, Cuba - Ferrer et al., 2000).

Fertilisation has been used to increase tree vigour and resistance to infection with mixed results. Siggers (1944) reduced infection and induced rapid height growth in *P. palustris* stands affected by BSNB, using applications of NPK (nitrogen, phosphorus and potassium) fertiliser, and mulching with dead grass and straw. A later study found that fertilisation increased *P. palustris* mortality as seedlings were outcompeted by surrounding ground vegetation. The increased humidity resulting from the more lush vegetation also slightly increased BSNB infection, and some phytotoxic effects of the products used, and the negligible impact of fertilisation on seedling growth resulting in its not being adopted widely as an effective BSNB management technique (Derr, 1957). Fertilisation treatments have had similar varied effects on DNB (Bulman et al., 2016). Little is known about the impacts of soil type (structure, micronutrient content, etc.) on susceptibility of trees to the pathogen, but an early study using a simple method of soil characterisation found no correlation between soil type and susceptibility (Toole, 1939).

In Europe, fungicides were used against some of the earliest outbreaks of *L. acicola*. In Croatia, copper products, probably Bordeaux Mixture, were applied to *P. halepensis* reducing crown infection and increasing needle lengths over time (Glavaš, 1979). In Spain cuprous oxide is used in most fruit crops, many herbaceous crops and in ornamental conifers, and in 2022 was authorised for terrestrial application to *P. radiata, P. pinaster* Aiton and *P. nigra* in the provinces of A Coruña and Lugo of the Autonomous Community of Galicia and in the Autonomous Community of the Basque Country. https://locatec.es/proyectos/fitoge st/excepcionales/400.pdf. Mancozeb and benomyl-based fungicides were used unsuccessfully to manage the disease on the first affected Austrian specimens in 1996, but felling and burning were ultimately used to control the infections (Cech, 1997).

Fungicidal active substances are under constant scrutiny, their continued availability in the EU dependent on the outcome of environmental and toxicological reviews and economic factors. While fungicide applications to nursery seedlings against pathogens such as *Dothistroma* and *Botrytis* spp. are routine, and could be used to control *L. acicola* outbreaks in nurseries (e.g. López Castilla et al., 2002), fungicide applications to forests are currently illegal in some European countries (e. g. Slovenia and Estonia). In addition, many of the specific actives used

against *L. acicola* in the past are no longer registered for use in the European Union and Britain or, in the case of copper actives, are currently under scrutiny. There is a need for efficacy trials using approved products with differing modes of action, on economically, ecologically and environmentally significant hosts. Fertilisation treatments may be more effective on European host species than the American *P. palustris*, particularly where ground vegetation is also controlled by chemical or cultural means.The impacts of underlying soil type, nutrient availability and drainage are also worthy of further investigation and are likely to affect overall tree condition and resilience to infection.

6.2.2. Silvicultural techniques

Silvicultural techniques used commonly against a range of foliar pathogens (such as *Dothistroma* spp.) have been recommended for effective BSNB management. Ensuring that plants for planting are healthy and not pre-stressed by inappropriate storage or wounded by rough handling increased establishment success. Generic good hygiene practices also minimised the dissemination of spores on tools and machinery (Nicholls et al., 1973; Kais, 1978) and possibly on clothing (Webster, 1930; Siggers, 1944; Jankovský et al., 2009a).

Controlled burns to destroy infected needle tissue (Verrall 1934, 1936; Baxter 1967) were one of the earliest methods used against *L. acicola* on the fire-tolerant *P. palustris* in the USA (e.g. Wyman, 1922; Chapman 1926; Hedgecock, 1929; Demmon, 1935; Wolf and Barbour 1941; Squires, 1947; Bruce 1954; Demers et al., 2010). Large areas (at least 100 acres) had to be burned to minimise impacts of encroaching inoculum from surrounding infected crops (Baxter 1967). Although burning caused some seedling mortality and terminal bud damage (Siggers 1932; Bruce, 1954), it resulted in more rapid height growth (Barnett et al., 2011). Management plans thus consisted of burning where foliar infection exceeded 20 % (Demers et al., 2010) or 30 %, continuing every-three to four years during the long establishment stage in *P. palustris* (Cordell et al., 1990). Environmental concerns over particulates and carbon emissions limit the practice of burning in many countries (e.g. Britain, Forestry Commission 2011). Burning specifically to reduce pest populations is thus rare in Europe, but it is regularly used to reduce fuel loads in southern European forests, minimising risks of wild-fire (Montiel and Kraus, 2010; Gazzard, Forestry Commission England, Pers. Comm. 20/11/18; Fernandes et al., 2022). Where *Pinus* forests are exposed to wildfire or deliberate burning, any secondary benefit of reducing both *L. acicola* and *Dothistroma* residues in fallen needles, has to be weighed against the fire-resistance of the host (De Ronde, 1982).

Forest structure influences the impacts of BSNB, and the more open, drier crowns of mature stands tend to be less susceptible to the disease than younger, closer-spaced plantations or dense, naturally regenerated forests, where high humidity is favourable to dissemination of conidia (Chapman, 1926). The microclimate can be deliberately manipulated to reduce inoculum. Increasing the spacing within and between seedling beds, reducing the initial stocking density in plantations (Derr, 1957; Kais, 1989, Munck et al., 2011) and Christmas tree plantations (Alexander and Skelly, 1977) and regularly thinning or pruning more mature crops will both decrease humidity, and physically increase the distance spores must travel to infect adjacent trees (Verrall, 1936; McIntire, et al., 2018). Thinning reduced defoliation of *P. strobus* affected by WPND (McIntire, et al., 2018), reduced BSNB impacts on *Pinus* spp. (Derr, 1957; Glavaš, 1979, 2001; CONIF - Corporacion nacional de Investigacion y Fomento Forestal, 1987; Kais, 1989 Glavaš and Margaletić, 2001; López Castilla et al., 2002; Demers, et al., 2010; Mesanza et al., 2021b), and has been used widely and successfully to manage DNB (Bulman et al., 2016), although Ortíz de Urbina et al., (2017) using a similar approach to manage DNB and BSNB in Spain, saw no appreciable benefits. To enhance successful control of the disease these silvicultural interventions could be used in combination with fungicides (Glavaš, 1979).

Heavily infected stands create a large source of inoculum and where

possible, susceptible hosts should not be established close to plantations containing infected trees (Tainter and Baker, 1996). Spores are largely disseminated in water droplets (Verrall, 1936; Kais, 1971, 1975b) and although studies have illustrated rapidly diminishing spore capture and *L. acicola* infections at distances over 1.5 m to 3 m (*P. palustris*, Verrall, 1936), conidia can travel at least 60 m (*P. strobus*, Wyka et al., 2018). The largely wind-disseminated ascospores are important drivers of long-distance dispersal, as is also the case with *Dothistroma* species (Kais, 1971, 1989; Mullett et al., 2016). Where both *L. acicola* mating types are present, enabling sexual reproduction, even widely spaced plantations may be vulnerable.

Uneven-aged and continuous-cover forestry management systems, promoted under the European Green Deal's Forest Strategy for 2030 (European Commission Forest strategy (europa.eu) accessed 19/04/2022; Lier et al., 2022) have a different canopy structure to plantations, and a different microclimate. *P. palustris* grown under the mature tree canopy of shelterwood regeneration systems seems to incur lower levels of infection (Boyer, 1975; Phelps et al 1978; Cordell et al., 1990) and artificial inoculation trials also showed shade reduced fructification (Siggers, 1944). In contrast, shaded ornamental *P. mugo* trees suffered severe infection, exacerbated by high humidity in the lower levels of the canopy (La Porta and Capretti, 2000). The mixed ages of trees in alternative silvicultural systems could also affect physiological susceptibility of trees to the disease, with some evidence that certain species, for example, *P. palustris* (Siggers, 1932), *P. taeda* (Toole, 1939) and *P. elliotti* (Gong and Liang, 1988), but not *P. strobus* (Broders et al., 2015; Wyka et al., 2017), become less susceptible with age. Mixed aged silvicultural systems are commonly practised across Europe and will need further study to determine what effect this may have on disease progression.

6.2.3. Breeding for resistance and tree species choice

Host resistance has played a key role in managing DNB (Bulman et al., 2016) and is also being developed and exploited in the management of *L. acicola*. By the 1970s the economic impacts of *L. acicola* on *P. palustris* in the southern States of the USA resulted in a 75 % decrease in the planted area of this species (Mann, 1969 cited by Kais 1975b). A subsequent breeding programme established after finding healthy seedlings in heavily infected nursery beds (Verrall, 1934; Derr, 1966; Derr and Melder, 1970; Boyer, 1972; Snyder and Derr 1972; Barnett et al., 2011) has been very successful. Hybrids of *P. palustris* × *P. elliottii* have also been developed balancing resistance to *L. acicola* and another serious pathogen, *Cronartium* species (Derr, 1966; Lott et al., 1996). Outbreaks of BSNB in exotic pine species in Southern China in the 1970s also stimulated breeding programmes for *P. elliottii* (e.g. Ye and Li, 1996).

Host susceptibility is influenced by a variety of heritable, constitutive and inducible defensive responses in *Pinus* spp., including production of phenolic compounds, terpenoids, pathogenesis-related proteins, and hypersensitive responses (Franceschi et al., 2005; Keeling and Bohlmann, 2006; Fraser et al., 2016). In the 1940s, resin production was linked to resistance of *P. palustris* to *L. acicola* (Siggers, 1944; Enebak and Starkey, 2012) where less susceptible varieties were found to have higher densities of resin canals (Verrall, 1934). Ye et al. (1994a) identified that more resistant *P. elliottii* clones had consistently higher concentrations of certain enzymes in their needle tissue. Enzymes involved in the production of terpenoids and other secondary metabolites could also be induced by exposure of tissue to toxins produced by *L. acicola* in culture (Ye et al., 1994a, b; Ye and Li, 1996; Ye and Qi, 1999; Yang et al., 2005; Cheng et al., 2012) and *P. elliottii, P. massoniana, P. taeda* and *P. thunbergii* seedling responses to these extracted toxins was a reliable indication of their susceptibility (Ye and Qi, 1999). Parallel studies indicated quantitative and qualitative differences in terpenoid concentrations between resistant and susceptible *P. elliottii* clones (Ye and Li, 1996) and almost disease-free clones of *P. elliottii* were developed in the 1990s (Ye and Li, 1996; Ye and Qi, 1999). This evidence of causal relationships between physiological responses and susceptibility should

now be explored in other *Pinus* species to increase the resilience of European forestry.

Many of these management options are not exclusive. For example, combining less susceptible *P. palustris* varieties with fungicidal root dipping has resulted in good disease control in the USA (Kais and Griggs 1986) and *P. palustris* has been re-included in planting programmes across the USA's Gulf States (Cordell et al., 1990; Enebak and Carey, 2002; Larson, 2002; Barnard and Mayfield, 2009). Resistance of *P. elliottii* clones in Chinese plantations has also been enhanced by fertiliser applications (Gong and Liang, 1988).

Prior to the successful tree breeding programmes, or where other management interventions have failed to prevent serious disease outbreaks, species change has been the only remaining choice. Where DNB outbreaks occurred on *P. radiata* in Kenya, Tanzania and Zimbabwe, and *P. nigra* subsp. *laricio* and 'Inland' and 'Coastal' origins of *P. contorta* subsp. *latifolia* in Britain, there was a large scale move towards planting less susceptible species (Bulman et al., 2016). Similarly, in the middle of the last century large areas of *P. palustris* affected by BSNB in the southern states of America were felled and replaced with *P. caribaea*, *P. elliottii* and *P. taeda* (Siggers, 1944; Derr, 1957). Profitable varieties of *P. sylvestris* Christmas trees in the North-Central States were replaced by naturally more resistant varieties, or with other species of *Pinus* or *Abies* in the 1970s after BSNB caused the loss of several hundred thousand trees (Prey and Morse, 1971; Nicholls et al., 1973; Alexander and Skelly, 1977).

Across Europe, the impacts of BSNB in natural and planted forests are currently relatively slight. However, should the pathogen's range and impact increase, and where control measures for *L. acicola* and other pathogens either cannot be used or are ineffective, species change may have to be considered.

6.3. Management case studies

There are few barriers to natural dispersal of the pathogen across Europe and eradication of *L. acicola* after detection in the wider environment is very difficult. The EUPHRESCO partnership highlighted several regional eradication and disease management efforts which have involved close collaboration between scientific institutes, foresters, local government, arboricultural workers and the local community. These case studies are outlined in further detail below:

Case Study 1: Outbreak of *L. acicola* in Slovenia

Lecanosticta acicola was first reported in Slovenia on *P. sylvestris* and *P. mugo* in 2008 in a park in Bled, and in 2009 in a park in Ljubljana (Jurc and Jurc, 2010). Following this, national surveys of forests were carried out from 2012 to 2016 by the Slovenia Forest Service and Slovenian Forestry Institute, and samples collected from symptomatic foliage. Survey locations included forest stands, parks, urban areas, and nurseries. Sixty-one locations were surveyed in 2012 (zero positive samples), 120 locations in 2013 (*L. acicola* confirmed at one site), 158 locations in 2014 (*L. acicola* confirmed at four sites), 58 locations in 2015 (zero positive records) and 70 locations in 2016 (*L. acicola* confirmed at three sites). Post 2016, sporadic observations have continued as part of regular forest monitoring, during specific research projects, and contributions from a citizen science initiative (https://www.invazivke.si Accessed 25/08/22). These have resulted in further reports from other urban areas (Čatež ob Savi, Kostanjevica na Krki, Celje, Mozirje park) and the first records from the wider environment in 2014 on *P. mugo* in Trenta in north-western Slovenia. In 2021, the pathogen was known to be present in 37 locations across Slovenia.

Prior to 2020, when it was required by EU law, all symptomatic pines were tested using molecular protocols (Ioos et al., 2010; EPPO, 2015), and those testing positive for *L. acicola* were cut and burnt. Further surveys have shown that these eradication efforts were not always successful as there have been new findings in some of these areas.

The Soča Valley study - In 2015, the Slovenian Forestry Institute discovered *L. acicola* in natural and planted forests, campsites and other

municipal areas in Soča Valley (46.17593 N, 13.73994E), an area of huge economic and ecological significance in western Slovenia. Population studies indicate *L. acicola* in the Soča Valley is distinctly different from the rest of Slovenia and might be more aggressive to the locally prevalent *P. nigra* (Sadiković et al., 2019a). A risk assessment highlighted the potential threat this posed to *P. nigra* forests throughout the rest of Slovenia and while eradication is no longer the aim, an action plan devised in 2019/20 attempts to mitigate further dissemination of these haplotypes (Jurc and Piškur, 2018; Benko-Beloglavec et al., 2019; Piškur et al., 2019a,b).

Eight areas heavily used by tourists were targeted due to their high levels of infection, an indication that humans and associated vehicles and equipment might be vectoring pathogen spores and infected needles (Fig. 4a). Leaflets (Fig. 4b) were handed out to the general public and forest owners explaining the risks posed to the local environment from this disease, and warning signs displayed at the edge of demarcated areas where measures were to be taken. Between November 2019 and April 2020 infected trees, all trees within 1 to 2 tree lengths, and any trees showing visible signs of BSNB within 100 m were felled (Zavrtanik and Kolšek, 2020). To minimise economic impacts on forest owners, transport of timber was permitted (except green wood chips). All logging residue with needles was burnt on site or transported in closed containers and burnt at an appropriate facility. All mechanization and equipment were thoroughly cleaned between sites and operations. All sites are currently under surveillance to evaluate the efficacy of these management operations, and spore traps, surveys and further sampling are underway.

This case study highlights the complexity of the operation in Slovenia and the importance of having a good communication strategy. Close collaboration was achieved between scientific institutes (the Slovenian Forestry Institute), government agencies (Phytosanitary Inspectors, the Slovenian Forest Service, the Slovenian Administration of the Republic of Slovenia for Food Safety, Veterinary and Plant Protection - NPPO), local municipal bodies, forestry and arboricultural workers, multiple private forest owners, fire brigades, legal bodies and the local communities. The awareness raising campaigns have been very successful and although eradication of the pathogen is probably not possible, huge efforts have been put in place to isolate the infection, minimise inoculum, and slow down further spread.

Case Study 2: Outbreaks in Hollenstein and Tyrole, Austria

Hollenstein/Ybbs Urban plantings:

In 1996, *L. acicola* was discovered on *P. mugo* hedging around a private property in Hollenstein/Ybbs (province of Lower Austria) (Cech, 1997; Brandstetter and Cech, 1999). From 1997 to 2000 intensive annual surveys of several hundred *Pinus* individuals were carried out in this location by Bundesforschungszentrum für Wald (BFW) researchers and community volunteers, finding 24 further infections on *P. mugo* and *P. sylvestris*. In all cases infected shrubs and trees were removed and burnt with full co operation from land owners. Less systematic surveys took place in this region from 2000 to 2008.

Hollenstein forest:

In 2008, the pathogen was detected on *P. sylvestris* a 17 ha mixed species forest near Hollenstein and all mature *P. sylvestris* were voluntarily felled and removed by the local forestry contractor (Cech and Krehan, 2008). This appears to have been a successful eradication as a follow up survey in 2016 revealed no further signs of infection.

Wider surveys:

Phytosanitary inspectors from regional authorities have conducted specific surveillance for *L. acicola* in forest stands, parks, urban areas, nurseries, and gardens, sending samples to BFW for analysis using morphological and molecular methods. Inspections have been annual in Tyrole (2014-present) but more sporadic in other areas, including Upper Austria (2010–2013), Saltzburg (2011–2020), Vorarlberg (2011 only) and Styria (2006–2017). Infections have been found on *P. sylvestris*, *P. uncinata* and *P. mugo* subsp. *mugo* (Kessler and Krehan, 2011). All *L. acicola* infected needle samples are stored in the herbarium of BFW

and entered in the database of BFW's damage diagnosis system (SDIS -https://bfw.ac.at/ws/sd.web?kat=Aandlang=1andgmp=2020).

Eradication in urban areas and public spaces has relied on felling and burning of all residues on site by the phytosanitary services or designated contractors, in accordance with the former EU plant protection legislation. At present, eradication efforts in urban areas appear to have been successful. Infections in the wider environment, in bogs/swamps and alpine protection forests have proved more difficult to control and active management plans are under development, following the Slovenian model discussed above. In 2022, the pathogen was known to be present in 18 locations (11 swamps and 7 alpine protection forests. Fig. 5).

Case Study 3: Tallinn Botanic Garden and wider environment, Estonia

Estonia, Tallinn Botanic Garden: *Lecanosticta acicola* was first recorded in Estonia in 2008 in the state-owned Tallinn Botanic Garden (59.469077 °N, 24.883476 °E) on ornamental specimens of *P. ponderosa*. Buffer zones were put in place until 2014 to restrict visitor access to the demarcated area, fungicides were applied, and approximately 20 *Pinus* trees including *P. mugo*, *P. mugo* subsp *mugo* and *P. mugo* subsp. *rotundata* were felled and burnt. Between 2011 and 2016 further specimens of these species and the closely related *P. uncinata*, *P. pumila* and *Pinus × rhaetica* (Adamson et al., 2015, 2018) were also found to be infected in the Botanic Gardens and wider environment.

All pine specimens in the gardens are currently inspected at least once per year, and samples of needles, shoots and cones (if present) collected. Between 2008 and 2013 a range of fungicide actives (chlorothalonil, propiconazole azoxystrobin and prochloraz; Kaur & Hermann, 2021) were applied every-three to four weeks throughout the growing season. This was reduced to Spring and Autumn applications of azoxystrobin, propiconazole and mancozeb from 2014, collecting and burning fallen needles under infected trees, and felling the worst affected trees. Disease intensity in the Botanic Garden has decreased since the first findings. Although the pathogen is still present, infection levels are considered stable, with no new trees infected in recent years. The control measures have also apparently succeeded in restricting this population of *L. acicola* to the Botanic Garden as these haplotypes have not been detected elsewhere in Estonia (Laas et al., 2019).

Estonia, wider environment: Between 2012 and 2015, *L. acicola* was recorded in western (Tori and Kärdla) and east-central Estonia (Vasula and Kärevere) on *P. mugo* in hedging and amenity plantings. Defoliation was severe and caused by different haplotypes to the original isolates found in the Botanic Garden (Adamson et al., 2015, Laas et al., 2019). In 2016 infection was found on young *P. sylvestris* in a mixed *P. sylvestris/ P. mugo* stand in central-eastern Estonia. Levels of infection and defoliation varied greatly between the trees. Although targeted surveys failed to find further *P. sylvestris* reports initially (Adamson et al., 2018), more recent surveillance revealed two more *P. sylvestris* sites, where infected trees were only found immediately adjacent to *P. mugo* with established infections (M. Laas Pers. Comm. 19/01/2022).

Monitoring is now carried out by specialists in a minimum of 50 permanent sampling plots encompassing non-native pines in urban greenspace and native *P. sylvestris* in forest stands (see Drenkhan and Hanso, 2009). Although owners are informed of positive findings and destruction of infected trees is recommended, in practice this is not always carried out, particularly in private gardens.

Additionally, *ca.* 50 *Pinus* samples are sent annually from nurseries to the Estonia Plant Health Laboratory and Estonian University of Life Sciences, Pathology Division where they are tested for *Dothistroma* spp. and *L. acicola* using morphological and molecular methods (Ioos et al., 2010). Plants are destroyed after any positive diagnosis of *L. acicola* in nurseries with no compensation to growers.

In summary, currently, *L. acicola* is known to be present in around 40 documented locations in Estonia predominantly on non-native pine species, and native *P. sylvestris* appears to have low susceptibility to the pathogen (Adamson et al., 2015, 2018; Laas et al., 2019, 2022).

7. Discussion

Lecanosticta acicola is just one amongst an increasing number of pests and diseases affecting Europe's forests but the EUPHRESCO Brownspotrisk project underpinning this study contributed significantly to raising the profile of this significant foliar pathogen. Data from 44 countries were compiled into the *Lecanosticta* species geo-database, and numerous scientific publications (e.g. Piškur, 2018; Sadiković et al., 2019a; Laas et al 2022; Raitelaitytė et al., 2022), national P&D updates (Steyrer et al., 2018, 2020, 2021), presentations (Cech, 2018; Sadiković et al., 2019b; Piškur et al., 2020), risk analyses, management guidelines, training events and provision of up to date advice for government ministers (Jurc and Piškur, 2018; Benko-Beloglavec et al., 2019; Piškur et al., 2019a,b) have been facilitated by the collaboration. Despite a downgrading of the quarantine status of the pathogen across much of Europe, *L. acicola* continues to be included in training for plant health inspectors in many countries, and surveillance activities in nurseries and forests are ongoing.

Currently, *Lecanosticta* species appear to be more restricted in their range than the similar *Dothistroma* species which are now found almost everywhere that susceptible hosts grow (Watt et al., 2009; Drenkhan et al., 2016a). However, over the past twenty years, *Lecanosticta* species' range has increased dramatically, with over half of the current 44 country reports received within this timeframe. This literature review combined with new records in the *Lecanosticta* geo-database have added eight countries (Belarus, Ecuador, Georgia, Jamaica, Poland, Slovakia, Turkey and Ukraine) to the global distribution of *L. acicola* reported by van der Nest et al., (2019a); molecular confirmation will be required, however, to confirm the reports from Ukraine, Ecuador (Evans and Oleas, 1983) and Jamaica (ANON, 1976 cited in Gibson, 1980), particularly where identification relied solely on foliar symptoms which could be confused with *Dothistroma* species (Drenkhan et al., 2016a).

The recent finding of *L. pharomachri* in exotic *Pinus* plantations in Colombia, and the damage caused, (Theron et al., 2022) is very concerning given the large scale planting of susceptible *Pinus* species across Colombia, Brazil, Chile and Argentina (Country Reports | Global Forest Resources Assessments | Food and Agriculture Organization of the United Nations (fao.org) Accessed 27/07/22). The forest industries in Colombia and Chile have been severely affected by DNB in the recent past (Dubin and Staley, 1966; Ahumada, 2013; Rodas et al., 2016) and considerable investment in the use of fungicides and silvicultural interventions maintains crop productivity (Bulman et al., 2016). Although regional authorities in South America have highlighted the additional threat posed by *L. acicola* (Auer et al., 2000; Auer and dos Santos, 2008),

Fig. 4a. Areas identified under the Action Plan in 2019/20 to concentrate efforts to minimise dissemination of more aggressive population of *Lecanosticta acicola* in Soča Valley in Slovenia.

surveillance efforts should be increased, and diagnostic assays updated to identify and discriminate between the full known range of *Lecanosticta* species.

To date, *Lecanosticta* species still appear to be absent from Britain, Finland, Africa, Australia, New Zealand and probably India, - all regions with substantial *Pinus* forest cover as native or exotic species (Country Reports | Global Forest Resources Assessments | Food and Agriculture Organization of the United Nations (fao.org) Accessed 27/07/22). Most of these areas have also been affected by DNB in the recent past (Drenkhan et al., 2016a) and it is especially important to maintain vigilance where forestry practitioners might assume foliar symptoms are *Dothistroma* spp. or other common foliar pathogens, rather than the early stages of a novel pathogen outbreak.

Whilst *Dothistroma* spp. have been recorded on 109 hosts (Drenkhan et al., 2016a), *L. acicola* appears to have a slightly narrower host range to date, with van der Nest et al., (2019a) listing 53, and the current study identifying 70 taxa vulnerable to *Lecanosticta* species. The collation of observations from the literature together with contemporary reports from the field has, for the first time, enabled the authors to assess the susceptibility of many of these hosts to *Lecanosticta* species, increasing our understanding of the risk posed to European forests by BSNB.

European coniferous forests are dominated by a relatively small number of conifer species. *Pinus mugo* and its subspecies are widespread across Europe from western Spain to Bulgaria and Romania (Farjon, 2010), and can be highly susceptible to *L. acicola* with heavy damage reported from locations as diverse as municipal plantings and high Alpine protection forests, although there is considerable variation in infection between individuals and regions. In more southern regions of Europe, *P. halepensis* has suffered significant mortality in some areas (Glavaš and Margaletić, 2001). However, there remains uncertainty over impacts of the pathogen on *P. nigra* (and its subspecies), *P. sylvestris* and *P. radiata*, all species of critical significance to European ecosystems and production forests, as levels of infection appear to vary across both the European continent and the United States (Skilling and Nicholls, 1974; Chandelier, 1994; Ortiz de Urbina et al., 2017; Adamson et al., 2018; Dubach et al., 2018; Sadiković et al., 2019a; Oskay et al., 2020).

Pinus sylvestris is the world's second most widespread conifer, after *Juniperus communis*, ranging from Portugal and Scotland in the west, to the Siberian taiga and Asia in the east. Extensive genetic variation arose during successive glacial periods, and many distinct varieties can be identified within this range (San-Miguel-Ayanz et al., 2016; Caudullo et al., 2017; Pyhäjärvi et al., 2020). Host genotype is likely to influence susceptibility to *L. acicola*, but as host origin and disease severity were not commonly reported in records compiled for this study, and in the historical literature, no obvious trends in BSNB severity across the host's European range could be detected. It would be interesting to establish whether the clear differences in disease severity between varieties observed in American *P. sylvestris* plantations in the 1970s (Skilling and Nicholls, 1974) manifest in the original varietal locations in France, Austria, Spain and Germany.

Pinus nigra originates from a narrower geographic range than *P. sylvestris*, and is largely restricted to Europe. Many regional varieties exist, including two particularly distinct *P. nigra* 'types' delineated by a large gap across the Adriatic Sea and the Po valley of Northern Italy (Olsson et al., 2020). There is no evidence yet to suggest these 'types' influence susceptibility to *L. acicola*, with heavy infection reported in sites as distant as Turkey and Spain. Encouraging future contributors to input more data on host provenance and disease impact into the developing geo-database, may highlight trends, allowing the development of a more robust risk assessment for European forests.

The apparent variability in susceptibility of two other hosts, *P. elliottii* and *P. palustris*, is largely the result of breeding programmes carried out during the latter part of the twentieth century in China and the USA which have significantly reduced disease impacts (Ye and Li, 1996; Enebak and Carey, 2002; Barnard and Mayfield, 2009). Similar breeding programmes are ongoing to reduce susceptibility to
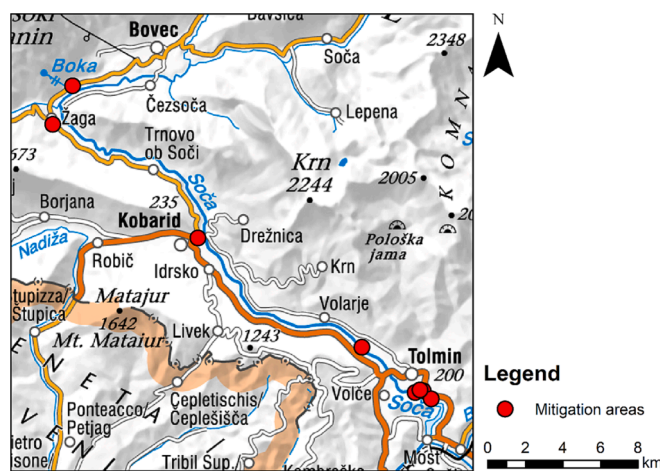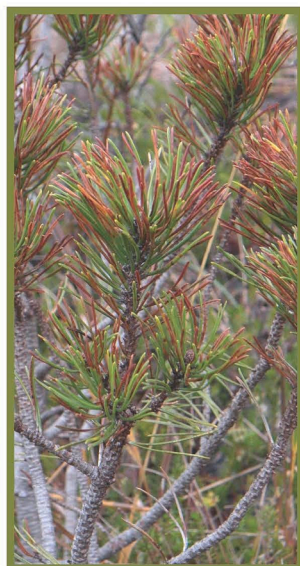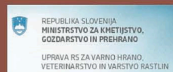
OBVESTILO OBISKOVALCEM

REPUBLIKA SLOVENIJA
MINISTRSTVO ZA KMETIJSTVO, GOZDARSTVO IN PREHRANO
UPRAVA RS ZA VARNO HRANO, VETERINARSTVO IN VARSTVO RASTLIN

ZAVOD za GOZDOVE SLOVENIJE
Slovenia Forest Service

Vstopate na območje, kjer se opravlja zatiranje karantenske bolezni borov z imenom **rjavenje borovih iglic** (*Lecanosticta acicola*). Zatiranje se vrši s posekom okuženih dreves in sežigom vej, vrhačev in iglic.

Ukrep se izvaja z namenom preprečevanja širjenja bolezni, ki je v Evropi omejeno razširjena in bi njeno nadaljnje širjenje lahko povzročilo velike gospodarske in okoljske škode v gozdovih.

PRIPOROČILA OBISKOVALCEM:
- Ne odnašajte vej z iglicami borov, sečnih ostankov ali iglic iz območja zatiranja bolezni.
- Odstranite iglice borov iz prevoznih sredstev preden zapuščate območje zatiranja bolezni.
- Očistite (operite) obutev ali opremo preden odpotujete domov.
- Upoštevajte navodila gozdarjev in izvajalcev sečnje in zatiranja glede gibanja po sečišču.
- Pazite na varnost vas in drugih obiskovalcev.

NOTICE TO VISITORS

You are entering the area where control of **brown spot needle blight** (*Lecanosticta acicola*) is performed (quarantine pest on pine trees). Pest control is carried out by removing infected trees and burning branches and treetops with needles.

The measure is implemented to prevent the spread of this pine disease, which is not widespread in Europe. Further spread of this disease could lead to major economic losses and ecological damage in forests.

Recommendations to visitors:
- Do not take pine branches with needles, cutting residues or pine needles from the disease control area.
- Clean (wash) your shoes or equipment before travelling home.
- Remove pine needles from your vehicle before leaving the area, where the disease is present.
- Follow the instructions of the foresters on how to move around the work area.
- Pay attention to your safety and the safety of other visitors.

AVVISO AI VISITATORI

State entrando nell'area dove si sta svolgendo un intervento contro l'organismo da quarantena che causa **l'ingiallimento a bande degli aghi di pino** (*Lecanosticta acicola*). L'intervento si svolge tramite il taglio delle piante infette e l'abbruciamento della ramaglia, dei cimali e degli aghi.

L'intervento si svolge allo scopo di prevenire l'espansione della malattia, che è limitatamente diffusa in Europa, ma una sua ulteriore diffusione potrebbe causare enormi danni economici e ambientali nelle foreste.

Raccomandazioni per i visitatori:
- Non asportare i rami con gli aghi dei pini, resti di taglio oppure aghi dall'area trattata
- Eliminare gli aghi dei pini dagli automezzi prima di abbandonare l'area oggetto di intervento.
- Pulire (lavare) le scarpe e zaini prima di ripartire verso casa.
- Rispettare le istruzioni dei forestali e degli operatori addetti al taglio e all'intervento per il passaggio nell'area di taglio.
- Fare attenzione alla sicurezza personale e degli altri visitatori.

Dodatne informacije lahko najdete na:

www.gozdis.si   *www.zgs.si*   *www.zdravgozd.si*   *www.gov.si*

Fig. 4b. Warning signs displayed at the edge of demarcated areas where measures were to be taken.

Fig. 5. Alpine protection forest of *P. uncinata* infested with BSNB. Isar Valley, Austria, Summer 2022 (photo by Thomas Cech, BFW).

Dothistroma species whilst maintaining timber productivity in New Zealand (*P. radiata* - Fraser et al., 2016) and more recently Britain (*P. sylvestris* - Burton et al., 2022). Given the expanding range and relevance of BSNB, silviculturalists might consider developing BSNB resistance of *Pinus* species grown in Europe through traditional phenotypic selection, or genetic engineering. Both methods would, however, require significant investment of time and resources, and where the value of the forest resides partly in its composition of native species or local provenances, any form of genetic manipulation of the hosts might face significant barriers.

While variation in host susceptibility will influence the impacts of BSNB on European forest ecosystems, genetic diversity within the pathogen itself is also likely to affect the vulnerability of Europe's forests. *Lecanostica acicola* is remarkably varied across Europe despite its relatively recent introduction. Multiple introduction events have resulted in both mating types of *L. acicola* being present (Janoušek et al., 2016; Mesanaza et al., 2021a) and numerous distinct populations exist (Laas et al., 2022; Sadiković et al., 2019a). Ongoing sexual recombination will facilitate dissemination as ascospores are largely wind dispersed. Extensive mixing within and between *L. acicola* populations also risks creating more virulent phenotypes, potentially facilitating adaptation to the varied European geography, climate and forest types (Janoušek et al., 2016; Mesanaza et al., 2021a). North American studies have identified inter- and intra-population variation in aggressiveness in northern and southern lineages (Phelps et al., 1978; Huang et al., 1995). Further laboratory and field-based studies will be needed to assess the

extent of variation between European populations (Sadiković et al., 2019a).

Although only *L. acicola* is currently known to be present in Europe, surveillance efforts may yet discover known or novel *Lecanosticta* cryptospecies, giving rise to further concerns. Interspecific hybridisation may not be common event but can have devastating impacts; riverine habitats across Europe were devasted following the hybridization of *Phytophthora* species in Central European forest nurseries, creating the aggressive heteroploid *Phytophthora alni* species complex, affecting *Alnus* spp. (Husson et al., 2015). Little is known about the existence of reproductive barriers within or between *Lecanosticta* species but to date there is no evidence for breeding or hybridisation between the northern and southern lineages which are known to co-occur in France (see Laas et al. 2022), or the different species present in Central America. Mixing of species or subspecies could however, facilitate accelerated evolution through genetic exchange.

Climate and climate change have significant, direct effects on both pathogen and host behaviour. (Anderegg, Kane, and Anderegg, 2013; Ray et al., 2010). Drought events and high temperatures have caused mass mortality of *Pinus* and other spp. since the early 2000s (Allen et al., 2010). Increased tree stress influences susceptibility to pathogens (Kliejunas et al., 2009) including *Lecanosticta* species, meaning that climate change is likely to change forest structure and species composition across Europe in the coming decades (Morin et al., 2018). In many European countries forestry policies encourage or require planting of indigenous species, and some areas, such as the Alpine 'protection

forests' stabilising steep slopes and protecting watersheds, are reliant on certain species silviculturally suited to the extreme conditions. Forestry policies are evolving within these constraints, with incentives to move towards mixed species forests, investigation of local provenances (Haufe et al., 2021; Taeger et al., 2013), and investment in genetic improvement programmes to increase resilience to climate change (Huber, 2011). In other regions, 'near- native' or 'new and emerging' species may be considered where forest condition is threatened by changing climate. Although some *Pinus* species listed in Table 1 are not currently common components of European forests, this might change. Consequently this review attempted to determine their susceptibility wherever possible. For species with unknown susceptibility to *Lecanosticta* species, artificial inoculation trials are ongoing, with results expected within the next few years.

The direct impact climate change could have on *L. acicola* itself, is the focus of a separate study supported by the Euphresco partnership (Ogris et al., in prep.), but preliminary results suggest that *L. acicola* could affect over 60 % of *Pinus* species area by the end of the 21st century globally. Climate change has resulted in an overall poleward shift of many fungal crop pathogens (Bebber et al., 2013) and has increased the incidence and severity of DNB in parts of the northern hemisphere (Woods et al., 2016), with recent, unprecedented levels of damage on *P. cembra* and *P. mugo* at high altitudes in the Eastern Alps (Ghelardini et al., 2020). Similarly, impacts of BSNB have increased in North America (Kais and Peterson, 1986; Broders et al., 2015; Wyka et al., 2017), and changes in climate across Europe are influencing the range of *L. acicola* with increases in temperature and spring and summer precipitation likely to have caused recent upsurges in disease in alpine forests in Austria, for example (Cech Pers. Comm., 2022). Climate change predictions suggest *L. acicola* may be able to progress further into Fennoscandia and Siberia, and it is possible that Europe may still be in the early stages of a BSNB epidemic, which will become increasingly severe in the next few decades. However, increasing temperatures and decreasing precipitation in more southern regions of the continent may decrease the rate of disease spread. In North America, the impacts of BSNB have already been increasing in northern States and Canada in the past 20 years (Broders et al., 2015; Wyka and Broders, 2016), and the pathogen may be able to progress further north and west. The ongoing modelling study hopes to explore these issues.

As well as demonstrating how far BSNB has spread across Europe in recent decades and increasing our understanding of the susceptibility of Europe's key forest species, this study has also illustrated how inconsistently the disease has been managed to date. The focus in Europe has been on surveillance and eradication, which in cases where infection loci were small and easily defined has been successful (Cech, 1997). However, if the ongoing collaborative effort in Slovenia's Soča Valley fails (Jurc and Piškur, 2018; Benko-Beloglavec et al., 2019; Piškur et al., 2019a,b), and where the pathogen has escaped eradication efforts in, for example, Bulgaria (Georgieva, 2020) and Lithuania (Markovskaja et al., 2011), the emphasis will have to switch to disease management. The downgrading in regulatory status is also likely to result in further outbreaks across Europe, despite concerted efforts by national teams. This study drew together a range of management options which have been used globally to tackle BSNB, drawing especially on the long history of BSNB management in the USA. Some North American methods are very specific to host species not likely to be planted in Europe. Other, more generic methods will vary in acceptability across Europe, but an immediate priority must be to test them under European conditions. Practitioners should also be encouraged to record their actions, successful and otherwise, in the geo-database to enable researchers, surveillance teams and forest managers to benefit from others' experiences. Without a coherent strategy for surveillance or management there is a danger that the pathogen will spread unchecked across vast interconnected pine forests.

Europe's forests support a huge diversity of life, andare critical to achieving climate neutrality objectives (e.g. The United Nations Sustainable Development Goal 15 | Department of Economic and Social Affairs (un.org); EU biodiversity strategy for 2030); New EU Forest Strategy | Legislative train schedule | European Parliament (europa.eu) all accessed 22/07/22). However, globalization and trade have facilitated the emergence of new pest and pathogen threats in our forests (Wingfield et al., (2015). There is a need for a collective effort to continue forest surveillance and monitor the movement of *Lecanosticta* species and many other pests and pathogens across Europe's relatively open borders. Programmes such as the BROWNSPOTRISK Euphresco partnership and the highly successful EU COST Action FP1102 DIAROD (Determining Invasiveness and Risk of Dothistroma; Bulman et al., 2016; Drenkhan et al., 2016) play a significant role in facilitating such collaboration. Countries cannot fully exclude pests by their individual efforts. The networks forged through the BROWNSPOTRISK project have helped raise the profile of this pathogen, fuelling efforts to develop new diagnostic protocols and explore effective management strategies.

8. Conclusions

The current distribution of *L. acicola* strongly suggests it has the capacity to adapt to a wide range of conditions across Europe. It affects 30 taxa, planted in Europe, 70 taxa globally, the majority *Pinus* species, and, together with *Dothistroma* species, *L. acicola* has the potential for landscape scale impacts on European forests. *Lecanosticta acicola* has been recorded in 24 European countries and its further dissemination to new naïve locations will depend to a large extent on the movement of infected *Pinus* planting stock. Whether the plants for planting 'pathway' will be facilitated by the recent downgrading of *L. acicola* from an A1 quarantine organism to a RNQP is not yet clear.

Ongoing modelling efforts will investigate the impacts of climate change on future distribution of the pathogen, but early indications suggest a potential expansion in range of *L. acicola*, particularly within Europe, into the latter part of this century.

To date, *Lecanosticta* species other than *L. acicola* have only been found in southern North America, Central America and the northeastern tip of South America, and all so far have been found on *Pinus* species native to these regions. However, there is an urgent need for revised molecular diagnostic assays with the capacity to detect and discriminate between the known *Lecanosticta* species and potentially, additional cryptospecies.

Although this study has highlighted the extensive range, and genetic diversity within *L. acicola* in Europe, there is an urgent need for further studies into the behaviour of *L. acicola* and the other *Lecanosticta* species. The economic impacts of BSNB have received little study in European forest, to date and even less attention has been paid to the potentially devastating impacts on vulnerable natural ecosystems such as the *P. mugo*-dominated 'protection' forests in Europe's mountain ranges, with their vital role in land stabilisation. Whilst this study outlines an extensive review of management options, decisions to intervene and actively manage the disease in Europe's forests will be dictated by its economic, socio-economic, ecological, and environmental impacts.

Data availability

The Geo-database maps are open access at: https://www.portaloff orestpathology.com).

CRediT authorship contribution statement

K. Tubby: Conceptualization, Investigation, Writing – original draft, Writing – review & editing, Supervision, Resources. **K. Adamcikova:** Resources, Writing – review & editing. **K. Adamson:** Resources, Writing – review & editing. **M. Akiba:** Resources, Writing – review & editing. **I. Barnes:** Resources, Writing – review & editing. **P. Boroń:** Resources, Writing – review & editing. **H. Bragança:** Resources, Writing – review & editing. **T. Bulgakov:** Resources, Writing – review & editing. **N.

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.

Data availability

a geo-database containing extensive surveillance data is open access available at http://www.portalofforestpathology.com

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.foreco.2023.120847.

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Further reading

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