Forest loss as a consequence of invasive pathogens and their interactions with climate change



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Abstract

The global forests are increasingly threatened by invasive tree pests and pathogens, and this trend is amplified by accelerating global trade and ongoing climate change. Although these biotic disturbances cause widespread tree decline, mortality, and degradation of forest ecosystem functions, their geographic distributions, climate-driven range dynamics, and consequences for forest carbon sequestration remain poorly understood and systematically underestimated. This doctoral thesis aims to address critical knowledge gaps by integrating machine learning text mining, systematic literature synthesis, species distribution modelling, remote sensing, and epidemiological–ecosystem coupling modelling to investigate three research questions: the global distribution of tree pest and pathogen research and disturbance impacts; how climate change reshapes the future geographic ranges of tree pests and pathogens; and the magnitude and mechanisms by which pest and pathogen outbreaks suppress forest carbon uptake.

This thesis begins with a literature review of the ecology of tree pests and pathogens, their life cycles, physiological interactions with host trees, and existing limitations in current monitoring, data availability, and carbon impact assessment frameworks. Then it goes to methodological aspect, introducing the main methods that are used in this thesis–integrated systematic review with natural language processing (NLP), geographic information system (GIS), species distribution modelling, remote sensing, and ecosystem modelling.

Chapter 4, the first research chapter, develops a machine-learning text-mining framework to automate large-scale synthesis of heterogeneous ecological literature. The aim of this chapter is to analyse the geographic distribution of tree pest and pathogen studies, as well as the distributions of the ecological impacts of tree pests and pathogens. A trained Naive Bayes classifier achieves extremely low false positive and negative rates, efficiently identifying survey papers that have field records, reducing manual screening labour by 87% across 16,355 publications. This research synthesises 12,933 georeferenced field records covering 160 host species and 53 priority pests and pathogens, revealing strong spatial, temporal, and taxonomic research biases concentrated in the Global North, with distinct continental patterns of infection and mortality. An open-access interactive web platform is developed to share the compiled dataset and support transparent forest health monitoring.

Chapter 5 models the geographic range shifts of 31 invasive tree pests and pathogens under multiple CMIP6 climate and Shared Socio-economic Pathway (SSP) scenarios. The results demonstrate a consistent northward range shift toward northern temperate and boreal forests between 2041 and 2080. Warming temperature is the primary driver of habitat suitability change, while precipitation regimes further regulate establishment and spread. High-emission scenarios substantially amplify

northward expansion, whereas southern European and other warming regions face declining pest and pathogen suitability. This cross-species consensus highlights rising biotic disturbance risks in carbon-rich boreal and temperate forests.

Chapter 6 integrates epidemiological modelling with a forest carbon cycle model to quantify ash dieback-driven carbon loss, contrasting conventional biomass-based estimates with dynamic net primary productivity (NPP) reduction estimates. Disease-induced NPP reduction is found to be substantially overlooked by traditional biomass-based carbon accounting, with an average 39.3% underestimation of total reduction in carbon sequestration potential across affected regions. Nonlinear carbon loss is driven by pathogen spread rate, as well as long-distance trade-mediated dispersal Neglected physiological suppression and prolonged post-disturbance recovery further enlarge the carbon sink deficit, indicating that pest and pathogen impacts should be more carefully incorporated into global carbon budget assessments. Though the results are confined to ash dieback disease, there are numerous damaging tree epidemics across the globe, and the subsequent changes in forest carbon sequestration potential could be substantial.

The thesis concludes that invasive tree pests and pathogens represent an underappreciated global forest disturbance driver with profound implications for biodiversity conservation, biosecurity, and climate mitigation. It provides novel methodological tools, synthesised global datasets, and generalisable ecological patterns, and delivers actionable management recommendations including enhanced cross-border biosecurity, systematic long-term monitoring, increased tree diversity, and the integration of pest and pathogen disturbances into forest resource assessment and global carbon modelling frameworks.

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1. Introduction: Tree Pests and Pathogens

Tree pests and pathogens are natural components of forest ecosystems. They contribute to natural selection, enhance species diversity by removing weakened individuals, and create ecological space for regeneration and succession (Dajoz 1998). However, accelerating international trade and transportation, combined with climate change, have significantly increased the introduction and establishment of invasive pests and pathogens in new regions (Ramsfield et al. 2016). These invasive pests and pathogens have caused widespread tree decline and mortality, in some cases fundamentally reshaping woodland landscapes (Urquhart et al. 2017). Many affected host species—including oak, apple, and poplar—are of substantial ecological and economic importance (Bebber et al. 2025). As a result, pest and pathogen disturbances are now recognised as major threats to global forest health. They have become a growing concern not only for governments, non-governmental organisations, and the scientific community, but also for the media and the broader public (Urquhart et al. 2017; Williams et al. 2023). However, pests and pathogens remain among the least understood types of forest disturbance due to their low detectability via satellite remote sensing, their complex biology, and their often latent effects. This thesis centres on tree pests and pathogens, aiming to improve understanding of their distributions, ecological dynamics, and functional impacts on forest ecosystems.

1.1 Thesis Outline

The scope of this thesis encompasses tree pests and pathogens, including invertebrate pests, as well as pathogens that are primarily fungal, with a small number of bacterial and oomycete agents. It quantifies research efforts, models climatic suitability, and assesses changes in carbon flux associated with tree pests and pathogens. The thesis does not directly account for the amount of forest loss attributable to pest and pathogen disturbances. Instead, it examines their ecological consequences, including patterns of disease severity, tree mortality, changes in the geographic distribution of pest and pathogen disturbances under climate change, and reductions in forest carbon sequestration potential.

The structure of this thesis is as follows. Chapter 1 defines the scope of the study—focusing on tree pests and pathogens—and outlines the significance of this research field. It then presents three research questions that reflect key gaps in current pest and pathogen research (see Section 1.6. Key Questions). These questions will be addressed in three research chapters (i.e. Chapters 4, 5, and 6) in this thesis, respectively.

Chapters 2 and 3 are literature review and methodology chapters, aiming to point out the existing

theory, map the current state of knowledge, identify research gaps, and finally justify the academic research in the thesis. Chapter 2 describes the ecology of tree pests and pathogens, reviews the current knowledge on how climate change affects pest and pathogen distributions, and explains how pests and pathogens influence forest carbon cycling through affecting host tree physiology. It then critically points out the key knowledge shortfalls within pest and pathogen studies: a data deficiency in the epidemiology of tree pest and pathogen outbreaks, a lack of comparative studies across multiple tree pests and pathogens on their interactions with the changing climate, and an inadequate methodology to accurately account the impact of tree pests and pathogens on reduced forest carbon sequestration potential. These knowledge shortfalls are essential, as Chapter 4–6 aim to address these gaps.

Chapters 4–6 are research chapters, each addressing one of the research questions proposed in Section 1.6. Each chapter is formatted as a peer-reviewed journal article and prepared for submission for publication. Chapter 4 addresses the question: What is the distribution of current research efforts on tree pests and pathogens? It synthesises epidemiological data of tree pest and pathogen outbreaks across the globe, covering 160 host species and 53 pest or pathogen agents. Then it analyses the spatial and temporal patterns of reported disease severity and tree mortality, identify the geographic research bias, and discusses the implications for global pest and pathogen research. As part of this research, an interactive web-based platform—the Tree Pests and Diseases Explorer (https://zjuhaoranwu.shinyapps.io/forestpestexplorer/)—was developed to provide open access to the compiled dataset and to offer tools for visualising epidemiological patterns. Chapter 5 addresses the question: how would climate change affect the geographic distribution of tree pests and pathogens in the future? It models the distribution of 31 pests and pathogens based on species distribution models (SDMs), and predicts their future ranges under different scenarios. Chapter 6 examines how a representative pathogen outbreak impacts on forest carbon sequestration potential, thus providing implications for global forest carbon budget accounting and international climate assessments. It models the reduction of forest carbon sequestration using a combination of an epidemiological model and an carbon cycling model. The model is parameterised using tree mortality outputs from Chapter 4 and pathogen distribution outputs from Chapter 5.

Finally, Chapter 7 concludes the thesis by summarising the main findings from the three research chapters. It discusses the implications for global forest management, biosecurity measures, and forest resource assessment. The closing section, Section 7.4, reflects on the lessons that tree pests and pathogens offer for ecosystem management. It calls for a need to recognise pest and pathogen outbreaks as an inherent component of forests. Improving tree diversity, promoting resistant genotypes, strengthening disease monitoring, enhancing early detection, fostering transboundary collaboration, and implementing stricter biosecurity measures should be integral components of forest management.

1.2 List of Terms

Prior to outlining the history and background of tree pests and pathogens, several key terms essential to defining the research scope are introduced below. These terms are used consistently throughout the thesis.

- **Aboveground biomass (AGB):** The total mass of living plant material above the soil surface, including stems, branches, and leaves, typically measured as dry weight per unit ground area. Researchers often assume a fixed proportion of total biomass to be carbon when estimating forest carbon storage.
- **Below ground biomass (BGB):** The total mass of living plant material below the soil surface, primarily roots. Together with AGB, it constitutes total biomass. BGB is more difficult to measure directly and is sometimes estimated from AGB using root-to-shoot ratios.
- **Bioclimatic variable:** Climate-derived variables based on monthly temperature and precipitation data that are biologically meaningful. Examples include maximum temperature of warmest month, precipitation of driest month, and annual precipitation.
- **Carbon stock:** The quantity of carbon stored within a specific pool, such as vegetation, soil, the ocean, or the atmosphere.
- **Ecosystem services:** The benefits humans derive from ecosystems, including clean air and water, food, flood and climate regulation, soil protection, recreation, and timber production.
- **Emerging infectious disease:** A disease recently detected in a population, caused by invertebrate pests or fungal, bacterial, or viral pathogens. It is characterised by a rapid increase in incidence, geographic range, or severity.
- **General Circulation Models (GCMs):** Complex computer models that simulate interactions among Earth's atmosphere, oceans, and land surface to project climate behaviour over long timescales.
- **Invasive species:** Non-native species that establish, spread, and cause harm to native ecosystems. Many destructive tree pests and pathogens are invasive species.
- **Gross primary productivity (GPP):** The rate at which photosynthetic organisms, typically plants, produce new biomass in an ecosystem over a period.
- Net ecosystem production (NEP): the rate at which organic carbon is captured by photosynthetic organisms, subtracted by total ecosystem respiration that stems from plants, animals, and microbes.
- **Net primary productivity (NPP):** The rate at which photosynthetic organisms capture and store as biomass after accounting for the energy they use for respiration.

- **Pathogen:** A microorganism—ranging from fungi, oomycetes, bacteria to virus—that causes disease in trees.
- **Pest:** In this thesis, it refers specifically to invertebrates that damage trees. Examples include defoliators (which consume leaves), borers (which tunnel into plant tissues), sap-sucking insects (which feed on plant fluids using specialised mouthparts), and gall-makers (which cause abnormal plant tissue growth by injecting chemicals or laying eggs).
- **Presence-only data:** Records that indicate where a species has been observed, without information on locations where it was searched for but not found. This data is used as input for species distribution modelling in Chapter 5.
- **Range shift:** A change in the geographic distribution of a species over time, often in response to climate or habitat changes.
- **Shared Socio-economic Pathways (SSPs):** Scenarios developed to describe potential future global developments—such as fossil fuel use, economic trends, and population growth—used to simulate future climate conditions.
- **Spatial resolution:** The size of the smallest unit (pixel) in a satellite image or other spatial dataset or map.
- **Species distribution modelling (SDM):** A modelling technique that quantifies the relationship between species occurrence data and environmental variables, and uses this relationship to predict potential distributions under current and future climate conditions.
- **Systematic review:** A rigorous and transparent literature review method that identifies, evaluates, and synthesises all relevant studies on a specific question using repeatable and well-documented procedures.

In addition, the thesis uses ‘tree pests and pathogens’ and ‘forest pests and pathogens’ interchangeably, as the thesis specifically focuses on the impact of pests and pathogens on forest ecosystems, rather than trees on urban, rural areas, savanna, and other ecosystems.

1.3 History

One of the earliest recorded tree epidemics is Dutch elm disease, a fungal vascular wilt affecting elm species (*Ulmus* spp.) (Karnosky 1979). The initial outbreak, caused by the fungus *Ophiostoma ulmi* (Buisman) Nannf., began in northwestern Europe around 1910 (Bernier 2022). The disease was named after a team of Dutch pathologists who first investigated it in the 1920s. According to the United Kingdom's Forest Research, this epidemic resulted in the death of between 10% and 40% of elms across various European countries before subsiding in the 1940s. In the 1930s, *O. ulmi* was

accidentally introduced from Europe to the United States, where it had devastating effects on the American elm (*Ulmus americana* L.) and related species in urban and riparian environments (Marcotrigiano 2016). In the late 1960s, a more aggressive strain, *Ophiostoma novo-ulmi* Brasier, was introduced to Britain from North America, leading to a second, far more destructive epidemic that caused widespread elm mortality in both regions (Harwood et al. 2010). Today, Dutch elm disease continues to threaten elm populations across Europe and North America, although numerous tree breeding programs have been established to enhance resistance and mitigate the long-term impacts of the disease (Sniezko and Nelson 2022).

Chestnut blight is another textbook example of an invasive tree disease, caused by the pathogen *Cryphonectria parasitica* (Murrill) M.E. Barr, which infects the American chestnut [*Castanea dentata* (Marsh.) Borkh.]. The disease was first reported in 1904 at the Zoological Park in New York City (Rigling and Prospero, 2017). Native to East Asia, the pathogen was accidentally introduced to North America through infected chestnut plants (Rigling and Prospero 2017). The subsequent outbreak killed an estimated four billion American chestnut trees during the first half of the twentieth century and is regarded as one of the most severe ecological disasters in U.S. history, resulting in the functional extinction of the species in the southern Appalachians (Wood 2024). The loss of the American chestnut—which had provided food for both people and livestock and served as a barterable commodity for goods and credit in local stores—was devastating to regional economies (Wood 2024). Numerous research programs have since been launched to breed blight-resistant chestnut trees for forest restoration (Burnham et al. 1986). However, chestnut blight remains highly destructive to the American chestnut and has also been reported to affect the European chestnut (*Castanea sativa* Mill.) across continental Europe.

During the 20th century, invasions of tree pests and pathogens increased exponentially (Santini et al. 2012; Boyd et al. 2013; Brockerhoff and Liebhold 2017; Ghelardini et al. 2017; Spence et al. 2019). In the United States, the cumulative number of non-native forest pest invasions rose from approximately 80 in 1900 to 250 in 1950 and to nearly 350 by 2000 (Brockerhoff and Liebhold 2017). In Europe, the number increased from about 60 in 1900 to 125 in 1950, reaching around 300 by 2000 (Brockerhoff and Liebhold 2017). Similarly, in the United Kingdom, around 25 major tree pests became established between 1900 and 2000, according to the Department for Environment, Food & Rural Affairs (Defra) (Spence et al. 2019). For pathogens, the total number of invasive forest species in Europe doubled over the same period (Santini et al. 2012).

Several destructive pests and pathogens emerged during this century, particularly in the United States. In 1923, *Phytophthora lateralis* Tucker & Milbrath was first reported in Washington State before spreading to British Columbia in the 1950s and northwestern California by 1980 ("*Phytophthora lateralis*", 2009). In 1940, the first specimen of the Fall webworm (*Hyphantria cunea* Drury) was captured in Hungary ("The Fall Webworm of North America in Europe" 1948). Native to North

America, this moth was introduced to Europe and East Asia, where it causes severe defoliation in pecan and fruit tree orchards (Schowalter and Ring 2017). Shortly afterward, in 1942, *Bretziella fagacearum* (Bretz) Z.W. de Beer, Marinc., T.A. Duong & M.J. Wingf., the causal agent of oak wilt, was reported in the United States (Henry, 1944). The ensuing epidemic killed millions of oaks and tanoaks, substantially altering forest composition and successional dynamics (Frankel et al. 2022). In 1946, pine pitch canker (*Fusarium circinatum* Nirenberg & O'Donnell) was first detected in North Carolina, affecting several pine species; the disease did not spread widely until the 1970s (Sanchez-Lucas 2022). During the 1950s and 1960s, extensive monoculture plantations of Monterey pine (*Pinus radiata* D. Don) in the Southern Hemisphere were severely affected by Dothistroma needle blight, caused by *Dothistroma septosporum* (Dorogin) M. Morelet (Barnes et al. 2022). In the Northern Hemisphere (including Canada, France, Hungary, and the United Kingdom), *D. septosporum*—together with *Dothistroma pini* Hulbary—caused increasing disease severity and mortality in pine plantations (Barnes et al. 2022). In 1951, the hemlock woolly adelgid (*Adelges tsugae* Annand), native to Japan, was first recorded in the eastern United States, where it caused widespread mortality of eastern hemlock (*Tsuga canadensis* [L.] Carrière) (McCarty and Addesso 2019). Later, in 1967, butternut canker (*Ophiognomonia clavigignenti-juglandacearum* Nair, Kostichka, and Kuntz) was reported in North America, leading to declines in butternut (*Juglans cinerea* L.) by as much as 70–90% in some regions (Broders and Boland 2011).

During the 1990s, the most well-known examples of fatal pests and pathogens emerged, many of which continue to cause substantial ecological and economic damage today. One of the most well-known epidemics is ash dieback, a severe fungal disease of the common ash (*Fraxinus excelsior* L.) caused by *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya (Carroll and Boa 2024). First identified in Poland in 1992, ash dieback spread rapidly across much of Europe before the pathogen was formally isolated in 2006 (Kowalski 2006). In the United Kingdom, the disease was first confirmed in 2012, although DNA evidence suggests that *H. fraxineus* had already colonised cankers on trees that died as early as 2004–2005 (Wylder et al. 2018). The common ash is both economically and ecologically significant: it provides high-quality timber for furniture and sporting equipment (Dobrowolska et al. 2011) and supports a variety of associated species, offering essential habitat and food resources (Hultberg et al. 2020). Consequently, the decline of ash populations poses a serious threat to forestry and biodiversity across the UK and Europe. The economic cost of ash dieback in the UK alone is projected to reach £15 billion over the next century (Hill et al. 2019). For safety reasons, weakened ash trees located near roads and public areas must often be felled, as the disease causes branches to become brittle and prone to falling. In addition, restrictions on the movement of ash material have caused significant economic disruption, leading to a near-total collapse of the ash timber market (Carroll and Boa 2024).

Around the same time, a highly destructive pest, the Asian longhorned beetle (*Anoplophora*

glabripennis), was discovered in warehouses and ports in North America in 1992 (Haack et al. 2010) and later in Europe in 2001 (Javel et al. 2017). Native to China and Korea (Lingafelter and Hoebeke 2002), the beetle's range expansion within Asia has been linked to large-scale afforestation and reforestation programs in China that began in the 1960s (Haack et al. 2010). The rapid increase in international trade from Asia since the early 1980s likely facilitated its global spread, as the beetle's larvae can remain concealed within untreated solid wood packing materials (Javel et al. 2017). Since its initial detection, *A. glabripennis* has spread to multiple U.S. states and several European countries, causing extensive tree mortality and resulting in economic losses estimated at hundreds of billions of dollars in the United States alone (Hu et al. 2009). Over the past twelve years, more than 45% of eradication programs targeting the beetle have been successful; however, it remains a persistent biosecurity threat, continuing to be intercepted at international borders (Branco et al. 2021).

In the mid-1990s, the sudden oak death (SOD) pathogen *Phytophthora ramorum* emerged simultaneously in North American and European forests (Grünwald et al. 2019). In central California, the pathogen quickly reached epidemic levels, killing tens of thousands of trees (Rizzo and Garbelotto 2003). In Oregon, repeated outbreaks have severely affected oak and tanoak populations, with control efforts costing over US$32 million during the past two decades (LeBoldus et al. 2022).

Since 2000, the number of new reports on emerging tree diseases has been doubling approximately every 11 years (Gougherty 2023). In the UK, for instance, the number of major tree pest introductions nearly doubled between 2000 and 2015 (Spence et al. 2019). Among these new pests and pathogens, the emerald ash borer (*Agrilus planipennis* Fairmaire) stands out as particularly destructive. Native to East Asia, it was first detected in the United States and Canada in 2002 (Haack et al. 2002), although dendrochronological evidence suggests that the species may have already been established in Michigan during the early to mid-1990s (Siegert et al. 2009). The pest was later discovered near Moscow in 2003 and officially reported in Russia in 2005 (Izhevskii and Mozolevskaya 2010). *A. planipennis* causes extensive damage and mortality in ash trees (Haack et al. 2015). Because both the emerald ash borer and the ash dieback fungus cause severe damage to ash populations, researchers are now investigating potential cross-resistance traits that could provide defense against both threats (Gossner et al. 2023).

1.4 Response from Society

In response to the growing need to control pests and protect forest health, numerous national and international regulations, integrated pest management strategies, media campaigns, and NGO initiatives have emerged. In the United States, several key legislative measures have been introduced to limit the import of non-indigenous plant-feeding pests and pathogens, beginning with the Plant Quarantine Act (1912), followed by the Organic Act (1944), the International Plant Protection

Convention (1952), the Federal Plant Pest Act (1957), the National Environmental Policy Act (1970), and the Plant Protection Act (2000) (Aukema et al. 2010). In Canada, legislation concerning tree pests and pathogens is primarily governed by the Plant Protection Act (1990), administered by the Canadian Food Inspection Agency (CFIA).

In the UK, the Plant Health Act (1967) was the first legislation requiring local authorities to prevent the introduction and spread of forestry pests and pathogens. The Dutch Elm Disease (Local Authorities) Order (1984) granted specific powers to local authorities to take measures against the spread of Dutch elm disease, including killing the infected trees. These were followed by subsequent regulations, including the Plant Health (Forestry) Order (2005), the Plant Health (Fees) (Forestry) (England and Scotland) Regulations (2015), and the Plant Health (Fees) (Forestry) (Wales) Regulations (2019).

In China, the Forest Law of the People's Republic of China (Standing Committee of the National People's Congress, 1998), the Regulations on the Prevention and Control of Forest Plant Diseases and Insect Pests (State Council, 1989), and the Regulation on Plant Quarantine (State Council, 1992) provide the fundamental legal framework for integrated pest management. These have been supplemented by a series of related regulations introduced after 2000, including those governing pesticide use (Ji et al. 2011). In Japan, the State's responsibility for preventing the spread of forest pests and pathogens is defined under the Forest and Forestry Basic Act, and the Forest Pest Control Act specifies concrete measures for the early detection and eradication of forest pests.

The international framework for plant health regulation was initiated in 1952 with the establishment of the International Plant Protection Convention (IPPC), aimed at harmonising phytosanitary measures among countries. Modern plant health regulation operates primarily under the Sanitary and Phytosanitary (SPS) Agreement of the World Trade Organization (WTO). However, these rules are often criticised as being largely ineffective for environmental protection, as their primary objective is to facilitate international trade rather than safeguard ecosystems (Roy et al. 2014). Furthermore, the associated legislation requires that a pest be formally identified and named before regulatory action can be taken (Roy et al. 2014), whereas in practice, pest and pathogen agents frequently become widespread before they are officially recognised in a given region (e.g. Wylder et al. (2018)). Within the European Union (EU), tree pest and pathogen regulations began with Council Directive 77/93/EEC (1977), which established protective measures against the introduction of harmful organisms affecting plants and plant products. This framework was later updated through Council Directive 2000/29/EC (2000) and subsequently replaced by the more proactive Regulation (EU) 2016/2031, which emphasises risk-based approaches, such as the implementation of plant passports and phytosanitary certificates.

Media coverage of tree pests and diseases plays a crucial role in raising public awareness, positioning

tree health as a major societal issue that requires coordinated responses from national governments, local authorities, woodland owners, wood traders, and citizens (Marzano et al. 2015). In the UK, the 2012 emergence of ash dieback fungus triggered a surge in newspaper reports describing the devastation caused by the disease. These media posts call on the government to ban ash tree imports (Tomlinson 2015). However, many of these reports were criticised for presenting inaccurate statistics and exaggerating the potential risks, such as claims that 90% of ash trees in Denmark had been killed and that ash comprised 30% of the UK's wooded landscape—figures that were considerably higher than reality (Tomlinson 2015). Despite these inaccuracies, the ash dieback outbreak became a viral public topic, prompting a broad governmental response and elevating the issue of invasive pests and pathogens to a high priority within the Department for Environment, Food and Rural Affairs (DEFRA) (Woodward and Boa 2013). The British public generally expresses concern about forest health and shows a moderate willingness to adopt biosecure behaviours, as evidenced by an online survey of 1,334 respondents (Urquhart et al. 2017). However, not all destructive pests and pathogens attract comparable attention. For example, the invasive pathogen *Phytophthora austrocedri* Gresl. & E.M. Hansen., which is killing the native juniper (*Juniperus communis* Thunb.), has received relatively little public concern (Woodward and Boa 2013).

In addition, the way information about invasive species is communicated in the news media can significantly influence the effectiveness of public engagement and responses. Based on a content analysis of 924 news articles published between 2002 and 2017 on the emerald ash borer in the United States, Clarke et al. (2020) found that invasion-militaristic framing—such as portraying environmental threats as "urgent," "defending enemy lines," or "fighting a losing battle"—may inadvertently lead to public desensitisation. Such language can convey a pessimistic message that tree mortality is inevitable, thereby discouraging proactive action by the public.

Numerous citizen science initiatives have been established to support the early detection, monitoring, and management of tree pests and pathogens (Hulbert et al. 2023). In the UK, the Observatree project, launched in autumn 2013, serves as a citizen science platform for the early warning of tree health threats. The project engages both tree health professionals and members of the public to report suspected pest or pathogen sightings as soon as possible, supported by a network of around 200 trained Observatree volunteers. Suspect cases can be submitted through the TreeAlert online portal, which is managed by Forest Research and funded by DEFRA, the Forestry Commission, Scottish Forestry, and the Welsh Government. In the United States, the TreeSnap project similarly encourages citizens to contribute tree health observations, enabling scientists to track the spread of pests and pathogens across regions (Crocker et al. 2019).

In contrast, China's response to forest pest and pathogen outbreaks is largely characterised by a top-down approach, involving intensive quarantines, clear-cutting, large-scale pesticide applications, and the use of biological control during major outbreaks such as those of the pine wood nematode

(*Bursaphelenchus xylophilus* Steiner & Buhrer) and the Asian longhorned beetle (Xu 2008; Wang et al. 2023). Despite the severe economic and ecological impacts of the pine wood nematode, public awareness of the pest remains low. Media coverage is predominantly limited to government-controlled outlets, such as the official websites of the National Forestry and Grassland Administration and various city- and county-level Municipal People's Governments. This centralised management structure is shaped by the fact that forest land in China is predominately state-owned rather than privately held. Consequently, the influence of the media, the general public, and NGOs on pest management and eradication efforts is relatively limited. Awareness of pest outbreaks among citizens typically arises through personal or professional interest—among those who enjoy woodlands, work in environmental sectors, or are otherwise directly engaged with forestry sector.

1.5 Ecological Consequences

Beyond the loss of forest and orchard products, outbreaks of tree pests and pathogens can substantially diminish forests' capacity to sequester and store carbon, regulate water quality, and mitigate flood risks (Boyd et al. 2013). Forest carbon sequestration plays a critical role in combating global climate change; however, disturbances caused by pests and pathogens can severely disrupt this function. Based on field survey data from 91,723 plots in the U.S. National Forest Inventory, Quirion et al. (2021) pointed out that live trees in plots recently impacted by insect disturbance sequestered on average 69% less carbon compared with plots with no recent disturbance, and for plots recently impacted by disease disturbances, this figure was 28%. Similarly, Zhou et al. (2024) estimated that pine forests (*Pinus* spp.) in the Northern Hemisphere store a total of 70,726 Tg C, yet outbreaks of pine wood nematode and Japanese pine sawyer beetle (*Monochamus* spp.) have resulted in a carbon sink deficit of 1,857 Tg C in northern pine ecosystems, equivalent to 18% of the carbon currently stored in European forests. Notably, the carbon loss attributed to pine wood nematode infestations exceeds that caused by wildfires (Zhou et al. 2024). In China, pine wood nematode infestations are estimated to threaten 483.23 Tg C of forest carbon, with an average recovery time of 13.95 years (Hu et al. 2024). Using field experimental data, Schafstall et al. (2024) parameterised a Biotic Disturbance Engine (BITE) model to simulate the potential impact of pine wood nematode introduction in a Central European forest landscape (40,928 ha). Depending on biological assumptions, the model predicted 40–95% pine mortality within 100 years of introduction, accompanied by a maximum annual carbon loss of 1.3–4.2%. In Britain, ash dieback has also caused substantial carbon losses. Soil carbon depletion alone was estimated at 5.8 million tonnes over five years (2016–2021)—more than half the amount of CO_2 sequestered by British broadleaf woodlands during the same period (Seaton et al. 2025).

Pest and pathogen disturbances also cause long-term disruptions in forest nutrient cycles by altering tree species composition, as different species vary in growth rate, tissue nitrogen concentrations,

allocation ratios, litter chemistry, and mycorrhizal associations (Lovett et al. 2006; Crowley et al. 2016). For example, using the forest ecosystem model Spe-CN, Crowley et al. (2016) simulated the effects of beech bark disease (BBD), hemlock woolly adelgid (HWA), and sudden oak death (SOD) on forest productivity, carbon storage, and nitrogen retention and loss over a 300-year period. They predicted a carbon loss ranging from 13% to 29% after 100 years and an increase in nitrate leaching of approximately +0.3 g m^{-2} $year^{-1}$ compared with uninvaded land.

Another consequence of the large-scale loss of a host species and its subsequent replacement by another is the decline in biodiversity. For instance, in the case of ash dieback disease, ash trees serve as food sources for many pests and mammals, provide nesting and breeding sites for certain bird species, and offer habitats for epiphytic bryophytes and lichens, as well as hunting grounds for various insects and birds (Broome and Mitchell 2017). In Sweden, 483 ash-associated species identified by Hultberg et al. (2020), of which 11% are exclusive to ash, and a further 23% show a strong preference for it. They also estimated that 115 species are at high risk of regional extinction due to the loss of ash. For other pests and pathogens, assessments of potential species loss are limited, as studies often focus on quantitative metrics of species diversity rather than identifying which species are on the Red List and would face high extinction risk if their host trees were lost (e.g., Schrader et al. 2021; Liu et al. 2023).

1.6 Key Questions and Innovations

This thesis seeks to address three central questions:

1. How are tree pests and pathogens, as well as associated research efforts, distributed globally?
2. How does climate change alter pest and pathogen distributions?
3. How do pests and pathogens affect forest carbon sequestration potential?

The reason for proposing question 1 is a significant data deficiency in tree pest and pathogen research. Epidemiological data on pests and pathogens is crucial: they help scientists to know where pests and pathogens currently occur, whether they have led to significant damages on trees, and where they would occur in the future. This would inform better surveillance, early disease detection, and interception strategies along high-risk trade routes. However, the current pest and pathogen data is not adequate: (1) Field surveys are labor-intensive and are therefore typically limited to national or regional scales, such as the National or State Forestry Inventory programs in the United States (Spencer and Czaplewski 1997), China (Zeng et al. 2015), the United Kingdom (Smith and Gilbert 2001), Russia (Alekseev et al. 2019), and the European forest monitoring network (Vidal et al. 2016). Therefore, although field research data reveals details on disease impacts and tree mortality, they are limited in geographic range, and is often not publicly accessible; (2) Remote sensing technologies,

such as satellite and drone imagery, are able to detect crown defoliation through vegetation indices; however, they often cannot determine whether defoliation is caused by pests, pathogens, or by other stressors. In addition, pests and pathogens often target specific host species rather than entire forest stands. Unlike stand-replacing disturbances such as wildfire or severe drought, their impacts may not be detectable by satellite imagery, particularly when the affected host species constitutes only a small proportion of the forest canopy. Therefore, these data are often limited to specific pest or pathogen outbreaks, and are heavily relied on prior knowledge of outbreak locations (e.g., Ye et al. 2022; Zhang et al. 2022); (3) Large-scale pest and pathogen occurrence databases, such as GBIF (Global Biodiversity Information Facility), EPPO (European and Mediterranean Plant Protection Organization), and CABI (Centre for Agriculture and Bioscience International), provide wide coverage across continents. However, these datasets are often confined to presence–absence records, rather than detailed information on disease severity or associated tree mortality. This limits its capability to analyse the functional impact of pests and pathogens on forests. Therefore, synthesising field survey data across the globe is a priority for tree pest and pathogen research. Such analysis can reveal the global distribution of disease impacts, identify geographic and knowledge gaps, and guide the allocation of research funding.

Although question 2 has been explored in pest and pathogen studies, findings are often inconclusive. They often conclude that, the effects of environmental variables on pest and pathogen biology are highly context-dependent, varying with species, functional traits, location, forest composition and density, etc. While acknowledging this complexity is important, such findings cannot be translated into practical management strategies. Generally, the impact of the environment on pest and pathogen performance can be summarised into two mechanisms: Firstly, changing temperature and precipitation affects the life cycle of pests and pathogens, altering their survival, growth, and reproduction rates. These direct impacts on pests and pathogens lead to geographic range shifts of pest and pathogen disturbances, and modify the severity of disturbance impacts (Ramsfield et al. 2016; Simler-Williamson et al. 2019). For instance, rising temperature can accelerate insect development rates (Deutsch et al. 2018), and shorten pathogen incubation periods (Singh et al. 2023), thus allowing them to survive in colder regions. Secondly, changes in temperature and precipitation can alter the regimes of abiotic stress—particularly drought—which may weaken host trees, suppress pest and pathogen populations, or affect both simultaneously. The net outcome depends on drought intensity, moisture availability, and whether the organism is a primary or opportunistic agent (Kolb et al. 2016). The above mechanisms may simultaneously exist in a host-pathogen system, and which mechanism is stronger would affect the net outcome of the pest and pathogen performance. Current research often focuses on a single species or a limited range of pests and pathogens. To provide meaningful implications for global forest management, it is necessary to conduct cross-scale comparative studies across a broad spectrum of pest and pathogen taxa. This broader approach is the primary contribution

of Chapter 5.

Question 3 remains poorly understood within academia, while it is important to global carbon budget reporting. The world's forest stores approximately 861 gigatonnes of carbon, with 44% in soil (to a one-metre depth), 42% in live biomass (above- and belowground), 8% in dead wood, and 5% in litter (Pan et al. 2011). This is roughly 90 times the fossil fuel emissions recorded in 2024 (Friedlingstein et al. 2025). The forest is a major component of the global land carbon sink, absorbing 2.3 ± 1.0 GtC annually—nearly one quarter of the 2024 fossil fuel emissions (10.1 ± 0.5 GtC; Friedlingstein et al. 2025). However, disturbances can substantially impact this sink. The global carbon budget report 2025 pointed out that, between January and September 2024, wildfires released an estimated 1.6–2.2 GtC across North and South America (Friedlingstein et al. 2025). Fires and severe drought in Brazil contributed an additional 0.2–0.3 GtC of carbon loss in September alone (Friedlingstein et al. 2025). However, the report overlooked the impacts of pest and pathogen outbreaks, even though these agents are increasingly driving a reduction of carbon sequestration. For example, the 15 most damaging non-native tree pests in the United States have caused tree mortality equivalent to 5.53 Tg C per year (Fei et al. 2019). Accurately quantifying the reduction in forest carbon sequestration caused by pests and pathogens would make carbon budget assessments more realistic and enhance the effectiveness of reforestation and afforestation initiatives by supporting precise carbon accounting.

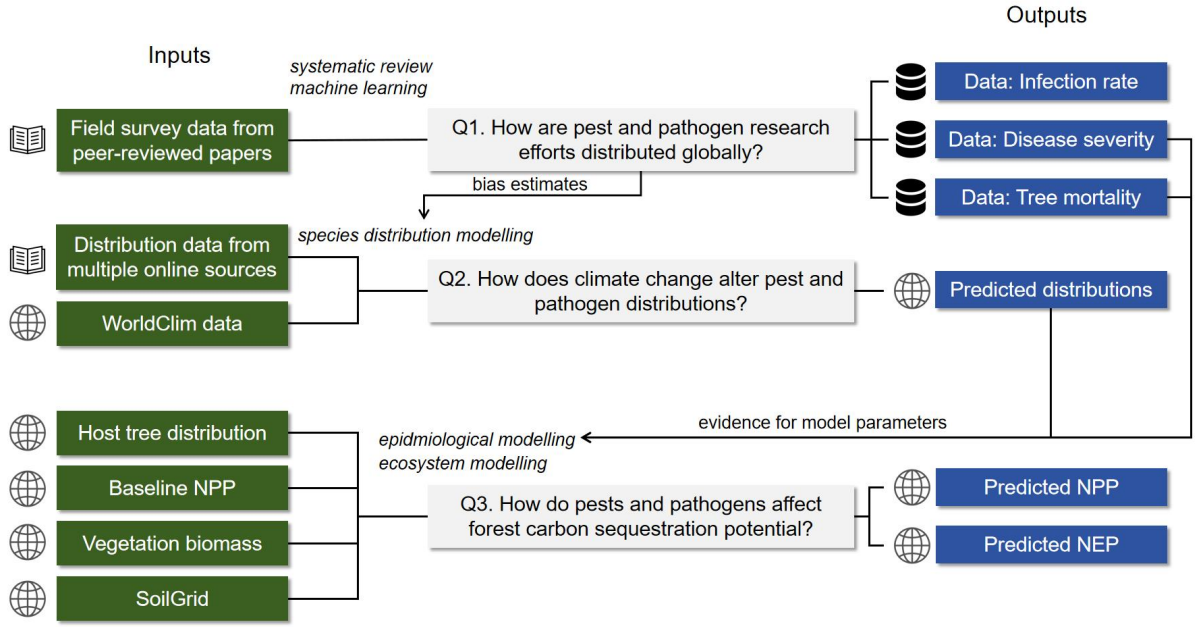


Figure 1.6. Schematic diagram of how three search chapters (Chapter 4–6, corresponding to Q1–3, respectively). The text boxes on the left hand show the main input data for each study, and boxes on the right hand side show the main outputs. The italic texts show the principle methods used in each research chapter. NPP is short for net primary productivity.

Chapters 4–6 address the three research questions, respectively. Figure 1.6 illustrates the relationships between these chapters, highlighting their main data inputs and outputs, as well as the dependencies between them. Overall, Question 1, addressed in Chapter 4, establishes the empirical foundation for investigating the ecological consequences of tree pests and pathogens for forest ecosystems. Specifically, answering this question provides (1) an approximate assessment of research intensity on tree pests and pathogens, which can be used to correct for sampling bias in species distribution models; and (2) estimates of disease impacts, measured by indicators such as crown defoliation and tree mortality rates, which are essential for modelling the effects of pest and pathogen disturbances on forest carbon cycling.

Building on the research intensity and pest and pathogen occurrence data compiled in Chapter 4, Question 2 is addressed in Chapter 5 through species distribution modelling. The predicted distribution of the ash dieback pathogen defines the epidemic region, and is thus the study extent for Chapter 6. As estimating reductions in forest carbon sequestration requires comprehensive evidence on pest and pathogen distributions, disease severity, tree mortality, and other baseline conditions, Chapter 6 integrates data and findings from both Chapters 4 and 5. Although the evidence compiled and generated in Chapters 4 and 5 is essential for estimating changes in forest carbon sequestration, uncertainties arising from these earlier analyses may propagate through the modelling framework and affect the results of Chapter 6. These sources of uncertainty and their implications are discussed further in Section 3.8.

2. The Ecology of Tree Pests and Pathogens

2.1 Introduction

Understanding the biological traits that drive pest and pathogen invasiveness is essential for predicting their impacts (Ghelardini et al. 2017). To successfully establish in a novel environment, invasive species often has multiple introduction pathways, higher fecundity, greater voltinism, larger genetic diversity, shorter lifespans, and faster development (Zhao et al. 2023). They may also differ significantly in key functional traits compared with native species (Mathakutha et al. 2019). Despite variations in their biology, tree pests and pathogens can facilitate their invasion success through adaptive reproductive strategies, dispersal capabilities, and an appropriate level of virulence to host trees (Brockerhoff and Liebhold 2017; Ghelardini et al. 2017). Understanding these mechanisms helps forest managers to identify where and how to intervene for effective disease mitigation.

The life cycle, or life history, is a central concept for studying biological traits. It encompasses a list of developmental stages an organism would undergo. This includes birth, growth, reproduction, aging, and death. In insects, life stages typically includes eggs, larva, pupa, and adults, although some species may lack one or more of these. The life cycle of fungal species are generally more complex, often alternating between asexual and sexual stages. The life cycle characteristics of a pest or pathogen determine how it spreads, invades, and damages new hosts. For instance, pathogens that infect plants through spores tend to have higher patch occupancy and colonisation rates than those that spread primarily through systemic infections or overwintering in rhizomes (van Dijk et al. 2022).

Temperature and precipitation patterns influence a pest's or pathogen's ability to complete its life cycle, thereby affecting its potential for invasion success. For example, *Hymenoscyphus fraxineus* (T.Kowalski) Baral, Queloz & Hosoya, the fungal pathogen responsible for ash dieback, is killed at temperatures above 30 °C (Kowalski and Bartnik 2010), limiting its impact during hot summers (Grosdidier et al. 2018). In contrast, the spruce bark beetle *Ips typographus* (L.), one of the most damaging forest pests in Central Europe, achieves optimal population growth near 30 °C (Wermelinger and Seifert 2008). Consequently, warmer summers increase its risk of establishment and spread (Webb et al. 2024), potentially exacerbating host stress and mortality.

This chapter will first discuss how tree pests and pathogens complete their life cycles. It will then review recent understanding on how environmental variables influence the pests' and pathogens' life cycles. It will identify the knowledge gap in this field, which is to be addressed in Chapter 5. Then this chapter will turn to discuss the host tree physiology, including how trees produce organic matters through photosynthesis, transport water via the vascular system, and lose water through transpiration. Then it will discuss how pests and pathogens disrupt normal tree physiology, affecting tree health and

forest carbon cycling. It will review recent progresses in estimating reduction of forest carbon sequestration potential driven by pest and pathogen outbreaks, highlighting the knowledge gap that is to be addressed in Chapter 6. Finally, it will discuss the recent advances in pest and pathogen monitoring across the globe, pointing out that there is a substantial data deficiency, thus highlighting the need of a synthesis research (i.e. Chapter 4).

2.2 Life Cycle of Pathogens

Although pathogens include viruses, bacteria, fungi, and protists, most of the pathogens discussed in this thesis are fungi. This is because the most prevalent and virulent epidemics are caused by fungus, while virus play a minor role in global forest biotic disturbances. A representative example is *H. fraxineus*, an ascomycete fungus responsible for ash dieback. Its life cycle begins when tiny, mushroom-like structures called apothecia develop on the previous year's fallen ash leaf litter. Apothecia, characteristic of some ascomycete fungi, are fruiting bodies that produce sexual spores for reproduction. The formation of apothecia by *H. fraxineus* can occur as early as spring (Marçais et al. 2023) and continue until early September (Inoue et al. 2019). The spores produced by these structures, known as ascospores, are dispersed by wind during summer and infect ash leaves (Landolt et al. 2016). Infection occurs when ascospores penetrate leaf cells and develop root-like mycelia that absorb nutrients from the host. Infected trees may initially show no symptoms but can later exhibit necrotic leaf spots (Bakys et al. 2009). When infected leaves fall, the pathogen persists in the leaf debris, completing its sexual stage and entering the asexual (anamorphic) phase. It can survive for several years on leaf stalks in the litter (Gross & Holdenrieder, 2013; Kirisits, 2015), forming dark, hardened structures called pseudosclerotia to overwinter effectively (Inoue et al. 2019). During the asexual stage, the fungus produces sticky conidia, which further develop into spermatia—one of the mating types (Fones et al. 2016). Spermatia fuse with ascogonia and undergo meiosis to form ascomata (Landolt et al. 2016). Finally, apothecia form once the weather becomes warm and moist, completing the cycle. In addition to leaf infections, *H. fraxineus* can also invade plant root systems via hyphae that develop from conidia (Fones et al. 2016).

Like *H. fraxineus*, many fungal species have both sexual (teleomorphic) and asexual (anamorphic) stages. These fungi are referred to as holomorphs and may have different names depending on the life stage being described—for example, the asexual stage of *H. fraxineus* is also known as *Chalara fraxinea*. The genus *Neonectria*, comprising ascomycete fungi that cause canker diseases, also includes holomorphic species. *Neonectria ditissima*, the pathogen responsible for European canker in apple and pear trees, can infect hosts using both ascospores and conidia (Gómez-Cortecero et al. 2016). *Neonectria faginata*, which causes beech bark disease in the United States, infects bark tissue using ascospores, microconidia, and macroconidia dispersed by wind and water (Houston 1994). Unlike *H. fraxineus*, *N. faginata* is an opportunistic pathogen that primarily attacks bark fissures

created by feeding damage from the beech scale insect (*Cryptococcus fagisuga*) (Houston 1994). *Cronartium ribicola*, a basidiomycete fungus that causes white pine blister rust, is notable for alternating between different host species during its sexual and asexual stages (Geils and Vogler 2011).

Some fungi, however, lack certain life stages or exhibit stages that are difficult to observe. *Ophiognomonia clavigignenti-juglandacearum*, the pathogen responsible for butternut canker in North America, reproduces primarily asexually. Its conidia infect trees and develop hyphae that penetrate the phloem, xylem, and other woody tissues ("*Sirococcus clavigignenti-juglandacearum*", 2005). Similarly, *Dothistroma septosporum*, the causal agent of Dothistroma needle blight (DNB), reproduces mainly asexually and spreads through conidia, though evidence suggests it also has a rarely observed sexual stage (Mullett et al. 2021).

In terms of dispersal, while fungal pathogens often rely on wind and water, some require vectors. A classic example is *O. novo-ulmi*, the fungus responsible for Dutch elm disease, which is transmitted by elm bark beetles (*Hylurgopinus rufipes* J.M.Swaine) (Gibbs et al. 1994). In spring and summer, adult beetles emerge from the bark of dead or dying elms carrying fungal spores. As they feed on healthy elms, they introduce *O. novo-ulmi* spores into the wood, leading to characteristic dark streaks and wilting symptoms. Later in the season, adult female beetles bore into the inner bark to construct breeding galleries and lay eggs. The developing larvae tunnel through the bark before pupating, becoming contaminated with the fungus. When these new adults emerge in spring, they carry the pathogen and continue the transmission cycle.

Similarly, *Raffaelea quercivora*, the pathogen responsible for Japanese oak wilt, is dispersed by the ambrosia beetle *Platypus quercivorus* (Mackesy et al. 2018). The beetle carries the fungus's conidia, transmitting them as it bores into sapwood and heartwood. The conidia germinate, producing hyphae that colonise the beetle galleries and surrounding wood. Female beetles lay eggs in these galleries, and the larvae feed on the fungus before pupating. The emerging adults acquire the fungus in their mycangia and spread it to new hosts. Other insect-vectored fungi include *Raffaelea lauricola* (the cause of laurel wilt; Hamilton et al. 2020) and *Geosmithia morbida* (the agent of thousand cankers disease; Utley 2013).

Several fungal pathogens employ multiple dispersal pathways. *Fusarium circinatum*, the causal agent of pine pitch canker, spreads via wind, rain, insect vectors, soil, and movement of infected materials (Gordon et al. 2001; Zamora-Ballesteros et al. 2019). *Cryphonectria parasitica*, the pathogen responsible for chestnut blight, disperses its conidia mainly through rain splash over short distances but can also spread over longer distances via birds, insects, mites, or windborne dust. Its ascospores are typically wind-dispersed over several hundred metres (Rigling and Prospero 2017).

Oomycetes are fungus-like eukaryotic microorganisms distinct from true fungi, being more closely

related to brown algae and diatoms. This group includes many devastating plant pathogens in agriculture and forestry. A well-known example is *P. ramorum*, which causes sudden oak death. Under high humidity and temperatures above 15 °C, the life cycle of *Phytophthora* begins when sexual spores (oospores) form and produce sporangia, its asexual spores (Silva et al. 2021). Sporangia are dispersed by wind and rain to infect plant tissues on the soil surface or aboveground, where they germinate directly or release zoospores that develop into mycelia (Silva et al. 2021). The mycelium typically reproduces asexually due to the efficiency of this mode (Janiszewska et al. 2020). Sporangia spread to new hosts, but under low temperatures (< 15 °C) and humidity, they form protective chlamydospores that persist in plant tissues or soil. When compatible mating types are present or under environmental stress, the mycelium undergoes sexual reproduction, forming stress-tolerant oospores through fusion of oogonia and antheridia (Silva et al. 2021).

Bacterial pathogens generally have simpler life cycles, reproducing exclusively asexually. *Xylella fastidiosa*, a pathogen infecting a wide range of ornamental and economically important plants, reproduces by binary fission. It is transmitted by xylem-feeding insect vectors, primarily sharpshooters (*Cicadellidae*) and spittlebugs (*Cercopidae*) (Hewitt et al. 1946). These insects acquire *X. fastidiosa* while feeding on infected plants and can immediately transmit it to new hosts without a latent period (Rapicavoli et al. 2017).

2.3 Life Cycle of Pests

One of the most common forest pests are beetles, which often tunnel beneath tree bark to feed and lay eggs. A typical example is the Asian longhorned beetle (*Anoplophora glabripennis*). Adult females create oviposition pits in the bark of living stems and branches by chewing, into which they insert a single egg into the cambial tissue, causing localized tissue death (Straw et al. 2015). The first-instar larva feeds on the dead cambial tissue within this oval patch. Upon molting into the second instar, it begins feeding laterally on undamaged phloem and xylem. Second- and third-instar larvae excavate a flat gallery beneath the bark. After molting into the fourth instar, they tunnel deeper into the wood and primarily feed within the xylem (Lingafelter and Hoebeke 2002). When fully grown, they construct a slightly enlarged chamber at the tunnel's end for pupation. The adult beetle emerges from the pupa within the chamber, chewing its way to the surface and leaving a circular exit hole approximately 10 mm in diameter (Haack et al. 2010; Sánchez & Keena, 2013; Straw et al. 2015). Other notable beetle species include *Tetropium fuscum* (Brown Spruce Longhorn Beetle) (Brandt 2024), *Ips typographus* (European Spruce Bark Beetle) (Wermelinger 2004), *Dendroctonus ponderosae* (Mountain Pine Beetle) (Furnissa and Kegley 2008), *Dendroctonus valens* (Red Turpentine Beetle) (Furniss 1995), *Agrilus anxius* (Bronze Birch Borer) (Barter 1957), *Malacosoma disstria* (Forest Tent Caterpillar), and *Agrilus planipennis* (Emerald Ash Borer) (Wei et al. 2007).

Moths typically damage trees during their larval stage, feeding on leaves, needles, or fruit. Well-known examples include *Hyphantria cunea* (Fall Webworm or American White Moth) (Schowalter et al. 2017), *Lymantria dispar* (Gypsy Moth) (Boukouvala et al. 2022), *Thaumetopoea pityocampa* (Pine Processionary Moth) (Jactel et al. 2014), *Dendrolimus sibiricus* (Siberian Silk Moth) (Pavlov et al. 2018), and *Choristoneura fumiferana* (Spruce Budworm) (Royama 1984). The life cycle of the Gypsy Moth (*L. dispar*) proceeds as follows (Boukouvala et al. 2022): mated females lay eggs on tree trunks near their pupation sites. The egg stage lasts about three weeks, comprising an embryonic phase followed by diapause, which is temperature-dependent. Eggs hatch from early spring to mid-May, and larvae feed on host foliage for six to eight weeks—initially cutting small holes in leaves during the first instar, and later feeding along leaf edges in subsequent instars. During the prepupal stage, larvae stop feeding and pupate in concealed locations such as branch undersides, bark crevices, and beneath stones or fallen trunks for one to two weeks. Adults do not feed and typically survive only about a week after mating.

Nematodes often cause fatal damage by feeding on the plant's vascular system, disrupting the water flow essential for tree survival (Topalović and Geisen 2023). Because nematodes have limited mobility, they rely on other organisms for long-distance dispersal. For instance, the pine wood nematode (*Bursaphelenchus xylophilus*) is transmitted by pine sawyer beetles (*Monochamus* spp.) (Tanaka et al. 2019). The nematode's life cycle includes both a phytophagous (plant-feeding) and a mycetophagous (fungus-feeding) phase (Kikuchi et al. 2011; Tanaka et al. 2019). It enters host trees during the beetle's maturation feeding, consuming plant epithelial cells around the cortex and xylem, spreading through the tree, and often causing death within a year. Once the tree becomes symptomatic, the nematode switches to feeding on invading fungi. The nematode has three propagative larval stages (L2, L3, and L4) before reaching adulthood; the L1 stage molts into L2 within the egg. Alternatively, L2 larvae may develop into the third-stage dispersal juvenile (D3) and subsequently the fourth-stage dispersal juvenile (D4), which migrates into adult vector beetles emerging from infected trees.

Sap-sucking pests possess piercing-sucking mouthparts that extract plant sap, weakening the host and potentially transmitting diseases (Wari et al. 2021). The Hemlock Woolly Adelgid (*Adelges tsugae*), an aphid-like insect, exemplifies this group. Its complex life cycle is typical of the Adelgidae (Havill et al. 2014). In Japan, where both host trees—the Japanese hemlock (*Tsuga sieboldi*i) and tigertail spruce (*Picea torano*)—are present, spruce serves as the primary host supporting the pest's sexual reproduction, while hemlock supports its asexual generations. There are two asexual generations per year, with a small proportion of the second generation developing into winged migrants known as sexuparae. These sexuparae settle on suitable spruce trees and produce a short-lived generation of sexual females and males. Mated females produce a single large egg that develops into an asexual female, or fundatrix, which overwinters near a bud. In spring, the fundatrix induces gall formation on

spruce buds to house her offspring. She lays numerous eggs, and the resulting crawlers feed inside the multi-chambered gall before maturing and returning to hemlock. In regions lacking spruce, such as North America, the insect completes only two asexual generations annually. Another example is the Spotted Lanternfly (*Lycorma delicatula*), which also feeds on plant sap and follows a one-year life cycle (Urban and Leach 2023). It overwinters as eggs that hatch in spring; the nymphs undergo four instars before becoming winged adults by mid-summer. Adults mate and lay eggs in the fall, dying off before winter.

Some pests induce abnormal plant tissue growth by injecting chemicals into plant cells, forming structures known as galls that provide both protection and nutrition for the pests. For instance, the oriental chestnut gall wasp (*Dryocosmus kuriphilus*) damages chestnut trees (*Castanea* spp.) by forming green or red galls on petioles, leaves, and stems (Mapes et al. 2022). This species reproduces asexually. Eggs and overwintering larvae remain within buds until spring, when larvae resume activity and induce gall formation. Pupation occurs within the galls, and adults emerge in summer (Mapes et al. 2022). Similarly, the Pine Needle Gall Midge (*Thecodiplosis japonensis*) completes one generation per year (EFSA Panel on Plant Health 2022). Adult females oviposit in pine needles, and the resulting larvae form galls at the base of needle fascicles for sap feeding. Third-instar larvae exit the galls and overwinter in cocoons in the soil, pupating at the end of winter.

2.4 Climate Change Effects on Pests and Pathogens, and Knowledge Gap

Temperature and precipitation influence the ability of pathogens to sporulate, spread, and survive within plant tissues. They also impact on the timing of pest life cycles, and the vulnerability of hosts to infection. Together, these factors affect the distribution ranges of both pathogens and pests (Sturrock et al. 2011; Ramsfield et al. 2016; Simler-Williamson et al. 2019; Linnakoski et al. 2019; Kliejunas et al. 2009). For many pathogens, global warming may drive latitudinal shifts in their distribution ranges, as increasing temperatures can make previously unsuitable regions favourable for spore production and dispersal (Raza and Bebber 2022).

For instance, the ash dieback pathogen *H. fraxineus* grows best at approximately 20 °C in pure culture (Kowalski and Bartnik 2010), with sporulation occurring between 15–21 °C (Mansfield et al. 2018). These temperature conditions are found across most of Europe, which helps explain the pathogen's rapid continental spread (PPQ 2022). Growth at 30 °C is very limited, and exposure to hot water at 36 °C for five hours can kill the pathogen (Hauptman et al. 2013). The northern limit of *H. fraxineus* is constrained by intolerance to cold winters and drought (Pautasso et al. 2013). However, ongoing climate warming is expected to create suitable conditions further north, promoting its expansion into northern Europe (Goberville et al. 2016). Similarly, *Ophiostoma novo-ulmi* (the causal agent of Dutch

elm disease) grows best around 20 °C (Oliveira et al. 2012), and maximal defoliation occurs at temperatures exceeding 17 °C under moderate sunlight (Sutherland et al. 1997).

Moderate precipitation generally provides favourable conditions for spore production, dispersal, and infection by fungal pathogens (Huber et al. 1998; Romero et al. 2022; Ji et al. 2024). *Dothistroma septosporum* and *Dothistroma pini*, the causal agents of Dothistroma needle blight, require water for spore germination and rely on water splash for transmission (Woods et al. 2005), with optimal activity at temperatures of 15–20 °C (McCulloch and Woods 2009). Consequently, warmer and wetter conditions are expected to increase their activity and disease impact (Sturrock et al. 2011). *Fusarium circinatum*, the causal agent of pitch canker, also prefers warm, wet, temperate to subtropical climates and is predicted to shift southward toward the central North Island of New Zealand and northern Tasmania (Ganley et al. 2011). Members of *Phytophthora* spp., though not true fungi, also require moist conditions for the motility of their zoospores, which swim to infect new plants (Rollins et al. 2016). Thus, milder and wetter winters, along with increased spring rainfall and summer temperatures, are expected to promote their reproduction and spread (Kliejunas et al. 2009; Sturrock et al. 2011). In contrast, some pathogens thrive under warmer and drier conditions, as drought and heat stress weaken host trees, increasing susceptibility to infection—typical examples include Armillaria root disease (*Armillaria* spp.) and oak decline (Sturrock et al. 2011).

Similar to pathogens, many invertebrate pests respond to warming temperatures by expanding their ranges into previously unoccupied areas formerly limited by cold winters, or by accelerating their life cycles due to increased thermal availability for growth and reproduction (Bale et al. 2002; Bracalini et al. 2024). For example, the Asian longhorned beetle (*Anoplophora glabripennis*) is projected to shift northward in the Northern Hemisphere, with its optimal host species dominating these new regions (Zhou et al. 2021). A similar pattern is predicted for the emerald ash borer (*Agrilus planipennis*), which is expected to expand its distribution across North America, Europe, and East Asia (Li et al. 2025). Using a cumulative growing degree day (CGDD) model, Bao et al. (2025) reported an increase in voltinism of 0.04 generations per decade for the pine caterpillar (*Dendrolimus spectabilis* Butler) under future climate scenarios. Conversely, in warmer regions, extreme summer temperatures may negatively affect pest populations by reducing individual size, fecundity, and dispersal capacity, while increasing mortality (Bracalini et al. 2024). For species requiring chilling periods to enter obligate winter diapause, milder winters and reduced snowfall can decrease overwinter survival (Bracalini et al. 2024). The direct effects of precipitation on pests are less documented than for fungal pathogens, as pests generally do not rely heavily on moisture for dispersal.

Besides direct effects on pathogens and pests, the changing climate also impacts on the host trees, particularly under heat stress, drought, wildfire, or wind disturbance (Itter et al. 2018; Jactel et al. 2019; Simler-Williamson et al. 2020). Abiotic stress, despite its negative impact on the pests' and pathogens' reproduction and survival, can weaken host defenses, thus making them vulnerable to

infection. For example, in a mixed evergreen and redwood forest in California, wildfire reduced the occurrence and density of susceptible hosts, thereby lowering infection rates of *Phytophthora ramorum* (Simler-Williamson et al. 2020). In contrast, increasing drought severity has been shown to favour the European spruce bark beetle (*Ips typographus*) by weakening host trees (Potterf et al. 2025).

Although the impact of climate change on pests and pathogens have been extensively studied, existing research often focuses on a single or limited number of species (e.g., Goberville et al. 2016; Barker et al. 2023; Zou et al. 2024), and often concludes that the climate change impacts are complex and highly context-dependent (Jactel et al. 2019). Comparative studies across multiple pest and pathogen species remain limited. The lack of cross-species analyses constrains our ability to identify general patterns, and draw broadly applicable conclusions about the invasion dynamics. As a result, there is a lack of general and useful principles for large-scale tree pest and pathogen management. Strategies that address shared drivers of pest and pathogen spread are needed based on evidence from cross-species research.

2.5 Host Tree Physiology

Accurate estimation of forest carbon loss caused by pests and pathogens requires a deep understanding of tree physiology. Plants synthesise carbon through photosynthesis and transport the assimilated organic compounds from leaves to roots via the phloem. The rate of carbon assimilation through photosynthesis is influenced by multiple factors, including light intensity, temperature, and stomatal conductance. The well-known Farquhar model (Farquhar et al. 1980), widely used in ecosystem modeling, describes the rate of carbon assimilation (i.e., photosynthetic rate) as a function of external environmental variables—such as photosynthetically active radiation (PAR) and ambient temperature—internal factors like intercellular carbon dioxide concentration, and species-specific parameters including the maximum rate of carboxylation and the maximum rate of electron transport. To solve for photosynthetic rate, ecosystem modelers often couple the Farquhar model with the Ball–Berry model (Medlyn et al. 2011), which establishes a relationship between intercellular CO_2 concentration, stomatal conductance, and vapor pressure deficit (VPD). By simultaneously solving these two coupled equations, modelers can estimate both stomatal conductance and photosynthetic rate. In summary, under normal physiological conditions, photosynthetic carbon assimilation is primarily determined by temperature, light intensity, and VPD. However, when stressors such as fungal pathogens are present, plants may close their stomata to prevent pathogen entry into leaf tissues (Gudesblat et al. 2009), thus the Ball–Berry relationship becomes invalid.

The total amount of carbon fixed through photosynthesis is referred to as gross carbon assimilation. A portion of this carbon is consumed through respiration by foliage, woody tissues, and roots. Across all

plant organs, respiration can be divided into maintenance respiration, which represents the metabolic energy required to sustain tissue health and function, and growth respiration, which accounts for energy used in building new tissues and supporting cell division. At the ecosystem level, the total carbon assimilated by primary producers is termed gross primary production (GPP). The sum of foliar and woody respiration across all trees constitutes aboveground respiration, while belowground respiration includes both root respiration and microbial (heterotrophic) respiration from the soil. Together, above- and belowground respiration make up ecosystem respiration, which typically exhibits a unimodal response to increasing temperature (Niu et al. 2024). Net Ecosystem Production (NEP) is defined as the difference between GPP and ecosystem respiration.

The net carbon balance of an individual plant equals its gross carbon assimilation minus all components of respiration. When considered across all producers, this becomes Net Primary Production (NPP) at the ecosystem scale. NPP reflects biomass gain—representing plant growth and, from a carbon ecology perspective, the extent to which vegetation acts as a net carbon sink. The assimilated carbon is allocated to different plant tissues according to specific allocation ratios, which depend on a range of internal and external factors such as resource availability, temperature, atmospheric CO_2 concentration, precipitation, and radiation (Holland et al. 2019; Prescott et al. 2020; Xia et al. 2023).

Water is essential for carbon assimilation and for maintaining vital cellular functions. Plants absorb water through their roots and transport it to the leaves via the xylem, a process driven by the force generated by the transpiration stream. Water loss occurs primarily through transpiration, the evaporation of water from leaf surfaces, but also to a lesser extent through lenticels on bark and cuticular transpiration through the waxy layer on leaves. Transpiration rate can be modeled using stomatal conductance and the leaf-to-air vapor pressure deficit (VPD), although it is important to note that stomatal conductance itself is strongly influenced by VPD (Bourbia and Brodribb 2024).

2.6 Pests and Pathogens' Effects on Forest Productivity, and Knowledge Gap

Dietze and Matthes (2014) summarised the effects of pests and pathogens on trees into five major groups:

(1) Defoliators, including pests that feed on leaves such as the spruce budworm (*Choristoneura* spp.) and the gypsy moth (*Lymantria dispar*), as well as foliar pathogens like Swiss needle cast (*Phaeocryptopus gaeumannii*) and ash dieback (*Hymenoscyphus fraxineus*). These organisms remove leaf biomass and thereby reduce photosynthetic capacity.

(2) Root rots (e.g., *Armillaria* spp., *Phytophthora* spp.), root-feeding weevils, and parasitic nematodes, which alter root turnover rates and consequently affect the rate at which plants contribute

organic matter to the soil.

(3) Stem rots (e.g., *Cryphonectria parasitica*), which increase tree mortality by destroying stem tissues such as xylem and phloem that are essential for water and nutrient transport.

(4) Xylem reducers, including bark beetles, cankers, and wilts, which impair water transport within trees.

(5) Phloem feeders, such as the hemlock woolly adelgid (*Adelges tsugae*), which directly remove a portion of the carbon assimilated by the host plant.

Some studies have quantified changes of forest carbon sequestration resulted from the change of species dominance followed by tree pest and pathogen outbreaks. In a simulation study, Crowley et al. (2016) reported a net carbon loss of 13% after 100 years in a stand where sugar maple (*Acer saccharum* Marsh.) replaced American beech (*Fagus grandifolia* Ehrh.) due to beech bark disease, and a 29% loss in plant and soil carbon where red maple (*Acer rubrum* L.) replaced red oak (*Quercus rubra* L.) following sudden oak death. Seidl et al. (2018) estimated that 1,027 Tg C (approximately 10% of European forest carbon stocks) is at risk in Europe from five major invasive alien pests—Asian longhorned beetle, pine wood nematode, sudden oak death, beech bleeding canker, and pitch pine canker—with an estimated carbon recovery time of 34 years. At a larger research scale, Zhou et al. (2024) further estimated a carbon sink deficit of 1,857 Tg C in northern pine ecosystems, driven primarily by the pine wood nematode (*Bursaphelenchus xylophilus*) and the Japanese pine sawyer beetle (*Monochamus* spp.), equivalent to approximately 18% of the carbon currently stored in Europe's living trees.

However, these studies often assume that the reduction of forest carbon sequestration potential equals to the amount of biomass carbon released by pests and pathogens through tree mortality. Based on this assumption, they calculate the biomass carbon stock at risk from tree mortality rates. When estimating forest recovery time, they assume that pest and pathogen outbreaks result in an instantaneous loss of tree biomass, followed immediately by a recovery phase with a constant rate of NPP input. This linear, mortality-based framework oversimplifies the complexity of real-world carbon dynamics, and may substantially underestimate the extent to which forest carbon sequestration is reduced: First, during both the outbreak and recovery phases, NPP is substantially reduced because pests or pathogens weaken host trees, impair physiological function, and suppress photosynthesis; Second, standing dead trees resulting from infestation no longer contribute to NPP and may occupy canopy and rooting space, limiting seedling recruitment and slowing forest regeneration. Therefore, accurate carbon accounting requires the consideration of both tree mortality and declines in NPP during outbreak and recovery phases. By integrating epidemiological dynamics with a carbon cycling model, Chapter 6 quantifies the extent to which previous mortality-based accounting frameworks have underestimated the reduction in carbon sequestration potential.

2.7 Ecological Data and Gap

Distribution data for tree pests and pathogens, records of their impacts on forest health are essential for analysing their interactions with climate change, and how they impact on forest carbon sequestration (Linnakoski et al. 2019; Simler-Williamson et al. 2019; International Tree Mortality Network 2025). Using more than 92,000 field plots from the U.S. National Forest Inventory, Fei et al. (2019) estimated that the 15 most damaging non-native forest pests collectively caused tree mortality equivalent to 5.53 Tg C per year nationwide. Based on 407 plots (36,000 observations) across 27 European countries from the ICP Forests dataset, George et al. (2022) reported that defoliation and mortality associated with ash dieback disease had doubled over the past three decades, with mortality hotspots concentrated in southern Scandinavia and northeastern Europe. Forzieri et al. (2023) further compiled 650,000 harmonised and georeferenced records of European forest tree pests and pathogens from ground surveys, remote sensing, and other sources, providing a valuable resource for understanding ecological processes under biotic disturbance.

Existing databases on tree pests and pathogens are constrained by both spatial and thematic limitations. While distribution platforms such as GBIF, EPPO, and CABI provide broad geographic coverage, they generally lack detailed information on the impacts of pests and pathogens on tree health (Linnakoski et al. 2019). Plot-based datasets, on the other hand, report details on disease severity and tree mortality, while they are geographically restricted. Notable example include National Forest Inventory (NFI) networks, the U.S. Alien Forest Pest Explorer (AFPE), and the DEFID2 database (Forzieri et al. 2023). In particular, NFI data often relies on country-specific survey methodologies within an individual nation, limiting cross-country comparability and broader spatial generalisation.

Thus, there is a lack of global pest and pathogen database that reports the disturbance occurrence, disease impacts, and tree mortality. Synthesising such a database is essential for understanding the distribution patterns of pests and pathogens, and mapping scientific research efforts on pests and pathogens, guiding research investments in pest and pathogen monitoring. Moreover, such a database would enable integrated and comparative analyses of pest and pathogen effects across regions and taxa, thereby strengthening our capacity to assess, predict, and mitigate biotic threats to the world's forests.

2.8 Summary

Ongoing changes in temperature and precipitation patterns are expected to alter the timing and capacity of tree pests and pathogens to complete their life cycles, thereby reshaping their impacts on forest health. Many pathogens undergo both asexual and sexual reproduction, with the former enabling rapid population growth and the latter enhancing evolutionary adaptability, although some

species reproduce exclusively asexually. The ability to survive as mycelium within host tissues, as well as to sporulate and disperse spores effectively, is critical for pathogen persistence. Optimal temperature ranges and humid conditions generally facilitate these biological processes, which explains why pathogen outbreaks are often concentrated in mild and moist regions. There are, however, exceptions where drier conditions favour infection, particularly when drought stress weakens host defenses and increases susceptibility.

Most pest species progress through egg, larval, pupal, and adult stages, though some may lack one or more stages. Certain pests also serve as vectors for pathogen transmission among trees. Pest populations are primarily regulated by temperature, especially through thermal budgets that influence growth and reproductive rates. Precipitation and other abiotic stressors mainly affect pest impacts indirectly by reducing host vigour and compromising defensive mechanisms. Studies consistently indicate that the interactions between climate change, pests, and pathogens are highly variable across species, host types, and environments. Systematic, multi-species assessments are therefore essential for evaluating how future climate change may broadly reshape the distribution ranges of forest pests and pathogens. Such analyses provide a more generalisable understanding of climate-driven invasion risks, inform global forest management and biosecurity strategies. This will be the central focus of Chapter 5.

Pests and pathogens disrupt host tree physiology through multiple pathways: by defoliating crowns, increasing root turnover rates, damaging stems, reducing xylem conductivity, or feeding on phloem. These processes interfere with photosynthesis, nutrient and water transport, and transpiration, often resulting in tree mortality. Such mortality events release significant amounts of carbon—comparable to emissions from large wildfires—yet their contribution is often overlooked in global carbon budget assessments. At the ecosystem level, the reduction of forest carbon sequestration potential caused by pests and pathogens remains uncertain. Numerous studies have estimated the loss of carbon through tree mortality driven by pests and pathogens, but they overlooked the impact of reduced forest productivity caused by pest and pathogen attacks. Therefore, these studies do not provide an realistic estimate of reduced forest carbon sequestration due to pest and pathogen outbreaks. Dynamic modeling that integrates epidemiology with forest carbon cycles can provide robust estimates of reductions in forest productivity. This allows for a accurate assessment of reduced forest carbon sequestration potential overlooked by previous mortality-based approaches. This will be the main objective of Chapter 6.

Currently, data on the ecological impacts of tree pests and pathogens are highly fragmented. National Forestry Inventory and several synthesised databases have detailed documentation on disease severity and tree mortality, but these data are restricted to certain regions, lacking geographic coverage. On the other hand, global sources such as GBIF, EPPO, CABI primarily focuses on the spatial occurrence rather than the disease impacts. To establish comprehensive understanding of global tree pests and

pathogens, synthesised database from field survey research across the globe is highly needed. It will help identify gaps in global forestry research, prioritising investment in tree pest and pathogen monitoring, and inform design of pest and pathogen research. This will be the aim for Chapter 4.

3. Methodology

3.1 Research Design

This chapter outlines the overarching methodological framework applied in the three research chapters (Chapters 4–6). Although each chapter provides a detailed description of its specific methods, it is useful to first present the broader methodological context. Providing this background helps readers understand the rationale for selecting particular methods in each chapter, especially for those who may not be familiar with the broader methodological concepts or terminology.

The following is the overall design of three research chapters:

Chapter 4 synthesised the field survey data on tree pests and pathogens, analysing its spatial and temporal distributions. Specifically, it aimed to:

1. Summarise the major taxa and systems that cause significant damage globally or regionally;
2. Characterise the spatial and temporal patterns of the locations of tree pest and pathogen surveys; and
3. Examine the spatial and temporal trends of the reported infection rates, disease severity, and tree mortality by tree pest and pathogen field surveys.

By mapping research patterns and trends, this chapter identified underrepresented regions, host groups, and research themes, and thus providing a meta-level understanding of the global geography of tree pest and pathogen monitoring research. The results also provided essential evidence for modelling the impact of pest and pathogen outbreaks to forest carbon sequestration potential in Chapter 6. Pest and pathogen data was collected through a systematic review (see Section 3.2).

Given the wide range of taxa analysed, the initial literature pool was expected to be extremely large, making manual screening impractical. Therefore, natural language processing (NLP) techniques were applied to develop an abstract classifier capable of efficiently filtering out peer-reviewed articles lacking field survey data. The training dataset for this classifier was developed during my MPhil research at the School of Geography and the Environment and was described in Section 3.2.

The compiled data from Chapter 4 were made openly accessible through an interactive web-based platform—Tree Pest and Disease Explorer (https://zjuhaoranwu.shinyapps.io/forestpestexplorer/)—developed using the R Shiny package (Chang et al. 2025).

Chapter 5 examined how climate change affects the distribution of tree pests and pathogens. The specific objectives were to:

1. Compile comprehensive global occurrence data for major tree pest and pathogen species;

2. Model their potential distributions under current climatic conditions; and

3. Forecast their future distribution ranges under different socio-economic scenarios (Shared Socioeconomic Pathways, SSPs).

This analysis identified regions most vulnerable to future pest and pathogen impacts, providing crucial insights for prioritising investments in biosecurity and disease prevention strategies. To achieve these objectives, pest and pathogen occurrence data were harmonised from multiple sources, including peer-reviewed literature, government reports, and international databases. The research used basic Geographic Information System (GIS) operations (introduced in Section 3.3) and used Species Distribution Modelling (SDM) techniques to establish statistical relationships between species occurrences and climatic variables. These relationships were then used to project both current and future potential distribution ranges (see Section 3.4).

Chapter 6 investigated the consequences of tree pests and pathogens on the forest carbon sequestration potential. Using the ash dieback disease as a model system, this chapter aimed to:

1. Estimate the Europe-wide net primary production (NPP) loss and associated reduction in forest carbon sequestration potential due to ash dieback over the time course 1992–2025.

2. Compare our dynamic model against static models to understand its potential and the role of NPP in forecasting carbon dynamics under the pathogen outbreak.

3. Explore how the reduction of forest carbon sequestration potential is affected by key disease-progression characteristics, including spread rate, international trade intensity, and virulence (defined by tree mortality and defoliation levels)

This research informed global carbon budget accounting by considering pest and pathogen impacts on forests—factors currently underrepresented in existing carbon budget assessments. The results provided valuable information to sustainable forest management, disease control strategies, and nature-based climate solutions such as reforestation and afforestation programmes.

To achieve these objectives, Chapter 6 combined an epidemiological model with a forest carbon cycling model (see Section 3.6) to simulate the forest carbon dynamics under the presence of ash dieback disease. The model was fitted by tree mortality and defoliation data synthesised from Chapter 4, pathogen distribution data from Chapter 5, biomass and forest fraction data derived from satellite images (see Section 3.5).

3.2 Data synthesis with Natural Language Processing (NLP)

The scope of this thesis, including three research chapters, focuses on tree pests and pathogens that cause significant and widespread damage globally or regionally. Defining a comprehensive list of

target pests and pathogens is therefore essential for all subsequent analyses. To compile this list, multiple governmental and non-governmental sources were reviewed, including: (1) The “Pest and Disease Resources” registry by UK Forest Research; (2) The “Key Tree Pests and Diseases” registry by the UK Woodland Trust; (3) The “Terrestrial Pathogens and Diseases” registry by the U.S. Department of Agriculture (USDA); (4) The “Top Forest Insects and Diseases” registry by the Government of Canada; (5) The “Forest Damage Caused by Pests and Diseases” registry by the Japanese Forestry Agency; and (6) The “National Survey of Forestry Harmful Organisms” by China’s National Forestry and Grassland Administration. Although these resources do not cover all countries, the listed species typically exert impacts that extend far beyond their regions of origin, causing widespread ecological and economic damage. This approach ensures that the final pest and pathogen list is balanced, comprehensive, and globally relevant. In Chapter 4, this compiled list was used as a set of search queries in Web of Science™ All Databases to identify all potentially relevant publications for subsequent screening.

The initial search for tree pest and pathogen research in Chapter 4 yielded more than 10,000 papers. The next step was to identify studies containing field survey data; however, manually screening abstracts from such a large corpus is infeasible. To address this, natural language processing (NLP) techniques were used. NLP is a text-mining approach designed to extract semantic information from unstructured text, enabling tasks such as classification, clustering, and information retrieval (Kao and Poteet 2007). In NLP, each text segment—such as an abstract—is treated as a document, and a structured collection of documents used for training or evaluation is known as a corpus. Within these documents, terms refer to words or multi-word expressions. Text classification is a popular application of NLP. It aims to categorise documents into predefined corpora based on the distribution of terms within each document. The underlying principle of classifier training is that certain terms occur with higher frequency in one corpus compared to another. In the context of Chapter 4, papers that include field survey data on disease severity or tree mortality belonged to one corpus, while papers without such data belonged to the other corpus. The goal of the classifier was to automatically identify and retain the former while excluding the latter.

The Naive Bayes classifier is a computationally efficient classification algorithm widely used in text classification. It assumes that words in a document are conditionally independent given the document’s class. This assumption simplifies computation by disregarding word order and dependencies between words. Based on word frequencies, the classifier estimates the posterior probability that a document belongs to a particular class and assigns it accordingly. Its computational efficiency and relatively low requirements for training data and memory make it well suited to processing large text corpora containing thousands of unique words. Therefore, it is an appropriate method for classifying large numbers of research papers on different tree pests and pathogens.

The training data for this text classifier were derived from my MPhil research at the School of

Geography and the Environment, University of Oxford. In that study, I evaluated the impacts of ash dieback disease on ash (*Fraxinus excelsior*) populations in a typical British woodland through a systematic review of 80 field survey papers, selected from an initial pool of 339 studies. Each paper was manually screened by reading its abstract to determine whether it contained field survey data. This curated dataset—containing both field survey and non-field survey examples—served as the training corpus for the classifier used in Chapter 4. Term frequencies were calculated separately for Corpus 1 (field survey papers) and Corpus 2 (non-field survey papers), and these frequency distributions were used as predictors for text classification based on Naive Bayes theory. This approach enabled efficient, automated identification of relevant literature containing empirical field data for the systematic review.

3.3 Geographic Information System (GIS)

A Geographic Information System (GIS) is a data science technology that integrates hardware and software to input, manipulate, analyse, and visualise location-based data. Each geographic data point is projected onto a world map according to a defined and standardised geographic coordinate system. GIS enables geometry manipulation, spatial data analysis, and numerical computation once data from multiple sources are aligned within the same geographic coordinate reference system.

In Chapter 5, pest and pathogen distribution data used for species distribution modeling (SDM) were compiled from multiple sources, including peer-reviewed literature, government databases (e.g., the U.S. Alien Forest Pest Explorer), the Global Biodiversity Information Facility (GBIF), and the EPPO Global Database. Because these sources differ in spatial format and resolution, all datasets were geo-referenced to a common coordinate system before analysis. Point-based data required no further conversion, as the MaxEnt modeling software directly supports point-location input. However, image-based maps that highlight pest outbreak regions—such as county-level disease occurrence maps from the U.S. Alien Forest Pest Explorer—required conversion to geospatial data formats. These maps were first imported into QGIS 3.18.3 as PNG files and then geo-referenced to the WGS 84 coordinate system. Since outbreak regions were delineated using specific colour codes, the highlighted areas were extracted by colour selection to produce a binary raster map. Alternatively, outbreak regions could be manually delineated by tracing their boundaries, resulting in vector polygons. In either approach, a regular point generation algorithm was then applied to convert the identified outbreak areas into evenly spaced occurrence points, ensuring compatibility with point-based SDM analyses.

3.4 Species Distribution Modelling

Species Distribution Modelling (SDM) establishes quantitative relationships between observed species occurrences (or abundances) and environmental variables, and uses these relationships to

predict potential distributions in unsampled regions or to project future ranges under changing climatic conditions (Elith and Leathwick 2009). SDMs play a central role in both fundamental and applied research in ecology and biogeography (Araújo and Guisan 2006). The key theoretical foundation of SDM is the concept of the ecological niche. A species' niche represents a multidimensional environmental space defined by the set of conditions under which the species can survive and reproduce. This is referred to as the fundamental niche, which differs from the realised niche, the subset of the fundamental niche that a species actually occupies in nature, constrained by factors such as dispersal limitation, interspecific competition, and predation.

SDMs have become increasingly important for studying biological invasions, assessing the effects of climate change on invasive species, and guiding conservation and biosecurity priorities (Srivastava et al. 2019). In Chapter 5, the MaxEnt algorithm (Phillips et al. 2006) is used to model the relationships between pest and pathogen occurrences and climatic variables, and to predict their potential future distribution ranges under different climate scenarios. MaxEnt is a widely used species distribution modelling tool, including in studies predicting the distributional shifts of tree pests and pathogens. Chapter 5 used MaxEnt to project future changes in the geographic distributions of tree pests and pathogens. This choice ensures methodological consistency with existing research in this field, thereby facilitating comparisons between studies.

However, the interpretation of SDMs requires caution, as sampling data are often incomplete and subject to spatial or taxonomic bias (Jarnevich et al. 2015). As shown in Chapter 4, research on tree pests and pathogens was heavily concentrated in the Global North—particularly in Europe, the United States, Canada, and Japan. For instance, many forest pests have emerged in the United States since 2000 and are currently restricted to North America. Consequently, SDMs trained solely on these data may predict future distributions limited to this region, even though these species could potentially establish elsewhere if introduced. Thus, SDM outputs should not be interpreted as definitive boundaries of potential spread.

Another critical consideration is whether SDMs accurately capture the biological reality of the modeled species (Jarnevich et al. 2015; Lee-Yaw et al. 2021). While environmental variables are often selected based on their percentage contribution to model performance—a statistically valid approach—such selection may not necessarily reflect biological relevance. From an ecological and physiological perspective, it is recommended that variables be chosen based on their direct influence on species' eco-physiological tolerances and life history traits (Jarnevich et al. 2015).

3.5 Remote Sensing (RS)

Remote sensing is a technique for collecting information about objects or phenomena from a distance, typically using sensors mounted on aircraft or satellites (Campbell and Wynne 2011). Remote sensing

data are multidimensional, typically stored as images, HDF files, or other structured data objects. Each pixel in an image represents two spatial dimensions (longitude and latitude), a temporal dimension (the acquisition time), and one or more spectral dimensions corresponding to the wavelengths measured, known as bands. A band refers to a specific range of wavelengths in the electromagnetic spectrum that a sensor uses to collect data, such as the red, green, blue, or near-infrared (NIR) bands. Most sensors capture data in multiple bands to better characterise surface features.

The resolution of a remote sensing image defines its level of detail. Spatial resolution refers to the ground area represented by each pixel (e.g., a 500 m resolution image means each pixel represents a 500 × 500 m area). Temporal resolution describes the time interval between successive observations of the same location—particularly relevant for satellites that periodically revisit specific areas. Spectral resolution refers to the number and width of spectral bands measured, determining the sensor's ability to distinguish between different wavelengths of electromagnetic energy.

Many remote sensing data products available in public archives are derived from raw imagery and often combined with ancillary information such as ground surveys. After image acquisition, preprocessing is required to correct for radiometric, geometric, and atmospheric effects, as data quality can be influenced by factors including sensor motion, atmospheric conditions, and illumination variability (Sowmya et al. 2017). Image enhancement techniques—such as brightness, contrast, and sharpness adjustments—are then applied to improve visual interpretation (Sowmya et al. 2017; Ablin et al. 2019). Subsequent image transformation combines and manipulates spectral bands to emphasise particular surface features (Kamusoko 2019). A commonly used index that combines multi-band information is the Normalised Difference Vegetation Index (NDVI), and its theory is as follows: Different materials on Earth's surface reflect and absorb electromagnetic radiation uniquely across wavelengths, creating characteristic spectral signatures (Xie et al. 2008). For instance, healthy green vegetation strongly reflects near-infrared light (NIR) due to chlorophyll and absorbs much of the red and blue light for photosynthesis. Consequently, researchers calculate NDVI as (NIR – RED) / (NIR + RED) to quantify vegetation cover. High NDVI values indicate healthy vegetation (e.g., forests, crops), while low values correspond to non-vegetated surfaces such as bare soil, urban infrastructure, water, or snow. Other commonly used transformation indices include the Enhanced Vegetation Index (EVI), Normalized Difference Water Index (NDWI), and Normalized Burn Ratio (NBR).

A key application of remote sensing is land cover classification. In Chapter 6, the MCD12Q1.061 MODIS Land Cover Type Yearly Global 500 m product (Friedl et al. 2010) was used to identify forested areas. Because different surface materials have distinct spectral signatures, classification algorithms can categorise pixels into vegetation, water, soil, snow, infrastructure, or other land types based on spectral values across all bands. A range of algorithms—such as Random Forest, Support

Vector Machine (SVM), and Artificial Neural Network (ANN)—are used for land classification with varying accuracy (Talukdar et al. 2020). The MODIS Global Land Cover product, for example, uses a supervised classification approach, trained and validated with reference site databases, to generate 17 International Geosphere-Biosphere Programme (IGBP) land cover classes (Friedl et al. 2002). Other recent high-resolution products include the WorldCover dataset (10 m resolution for 2020–2021) based on Sentinel-1 and Sentinel-2 data (Zanaga et al. 2022), and GLC_FCS30D, a 30 m global land cover dynamics dataset derived from Landsat imagery using a spatiotemporal refinement algorithm and validated with 84,526 global samples (Zhang et al. 2024). Accurate land cover classification, particularly the identification of forested areas, is essential in Chapter 6 for estimating forest carbon loss.

In addition, ecosystem productivity data products are used in Chapter 6 to quantify the total carbon fixed through photosynthesis. Remote sensing–based Gross Primary Productivity (GPP) estimation typically use several approaches (Zhu et al. 2024): (1) Empirical models, establishing statistical correlations between vegetation indices and observed GPP; Light Use Efficiency (LUE) models, estimating GPP as the product of photosynthetically active radiation (PAR), the fraction of absorbed PAR (fPAR), maximum LUE, and environmental scalars, with fPAR often approximated by NDVI; (2) Light Use Efficiency (LUE) models, estimating GPP as the product of photosynthetically active radiation (PAR), the fraction of absorbed PAR (fPAR), maximum LUE, and environmental scalars, with fPAR often approximated by NDVI; (3) Process-based models, simulating carbon, water, and energy exchanges within ecosystems; and (4) Machine learning approaches, integrating multi-source environmental data. For instance, the MOD17 GPP product estimates GPP using an LUE model calibrated with data from a global network of 352 eddy covariance (EC) flux towers (Endsley et al. 2023). Net Primary Production (NPP) is then derived by subtracting maintenance and growth respiration from GPP (Endsley et al. 2023). In Chapter 6, MOD17A3HGF V6.1 NPP data for 2002–2021 (Running and Zhao 2021) will be used to estimate baseline NPP, from which the NPP reduction attributable to ash dieback will be subtracted to quantify its impact on ecosystem productivity. This product was selected for three reasons: (1) its temporal coverage aligns well with the period during which ash dieback became widespread; (2) its spatial resolution of 500 m is sufficiently fine to model disease dynamics across large geographic areas; and (3) MODIS provides regular, global land-surface coverage, ensuring broad and consistent spatial coverage for the analysis.

The WorldClim v2 dataset used in Chapter 5 also integrates satellite data with weather station observations. It incorporates monthly temperature (minimum, maximum, and mean), precipitation, solar radiation, vapor pressure, and wind speed data from 9,000–60,000 stations, interpolated globally using covariates such as elevation, distance to the coast, and three satellite-derived variables: maximum and minimum land surface temperature, and cloud cover obtained from MODIS (Fick and

Hijmans 2017). Incorporating satellite data improved temperature prediction accuracy by 5–15% (Fick and Hijmans 2017).

Finally, Google Earth Engine (GEE) is a cloud-based platform for large-scale geospatial analysis and remote sensing applications. It supports research on deforestation, drought, natural disasters, food security, water management, climate monitoring, and environmental protection (Gorelick et al. 2017). Many datasets used in this thesis, including MODIS land cover and GPP products, can be accessed, processed, and visualized directly on GEE. Its powerful cloud computing infrastructure enables efficient handling of massive geospatial datasets without the computational and memory constraints of local systems. In this thesis, GEE was used in Chapter 6 to access and download remote sensing datasets.

3.6 Ecosystem Modelling

Ecosystem modelling used mathematical and computational tools to represent complex ecological systems, enabling researchers to understand and predict how species, populations, communities, and entire ecosystems respond to environmental change and disturbances. It also supports decision-making by allowing comparison of alternative management strategies through scenario analysis (Geary et al. 2020). Ecosystem models vary widely in scope and detail. Some focus on the dynamics of populations or communities while ignoring individual-level processes. Others simulate fine-scale mechanisms, such as how individual trees regenerate, grow, and die, and how these biological processes are influenced by environmental variables. Similarly, a model may rely on empirical relationships—such as correlations between mortality and climatic factors—or it may incorporate mechanistic detail, for example by explicitly representing how a pest or pathogen disrupts vascular tissues, extracts plant resources, damages bark or foliage, and ultimately increases the probability of tree mortality. Therefore, ecosystem models can differ substantially in complexity. There is no universal standard for the "right" level of detail; rather, a model should be as simple as possible to minimise unnecessary uncertainty, yet as complex as necessary to adequately represent the processes of interest (Kimmis et al. 2008).

To simulate pest or pathogen outbreaks, researchers use epidemiological models to characterise patterns of disease spread. For large-scale spatial dynamics, cellular automata (CAs) are frequently used (Dai et al. 2020). CAs are discrete, grid-based models in which each cell evolves through time according to a set of local, uniform rules. When a disease first emerges in a given grid cell, its neighboring cells may become infected in subsequent time steps, depending on predefined transmission probabilities. Disease spread rates can be modelled in different ways. In a simplest way, the spread rate is assumed to be constant. Sometimes, it is assumed to be dependent on population density, that is, proportional to the number of infectious and susceptible individuals. This approach is

known as a compartmental model, in which individuals transition among discrete states or "compartments". The classic structure includes S (susceptible), I (infectious), and R (recovered), and may also incorporate additional states such as exposed (latent) or dead (Brauer 2008). In addition to local spread, long-distance dispersal must often be considered, particularly for tree pests and pathogens that are transported through trade and human movement (Strona et al. 2020). Chapter 6 will use a CA model to simulate the spread of ash dieback. The model can capture local pathogen dispersal and transmission between host populations in neighbouring grid cells, as well as long-distance dispersal across non-adjacent grids associated with international transport and trade. By explicitly representing the spatial and temporal dynamics of disease spread, the CA model will also enable the mapping of pathogen invasion pathways and the assessment of how the resulting NPP reduction evolves across geographic space and over time.

Forest carbon dynamics are commonly simulated using Dynamic Global Vegetation Models (DGVMs), which are process-based, computer-driven tools designed to represent vegetation structure, distribution, and the cycling of carbon and water under changing environmental conditions, including climate change, elevated CO_2 concentrations, land-use change, and disturbances (Schulze et al. 2018). DGVMs simulate carbon stocks and fluxes among vegetation, soil, and the atmosphere, ultimately estimating the carbon sequestration potential of forests. At each time step, the vegetation carbon pool is increased through net primary production (NPP), while a portion of carbon is transferred to the soil via litterfall and other dead plant materials, such as twigs and branches. The soil organic carbon pool is replenished by these vegetation-to-soil fluxes, but carbon is simultaneously lost through heterotrophic (soil) respiration. DGVMs also vary in complexity. At a basic level, they may represent only these core carbon fluxes. More advanced models incorporate detailed ecophysiological processes, including photosynthesis, autotrophic respiration, transpiration, tissue turnover, and competition for light and nutrients. Well-known examples include the Lund-Potsdam-Jena (LPJ) model (Smith 2001), Ecosystem Demography model (ED2) (Medvigy et al. 2009), and the Joint UK Land Environment Simulator (Best et al. 2011; Clark et al. 2011).

In Chapter 6, an epidemiological model coupled with a forest carbon dynamics model was developed to quantify reductions in carbon sequestration potential driven by a pathogen outbreak. Pathogen spread was simulated using a CA framework within a spatial grid system, enabling representation of local transmission dynamics. Probabilistic long-distance dispersal events were also incorporated to capture the effects of international transport and trade. Empirical relationships between disease progression, tree defoliation, and mortality—synthesised in Chapter 4—were used to parameterise the model. The dynamics of vegetation and soil organic carbon pools were then simulated to estimate changes in net ecosystem productivity (NEP).

3.7 **Data Dependencies**

The data dependencies across three research chapters are explicitly shown in Figure 3.7:

(1) The database developed in Chapter 4 includes a geographic map of tree pest and pathogen research. This map reflects where tree pest and pathogen research efforts are concentrated, and is used in Chapter 5 for correct sampling bias for species distribution modelling. Without sampling bias correction, the species distribution model implicitly assumes that the modelled species can be sampled by researchers with equal probability, with leads to the result that regions where the modelled species is not studied are tend to be predicted as unsuitable habitats.

(2) The output of the species distribution model for ash dieback disease in Chapter 5 is used as an input to confine the extent of the epidemiological model in Chapter 6. To model the disease spread and the subsequent forest NPP reduction, the model has to be confined in regions where ash dieback does occur. Therefore, the model is confined to regions where both the pathogen and the host tree are available. This region is predicted by MaxEnt model using the pathogen's and the host's presence-only data. In addition, predicted distribution data for common ash is also used as an approximate for the abundance of ash trees in forests.

(3) The disease severity (primarily tree crown defoliation) and tree mortality metrics collected in Chapter 4 for ash dieback are used in Chapter 6. These data are used to generate a curve describing how the crown defoliation rate and tree mortality rate change over time since a forest is infected by the ash dieback fungus. With the predicted crown defoliation rate and tree mortality rate, the reduction of NPP can thus be calculated.

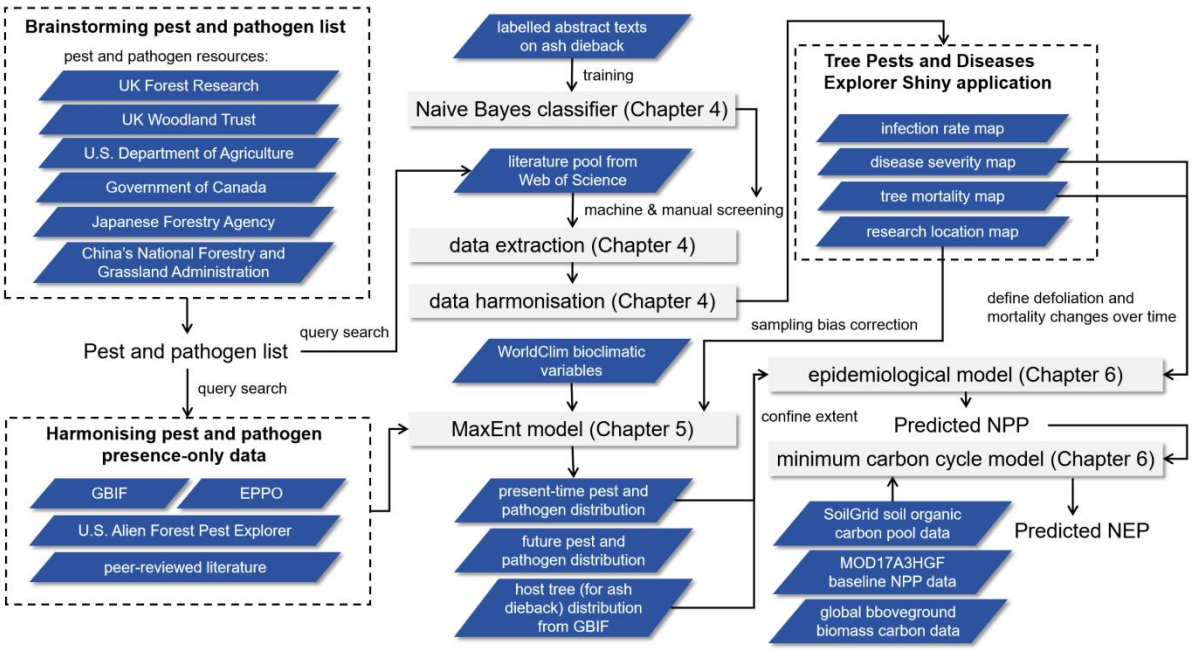


Figure 3.7. Flow chart showing the data dependencies across three research chapters. The blue diamond text boxes represent data resources or datasets, either in a form of literature or a geographic map that can be visualised through GIS. The gray shaded text boxes represent specific methods used in the research, with Chapter number attached.

3.8 Key Assumptions and Uncertainties

Chapter 4 is based on four main assumptions: (1) the language used in the abstracts of research papers on tree pests and pathogens contains sufficient information to identify whether a paper reports field survey data; (2) a text classifier trained on abstracts of ash dieback research papers, based on the first assumption, can be generalised to research papers on other tree pests and pathogens; (3) peer-reviewed field survey data on disease incidence, severity, and tree mortality are generally reliable and can therefore be synthesised into a global database that characterises the impacts of tree pests and pathogens; and (4) a systematic review of English-language publications indexed in the Web of Science database can capture a substantial proportion of the published evidence on tree pests and pathogens that threaten northern temperate forests. The main sources of uncertainty in the analyses are: (1) classification errors arising when papers on particular tree pests or pathogens describe field survey data using specialised terminology or phrasing that the text classifier fails to recognise, resulting in relevant survey data being overlooked; (2) publication bias and uneven research coverage, as research efforts are concentrated in the Global North, while studies conducted in developing countries and published in languages other than English may be underrepresented, leading to the omission of some field survey data; and (3) inconsistencies in data collection protocols across field surveys, particularly for subjective measures such as the severity of tree damage caused by pests and pathogens.

The main assumptions underlying Chapter 5 are as follows: (1) niche conservatism: the climatic and ecological niches of tree pests and pathogens do not evolve rapidly over the modelling period, and their temperature and precipitation tolerances remain relatively stable; (2) distributional equilibrium: the current distributions of tree pests and pathogens are sufficiently close to climatic equilibrium and are not undergoing rapid changes that would substantially undermine model predictions; (3) climatic dominance: climate is a primary determinant of the geographic distributions of tree pests and pathogens, while the effects of host–pathogen interactions and dispersal limitations are assumed to be comparatively less influential; (4) representativeness of occurrence data: distribution records compiled from multiple sources, including EPPO, governmental databases, and peer-reviewed publications, adequately represent the geographic occurrences of tree pests and pathogens; and (5) representativeness of research effort: the database constructed in Chapter 4 provides a reasonable proxy for spatial variation in research and sampling effort, allowing a bias raster to be developed to account for sampling bias in GBIF and other major distribution data sources. The main sources of uncertainty in Chapter 5 include: (1) Temporal mismatch between species occurrence records and bioclimatic data: Chapter 5 will use historical WorldClim bioclimatic data representing the period 1970–2000 for species distribution modelling, whereas many tree pest and pathogen species became widespread or began causing substantial damage primarily after 2000. Because historical temperatures

were generally lower than those experienced in recent decades, this temporal mismatch may lead models to overestimate the cold tolerance of these species and, consequently, their potential distributions in colder regions. To address this limitation, the study assumes that the spatial distribution of occurrence records collected after 2000 is broadly comparable to that of records collected before 2000, such that the combined occurrence data can be used with the historical bioclimatic baseline; (2) Sampling bias in occurrence data: although a bias raster can partially account for uneven sampling effort in GBIF and other distribution data sources, residual sampling bias may remain. Furthermore, uncertainties originating in Chapter 4, including publication bias and text-classification errors, may propagate into the species distribution models developed in Chapter 5 through the bias correction procedure; (2) Changes in geographic distributions: new colonisation events and ongoing range expansions may cause the distributions of tree pests and pathogens to diverge from those represented by historical occurrence records; (3) Host availability and resistance: tree pests and pathogens depend on the presence of suitable host trees for survival and establishment. Therefore, they cannot establish in areas where host trees are absent or where the available host trees exhibit resistance to the pest or pathogen; (4) Climate model uncertainty: differences in climate projections generated by alternative global climate models (GCMs) may lead to divergent estimates of future climatic suitability; and (5) Socioeconomic pathway uncertainty: alternative Shared Socioeconomic Pathways (SSPs) represent different trajectories of socioeconomic development, greenhouse gas emissions, and environmental change, resulting in different future climate projections and, consequently, different estimates of the potential geographic distributions of tree pests and pathogens.

Chapter 6 is based on five main assumptions: (1) the spread of ash dieback can be represented by short-distance dispersal driven by the movement of pathogen spores and long-distance dispersal associated with international transport and trade; (2) changes in tree canopy defoliation and tree mortality rates can be described using logistic functions of the time elapsed since infection; (3) the effects of interannual climate variability and changes in atmospheric CO_2 concentrations on vegetation dynamics and soil organic carbon pools are negligible relative to the impacts of ash dieback outbreaks; and (5) the turnover rates of vegetation and soil organic carbon pools remain constant throughout the simulation period. The main sources of uncertainty in Chapter 6 are as follows: (1) uncertainty in the tree canopy defoliation and mortality curves derived from Chapter 4. Publication bias and inconsistencies in field survey protocols may affect the reliability of these curves and, consequently, the modelled impacts of ash dieback on ecosystem carbon dynamics; (2) uncertainty in the geographic boundary of the disease spread model, which is constrained by the predicted distribution of the ash dieback pathogen (*Hymenoscyphus fraxineus*). Bias in the species distribution models developed in Chapter 5, potentially arising from biases in pathogen occurrence data, may therefore propagate into the spatial extent of the simulations in Chapter 6; (3) a potential

detection lag between the pathogen's actual arrival at a location and its first reported occurrence, which may introduce uncertainty into the timing and reconstruction of disease spread; (4) sampling bias in the host tree distribution data used to estimate common ash abundance through species distribution modelling; (5) the omission of other ecosystem processes, including drought, forest management practices, and biotic interactions, which may interact with ash dieback and alter forest carbon dynamics; and (6) uncertainty in the MOD17A3HGF V6.1 NPP data, potentially arising from biases in meteorological inputs and errors in land-cover classification.

3.9 Data and Code Availability Statements

The web-based tree pest and pathogen database developed in Chapter 4 is available at https://zjuhaoranwu.shinyapps.io/forestpestexplorer/. Analysing code for Chapter 4 is available at https://oxris.ox.ac.uk/viewobject.html?cid=1&id=2466247. Data and analysing code for Chapter 5 is available at https://oxris.ox.ac.uk/viewobject.html?cid=1&id=2466277. Data and analysing code for Chapter 6 is available at https://oxris.ox.ac.uk/viewobject.html?cid=1&id=2466358.

4. A machine-learning text-mining framework for large-scale synthesis of heterogeneous scientific literature: a case study of forest pests and pathogens

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Statement of authorship: HW designed and implemented the project, as well as data analysis. HW and CZ implement data collection from peer-reviewed tree pest and pathogen surveys. HW wrote the manuscript with significant contributions from CALD and advice from YM.

Keywords: invasive forest pest; disease outbreak; ecological monitoring; emerging infectious disease; forest conservation

Data accessibility statement: Data used in this paper is openly accessible at a web-based interactive tool Tree Pests and Diseases Explorer (https://zjuhaoranwu.shinyapps.io/forestpestexplorer/).

Word Count (Abstract): 245
Word Count (Main Text): 3196
Reference Count: 35
Figure Count: 6
Table Count: 0
Text Box Count: 0

Abstract

Large-scale data synthesis in ecology and forestry research is severely constrained by labour-intensive manual literature screening. Here, we present a novel text mining-driven framework designed to automate the identification and extraction of field survey data from thousands of peer-reviewed publications, applied to studies on forest pests and pathogens threatening European forests. To our knowledge, this is the first study to use a text-mining-based abstract classifier to analyse the research literature on forest pests and pathogens. We trained a Naive Bayes abstract classifier on a human-labelled corpus of ash dieback studies, achieving a false positive rate of 1.27% and false negative rate of 1.54% on the training dataset, enabling highly reliable automated literature filtering. When applied to a pool of 16,355 publications covering 44 priority pests and pathogens, the text mining pipeline reduced manual screening effort by 87% and efficiently identified 472 field surveys, from which we further manually checked field survey data, and synthesised 12,933 georeferenced records of infection rate, disease severity, and tree mortality. The resulting dataset reveals strong spatial, temporal, and taxonomic biases concentrated in the Global North, with distinct continental differences in pest and pathogen impacts: Europe exhibits high infection rates while North America experiences greater tree mortality. We further developed an interactive Shiny web application, Tree Pests and Diseases Explorer (https://zjuhaoranwu.shinyapps.io/forestpestexplorer/), to openly visualise and share the synthesised data. This study demonstrates that text mining drastically accelerates evidence synthesis in forest pathology, and could help manual review in scalability and consistency. It also provides a transferable workflow for large-scale ecological research. We acknowledge that our synthesis could have geographical bias as we primarily explored English-language literature on Web of Science, focusing on UK pest and pathogen watchlists as a query set. However, the synthesised database still has the potential to support evidence-based biosecurity decision-making and enables more proactive, targeted monitoring of forest health threats in Europe.

1. Introduction

Ecological research increasingly relies on large-scale data synthesis to reveal generalisable patterns across systems, taxa, and regions (Folk and Siniscalchi 2021; Spake et al. 2022). However, the manual extraction and integration of empirical data from thousands of peer-reviewed publications remain the dominant workflow in ecological meta-analyses and systematic reviews. This labour-intensive process is prone to human error, inconsistent screening, and long working hours, severely limiting the scale, speed, and reproducibility of evidence synthesis (Westgate and Lindenmayer 2017; Haddaway et al. 2020). For research domains involving diverse taxa, heterogeneous study designs, and scattered field observations, the manual literature processing has become a major barrier to translating published evidence into actionable insights for management and policy.

Text mining and automated document classification offer a powerful solution to these challenges (Farrell et al. 2022). By quantifying word frequencies, learning statistical patterns from labelled text, and predicting the relevance of unread documents, machine learning–driven text mining can rapidly filter large literature databases, identify studies containing targeted field data, and streamline the transition from raw publications to structured datasets (Westgate and Lindenmayer 2017; Farrell et al. 2022). When integrated into systematic review frameworks, text mining drastically reduces manual screening effort, improves consistency, and enables synthesis at scales that are logistically unfeasible with fully manual pipelines. Despite these advantages, the adoption of text mining for evidence synthesis remains limited in applied ecological fields (Farrell et al. 2022), including forest health and forest pathology.

Forest pests and pathogens represent an ideal case study field for demonstrating the value of text mining–assisted synthesis. Invasive and native pest–pathogen systems are highly diverse, with hundreds of damaging agents affecting thousands of host tree species worldwide (Boyd et al. 2013; Gougherty 2023). Conventional systematic reviews in this domain require repeated searches using individual pest or pathogen names, yielding massive, unstructured literature pools that demand exhaustive manual screening. This complexity slows the assembly of global impact datasets, delays the detection of spatial and temporal outbreak patterns, and hinders cross-system comparisons needed for biosecurity and forest conservation. For threats targeting European forests, where trade and climate change drive

recurrent disease outbreaks (Dahlsjö 2023), scalable, automated evidence synthesis is especially urgent to identify high-risk pathways and prioritise monitoring.

Here, we present a novel, reproducible text mining framework designed to automate large-scale evidence synthesis from heterogeneous forest health literature. The core innovation of this work is a Naive Bayes abstract classifier trained to identify field survey data from peer-reviewed abstracts, enabling efficient filtering of tens of thousands of papers with minimal manual input. We apply this framework to a large set of publications on forest pests and pathogens threatening European forests to (1) establish a complete workflow for text mining–assisted systematic review; (2) validate classifier performance against manual screening; (3) demonstrate the production of a harmonised, spatially explicit dataset on the impacts of forest pests and pathogens, including infection rates, disease severity, and host tree mortality; and (4) highlight how automated synthesis reveals global gaps in monitoring coverage. By centring the text mining pipeline, this study provides a transferable model for accelerating large-scale data synthesis in forest pathology and broader ecology.

2. Methods

2.1. Framework overview

We developed a four-stage automated synthesis pipeline centred on text mining and supervised document classification (Figure 1):
1. Construct a labelled training corpus using manually screened papers on a model pathogen (ash dieback).
2. Train a Naive Bayes text classifier to identify abstracts containing field survey data.
3. Apply the classifier to filter a large-scale literature pool of forest pest and pathogen publications.
4. Validate the filtering result through a manual screening and extract structured field data from retained papers to produce a harmonised dataset.

This framework drastically reduces manual effort by eliminating irrelevant documents early, allowing researchers to focus only on high-value field survey studies.

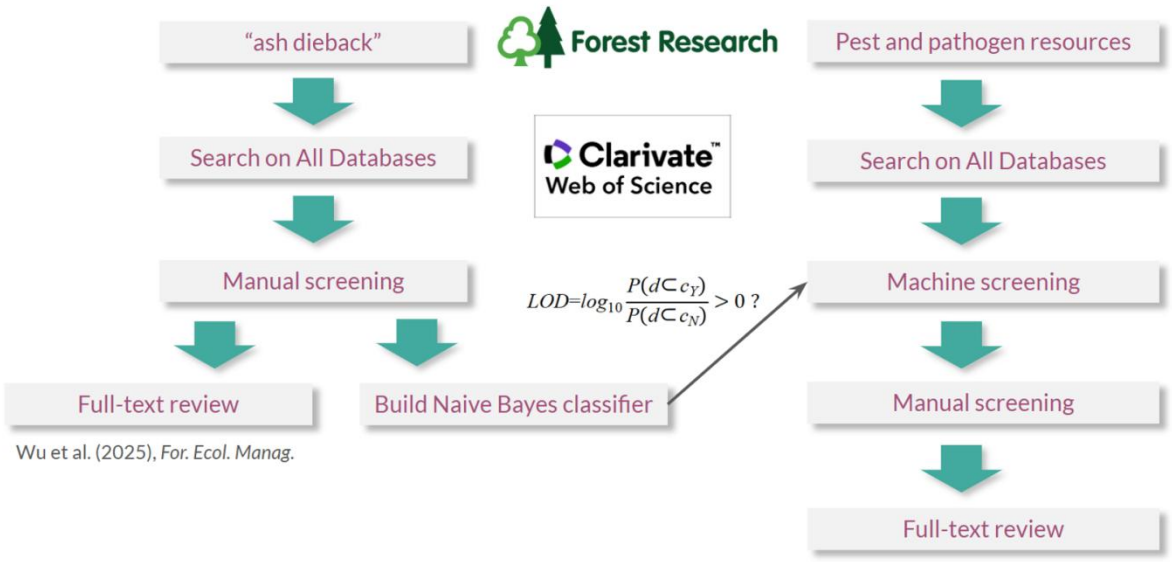


Figure 1. Framework of collecting field survey data from peer-reviewed journal articles on forest pests and pathogens.

2.2. Training corpus construction

We used ash dieback (*Hymenoscyphus fraxineus*) as a model system to build a high-quality labelled training dataset. In our previous work (Wu et al. 2025), we searched Web of Science ™ All Databases using a targeted query for ash dieback – related studies, yielding 339 publications. The search term used was 'TS = ("ash dieback" OR "*Chalara dieback*") OR (TS = ("common ash" OR "European ash" OR "*Fraxinus excelsior*" OR "F. excelsior") AND TS = ("*Chalara fraxinea*" OR "*C. fraxinea*" OR "*Hymenoscyphus albidus*" OR "*H. albidus*" OR "*Hymenoscyphus pseudoalbidus*" OR "*H. pseudoalbidus*" OR "*Hymenoscyphus fraxineus*")'. All abstracts were manually screened and labelled as:

- Y (positive): contained plot-based field survey data (mortality, defoliation, infection rate, severity).
- N (negative): focused on genetics, chemistry, modelling, or reviews without field data.

This process produced 80 positive (Y) and 259 negative (N) labelled abstracts, forming a gold-standard training corpus. This labelled corpus enabled the model to learn linguistic patterns distinguishing field survey papers from non-survey publications.

2.3. Text mining classifier design and training

We built a Naive Bayes abstract classifier—a robust, interpretable text mining algorithm widely used in document classification.

The classifier computes a log-odds (LOD) score for each abstract to estimate the likelihood that it contains field survey data:

$$LOD=log_{10}\frac{P(d\subset c_Y)}{P(d\subset c_N)}$$

where:

- c_Y = corpus of papers with field data
- c_N = corpus of papers without field data
- d = incoming unlabelled abstract

The probability of an incoming abstract belonging to a corpus is estimated as:

$$P(d\subset c)=p(w_1\in c)\cdot\ p(w_2\in c)\cdot\ \ \ldots\cdot\ p\left(w_{|V_c|}\in c\right)\cdot\ P_0(c)$$

where:

- $p(w_i\in c)$ is the probability of observing word w_i in corpus c,
- $|V_c|$ is the number of words in corpus c (vocabulary size), and
- $P_0(c)$ is a prior probability, calculated as the number of documents in corpus c divided by the total number of documents in the training dataset.

Word probabilities were estimated using Laplace smoothing to avoid zero frequencies:

$$p(w_i\in c)=\frac{count(w_i,\,c)+1}{\sum_{w\in c_Y}count(w,\,c)+|V_c|}$$

where $count(w_i,\,c)$ is the frequency of word w_i in corpus c, and $|V_c|$ is the vocabulary size.

2.4. Large-scale automated literature screening

We scaled the text mining framework for all major pests and pathogens threatening European forests. We selected 44 high-priority pests and pathogens from UK Forest Research (the research agency of the Forestry Commission (FC), the UK's principal organisation for forestry and tree-related research) and Woodland Trust (the UK's largest woodland conservation charity) watchlists (Supplementary Table S1), representing the most ecologically and economically important threats to European forests.

In August 2024, we searched Web of Science™ using all pest and pathogen common names, retrieving 16,355 publications. Duplicates and papers without abstracts were removed. The full abstract corpus was fed into the trained text classifier. The classifier scored every abstract and retained only papers with LOD > 0 (high probability of containing field survey data). Then, the retained papers were manually checked to confirm field survey availability, ultimately yielding a high-quality literature pool for data extraction.

2.5. Standardised data extraction

To ensure synthesis consistency, we extracted three core forest health metrics from full texts:

- Infection rate (%): proportion of host trees showing disease symptoms.
- Severity (%): weighted average crown damage, defoliation, or vitality scores (converted to percentage).
- Mortality (%): host tree mortality from pest or pathogen impacts.

Values were aggregated by location, host species, pathogen, and survey year using weighted averages to avoid duplicate records. All analyses were implemented in R 4.4.3.

A Shiny-based interactive web application—Tree Pests and Diseases Explorer (https://zjuhaoranwu.shinyapps.io/forestpestexplorer/)— was developed to visualise, map, and explore the spatially explicit dataset synthesised in this study.

3. Results

3.1. Validation of the text mining classifier

We first validated the performance of the Naive Bayes text classifier using the ash dieback benchmark dataset (339 publications), which had been fully human-labelled to establish ground truth. This labelled corpus served as both the training set and the independent test set, allowing direct assessment of classification accuracy against manual annotations.

We applied the trained classifier to all 339 abstracts to predict labels (Y = contains field survey data; N = no field survey data). Predicted labels were then compared to the manually assigned ground truth. The classifier achieved a false positive rate (FPR) of 1.27% on the training dataset, representing the proportion of true negative abstracts incorrectly identified as positive. It also achieved a false negative rate (FNR) of 1.54% on the training dataset, representing the proportion of true positive field survey papers incorrectly rejected as negative.

3.2. Efficiency of the text mining framework

After applying the validated classifier to the full literature pool of 16,355 publications targeting forest pests and pathogens, the literature pool was reduced from 16,355 to 2,124 papers (Figure 2). This represents an 87.0% reduction in the manual screening burden. After a further manual screening step, 472 high-quality survey papers were used for data extraction.

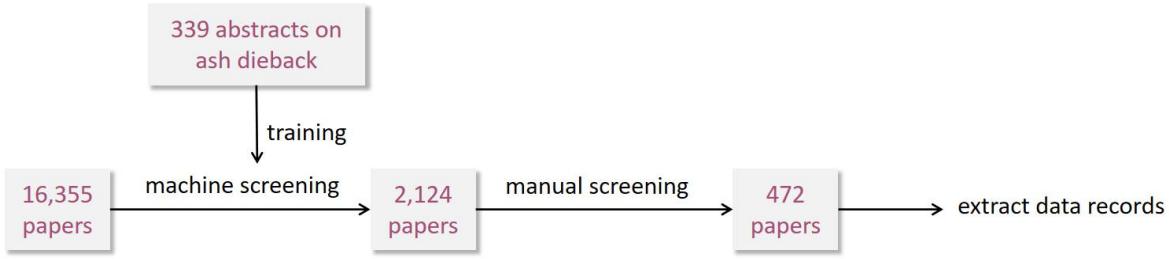


Figure 2. Flow chart of the number of papers in the literature pool before and after the screening process.

3.3. Output of the automated synthesis pipeline

The validated text mining framework, combined with final manual curation, yielded a structured, globally comprehensive dataset of forest pest and pathogen impacts. In total, we extracted 12,933 georeferenced records from 472 peer-reviewed field surveys spanning 1953 to 2024, covering 160 host tree species across 40 genera and 44 focal pest and pathogen agents threatening European forests.

Spatially, studies were heavily concentrated in the Global North, with North America (208) and

Europe (197) accounting for the vast majority of surveys, followed by Asia (59); Oceania, Africa, and South America were markedly underrepresented (Figures 3–4). Temporally, research activity rose sharply after 2000, with distinct continental trends: North America dominated surveys before 2000, particularly in eastern temperate forests, while Europe emerged as a major monitoring hotspot in the 2000s, driven by widespread outbreaks such as ash dieback; East Asia saw expanded monitoring from the 2000s onward, led by Japan and Korea (Figure 4). However, most studies remained short-term (<2 years); long-term monitoring (>20 years) comprised only 8.8% of records (Figure 3).

The dataset was dominated by surveys in natural forests (59.56%), followed by plantations and orchards (10.9%). Taxonomically, *Pinus* spp. (pines) was the most widely studied host group, associated with the highest diversity of pests and pathogens, followed by *Quercus* spp. (oaks), *Fraxinus* spp. (ashes), and *Castanea* spp. (chestnuts).

In field surveys where infection rate, disease severity, and tree mortality are reported, we could see that: Europe showed consistently high infection rates, whereas North America was associated with higher tree mortality (Figure 5–6).

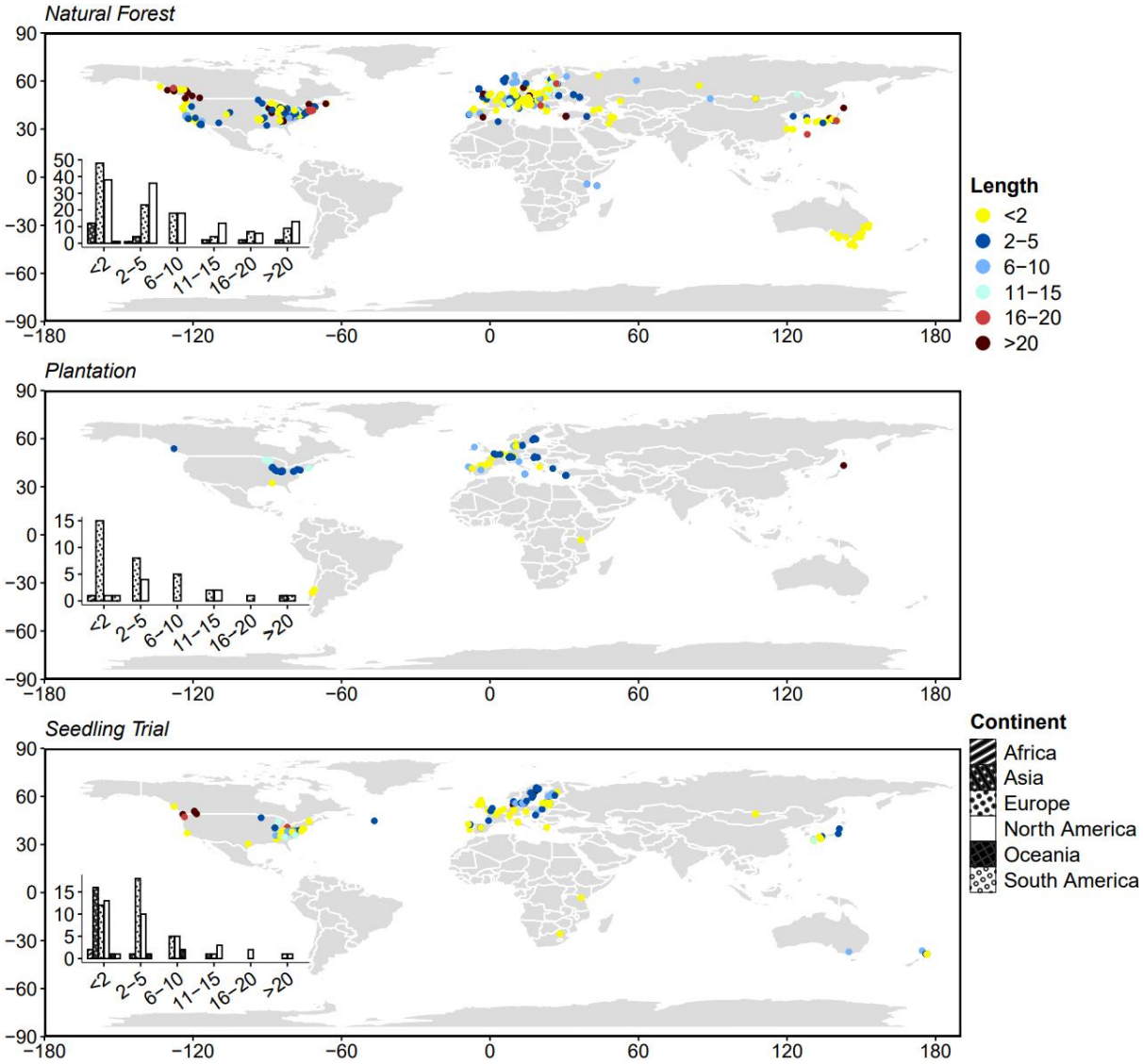


Figure 3. Length of published surveys on tree pests and pathogens. Each point on the map represents a survey, with colour indicating its duration. The accompanying bar plots show the number of surveys within each duration category, grouped by continent.

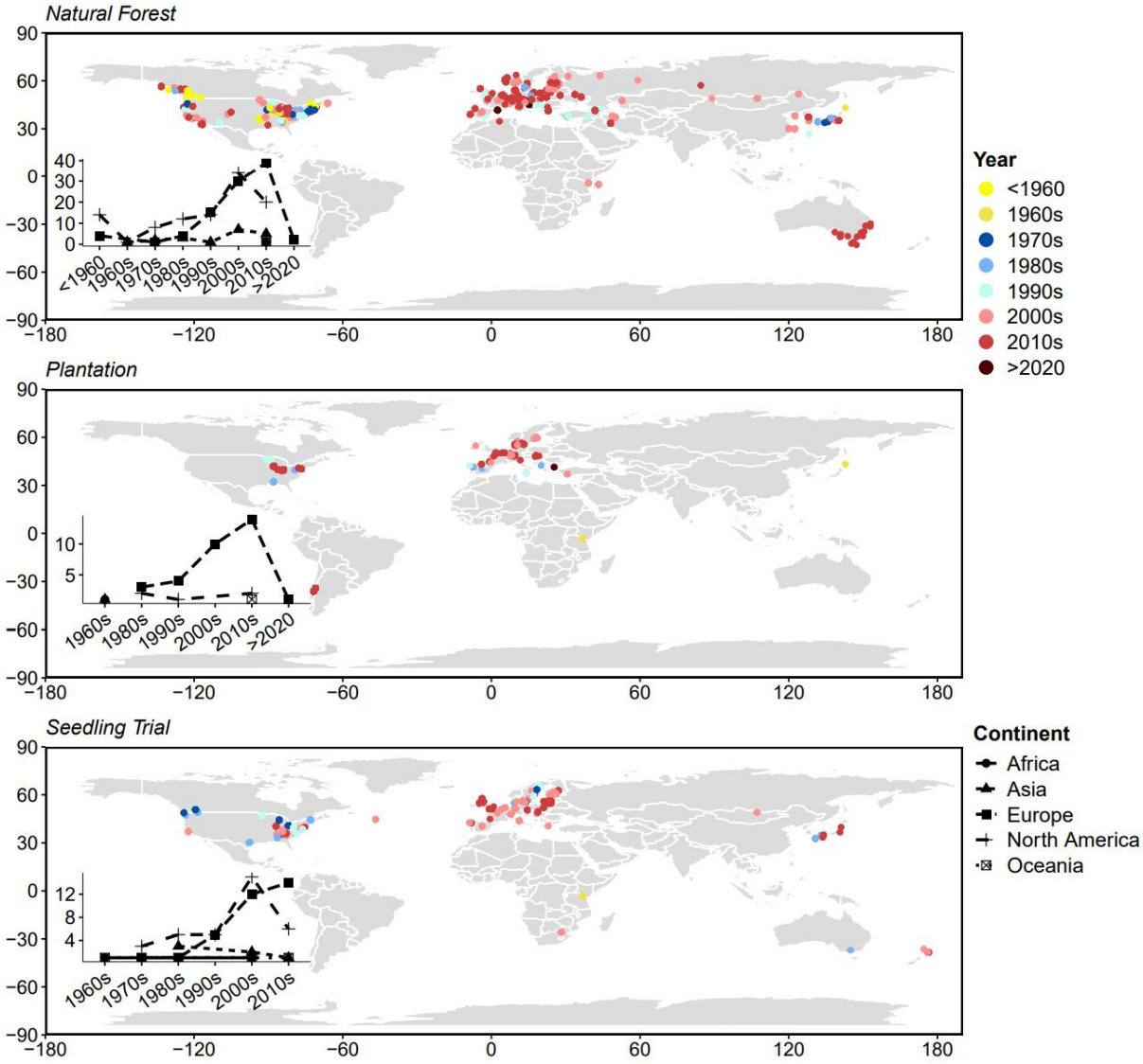


Figure 4. Geographic distribution and temporal trends of published surveys on tree pests and pathogens. Each point on the map represents a survey, with its colour indicating the year of publication. The line plots depict the number of surveys published within specific time periods, categorised by continent.

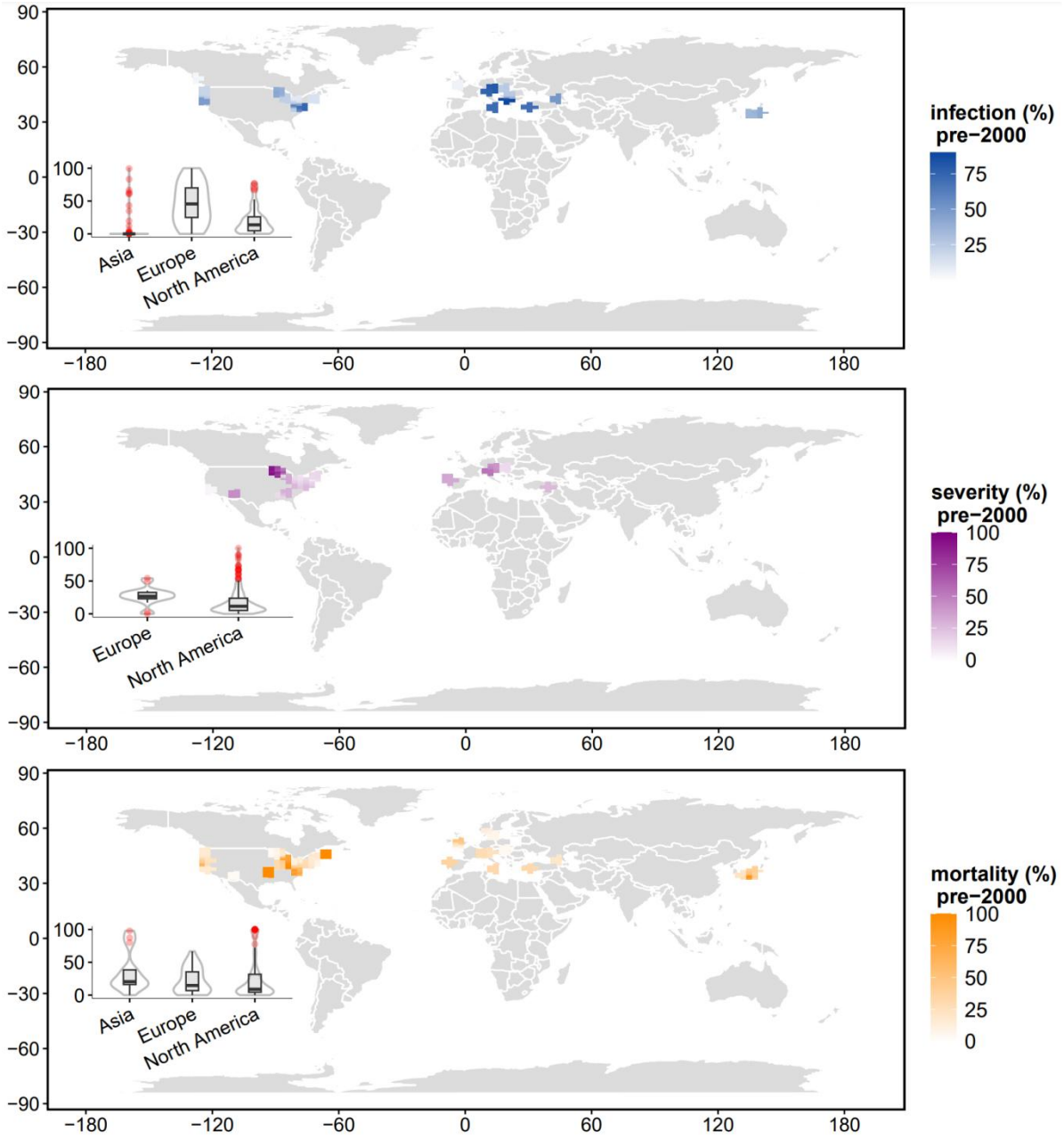


Figure 5. Geographic distribution of disease metrics—namely infection (%), severity (%), and mortality (%)—based on pre-2000 disease surveys in natural forests and plantations. Disease metric data points were mapped onto a raster grid using the ordinary kriging method. The krige() function from the gstat R package was used to automatically fit a default variogram model from empirical data, and the maximum search distance of the ordinary kriging model was set to 3 units for neighbouring point selection during prediction. The inset plots show a different set of continents in each panel because there is no survey data for certain metrics for some continents.

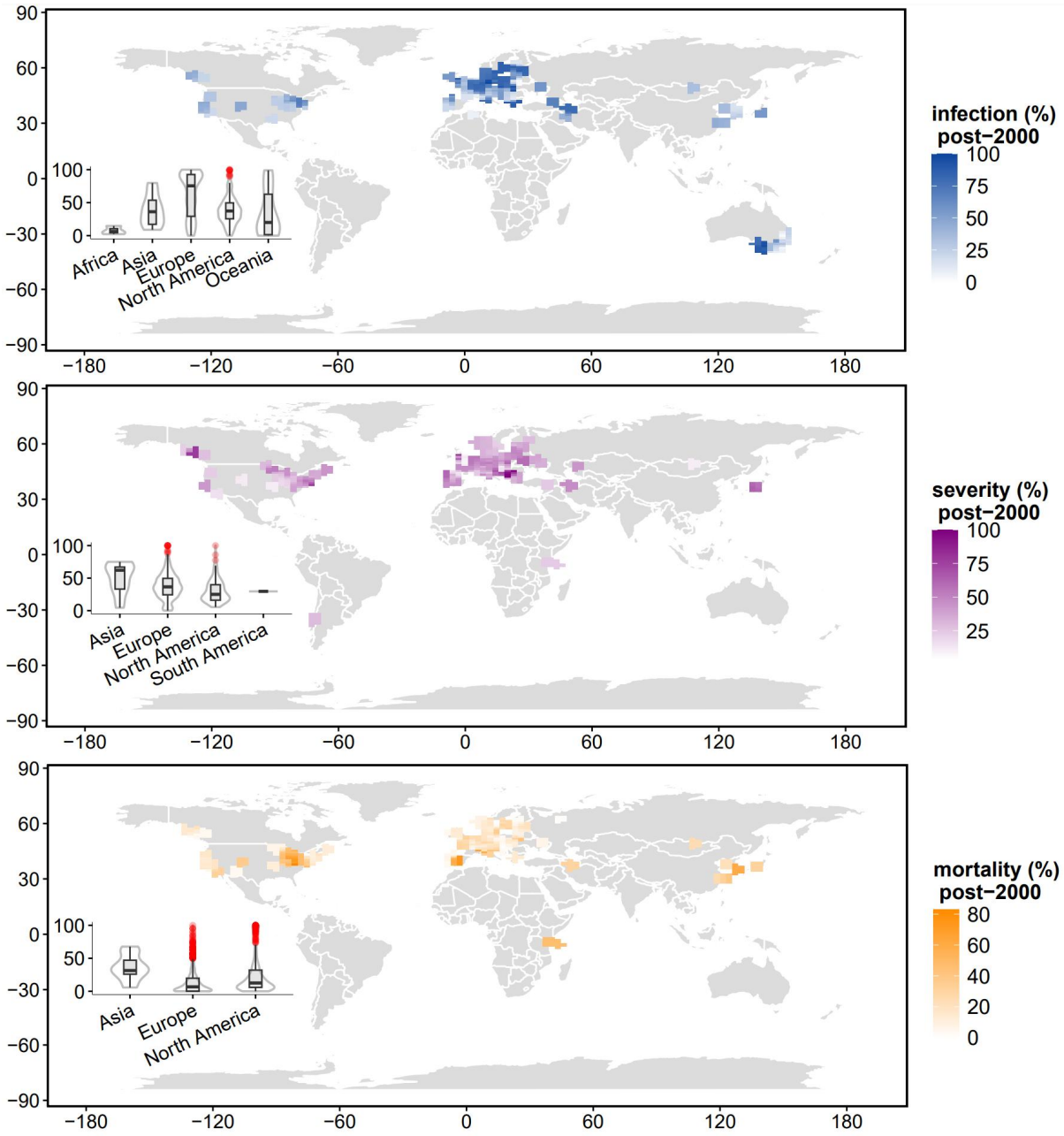


Figure 6. Geographic distribution of disease metrics—namely infection (%), severity (%), and mortality (%)—based on post-2000 disease surveys in natural forests and plantations. Disease metric data points were mapped onto a raster grid using the ordinary kriging method. The subplot shows distributions of survey values categorised by continent. The krige() function from the gstat R package was used to automatically fit a default variogram model from empirical data, and the maximum search distance of the ordinary kriging model was set to 3 units for neighbouring point selection during prediction. The inset plots show a different set of continents in each panel because there is no survey data for certain metrics for some continents.

4. Discussion

4.1. Performance, strengths, and limitations of the text mining framework

The growing volume of ecological literature and the need for large- scale evidence synthesis have made manual systematic reviews increasingly time-consuming, inconsistent, and prone to human error. Text mining offers an effective solution: when integrated into the screening process, it can substantially reduce the workload for researchers (O'Mara-Eves et al. 2015). In addition, it can even outperforms human screening to offer consistency in categorising abstracts in some cases (Goh et al. 2020).

This study establishes a scalable text mining-driven framework for automating large-scale synthesis of forest pest and pathogen field surveys, addressing a longstanding bottleneck in ecological evidence synthesis. The Naive Bayes classifier achieved exceptionally low error rates on human-labelled ground-truth data on ash dieback, demonstrating that automated abstract screening may have the potential to significantly aid manual review through reducing labour and time costs. By processing 16,355 publications and reducing the manual screening burden by 87%, this framework helps manual systematic review to increase its speed, scalability, and reproducibility, particularly for research domains involving hundreds of pest-pathogen systems and fragmented literature.

A particular strength of this approach is its transferability. Unlike custom pipelines built for a single pathogen, our classifier can be readily adapted to other taxa, disturbance types, or ecological themes by updating the training corpus and search terms. This makes the method suitable for synthesising data on invasive species, climate impacts, wildlife monitoring, and other fields where literature volume outpaces manual capacity. Furthermore, the framework retains a manual validation step after automated filtering, balancing automation with quality control to ensure only high-confidence field surveys enter the final dataset.

Despite its strong performance, the framework has limitations worth noting. First, the classifier was trained on abstracts alone and cannot access information hidden in figures, tables, or full-text methodological descriptions that might confirm field survey presence. Second, performance depends on the quality of the training data; expanding the corpus to include more pathogens, regions, or languages could further improve generalisability. Third, the approach relies on standardised terminology in abstracts (e.g., "field survey," "tree mortality," "infection rate"), meaning highly idiosyncratic phrasing may reduce classification confidence. Nonetheless, these limitations are minor relative to the efficiency gained, and they can be mitigated by incremental retraining and expanded corpus design.

4.2. Implications for European forest health and biosecurity

Beyond methodological advances, the synthesised dataset provides actionable insights for European forestry and biosecurity governance. The spatial and temporal patterns recovered by the text mining pipeline highlight the data availability on pests and pathogens that threat European forests: North America dominated early survey efforts, while Europe emerged as a global hotspot for forest pest and pathogen research after 2000. Many pests and pathogens can attack both North American and European forests, such as,the Emerald ash borer (*Agrilus planipennis*), which first caused severe impacts in North America before spreading to Eastern Europe and continuing to expand westward toward Western Europe (Baranchikov et al. 2008). Our synthesis also found that tree pest and pathogen surveys in Europe appear to report a high infection rate, while those in North America tend to report a high tree mortality, though there is no strong evidence to confirm if this reflects the real differences in pests' and pathogens' virulence in different continents. Despite this, we suggest that European forestry agencies could proactively monitor newly reported pests and pathogens in North America, especially those that target host taxa closely related to dominant European tree species, to strengthen border control, quarantine, and pre-emptive biosecurity preparedness.

The underrepresentation of field data in regions such as Asia, Africa and South America can be resulted from a sampling bias towards English-based literature, but can be also stemmed from a real data deficiency. Many high-impact threats to European forests, including pine wood nematode (*Bursaphelenchus xylophilus*), have caused severe damage in parts of Asia (Mamiya 1988; Hu et al. 2024; Lee and Kim 2025), yet consistent, plot-based field survey data from these source regions remain scarce. For instance, although we tried to search field surveys papers on pine wood nematode in China's CNKI database, even we used Mandarin Chinese as search term, we could not find relevant field surveys where monitoring data of pine woode nematode could be extracted for anlaysis. Such data gaps hinder robust risk assessment, pathway analysis and early warning for Europe. Increased research investment, expanded long-term monitoring, and tighter phytosanitary controls targeting these data-sparse regions are therefore critical to reducing the risk of unintentional introductions via trade and live plant movement.

By providing a standardised, open, and interactive dataset (via the Tree Pests and Diseases Explorer), this study supports evidence-based forest health policy at the European scale. Regular, automated updates using the text mining framework could enable near-real-time monitoring of emerging outbreaks, improving early warning and rapid response capacity.

4.3. Future directions

To maximise the impact of text mining in forest health research, we recommend three directions: First, a critical step is to expand and diversify the training corpus to improve generalisability and multilingual coverage. Our classifier was trained on a single model system (ash dieback) as a proof-of-concept, but performance and transferability can be greatly enhanced by incorporating field survey data from a broader range of forest pests, pathogens, and even other forest disturbance types (e.g., drought, windthrow, fire). Shared ecological terminology such as "tree mortality", "defoliation", and "stand damage" is consistent across disturbance studies, meaning a generalised corpus can enable the same classifier to screen literature at scale for nearly any forest impact topic. Equally important is addressing the English-language bias in current ecological synthesis (Hannah et al. 2024). Expanding the training corpus to include non-English abstracts would allow the framework to identify relevant literature across Europe, Asia, and South America more comprehensively. Multilingual text mining models are needed in conservation science to reduce geographic inequities in evidence synthesis, and a similar approach would make our framework truly global, robust to publication language, and capable of uncovering data from historically underrepresented regions.

Second, we suggest advancing beyond abstract-only screening to full-text mining and automated data extraction from tables, figures, and methodological sections. The growing availability of open-access publications removes barriers to full-text processing, allowing richer information to be captured beyond what brief abstracts provide. A major bottleneck in current synthesis workflows is the manual digitisation of data from graphs and maps; however, recent tool development in ecology now enables semi-automated and AI-assisted extraction. For example, the R package metaDigitise supports high-throughput, reproducible data extraction from figures including bar plots, boxplots, and scatter plots within standard analytical workflows (Pick et al. 2018). Similarly, WebPlotDigitizer, an interactive web tool for data extraction from figures, now includes AI-assisted features for automatic axis calibration and data point detection, drastically reducing manual effort (Rohatgi 2024). Fully integrating such tools into our text mining pipeline would enable end-to-end automation: from identifying relevant papers, to extracting numerical values, to populating a standardised database. This would allow near-real-time updates of synthesised datasets as new papers are published, transforming static systematic reviews into living databases.

Finally, we recommend integrating text-mined literature synthesis with remote sensing and forest inventory data to create a hybrid, multi-source forest health monitoring system. Text mining efficiently compiles ground observations from published field surveys, a resource that satellites often cannot fully capture due to the host-specific, patchy nature of pest and pathogen impacts. Integrating multiple data sources would benefit global forest health monitoring, enabling cross-validation

between in situ evidence and landscape-scale observations. By positioning automated literature synthesis as an important component of the ecological big-data ecosystem, we can better convert plot-level impacts to continent-wide risk maps, supporting more robust early warning systems for invasive pests and pathogens under climate and global change.

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5. Climate change drives northward range shifts in invasive forest pests and pathogens

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Statement of authorship: HW designed and implemented the project and wrote the manuscript with significant contributions and advice from JG and CALD. CZ implemented the visualisations of the model. The project is supervised by CALD and YM.

Keywords: invasive forest pest and pathogen; disease outbreak; forest conservation; global change; range shift; species distribution modelling

Data and code availability: Data and analysing code for the manuscript is available at zenodo https://zenodo.org/records/22843856.

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Table Count: 0

Text Box Count: 0

Abstract

Invasive tree pests and pathogens are increasingly threatening forests worldwide. Understanding how a warming climate and changing precipitation patterns will affect the future distribution ranges of these pathogenic species requires systematic analysis across a variety of host trees and pathogenic species. We analysed 31 major tree pests and pathogens that have caused widespread and extensive damage globally, predicting their current and future distribution under various climate change scenarios using species distribution modelling. Our results showed that tree pests and pathogens will consistently shift northward, threatening northern temperate and boreal forests between the years 2041 and 2080. On the other hand, some warmer regions, including southern Europe, were expected to experience fewer pest and pathogen outbreaks in the future. Annual mean temperature, mean temperature of the warmest quarter, precipitation of the warmest quarter, and precipitation of the driest month contributed to the species distribution models, indicating that warming temperatures and moderate precipitation may promote the survival, reproduction, and spread of the pathogenic agents. Our research highlights the need for enhanced monitoring, early pest and pathogen detection, stricter biosecurity measures, and improved silvicultural strategies in temperate and boreal forests in the northern hemisphere. Moreover, forest assessments, including those focused on carbon budgets, biodiversity, and ecosystem services, should account for the effects of tree pests and pathogen outbreaks, as they may drastically alter future functioning of forests globally.

2. Methods

1. Introduction

Tree pests and pathogens are natural components that regulate host tree population dynamics, forest nutrient cycles, and overall forest health. However, due to increasing global change and human trade, some pests and pathogens have moved beyond their native ranges, where they cause severe tree diseases, tree mortality events, and subsequent carbon loss, resulting in substantial economic losses and damage to ecosystem services (Boyd et al. 2013; Fei et al. 2019; Gougherty and Davies 2022). Currently, new records of emerging forest diseases are doubling approximately every 11 years (Gougherty 2023), with e.g., Ash Dieback and Dutch Elm Disease continuing to raise concerns (Copeland et al. 2023; Carroll 2024).

Despite their global prevalence, numerous studies suggest that tree pests and pathogens appear to be particularly destructive to northern temperate and boreal forests (Fei et al. 2019; Venäläinen et al. 2020; Forzieri et al. 2023; Wang et al. 2023). Boreal forests account for approximately 32% of the carbon sequestered in the world's forests (Pan et al. 2011), and their biomass is predicted to increase due to global warming, highlighting their importance in global timber production, forest management, and carbon policies (Xu et al. 2024). However, these forest ecosystems are relatively simple, often dominated by only a few species, which makes them especially susceptible to large-scale disease outbreaks. Tropical forests, on the other hand, have higher biodiversity which has been shown to reduce the effects of tree pests and pathogens (Ciesla 2001).

Warming trends and milder winters enable pests and pathogens to expand their ranges, reproduce more frequently, and survive in regions previously protected by cold winters (Goberville et al. 2016; Goodsman et al. 2018; Szyniszewska et al. 2024). Furthermore, forests in northern temperate and boreal zones are major hubs for timber production and international trade (Hashiramoto et al. 2004), which further promotes the spread of pests and pathogens (Ramsfield et al. 2016). It is therefore vital to assess how tree pests and pathogens are likely to spread in northern regions and to identify the most vulnerable regions.

Although studies have projected the future distribution of individual forest pests or pathogens (e.g. Watt et al. 2009; Goberville et al. 2016; Aierken et al. 2024), the cumulative climate-driven redistribution of multiple high-impact species remains poorly understood. Such a synthesis is essential as simultaneous range expansions across taxa may generate emergent disturbance regimes that disproportionately threaten carbon-rich northern temperate and boreal forests.

Here, we analyse the geographic distributions of 31 high-impact tree pests and pathogens responsible for widespread tree mortality. Using ensemble climate projections under multiple Shared

Socioeconomic Pathways (SSPs), we (1) estimate their current potential distributions, and (2) quantify projected shifts in cumulative pest and pathogen pressure through the mid- and late-21st century. By identifying regions where multiple agents are likely to converge, we aim to assess the vulnerability of global forests to future biologically driven disturbance under climate change.

2.1. Pest and pathogen selection

In this study, 31 tree-infecting pests and pathogens were evaluated (see Supplementary Table S1 for details). The compilation of this pest or pathogen list followed dual criteria: (1) the organism is documented to cause extensive, widespread, or economically important damage in at least one country or region, based on peer-reviewed literature, forest health surveys, or official reports from national forestry agencies, and (2) the organism has been formally recognised or prioritised by relevant authorities, being designated as a regulated pest or pathogen, quarantine organism, notifiable pathogen, or listed species on official forest health databases. Selection was done through a systematic review of pest and pathogen inventories from authoritative sources across major regions, including:

- The "Pest and Disease Resources" registry by the UK Forest Research
- The "Key Tree Pests and Diseases" registry by the UK Woodland Trust
- The "Terrestrial Pathogens and Diseases" registry by the U.S. Department of Agriculture (USDA)
- The "Top Forest Insects and Diseases" registry by the Government of Canada
- The "Forest Damage Caused by Pests and Diseases" registry by the Japanese Forestry Agency
- The "National Survey of Forestry Harmful Organisms" by China’s National Forestry and Grassland Administration

From these sources, we selected organisms that met our predefined criteria. While the consulted sources do not cover all countries globally, many of the documented pests and pathogens extend their damage beyond the countries hosting the source websites, thereby ensuring regional or global representativeness. For instance, the Pine wood nematode (*Bursaphelenchus xylophilus*) appears on the UK Forest Research list, although its most severe impacts have been documented in East Asia. In addition, though this list may miss organisms that cause damages in many Global South countries, it still covers major pests and pathogens in temperate and boreal forests of the northern hemisphere, and therefore, it allows us to accurately estimate the geographic shift of pests and pathogens in this region, which is the key focus of this paper.

The complete list of pests and pathogens included in the analysis is provided in Supplementary Table S1.

2.2. Pest and Pathogen Distribution Data

To model the geographic areas affected by these pests and pathogens, we compiled presence data from a range of sources, including peer-reviewed literature, government agency databases (e.g., the U.S. Alien Forest Pest Explorer), the Global Biodiversity Information Facility (GBIF), and the EPPO Global Database. Priority was given to literature that synthesises multiple data sources to generate comprehensive pest and pathogen presence datasets (see Supplementary Table S1 for details on these literary sources), with GBIF occurrence points used to supplement these primary datasets. For pests and pathogens lacking robust literature sources, GBIF occurrence data served as the primary presence dataset. All presence points were subsequently cross-validated against state- or province-level records of pest and pathogen presence from the EPPO database. A detailed account of the data collection process for each pest or pathogen is provided in Supplementary Table S1.

Some locations with recorded pest or pathogen presence may experience only minimal forest damage. For instance, the emerald ash borer (*Agrilus planipennis*) is highly destructive to several ash species (e.g. white ash (*Fraxinus americana*), black ash (*Fraxinus nigra*), green ash (*Fraxinus pennsylvanica*)) in North America and common ash (*Fraxinus excelsior*) in Europe, but its impact in East Asia, its native area, is limited due to long-term co-evolution with its host tree species there. In this paper, we excluded presence points where the pest or pathogen was documented to co-evolve with its native hosts and do not cause destructive epidemics, evidenced by peer-reviewed research papers, official websites, and EPPO database.

2.3. Climatic Data

We used the WorldClim version 2 bioclimatic variables, with a spatial resolution of 10 arc-minutes. The dataset represents average values for the period 1970–2000. The definitions of WorldClim bioclimatic variables are displayed in Supplementary Table S2.

To project the future range of pests and pathogens, WorldClim future climate data was used. The dataset consists of downscaled future climate projections from the Coupled Model Intercomparison Project Phase 6 (CMIP6). We focused on 10 arc-minute resolution bioclimatic variables for two time periods: 2041–2060 and 2061–2080.

Projection datasets were downloaded for four Shared Socio-economic Pathways (SSPs): SSP126 (sustainable and green pathway, with an anthropogenic radiative forcing of 2.6 W/m^2), SSP245 (the "middle of the road" pathway with moderate global population growth, a certain degradation of ecosystems, and an anthropogenic radiative forcing of 4.5 W/m^2), SSP370 (regional rivalry pathway, with rising inequality and an anthropogenic radiative forcing of 7 W/m^2), and SSP585 (fossil-fuelled development, with an anthropogenic radiative forcing of 8.5 W/m^2), and 11 global climate models

(GCMs): ACCESS-CM2, BCC-CSM2-MR, CMCC-ESM2, EC-Earth3-Veg, GISS-E2-1-G, INM-CM5-0, IPSL-CM6A-LR, MIROC6, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL.

2.4. Modelling Procedure

We used the Maximum Entropy (MaxEnt) algorithm to estimate both current and future distributions of pest- or pathogen-damaged areas. The MaxEnt software version 3.4.4 (Phillips, Anderson & Schapire 2006) was used to run the algorithm. For each pest or pathogen, we first ran MaxEnt using an initial set of bioclimatic variables that could potentially best describe a pest's or a pathogen's ecological tolerance: bio_1 (Annual Mean Temperature), bio_5 (Max Temperature of Warmest Month), bio_6 (Min Temperature of Coldest Month), bio_12 (Annual Precipitation), bio_16 (Precipitation of Wettest Quarter), bio_17 (Precipitation of Driest Quarter). The annual mean temperature and annual precipitation are approximates of the pests' and pathogens' suitable ecological niche to thrive. The maximum temperature of warmest month and precipitation of driest quarter represent heat and drought stress that could reduce the sporulation of pathogen species, reproduction success of pest species, but may also increase host tree vulnerability. The minimum temperature of coldest month represents cold stress in the winter, which defines the northern boundary for some pests and pathogens to survive. Precipitation of wettest quarter represents the moisture condition, which is essential for some pathogens to sporulate, spread, and infect new trees.

With the result from the initial MaxEnt model available, we then selected bioclimatic variables from them for a refined model based on four criteria:

1. Variables must have contributed at least 5% to the initial MaxEnt model incorporating six bioclimatic variables.

2. Selected variables must exhibit a Pearson correlation coefficient below 0.8 to avoid collinearity.

3. Each model must include no more than four variables, as additional variables do not significantly improve model accuracy (Goberville et al. 2016).

4. Selected variables should generally be supported by evidence from existing literature demonstrating that they constrain the biological performance of the pest or the pathogen. When such evidence is unavailable, variable contribution and permutation importance in the initial MaxEnt model are used as the primary selection criteria.

Using the filtered bioclimatic variables, we re-ran a refined MaxEnt model for each pest or pathogen to predict its current distribution range. We then projected the effects of climate change on future pest and pathogen ranges for the periods 2041–2060 and 2061–2080 under the four SSPs and 11 GCMs, utilising the WorldClim future climate dataset. For each SSP, the future pest or pathogen range was determined by averaging prediction values across the 11 GCMs.

To address uneven sampling efforts in GBIF and other occurrence datasets, we used a bias-corrected sampling approach to generate background points for the MaxEnt model. Specifically, we sampled 10,000 background points from a bias raster representing spatial variation in sampling effort, using probability-weighted random sampling. The bias raster was created based on synthesised data from the literature. In our previous work, we synthesised plot-based monitoring data of tree pests and pathogens from 472 peer-reviewed papers, selected from an initial pool of 16,355 (Chapter 4). 12,933 field survey records, spanning 1953 to 2024 and a wide range of forest pests and pathogens are used to reflect the scientific sampling intensity across the globe.

To evaluate the model performance, the presence data were split into two subsets: 75% of the data were used to build the model (training data); and the remaining 25% served to evaluate model performance (testing data). The Area Under the Curve (AUC) values on both training and testing data were calculated. The AUC values quantify the performance of MaxEnt models, with values ranging from 0 to 1. Higher values indicate better model accuracy. The calculated values for each pest's or pathogen's MaxEnt model are provided in Supplementary Table S3.

For the output format, the cloglog value (complementary log-log) was used to estimate the probability of pest or pathogen occurrence. This value represents suitability of a habitat for a pest or pathogen species.

Next, a threshold provided by MaxEnt that balances training omission and predicted area was applied to generate a binary distribution map for each pest or pathogen. These individual distribution maps were then summed to produce the final species richness map.

2.5. Calculate Pest and Pathogen Richness Map

To estimate pest and pathogen richness under both current and future conditions, we first applied spatial masks to each pest's or pathogen's prediction map to restrict calculations to relevant regions. This step was necessary because some areas predicted as suitable may correspond to regions where the pest is present but does not cause significant damage, often due to host adaptation or resistance.

Based on available information on pest- or pathogen-damaged ranges from EPPO, we restricted projections to regions within the documented invaded range to avoid unrealistic extrapolation beyond dispersal constraints. Details of the invaded range for each pest or pathogen are provided in Supplementary Table S1.

3. Results

The current global distributions of 31 major tree pests and pathogens that threaten European forests were successfully mapped (Figure 1, see individual distributions in Figure S1). North America (22

species) and Europe (17 species) were found to be hotspots, while East Asia harboured a sizeable number of pathogenic species (10 species) (Figure 1, see Figure S2 for the standard deviation of model projections across 11 GCMs).

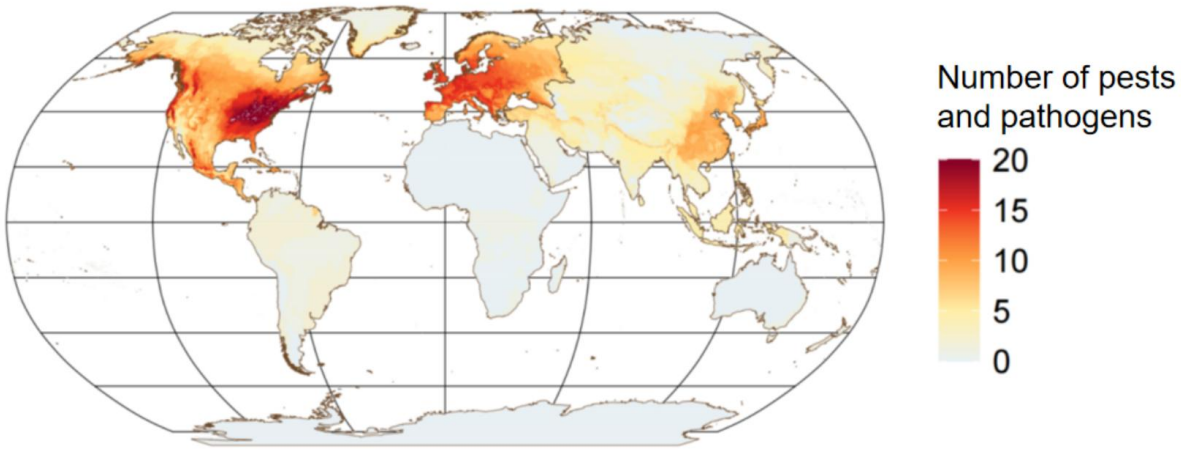


Figure 1. Modelled pest and pathogen species richness under current conditions. Presence-only data for 31 major forest pests and pathogens were used as input for the MaxEnt program. Species richness was calculated by summing the predicted distribution map for each pest or pathogen, where predicted presence regions are places with larger predicted probability of occurrence than a selected threshold. This balanced training omissions and predicted areas in the MaxEnt model.

Between 2041 – 2080 we found that pests and pathogens are expected to expand into new areas at a rate of 16,747 km^2/year (SD = 9,562 km^2/year for 11 GCMs) under the green emissions (SSP126) scenario and 59,304 km^2/year (SD = 16,179 km^2/year for 11 GCMs) under the fossil fuel (SSP585) scenario. Regardless of the climate scenario, eastern parts of North America are expected to experience the highest increase in the number of novel pests and pathogens from 2041 (Figure 2). The expansion in Europe is expected to take place in eastern and northern regions, while the current southeastern hotspot is expected to experience little increase (Figure 2). While the expansion of pests and pathogens in East Asia is projected to be limited in the near term (2041–2060), under a high emissions scenario (SSP585), we expect to see an expansion of the modelled species into large parts of north Asia during 2061–2080 (Figure 2). The predicted pest and pathogen richness is given in Supplementary Figure S3, and the changes in individual pest or pathogen distributions are shown in Supplementary Figure S4. When summarising the changes in pest and pathogen richness across the globe, we found that most regions will experience an increase in the number of pests and pathogens (Supplementary Figure S5).

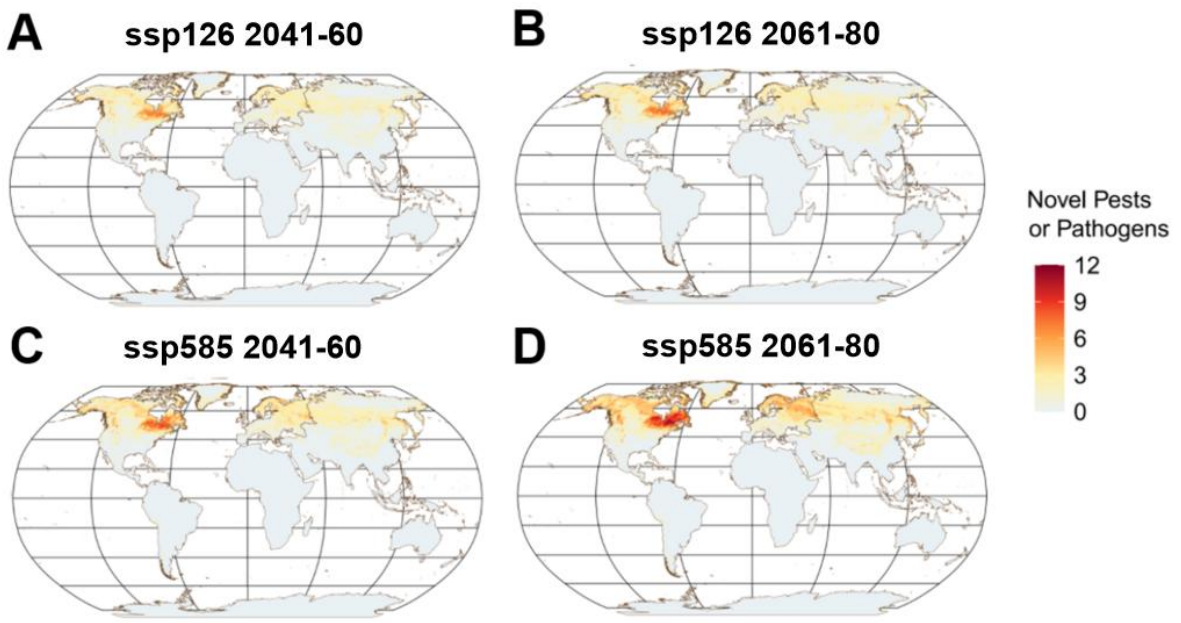


Figure 2. Number of newly emerged pests and pathogens (novel pests and pathogens) for the periods 2041–2060 and 2061–2080 under the lowest (SSP126) and highest (SSP585) emission scenarios.

The six most damaging forest pests and pathogens included in our model (*Hymenoscyphus fraxineus*, *Anoplophora glabripennis*, *Ophiostoma ulmi*/*O. novo-ulmi*, *Agrilus planipennis*, *Bursaphelenchus xylophilus*, and *Cryphonectria parasitica*) all show a consistent northward expansion in suitable habitat between 2041 and 2080 (Figure 3). Across taxa, occurrence probabilities increase in northern temperate and boreal regions, including northern Europe, Canada, and parts of western Siberia, while declining in some currently affected southern regions (Figure 4). This pattern is particularly pronounced in Europe and North America. For example, *H. fraxineus* is projected to expand into northern Europe and Scotland while retreating from southeastern Europe and southern England (Supplementary Figure S4). Similarly, *A. planipennis* and *Ophiostoma* spp. show increased suitability across Canada, Alaska, and northern Europe, indicating an elevated risk to ash and elm populations in these regions. In Asia and Eurasia, *B. xylophilus* is projected to expand into Europe and western Siberia, while *C. parasitica* shows increased suitability across northern and western Europe and the United Kingdom (Supplementary Figure S4).

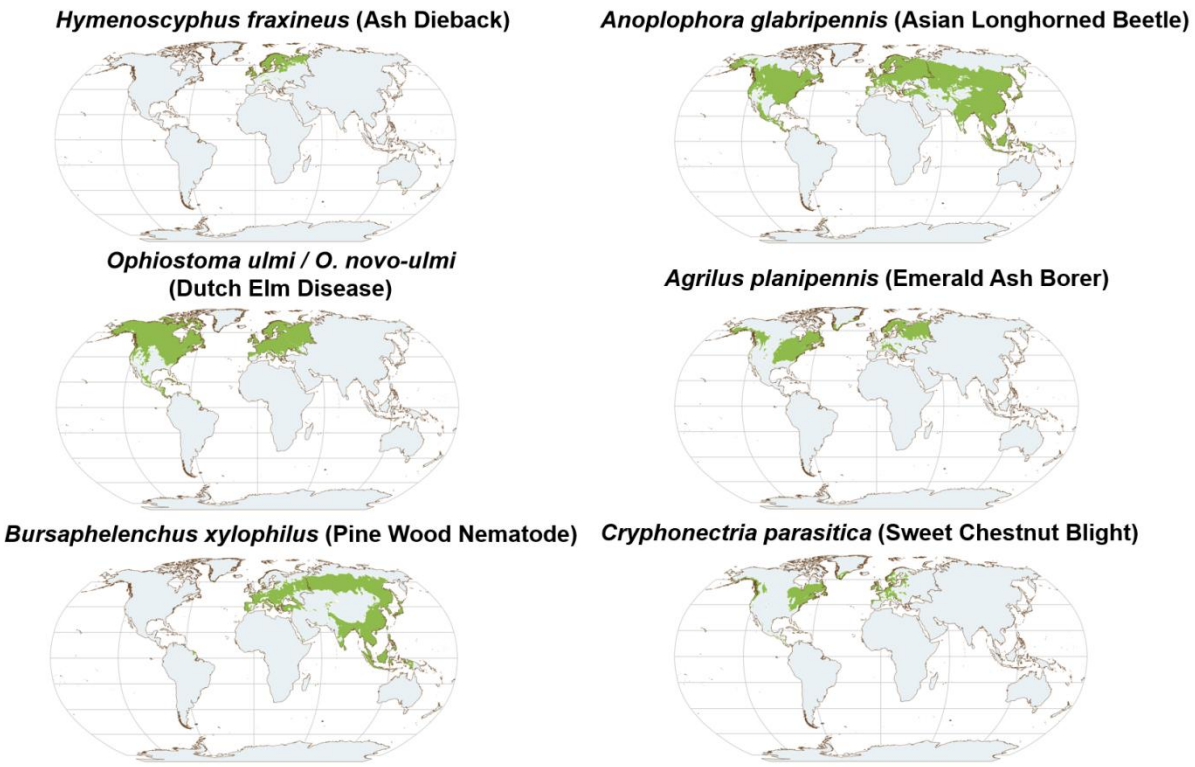


Figure 3. Projected distributions of six important pests or pathogens (*Hymenoscyphus fraxineus* (Ash Dieback), *Anoplophora glabripennis* (Asian Longhorned Beetle), *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* (Dutch Elm Disease), *Agrilus planipennis* (Emerald Ash Borer), *Bursaphelenchus xylophilus* (Pine Wood Nematode), C*ryphonectria parasitica* (Sweet Chestnut Blight)) for 2061–2080 under scenario SSP585.

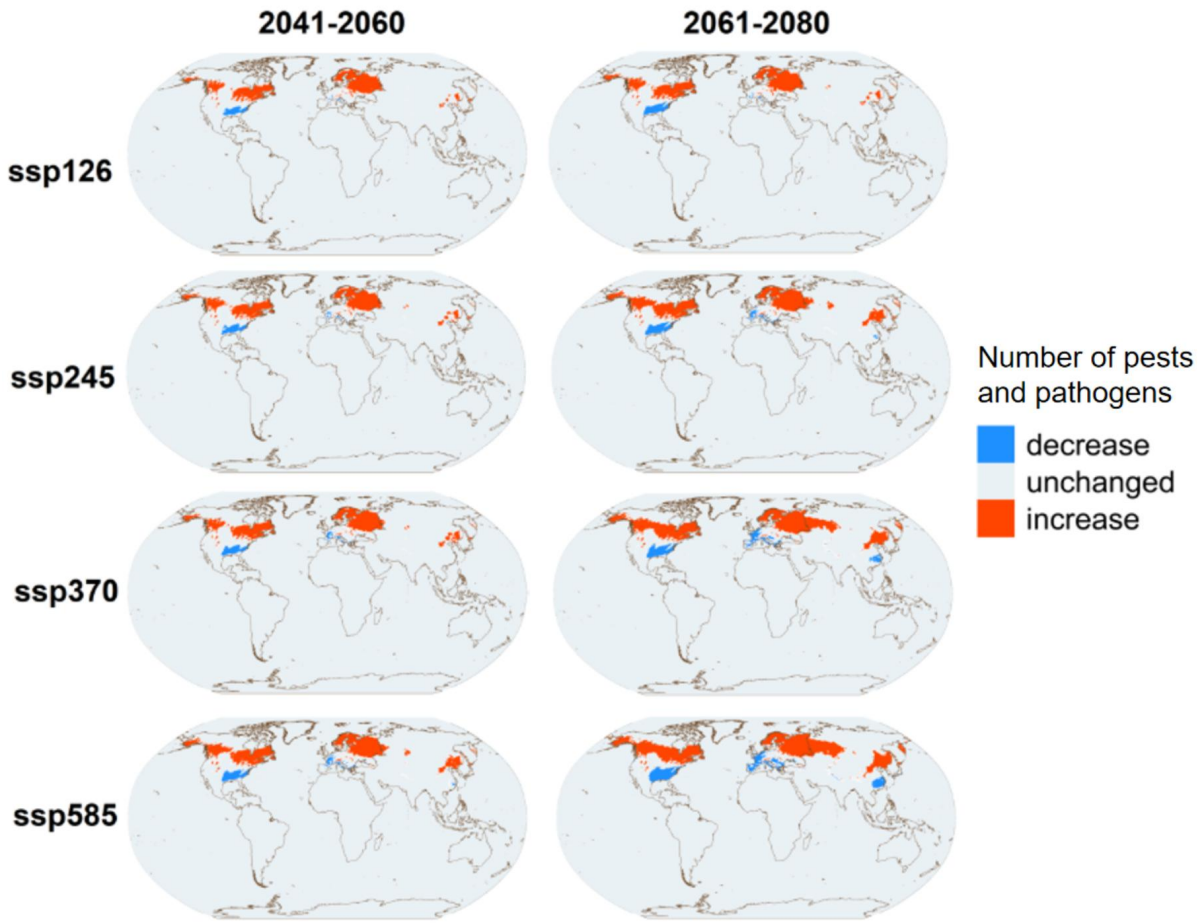


Figure 4. Projections of changes in the number of pests or pathogens for 2041–2060 and 2061–2080 under four Shared Socio-economic Pathways (SSPs): SSP126 (the most climate-positive scenario, characterised by low greenhouse gas emissions), SSP245, SSP370, and SSP585 (the most high-emission, climate-negative scenario). The number of pests and pathogens was calculated by summing the binary distribution maps of individual pest or pathogen species. Each binary distribution map was generated by applying a threshold that balances training omission and predicted area. A pest or pathogen was considered present at a given location if its predicted occurrence probability exceeded the corresponding threshold.

4. Discussion

4.1. Temperature and Northward Range Shifts

Across the provided 31 tree pests and pathogens, we detect a consistent poleward intensification of climatic suitability, suggesting a systemic redistribution of forest disturbance pressure toward northern temperate and boreal forests. Warming temperatures appear to be a key driver of this trend.

For insect pests, the rate of development increases with temperature, but declines rapidly beyond an upper thermal limits (Jactel et al. 2019). Warmer temperatures both shorten generation times and

increase the number of offspring, facilitating insect outbreaks (Jactel et al. 2019). For fungal pathogens, warmer temperatures may favour sporulation and dispersal for some species (La Porta et al. 2008). However, temperatures above 30°C can strongly limit pathogen germination and growth. At the same time, extreme heat and drought can weaken tree health, making them more vulnerable to pest and pathogen attacks (Jactel et al. 2019; Chen et al. 2024; Tabassum et al. 2024). These patterns align with our results, which show that almost all pests and pathogens analysed have increased occurrence probabilities in northern temperate and boreal regions, while probabilities decrease in the southeastern United States, southwestern Europe, and eastern China. Although the effects of temperature on the geographical range shifts of pests and pathogens are influenced by many complex factors (Jactel et al. 2019; Singh et al. 2023), we can still predict their net effect using niche-based species distribution models.

These mechanisms are consistent with the thermal biology of many tree pests and pathogens. For instance, both insect pests such as the Asian Longhorned Beetle and fungal pathogens, such as those causing Dutch elm disease, exhibit optimal performance at moderate temperatures (Zhou et al. 1984, Zhou et al. 1984, D'Arcy 2000, Straw et al. 2015), suggesting that warming conditions will enhance their spread into northern regions. In addition, warming temperature may increase drought events, thus having an indirect effect on intensifying the disease outbreaks through weaking the host trees. For example, plantations of poplars with a shortage of water were found to be attacked by Asian Longhorned Beetle, causing serious epidemics (Luo et al. 2003). These provide a mechanistic basis for the northward shifts observed in our models.

4.2. Impact of Precipitation on Pest and Pathogen Range

Many fungal pathogens generally benefit from increased rainfall and high moisture, which support spore production and transmission (Milici et al. 2020). *Hymenoscyphus fraxineus*, the pathogen responsible for Ash Dieback, exemplifies this, as it requires moist spring and summer conditions for sporulation and spread across host trees (Marçais et al. 2023). Similarly, *Cryphonectria parasitica*, the causal agent of Sweet Chestnut Blight, also depends on humid conditions for growth, spore germination, and dispersal. Elevated precipitation increases splashing and water flow, potentially enhancing the efficiency of fungal spore dispersal (Metreveli et al. 2024).

For insect pests, the effects of precipitation are complex. Moderate precipitation may support pest survival, whereas both excessive dryness and excessive wetness can negatively affect their life cycles. These hydrological extremes may also damage tree health, making host trees more vulnerable to infestation (Kolb et al. 2016; Dahlsjo and Malhi 2024). Generally, pests that primarily feed on woody tissues (e.g., moths boring into pine shoots or stems) are adversely affected by drought, whereas bark beetles, leaf chewers, miners, gall makers, and sap feeders often benefit from drier conditions (Jactel

et al. 2019). Our results indicates that many pests (e.g., emerald ash borer) require a moderate level of precipitation for egg hatching and larval survival. The Asian Longhorned Beetle, on the other hand, showed exceptionally high occurrence under extreme drought. This may have been due to a weakened host trees affected by water stress, although such a conclusion must be supported by empirical evidence.

4.3. Management Considerations

The projected northward range shifts highlight the need for strengthened forest management strategies in northern temperate and boreal regions. These include enhanced monitoring and early detection, stricter biosecurity controls on potentially infected plant material, and silvicultural practices that increase forest resilience, such as promoting tree species diversity and reducing connectivity among susceptible hosts (Dahlsjo 2023). Given that many of these pests and pathogens target economically important species, mixed-species plantations may help balance productivity with resistance to disease outbreaks.

Global forest resource assessments should also account for the effects of pests and pathogens, particularly in northern temperate and boreal zones. For example, an outbreak of spruce budworm in Canada was estimated to cause a carbon sink loss of approximately 2.87 t C ha^{-1} yr^{-1}, shifting eastern Canadian boreal forests from a net carbon sink to a carbon source (Zhang et al. 2014). In a study of ~92,000 field plots, mortality caused by 15 major non-native forest pests and pathogens in the United States was estimated at ~5.53 Tg C per year (Fei et al. 2019). Similarly, pine wilt disease, a major threat to Chinese pine forests, is estimated to cause 483.23 Tg C loss even under current climate conditions (Hu et al. 2024). To accurately assess forest carbon sinks, carbon budget models should incorporate the effects of pests and pathogens to project future forest productivity (Volney et al. 2000); however, this is still a major gap in global forest carbon accounting.

Biodiversity would also be adversely affected by pest and pathogen outbreaks due to large-scale tree mortality, which alters species competition and habitat structure (Mitchell et al. 2021). For instance, in the United Kingdom, 953 species were identified as associated with *Fraxinus excelsior* (common ash), including 1 fungus, 29 invertebrates, and 4 lichens that are obligately dependent on ash trees. Thus, substantial declines of ash trees has wider implications than tree mortality alone (Mitchell et al. 2014). Assessments of other ecosystem services, such as water retention, nitrogen cycling, flood risk reduction, and cultural values, in northern temperate and boreal forests, should also be reconsidered, particularly in high pest- or pathogen-risk areas.

4.4. Limitations

One important limitation in this study is the temporal mismatch between bioclimatic data and the species occurrence data used for MaxEnt modelling. When the baseline periods of these datasets do not align, the reliability of species distribution models may be reduced (Roubicek et al. 2010). For example, D'Amen et al. (2024) found that the temporal resolution of input data substantially influenced estimates of thermal niche overlap between Lessepsian fish in their native and invaded ranges. In the present study, the historical WorldClim bioclimatic data represent the period 1970–2000, whereas many of the epidemics considered in this study have caused substantial damage primarily since 2000. Examples include Ash Dieback, Beech Leaf Disease, Emerald Ash Borer, Laurel Wilt, and Spotted Lanternfly. Because historical temperatures were generally lower than those experienced in recent decades, using these historical climatic data may lead to an overestimation of the cold tolerance of pests and pathogens that emerged or became prominent after 2000. Consequently, their climatic niches may be estimated to extend into colder environments than they can actually tolerate. This could, in turn, lead to overestimation of both the magnitude and rate of their projected northward range shifts.

Other methodological constraints include: Firstly, the models rely on presence-only data, which may reflect uneven sampling effort despite bias correction. Geographic bias on the bias raster that is determined by synthesised tree pest and pathogen research data (Chapter 4) can propagate to species distribution modelling. Secondly, projections of species climatic suitability rely on the assumption that tree pests and pathogens have occupied all geographically and environmentally suitable areas. This equilbrium assumption can be violated for newly emerged pests and pathogens. Thirdly, the model does not account for host availability, which is essential for survival and spread of a pest or a pathogen. Areas that are suitable for pests and pathogens to invade should be areas where host trees exist. Fourthly, model projections are restricted in documented invaded continents, which mean that continents where a pest or a pathogen arrives but is not documented would be missed. Finally, the AUC values reported in Supplementary Table S3 should be interpreted with caution. The MaxEnt models in this study were evaluated using random partitioning of occurrence records into training and testing subsets rather than spatially blocked cross-validation. This approach may inflate estimates of model performance because of spatial autocorrelation among geographically clustered occurrence records. Accordingly, greater confidence should be placed in the multi-species consensus pattern than in the predicted distributional changes of individual taxa. As shown in Supplementary Figure 4, the predicted distributional changes of all individual pest and pathogen species exhibited a consistent signal of northward expansion, regardless of model performance (i.e. AUC values). This indicates that, even if we exclude or down-weighted models with low AUC values, the principal patterns displayed in Figure 4 remains unchanged.

Overall, our results indicate a consistent poleward redistribution of tree pests and pathogens, with increasing convergence of multiple high-impact species in northern temperate and boreal regions. This emerging pattern has important implications for forest resilience, as these ecosystems play a critical role in global carbon storage, biodiversity, and ecosystem services. Incorporating biotic disturbance agents into future forest assessments will be essential for accurately predicting ecosystem responses to climate change. Without such integration, projections of forest function and stability are likely to underestimate the risks posed by biologically driven disturbances in a warming world.

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6. Disease-driven suppression of forest carbon uptake rivals mortality-based estimates

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Statement of authorship: HW designed and implemented the project, and wrote the manuscript with significant contributions from CALD and HZ. HZ provides the model for simulating land carbon emission from net primary production loss. The project is supervised by CALD and YM.

Keywords: invasive forest pest; disease outbreak; forest conservation; global change; carbon sink; net primary productivity

Data and code availability: the modelling codes and the input and output data is available at https://zenodo.org/records/22858594

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Abstract

While invasive tree pests and pathogens have caused widespread tree mortality events, their subsequent impacts on reduced carbon sequestration remain poorly quantified in the global carbon budget. Previous carbon accounting methodologies have calculated forest carbon storage losses due to pests and pathogens-induced mortality, and assumed that forest net primary production (NPP) remains unchanged both during outbreaks and throughout the recovery phase. Here we consider both NPP reduction and tree mortality-caused loss of forest carbon sequestration potential. By integrating epidemiological and ecosystem models for ash dieback disease, we demonstrate that the loss of carbon sequestration potential is 39.3% high than previously thought. This overlooked carbon loss arises from nonlinear reductions in forest NPP, which are strongly influenced by pathogen spread rates and the intensity of international transport and trade. Early detection and eradication can substantially mitigate this hidden carbon source resulting from declining NPP. Once a pathogen population becomes established, however, nonlinear NPP losses become difficult to prevent; instead, mitigation strategies—such as active tree removal, planting of alternative species, and boosting resistant genotypes—can help reduce the maximum potential carbon losses caused by these pests.

Main

Forests cover approximately 30% of the Earth's land surface and generally act as a net carbon sink (Harris et al. 2021). However, intensifying global change and an increase in both natural and human-driven disturbances—including wildfires, deforestation, management practices, and biotic agents—are turning forests into carbon sources (de-Miguel et al. 2025). Invasive tree pests and pathogens pose a substantial, and growing, threat to global forest carbon stocks and production. With outbreaks doubling approximately every 11 years (Gougherty 2023), these organisms affect millions of tons of carbon annually worldwide (Seidl et al. 2018; Fei et al. 2019; Hu et al. 2024). An analysis of over 90 000 forest plots in the United States found that the 15 most damaging non-native pests caused additional tree mortality equivalent to 5.5 TgC per year (Fei et al. 2019). Similarly, a synthesis of nearly 80 000 field plots estimated that carbon sequestration by live trees was reduced by almost 13 TgC yr^{-1} from insect disturbances and pathogen outbreaks (Quirion et al. 2021). Pine wilt disease—caused by the pine wood nematode (*Bursaphelenchus xylophilus*) through Japanese pine sawyer beetles (*Monochamus* spp.)—has led to a carbon sink deficit of 1,857 TgC in northern pine ecosystems, equivalent to 18% of the total live carbon stock in European forests (Zhou et al. 2024). However, such carbon emission induced by forest disease have not been considered in the global carbon budget and vegetation modelling (Friedlingstein et al. 2025). Thus it is important to assess this carbon flux and provide a pathway for models' incorporation.

The mechanisms that a pest or a pathogen outbreak reduce forest productivity can be summarised by the following: (1) leaf defoliators, such as *Hymenoscyphus fraxineus*, the cause of European ash dieback, directly reduce photosynthesis through crown damage; (2) xylem reducers, such as the pine wood nematode, could feed and reproduce rapidly in resin ducts and cortex tissue, restricting plant water transport and subsequently transpiration; (3) phloem-feeders like the hemlock woolly adelgid (*Adelges tsugae*) divert non-structural carbohydrates; root rot diseases and root-feeding insects accelerate root turnover, increasing carbon transfer from biomass to the soil organic pool (Dietze and Matthes 2014; Estorninho et al. 2022). Despite these complexities, current estimates of forest carbon loss from pest and pathogen outbreaks are primarily based on observed tree mortality. this method assumes that carbon emission results solely from tree death and that net primary productivity (NPP) remains unaffected throughout both the outbreak and recovery periods. Examples range from models that are based on tree mortality rates from forest inventory data (Fei et al. 2019; Quirion et al. 2021) to those where static NPP parameters are considered, but in an unchanged state (Seidl et al. 2018; Hu et al. 2024).

In reality, pest and pathogen outbreaks can significantly reduce forest NPP, not only through direct tree mortality, but also via sub-lethal effects such as reduced photosynthesis, impaired growth, and

increased autotrophic respiration (Pinkard et al. 2011). For example, ash dieback contributes to the mortality of European ash (*Fraxinus excelsior* L.) where the fungus (*H. fraxineus*) colonises leaves and woody tissues, leading to necrosis, premature defoliation (Gašparović et al. 2023), and, in severe cases, blockage of water and nutrient flow in the stem (Gross et al. 2014). As a result, trees can either (1) stand defoliated, thus having smaller NPP and a reduced growth, or (2) stand as dead wood for decades, ceasing to contribute to NPP while slowly decaying and releasing carbon into the soil pool. For example, in a study on five mature woodlands in the UK, ash trees with > 75 % canopy loss due to ash dieback accounts for 27.4 % (or 20.7 Mg) of the carbon stocked by ash trees (Mailes et al. 2026). Calculations of carbon mitigation capacities of these affected forests require further reconsideration of the role of severely affected host trees.

Dynamic forest carbon modelling provides a powerful tool to simulate carbon storage, sequestration, and emission fluxes under changing environmental and disturbance regimes, including pest and pathogen outbreaks (Fuller et al. 2025). Moving beyond static mortality multipliers, mechanistic models offer several advantages. First, they can simulate processes such as reduced photosynthesis, track the spatiotemporal dynamics of NPP reduction, and capture non-linearities in disease progression, thereby improving the realism of forest carbon budget assessments. Second, by incorporating biological and ecological processes as parameters, such models help identify which factors disproportionately influence NPP and subsequent carbon dynamics during biotic disturbances. Third, mechanistic models enable the testing of hypothetical management scenarios to evaluate strategies for minimising reductions in NPP.

In this paper, we focus on a typical forest pathogen outbreak (ash dieback), aim to model the reduction of forest carbon sequestration potential both from tree mortality and reduced NPP. We achieved this through coupling disease spreading pattern and a minimal carbon cycling model. We also calculated mortality-only estimates for comparison. Specifically we aim to: (1) estimate the Europe-wide NPP loss and associated carbon storage loss due to ash dieback over the time course 1992–2025; (2) Compare our dynamic model against static models to understand its potential and the role of NPP in forecasting carbon dynamics under the pathogen outbreak; and (3) attribute loss of NPP potential to key disease-progression characteristics, including spread rate, international trade intensity, and virulence (defined by tree mortality and defoliation levels).

Results

Dynamics of carbon loss

In this study, we make use of the percentage of crown defoliation ($p_{\text{defoliated}}$) and the percentage of tree

mortality induced by ash dieback calculated by $p_{\text{mortality}}$ to model the progression of ash dieback disease. We further spin up a minimal carbon model (u-model) without annual change in climate variables nor CO_2 (NEP = 0), in order to model the effect of the disease outbreak to changes in forest carbon cycle, without considering other drivers that might change NEP. After the spin-up, NPP decrease significantly following the spread of ash dieback, leading to a negative NEP through the simulation.

Table 1 shows the amount of reduced carbon sequestration resulted from reduced net primary production (NPP) is substantial. In nations such as Sweden and Estonia, the order of magnitudes of NEP is comparable to annual fossil fuel emissions by car (around 10 ~ 60% of the fossil fuel emission by car in 2022). In Germany, while fossil fuel emissions are far greater, the negative NEP due to ash dieback is ~0.002 kg C/m², which is the largest among the listed countries. This contrasts with France, where large areas remain uncolonised, resulting in a lower aggregate impact. The reduction in NPP resulted from ash dieback disease is displayed in Supplementary Table S1.

Table 1. Predicted net ecosystem production (NEP = NPP – heterotrophic respiration) due to ash dieback disease by country. A negative NEP means that the forest acts as a carbon source rather than a carbon sink, under the impact of the pathogen's disturbance.

Country	NEP due to ash dieback 2005 (kg C/m²/year)	NEP due to ash dieback 2015 (kg C/m²/year)	NEP due to ash dieback 2025 (kg C/m²/year)	Fossil fuel emission by car 2022 (kg C/m²/year)**
United Kingdom	NA*	–0.000316	–0.000722	0.0667
Sweden	–0.00165	–0.0031	–0.00114	0.00503
Norway	NA	–0.000103	–0.0000599	0.00608
Germany	–0.00542	–0.00779	–0.0022	0.068
France	NA*	–0.0000748	–0.0000683	0.0291
Poland	–0.00442	–0.00178	–0.00046	0.0314
Estonia	–0.000827	–0.00111	–0.000394	0.00848

*: Disease not predicted to arrive at the country yet.

**: Yearly fossil emission data sourced from Open climate data (https://openclimatedata.net/)

The decline of NPP exhibits nonlinear dynamics over both time and space (Figure 1). Although the pathogen was reported in many European countries around 2000, the continental-scale NPP loss at that time remained below 0.0003 kg C/yr/m². After 2000, however, NPP loss increased substantially, reaching with an annual removal rate of approximately 0.0015 kg C/yr/m² around 2010. Losses subsequently stabilised after 2020, roughly 30 years after the disease was first reported in Poland.

Spatially, change of NPP and NEP also followed a nonlinear pattern (Figure 1B; Supplementary Figure S2). In 2005, most affected regions showed an NPP removal rate below 0.0002 kg C/m². By 2015, this rate had risen sharply, exceeding 0.0025 kg C/m² across much of the infected range. This spatial trend reflects the disproportionate expansion of infected area over time. After 2020, the pathogen reached the limits of its climatically suitable range, and further increases in NPP loss were driven primarily by intensified defoliation and mortality within already infected areas (Figure 2).

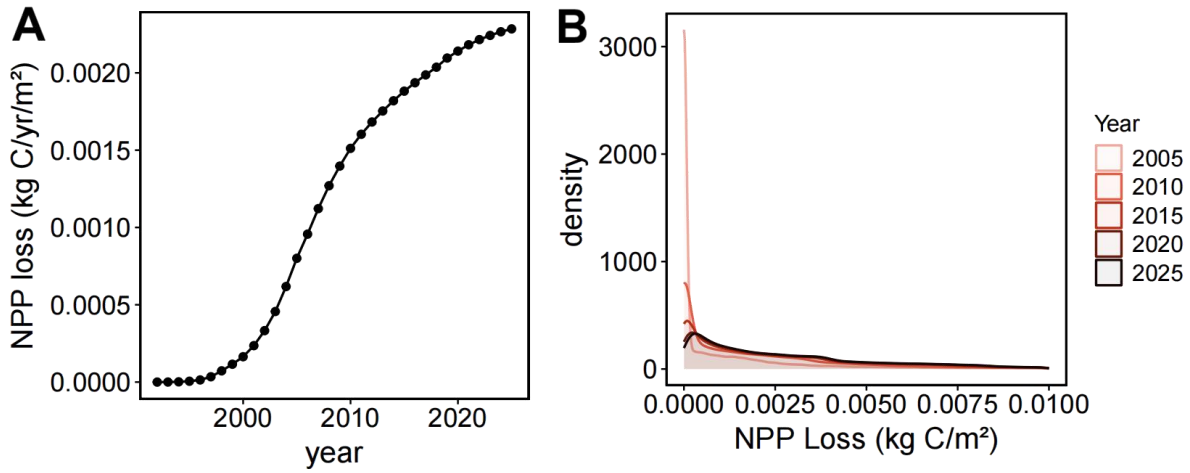


Figure 1. Temporal and spatial dynamics of forest NPP loss. (A) Total forest NPP loss across Europe over time since disease establishment. (B) Density distribution of pixels experiencing various levels of NPP loss.

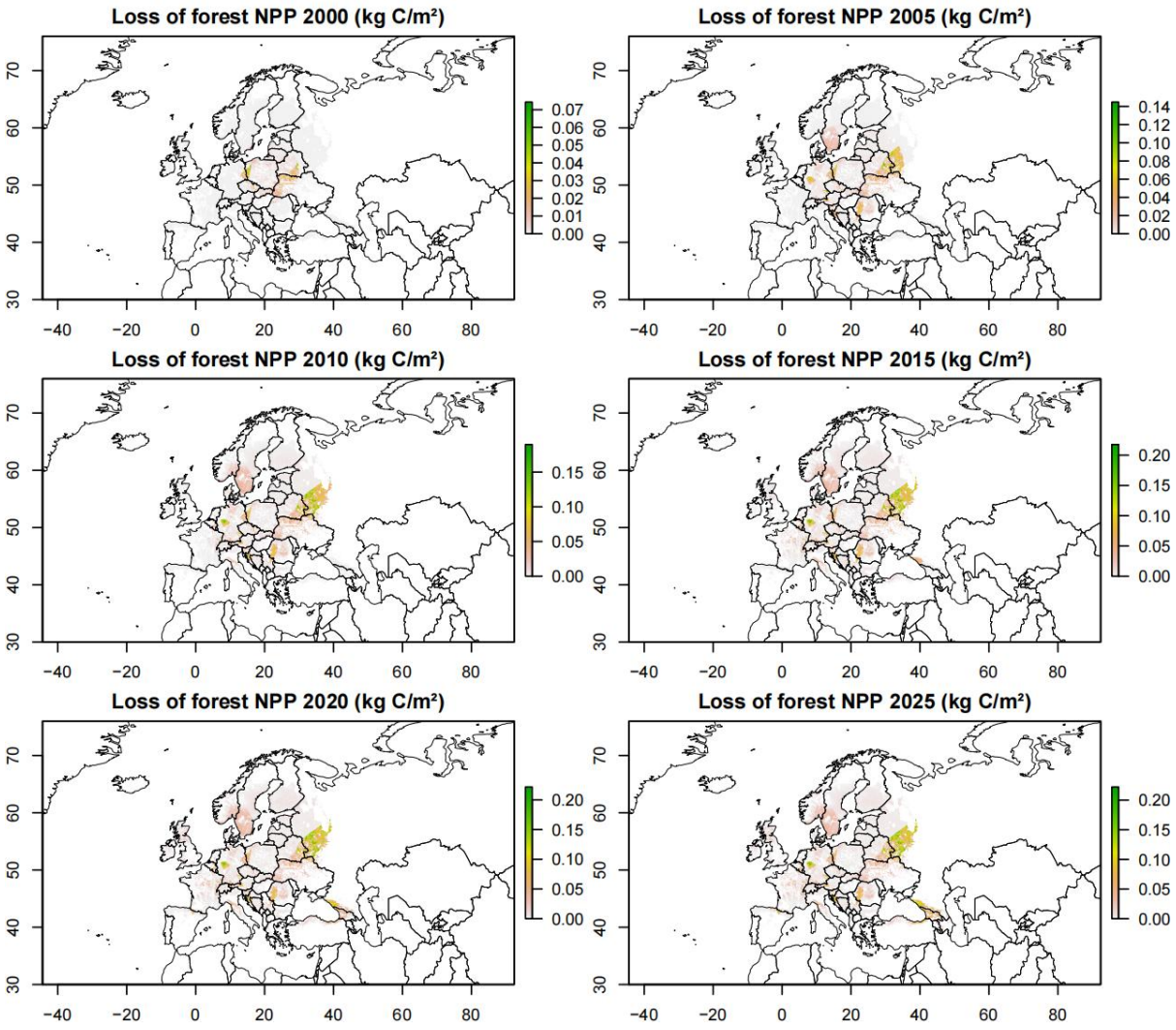


Figure 2. Evolution of forest NPP loss as the ash dieback disease progresses in the Europe.

Tree mortality ($p_{\text{mortality}}$), rather than crown defoliation ($p_{\text{defoliated}}$), represents the primary driver of NPP loss (Figure 3). Although defoliation dominates NPP reduction in newly infected areas during the initial stages of disease spread, tree mortality rapidly surpasses it as the infection progresses. By 2020, mortality accounted for over 60% of total NPP loss in nearly all affected regions.

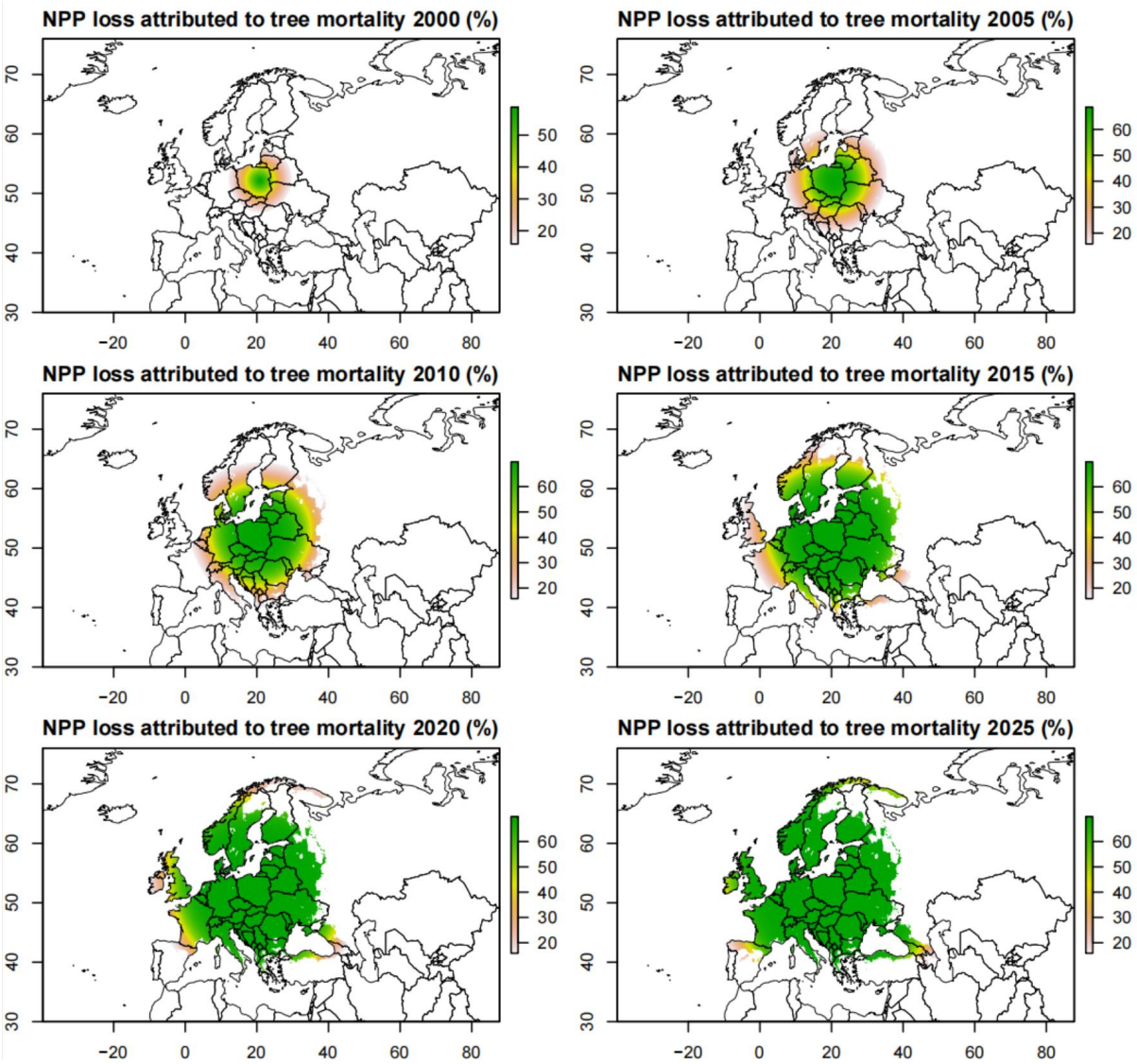


Figure 3. Proportion of NPP loss attributed to tree mortality, rather than crown defoliation, as the ash dieback disease progresses in the Europe.

Sensitivity Analysis

We explored how disease spread rate, intensity of long-distance introductions, and disease virulence affect NPP reduction through simulated the model using different parameter values. Scenario modeling revealed that increased short-distance dispersal induces a nonlinear rise in net primary productivity (NPP) loss, particularly within a range of 20–40 km yr^{-1}. Long-distance dispersal also disproportionately amplifies NPP loss; even a minor increase in its intensity (e.g., raising C_{max} from 0.5 to 1) can produce a substantial surge, though further elevation does not cause significant change of NPP loss anymore. Both dispersal mechanisms primarily influence the rate at which NPP loss approaches its maximum potential.

On the other hand, the biological traits of hosts and pathogens, reflected by maximal mortality and maximal defoliation parameters, contribute linearly to increased NPP loss. They determine the ultimate potential of the pathogen to remove NPP in a specific place after the epidemic stablises, rather than the speed of NPP loss.

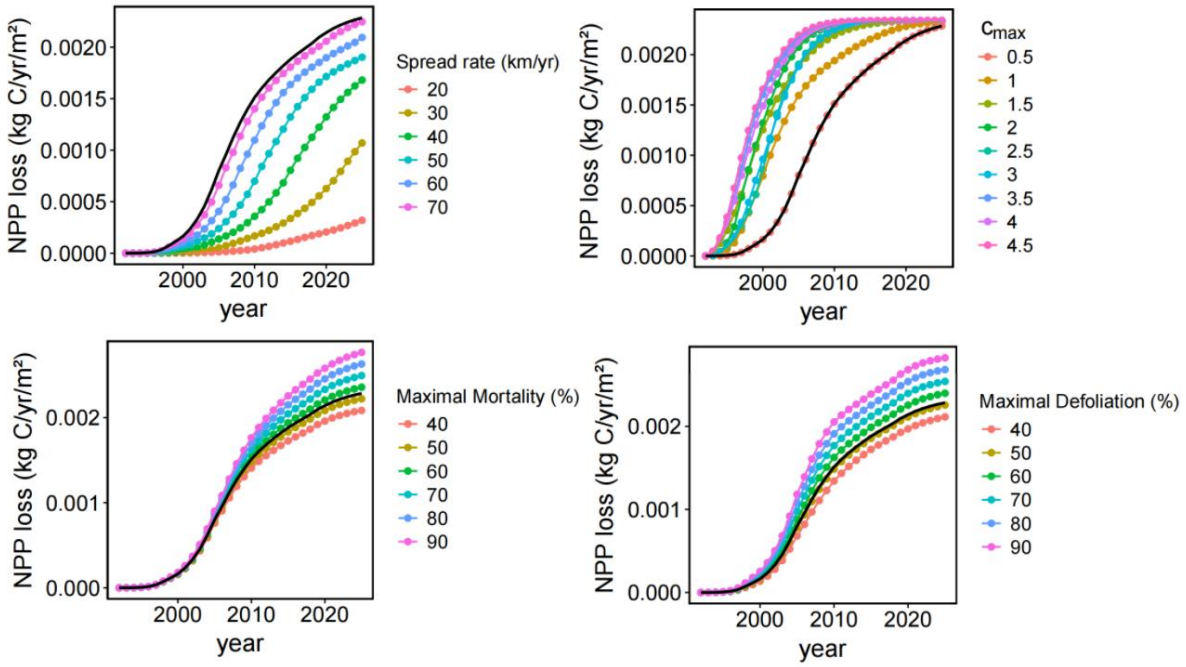


Figure 4. Sensitivity of forest NPP loss to model parameters: spread rate, maximum number of annual long-distance introductions (C_{max}), maximal mortality ($A_{sym,death}$), and maximal defoliation ($A_{sym,defoliated}$). The black line represents the result outputs when using parameters in the present study: spread rate = 75 km/yr, C_{max} = 0.3, $A_{sym,\ death}$ = 54.65%, $A_{sym,defoliated}$ = 51.98%.

Carbon impacts underestimated by biomass-based models

The above findings consider addition loss of forest carbon sequestration potential due to NPP reduction under pest and pathogen outbreaks. How does the above compare to carbon emission calculated by previous tree-mortality based estimates? Our result showed that when accounting for NPP reduction, the reduced carbon sequestration potential was on 39.3% (median, SD = 4.5%) higher than previously thought, across all regions affected by ash dieback (Figure 5). In earlier-infected regions, such as Poland and Ukraine, the magnitude of underestimation are 32.2% and 38.3%, respectively. In the United Kingdom, there was a 41.3% underestimation of reduced forest carbon sequestration potential, and France, this figure was 39.4%. Even in newly infected areas, such as Spain (infected post-2020), the underestimation of the biomass-based method are about 54.4%.

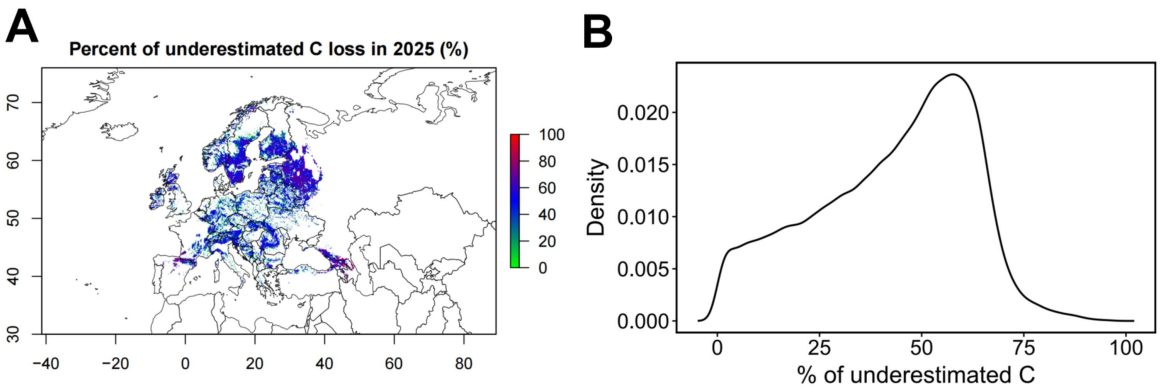


Figure 5. Percentage underestimation of foregone carbon uptake by biomass-based models. Proportion of foregone carbon uptake related to reduced NPP, relative to the total carbon effect (i.e. biomass-based + NPP-related) (A). Density distribution of the proportion across all pixels in (A) is shown in panel (B).

Discussion

Carbon loss from nonlinear NPP reduction

While biomass-based metrics (e.g. Seidl et al. 2018; Fei et al. 2019; Quirion et al. 2021; Hu et al. 2024) are useful to quantify the amount of carbon storage directly loss from pest and pathogen outbreaks, the total amount of reduced forest carbon sequestration potential can be much higher. In this study, we incorporated the impact of reduced NPP on carbon sequestration potential, and we suggested that the total amount of reduced carbon sequestration potential due to ash dieback outbreak is 39.3% large than direct carbon loss induced by tree mortality. The order of magnitude of NEP (kg C/m²/yr) under disease outbreak can be comparable to annual fossil fuel emissions by car in kg C/m²/yr from some affected regions (Table 1). There are other examples which also demonstrate that reduced NPP resulted from pests and pathogens cannot be overlooked: Flower and Gonzalez-Meler (2015) synthesised nine studies on defoliators, phloem feeders, and wood borers, reporting post-disturbance NPP reductions mostly ranging from 0 to 0.2 kg C/m², with the greatest losses caused by wood borers and invasive pests. Similarly, a gypsy moth (*Lymantria dispar*) outbreak in New Jersey's Pinelands National Reserve during 2007–2008 reduced NPP by 78% over the following decade relative to pre-disturbance levels (Clark et al. 2018). The resulting defoliation increased tree mortality and dead wood, elevating ecosystem respiration to a point where it consumed 97% of gross ecosystem production (Clark et al. 2018). In another simulation study, Liu et al. (2019) modelled spruce

budworm (*Choristoneura fumiferana*) outbreaks in Canadian boreal forests and estimated maximum NPP reductions of 30.54% in fir, 29.36% in spruce, and 36.24% in mixed fir-spruce stands.

Therefore, our analysis suggests that: (1) It is not accurate to equate carbon loss directly with mortality-induced biomass loss from pests; (2) Disturbance and recovery processes are not linear. Previous forest carbon recovery models often assume that an outbreak instantly removes all host-tree carbon, followed by a linear recovery at a constant NPP rate (Seidl et al. 2018; Hu et al. 2024). In reality, however, an outbreak result in a large amount of standing deadwood and severely weakened trees. Decomposer need decades to process the enlarged deadwood pool, and thus dead trees continue to occupy growing space, leading to a prolonged NPP reduction of the forest community and slow forest functioning recovery. Consequently, the actual trajectory of forest recovery would be slow without active cutting of severely diseased wood (Boyd et al. 2013; Coker et al. 2019).

Disease-driven carbon loss shouldn't be overlooked

Disease-driven forest carbon loss has been systematically underestimated and poorly incorporated into global carbon emissions accounting frameworks, leading to its persistent neglect in climate and forest policy. The Global Carbon Budget 2025, for example, explicitly quantifies and integrates carbon emissions from deforestation and wildfires, including dedicated analyses of fire-related CO_2 fluxes and land-use change emissions, while it does not consider carbon losses attributable to forest pests and pathogens (Friedlingstein et al. 2025). These carbon accounting reports rely heavily on comprehensive simulations from dynamic global vegetation mvodels (DGVMs); currently, these models require more explicit methods to incorporate the effect of forest pests and pathogens on carbon loss dynamics.

Our research also suggests that the order of magnitudes of reduced NPP resulted from ash dieback can be sometimes comparable to fossil fuel emissions by car in some countries. This underscores that ash dieback is not a trivial ecological disturbance but a contributor to carbon budget imbalances that could not be neglected, one that demands more attention in climate and forest management policies.

Although the reduced carbon sequestration resulted from ash dieback pathogen is still smaller than fossil fuel emissions by car, it should be noted that: (1) the present research only focuses on the impact of ash dieback on the reduction of forest carbon sequestration, rather than a wide range of pest and pathogen disturbances in general. Ash dieback is just one of the numerous forest diseases globally. However, there has already been other widespread pests or pathogens such as those causing Pine Wilt Disease, Dutch Elm Disease, Oak Wilt, etc. All of those independently drive substantial carbon sequestration losses and emissions. As a typical estimate, Zhou et al. (2024) reported a carbon sink deficit of 1,857 TgC in northern pine ecosystems caused by the pine wood nematode and Japanese pine sawyer beetles. In the United States, the chestnut blight spread quickly throughout the

American chestnut's native habitats quickly since its discovery in 1906, and kills around 90% of the population (Powell et al. 2019). These epidemics could cause equal or even greater impact than ash dieback over the same or even broader geographic range. However, many of these epidemics are not well documented in terms of their impacts on forest ecosystem productivity. If relevant data is available for tree pests and pathogens besides ash dieback, the reduction of forest carbon squestration could be much higher than the figure given in the present study; (2) Ash is not a dominant tree species across Europe. Rather, its relative abundance is around 0.1–0.2 in many forest plots (Supplementary Figure S5), indicating that the ash dieback pathogen is unlikely to eliminate a significant proportion of trees within a forest. Consequently, its potential to cause extremely large reductions in net primary production (NPP) is limited. However, this may not be the case for other pests and pathogens. For example, Pine Wilt Disease can affect pine monocultures, where the host trees dominate the forest canopy, potentially leading to the mortality of most or even all trees within an affected forest. This further emphasises the urgency of conducting more ecosystem research in pest and pathogen disturbances.

Uncertainty in carbon loss estimation

The present study provides a modeling framework to estimate land carbon losses resulting from forest pest or pathogen outbreaks. Using core inputs—including empirical mortality and defoliation curves, reference NPP data, and host and disease occurrence records—the model simulates annual changes in NPP and NEP, enabling the calculation of the cumulative carbon source over a defined period, thereby assisting carbon emission assessments.

While our results highlight the large hidden carbon sink deficit from ash dieback, several key uncertainties remain in the estimation: First, genetic evidence suggests that *Hymenoscyphus fraxineus* often establishes years (Carroll and Boa 2024). This detection lag is difficult to be integrated into the model, because no evidence can be found for the exact year when the pathogen establishes. Second, parameter uncertainty in logistic functions for mortality and defoliation propagates through NPP and net ecosystem production (NEP) calculations. Disease characteristics parameters vary in stand age, site conditions, climate, and sampling intensity. However, to make an continental-scale prediction, parameters derived from a synthesis of published studies still remain to be a balanced choice. Third, uncertainty in host density and forest fraction affects the scaling of NPP reductions from pixel to continental scales. Fourth, turnover rate could change under disease outbreaks. This study has to use fixed carbon turnover rate and base respiration rate due to lack of studies in the literature, but these values could change during disease outbreaks. Finally, uncertainty in interactions with co-occurring stressors is not addressed. In reality, ash dieback coincides with drought, nitrogen deposition, other pests, and management activities, which can mitigate or deteriorate NPP reductions. The recovery

speed and changes of species dominance followed by a pest or a pathogen outbreak can also change the long-term NEP. The outcome differs among forests. However, no mature and reliable studies have achieved effective coupling of climate, multiple stressors and forest disease dynamics currently. Arbitrary incorporation of unvalidated interaction parameters would instead introduce greater noise and reduce model prediction accuracy and robustness. Future targeted controlled observation and manipulative experiments will clarify multi-stressor interaction effects to support model iteration.

Methods

Management implications

The global forest carbon stock is consistently threatened by invasive pests and pathogens. Our modelling work suggests that, during epidemic outbreaks, the loss of NPP increases nonlinearly over time and space. Even a small change in the dispersal rate of a pest can significantly accelerate the progress (Figure 4) that an outbreak releases stored forest carbon. To prevent disease spread from entering this high-loss nonlinear zone, forest managers should prioritise early detection systems, establish pest monitoring networks, and, where feasible, implement localised chemical or biological control measures. We also show that, even low levels of international transport and trade can disproportionately accelerate forest carbon loss. This implies that a zero-tolerance approach should be applied to wood imports from infected regions, as even minimal trade can establish an invasion. Once a highly infectious pest or pathogen becomes established, stricter border controls become far less effective.

The maximum levels of tree mortality and defoliation, which are determined by the biological traits of both the host and the pest or pathogen, directly determine the scale of NPP loss. The amount of NPP removed increases linearly with the severity of these impacts. In other words, the specific characteristics of the trees and pest invaders set the upper limit for long-term carbon loss once an epidemic stabilises.To mitigate this long-term decline in forest carbon storage, one management strategy is to prioritise planting alternative tree species with high photosynthetic efficiency, or to select host varieties with greater genetic resistance, thereby accelerating canopy recovery. In practice, however, recovery goals are more complex. Managers must balance carbon sequestration targets with the imperative to protect biodiversity. The widespread loss of a foundational host tree can drive associated obligated species to extinction, as alternative tree species may not offer equivalent habitat or ecological functions (Hultberg et al. 2020).

Our results also underscore the importance of actively removing dead wood to mitigate forest carbon loss. A reduction of forest NPP could not only result from carbon emission from the dead tree body, but also from soil beneath the dead trees, because no litterfall, woody debris or other fresh carbon will

be input into the soil, while the remaining soil organic carbon would be persistently decomposed. Large volumes of standing deadwood can substantially increase carbon emissions through decomposition. For instance, the mountain pine beetle (*Dendroctonus ponderosae*) outbreak in British Columbia affected an estimated 270 megatonnes of carbon across 374,000 km² from 2000–2020. During the peak period of 2003–2007, the transfer of biomass to dead organic matter pools increased heterotrophic respiration from 408 to 424 g C m^{-2}, accelerating overall carbon release (Kurz et al. 2008). Similarly, Flower et al. (2013) estimated that an emerald ash borer (*Agrilus planipennis*) outbreak in the Great Lakes region could lead to the decomposition of 0.156 Pg C from existing aboveground biomass. These are carbon emission from tree mortality only, without considering NPP reduction. The actual amount of reduced forest carbon sequestration potential could thus be even higher when a reduction of forest productivity is considered in these studies. Additionally, accumulated deadwood elevates wildfire risk, necessitating integrated management strategies—from selective thinning to physical harvesting (Parajuli et al. 2025). Proactive removal not only reduces this hazard but can also promote seedling regeneration of replacement tree species. Finally, during active disease spread, strategic clear-cutting of infected stands can help slow pest advance, significantly reducing the potential for nonlinear, large-scale NPP loss (de la Fuente et al. 2018).

Study system

One of the key characteristics of ash dieback to be simulated in this study is its decadal spatial spreading. European ash dieback (Thomas 2016; Carroll and Boa 2024) was first formally identified in Poland in 1992 (Przybył 2002) and subsequently spread rapidly westward across the continent with the latest detection in Spain in 2021 (Carroll and Boa 2024). There is likely a lag between the first introduction of *H. fraxineus* and the first report of disease symptoms (Carroll and Boa 2024). For example, in United Kingdom, genetic evidence suggests that the pathogen may have been present as early as 2004, several years before the symptomatic detection in 2012 (Wylder et al. 2018). Similarly, research indicates *H. fraxineus* may have existed in Poland as far back as the 1960s (Sønstebø et al. 2017).

Second, unlike pest disease, ash dieback could sustain in many consecutive years. The life cycle of *H. fraxineus* proceeds as follows (Carroll and Boa 2024): during spring and summer, fungal ascospores infect new leaves, penetrating either directly through the leaf cells or via stomata. The spores develop into mycelium, which colonizes the leaves and subsequently spreads into adjacent woody tissues. Infected leaves are shed prematurely in summer. The mycelium persists within this leaf debris, undergoing an asexual stage and overwintering. The following spring, small fruiting bodies (ascocarps) emerge from the debris and release ascospores, thereby initiating a new infection cycle. Tree mortality from ash dieback is highly variable, with reported rates reaching up to ~70% in natural

woodlands and ~85% in plantations (Coker et al. 2019). Therefore, the last key characteristic of ash dieback infection is that ash population was not wiped out immediately – many trees could remain alive but ill for decades, making consideration of reduced NPP (beyond mortality) imperative.

Disease spread model

In our model, the spread of the ash dieback fungus *H. fraxineus* was simulated on a 0.05 × 0.05° raster, with the initial outbreak located in northeastern Poland in 1992. The fungus was assumed to spread via both short- and long-distance dispersal mechanisms. For short-distance dispersal, the fungus was assumed to spread to neighbouring pixels at a constant rate of r_{spread} =75 km yr^{-1} (km/yr), based on its estimated annual spread reported by Gross et al. (2014). For long-distance dispersal, the fungus was assumed to infect all regions with equal probability, representing the impact of international transport and trade. The expected number of new long-distance introductions per year was modelled following Levin's metapopulation framework (Levins 1969). In Levin's metapopulation model, the rate of change of occupied patches is described as,

$$\frac{dp}{dt}=cp(1-p)-ep$$

where p is the proportion of occupied patches or habitats, c and e are the colonisation and extinction parameters, respectively. The term $C=cp(1-p)$ is the colonisation rate, indicating the number of new introductions per year, and the term $E=ep$ is the extinction rate, indicating the rate of natural mortality of the pathogen. When $p=\frac{1}{2}$, the colonisation rate $C=cp(1-p)$ reaches its maximum $C_{max}=\frac{1}{4}c$. In context of ash dieback, the past decades have seen the pathogen becoming widespread and highly virulent across the Europe. In the pathogen's distribution range, there is currently very limited evidence indicating that the pathogen may undergo local extinction. We thus ignored the extinction term ep, as the pathogen shows high fitness across different ash woodlands and mixed forests. In each year, the number of new introductions was assumed to be the expected number of the colonisation rate, $E(C)$. $E(C)$ was proportional to the proportion of infected pixels p, and the proportion of uninfected pixels:

$$E(C)=4\times C_{max}\times p(1-p)$$

where C_{max} is a model parameter representing the maximum possible number of new introductions per year. We converted the continuous Levins population model to a discrete form in order to fit our goal for simulating disease spread in discrete time step with a cellular automaton model. A range of C_{max} values were tested, and the optimal value was selected by comparing the predicted first year of disease occurrence with observed first-incidence records from several locations (Supplementary Figure S1A). Model fit was quantified using a quadratic loss function defined as the sum of squared

deviations between predicted and observed first-incidence years (Supplementary Figure S1B).

With the initial outbreak in Poland in 1992, the model iteratively calculates the number of occupied pixels and then determines whether long-distance dispersal occurs. For each outbreak point—whether the initial site or a new long-distance introduction—a short-distance dispersal algorithm was used to simulate continuous pathogen spread. The model output is a raster representing the first year of disease occurrence for each pixel, obtained by taking the minimum first-incidence value across all short-distance dispersal layers.

Reduction in NPP

The reduction in NPP at time *t* (year) due to ash dieback was estimated as:

$$\text{Reduction in NPP}(t)=\text{NPP}\times D-\text{NPP}(t)\times D\times\left(1-p_{\text{death}}(t)\right)\times\left(1-p_{\text{defoliated}}(t)\right)$$

where: NPP is the mean annual net primary production (kg C m^{-2}), calculated from MOD17A3HGF V6.1 data for 2002–2021 (Running and Zhao 2021). *D* is the relative abundance of the host species, *F. excelsior*. We used data from 887 forest plots in the sPlotOpen dataset (Sabatini et al. 2021; Supplementary Figure S5), distributed across Europe, that recorded the abundance of ash trees. These data were then used to generate a continuous map of host tree abundance through nearest-neighbour interpolation.

p_{death} is the proportion of dead trees in the population (i.e. the number of dead trees divided by population size), and $p_{defoliated}$ is the mean percentage of crown defoliation in the tree population (i.e. the proportion of leaves removed in an entire tree crown, averaged over all trees in the host population), respectively, both of which increase over time since pathogen arrival. These proportions were modelled as logistic functions of years since infection, parameterised using field observations on tree defoliation and mortality from 80 peer-reviewed papers on ash dieback (Wu et al. 2025):

$$p_{death}(t)=\frac{A_{sym,death}}{1+\exp\left(\frac{x_{mid,death}-t}{s_{death}}\right)}$$

$$p_{defoliated}(t)=\frac{A_{sym,defoliated}}{1+\exp\left(\frac{x_{mid,defoliated}-t}{s_{defoliated}}\right)}$$

where:

A_{sym} determines the asymptotic maximum mortality or defoliation, x_{mid} is the inflection point at which the response reaches $A_{sym}/2$ is reached, and s is a scale parameter.

The field data and fitted curves are displayed in Supplementary Figure S2.

The model domain was restricted to the predicted disease range (Supplementary Figure S3), obtained using MaxEnt distribution modelling for *H. fraxineus* in our previous work (Chapter 5). All layers—including forest fraction, host density, NPP, and disease-incidence year—were analysed only within this range.

Net Ecosystem Production

The net ecosystem production (NEP) in areas impacted by ash dieback disease was modelled using a minimum carbon cycle model. The model partitions forest carbon storage into two parts: vegetation carbon pool (C_{veg}) and soil organic carbon pool (C_{soil}). The dynamics of vegetation carbon pool was modelled as:

$$C_{veg}(t) = \begin{cases} NPP(t) - Flux_{veg_to_soil}(t), & t < 1992 \\ NPP(t) \cdot \left(1 - \frac{Reduction\ in\ NPP(t)}{NPP(t)}\right) - Flux_{veg_to_soil}(t) - C_{veg}(t-1) \cdot p_{death}(t-1), & t \geq 1992 \end{cases} \dots (5)$$

where $Flux_{veg_to_soil}(t)$ is the amount of carbon moved from vegetation to soil organic carbon pool due to dead plant tissues. It was assumed to be proportional to C_{veg}, and thus $Flux_{veg_to_soil}(t) = K_1 \cdot C_{veg}(t)$, where the value of fixed turnover rate K_1 was calculated with known vegetation biomass data (Liu et al 2015) and NPP data (Running and Zhao 2021) in year 1993: $K_1 = C_{veg1993}$ / NPP_{1993}. Before 1992, a proportion of vegetation biomass goes to soil organic carbon pool (C_{soil}) naturally. Since ash dieback occurs in 1992, the amount $C_{veg}(t-1) \cdot p_{death}(t-1)$ represents carbon removal due to tree mortality driven by ash dieback. The removed carbon would be put into a necromass carbon pool (C_{necro}). Though necromass should be part of soil organic carbon pool, we made it a separated component from C_{soil}, in order to distinguish the amount of carbon removed due to natural turnover from that removed due to pathogenic reasons.

The dynamics of soil organic carbon pool (C_{soil}) was modelled as:

$$C_{soil}(t) = Flux_{veg_to_soil}(t) - K_2 \cdot C_{soil}(t) \cdot 1.4^{(T - T_{ref})/10} \dots (6)$$

where K_2 depicted the intensity of soil respiration, and was calibrated using soil organic carbon data downloaded from SoilGrids (https://soilgrids.org/). To calibrated K_2, we first assumed that soil organic carbon pool was in equilibrium in 1903, namely NPP equals to soil respiration. Then, K_2 can be estimated by NPP_{1903} divided by the Q10 function $f_{Q10} = 1.4^{(T_{1903} - T_{ref})/10}$ and then further divided by the soil organic carbon pool in 1903, given by SoilGrid data.

T is temperature, and T_{ref} is constant 46.02℃. The Q10 value was set as 1.4. Similarly, respiration on necromass was also modelled by this Q10 function:

$$\text{Necro_respiration}(t) = K_2 \cdot C_{necro}(t) \cdot 1.4^{(T-T_{ref})/10} \ldots (7)$$

The model started from the year 1903, which was an arbitrarily chosen value, as any time before 1992 allows the model to generate baseline maps of vegetation and soil organic carbon pools before the ash dieback occurs. in each time step (year), the model simulated the dynamics of vegetation and soil (including necromass) carbon pools. When the model proceeded to year 1992, the effect of foregone NPP due to ash dieback was incorporated into the model. A proportion of annual NPP at each year was removed, determined by the ratio $Reduction\ in\ NPP(t)/NPP$.

Finally, we compared the amount of reduced forest carbon sequestration potential resulting from tree mortality with that resulting from reduced productivity. The reduced amount of carbon resulting from tree mortality can be seen as the amount of carbon released from necromass respiration. This proportion of carbon was released slowly from dead trees to the air. Then, the percent of underestimated carbon sequestration potential up to a specific year was calculated as,

$$\text{Underestimated C (\%)} = \left(1 - \frac{\sum_{i=1992}^{t} \text{Necro_respiration(i)}}{\sum_{i=1992}^{t} |\text{NEP(i)}|}\right) \times 100 \ \ldots (8)$$

$$NEP(t) = NPP(t) - K_2 \cdot [C_{soil}(t) + C_{necro}(t)] \cdot 1.4^{(T-T_{ref})/10} \ \ldots (9)$$

where numerator in equation (8) represents tree-mortality based estimate, which assumes that foregone carbon sequestration relative to disease-free scenario is the amount of carbon released to air from necromass. The denominator represents NPP-based estimate, the main focus of the present research, which assumes that foregone carbon sequestration relative to disease-free scenario stem from both a reduction of photosynthesis and the amount of carbon released from necromass. NEP reflects the net outcome after accounting for a changed NPP and a change on soil respiration intensity.

To analysis the sensitivity of the "Underestimated C (%)" metric to major model parameters (i.e. spread rate, C_{max}, $A_{sym,death}$, and $A_{sym,defoliated}$, we introduced a ±15% perturbation of these parameters, ran the disease spread model and subsequently the minimum carbon cycle model 100 times. Parameters are sampling based on a Monte-Carlo sampling method. We calculated the "Underestimated C (%)" metric for each independent simulation, and finally calculated the standard deviation as the uncertainty range of the metric.

It should be acknowledged that this estimate does not account for the compensatory regrowth of other tree species, such as sycamore, beech and oak, following ash mortality and defoliation. Consequently, the potential recovery of forest carbon sequestration capacity through compensatory growth is not captured by this estimate.

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7. Conclusion

7.1 Argument Summary and Key Contributions

This thesis demonstrates that current understanding and projections of tree pest and pathogen impacts are systematically biased, geographically incomplete, and overly conservative. As a result, future risks to forest health and carbon storage are substantially underestimated. These biases are particularly pronounced in northern temperate and boreal regions, where pest and pathogen outbreaks are expected to become more frequent under climate change, leading to largely overlooked reductions in forest carbon sequestration potential. Knowledge gaps are also severe in the Global South, where pest and pathogen distributions, outbreak severity, and associated carbon losses remain poorly documented, leaving both present and future global risks insufficiently understood.

Chapter 4 addresses two questions (1) How are tree pests, pathogens, and their associated disease impacts distributed globally, and (2) how may machine learning text-mining facilitate the compilation of such data from heterogeneous literature sources? Although a complete list of all global pests and pathogens is not available, it is possible to conduct a systematic synthesis of the existing literature to partially capture global patterns of pest and pathogen occurrence. The chapter reveals strong geographic and temporal biases in research effort showing that (1) monitoring and research are heavily concentrated in the Global North, particularly in temperate forests of North America and Europe; and (2) the Global South—including much of China, Africa, and South America—remains severely underrepresented in pest and pathogen data. To address accessibility barriers, Chapter 4 introduces the Tree Pests and Diseases Explorer (https://zjuhaoranwu.shinyapps.io/forestpestexplorer/), an open-access web portal that compiles observation data and highlights global data gaps. This chapter highlights the value of text-mining to facilitate data gathering and underscores the need for more coordinated and comprehensive monitoring to improve forest health assessments and inform global biosecurity policy.

Chapter 5 examines how climate change is likely to reshape the global distribution of forest pest and pathogen outbreaks. Using species distribution models for 31 major tree pests and pathogens, this chapter produces estimates of current and future outbreak risk under multiple climate and socioeconomic scenarios. The results indicate that (1) pest and pathogen ranges are projected to shift consistently poleward, posing increasing threats to northern temperate and boreal forests during the period 2041–2080; and (2) the severity of future impacts depends on socioeconomic pathways, with more high emission trajectories (i.e. increased radiative forcing and expansion in fossil fuel use) leading to substantially greater risks for northern forests; (3) prevalence of pests and pathogens reduced in regions that are becoming too hot, such as southern Europe. While previous modelling

studies often focus on single species, Chapter 5 reveals a robust, cross-taxa pattern of northward range expansion. These findings highlight the need to prioritise monitoring, early detection, and adaptive silvicultural strategies in northern and boreal regions.

Chapter 6 investigates how pest and pathogen outbreaks influence forest carbon budgets using ash dieback as an example. Conventional carbon accounting approaches typically attribute pest- and pathogen-induced carbon losses exclusively to tree mortality, equating carbon impacts with biomass released from dead trees. However, when considering the total impact on reduced forest carbon sequestration, Chapter 6 points out the importance of disease-driven suppression of forest carbon uptake. Using an integrated epidemiological and ecosystem modelling framework applied to ash dieback, this chapter shows that (1) nearly half (39.3%) of the total reduction in carbon sequestration potential arises from overlooked slow-down of net primary production, of which the loss of carbon potential is comparable in magnitude to carbon losses from tree mortality; and (2) disease spread rate and long-distance dispersal through international timber trade strongly amplify carbon sequestration losses, whereas biological traits such as maximum mortality or defoliation rates exert more linear effects. These results emphasise the importance of early detection, rapid eradication, and strict controls on diseased timber imports to prevent declines in future carbon storage potential.

Collectively, this thesis advances understanding of forest pest and pathogen disturbance through an integrated analytical framework. Compared with other major disturbances such as wildfire and drought, pest and pathogen outbreaks remain poorly understood due to complex biological interactions among pests, pathogens, host trees, and climate variables, as well as limited detectability via remote sensing. By synthesising global literature, compiling multi-source occurrence data, and integrating spatial datasets and ecosystem models, this research identifies critical data gaps and reveals general patterns across multiple pest and pathogen systems. This comparative, cross-scale approach enables the identification of broad rules governing pest dynamics and carbon impacts, rather than isolated, species-specific insights.

7.2 Implications for Improved Pest Management

Based on the findings of this thesis, several strategies are recommended to enhance forest resilience to pest and pathogen outbreaks:

(1) Address geographic biases in monitoring and early detection. As demonstrated in Chapter 4, pest and pathogen research remains heavily concentrated in temperate forests of the Global North, while a lack of monitoring efforts persist across much of the Global South. This may have global implications if the lack of understanding fails to prevent the introduction of unknown species. Regular monitoring and early disease detection can substantially reduce the likelihood and severity of carbon sequestration losses. Once a pest or pathogen becomes established, eradication is often infeasible, as

illustrated by the spread of ash dieback in Chapter 6. Looking ahead, intensified monitoring will also be essential in boreal forests, which are projected to face increasing pest pressure under climate change, as revealed in Chapter 5. Given that boreal forests account for approximately one-third of global forest cover (UNEP et al. 2009) and represent a major global carbon sink (Pan et al. 2011), proactive detection and eradication programs are critical to maintaining their long-term carbon sequestration function.

(2) Strengthen cross-scale and cross-border coordination. Global disparities in funding and capacity limit pest and pathogen research in many regions. Support from the Global North and international organizations could facilitate monitoring efforts across Asia, Africa, and South America. Harmonised monitoring protocols are also essential, as current field surveys often rely on inconsistent rating systems that hinder comparability. Existing global forest plot networks, such as ForestGEO (Davies et al. 2021), provide valuable models for standardising data collection. Furthermore, the poleward shifts identified in Chapter 5 imply rising transboundary risks, underscoring the need for coordinated international responses, particularly with respect to timber transport. Strict regulation of wood materials from diseased regions is crucial, as even low-intensity trade can markedly amplify carbon sequestration losses.

(3) Prepare forests for novel pest pressures through integrated management. As boreal forests may encounter increasing pest pressure in the future, enhancing species and genetic diversity is needed to buffer against rapid spread. Where eradication is no longer possible, active management—such as planting alternative or resistant tree species—may accelerate recovery more effectively than passive regeneration. Chapter 6 suggests that extensive mortality and prolonged decomposition can suppress net primary production for extended periods, reducing carbon sequestration capacity. Targeted harvesting and restoration can mitigate these effects and support a faster return toward pre-disturbance carbon baselines.

7.3 Implications for Global Forest Resource Assessment

First, the strong geographic bias in pest and pathogen research suggests that current forest resource assessments may substantially underestimate disturbance impacts from pest or pathogen outbreaks, relative to better-documented drivers such as wildfire and drought. For example, FAO's Global Forest Resources Assessment 2025 reports that 6.13 million ha of forests was affected by disease in 2020, and an average of 34.1 million ha was affected by insects in 47 reported countries (FAO 2025), yet the reported countries are disproportionately concentrated in the Global North. As revealed in Chapter 4, large regions of Africa, Oceania, South America, and much of Asia remain poorly studied, indicating that true impacts on forest health, carbon sequestration, and even regional climate regulation may be far greater than currently assessed. When exploring questions such impacts of climate change on the

pest behaviour, it should also be noted that conclusions may be made based on data points that are centred around Global North.

Second, closer integration of monitoring and modelling is urgently needed. Many assessments rely on static indicators—such as outbreak area or annual mortality rates—that implicitly assume stable disturbance regimes. This assumption is increasingly invalid. Invasive forest pests and pathogens are doubling approximately every decade (Gougherty 2023), and many of the most damaging species have become widespread only since the early 2000s. These nonlinear dynamics are poorly captured by linear extrapolations from past trends. Similarly, reductions in carbon sequestration often remain latent during early disease stages before accelerating rapidly during outbreak expansion, leading to abrupt declines in net primary production and recovery potential. Species distribution modelling in Chapter 5 further demonstrates nonlinear shifts in pest pressure under future climates, particularly in boreal forests. Together, these findings argue for forward-looking, climate-adjusted assessment frameworks that anticipate emerging risks rather than relying on historical baselines.

Thirdly, carbon accounting frameworks—particularly those that consider pest and pathogen outbreaks—require revision. While the effects of wildfire and drought on forest carbon loss are reflected in the Global Carbon Budget report (Friedlingstein et al. 2025), the impacts of pest and pathogen outbreaks remain not considered. Global dynamic vegetation models (DGVMs), such as LPJ (Lund–Potsdam–Jena) (Calle and Poulter 2021) and ED2 (Ecosystem Demography 2) (Longo et al. 2019), explicitly include wildfire modules to assess its impact on forest carbon but lack simulations of pest and pathogen disturbances due to the complexity of the underlying biological processes. Several studies have estimated the potential reduction in forest biomass loss caused by pest and pathogen outbreaks using one or several pest or pathogen species as case studies (Seidl et al. 2018; Fei et al. 2019; Hu et al. 2024). However, these estimates primarily focus on carbon losses associated with tree mortality. In reality, reductions in forest carbon sequestration arise not only from carbon release due to tree mortality but also from decreased net primary production resulting from widespread tree death or weakening, as demonstrated in Chapter 6. Explicit incorporation of pest- and pathogen-induced mortality, associated reductions in net primary production, and forest recovery rates are therefore needed in DGVMs. Doing so would enable more realistic estimates of pest- and pathogen-driven reductions in carbon sequestration potential within the forest carbon budget. Nature-based solution projects, such as those certified under the Gold Standard, should also account for pest and pathogen risks when estimating achievable carbon sequestration. Ignoring these risks would lead to overly optimistic estimates of carbon sequestration rates.

7.4 Limitations

This thesis uses a sequential, interconnected analytical workflow. Chapter 4 synthesizes georeferenced

empirical field records extracted from heterogeneous literature. Chapter 5 develops species distribution models using a bias raster derived from the spatial distribution of tree pest and pathogen research intensity mapped in Chapter 4. Chapter 6 integrates the predicted distributions of the ash dieback fungus with tree defoliation and mortality parameters compiled in Chapters 4 and 5 to model the reduction in carbon sequestration attributable to ash dieback. Limitations originating in earlier chapters may propagate through this analytical pipeline, thereby influencing the interpretation and constraining the conclusions that can be drawn from downstream analyses.

Firstly, the sampling bias correction applied in the species distribution models in Chapter 5 depends on the accuracy of the research intensity map developed in Chapter 4. However, the workflow in Chapter 4 has two main limitations. (1) The Naive Bayes text-mining classifier relies primarily on a training corpus derived from ash dieback literature. Independent cross-validation using literature on other pests and pathogens would help establish whether the classifier performs reliably across a broader range of taxa and, consequently, whether it is likely to identify relevant field survey studies across different taxonomic groups. (2) The literature search is restricted to English-language publications. The exclusion of non-English sources may lead to an underestimation of research effort, particularly in countries of the Global South where scientific publications are frequently produced in languages other than English. These limitations may propagate into Chapter 5. Despite the application of sampling bias correction in MaxEnt, uneven field survey coverage may still lead to an under-representation of pest and pathogen occurrences in data-deficient regions. Consequently, the projected northward range shifts in Chapter 5 are likely to be most reliable in European and North American countries, where observational records are relatively abundant. Projections for Russia, China, and other countries where relevant research may be under-represented in English-language literature require further assessment following the inclusion of field survey studies published in other languages. Furthermore, the limited geographical coverage of the underlying occurrence data precludes robust extrapolation to tropical and Southern Hemisphere forest systems.

Secondly, the accuracy of the MaxEnt outputs in Chapter 5 affects the spatial extent of the epidemiological model in Chapter 6. Uncertainty in the predicted distribution of the pathogen may therefore propagate into estimates of mean NPP, the total reduction in carbon sequestration across Europe, and, subsequently, mean NEP predicted by the minimal carbon cycle model. This is because changes in the spatial extent of the modelling domain alter the number of grid cells included in the analysis, potentially affecting both spatially averaged values and cumulative estimates. The assumptions underlying the MaxEnt model in Chapter 5 include (1) niche conservatism, which assumes that the ecological niche of the ash dieback fungus remains relatively stable over time, although *Hymenoscyphus fraxineus* may evolve to tolerate warmer temperatures; and (2) distributional equilibrium, which assumes that the fungus has colonised all climatically suitable habitats. These assumptions may lead to an underestimation of the fungus's potential distribution,

particularly if its climatic tolerance is still evolving or it has not yet reached all suitable habitats. In addition, there is a temporal mismatch between the bioclimatic data and species occurrence records used in Chapter 5. The historical bioclimatic data from WorldClim represent the period 1970–2000, whereas the occurrence records for *H. fraxineus* were downloaded from GBIF in 2025. If the historical climate data are colder than the current climate, the MaxEnt model may infer that the fungus can survive in colder regions than it can under present-day conditions. Consequently, the model outputs used in Chapter 6 may overestimate the reduction in net primary productivity (NPP) in colder regions while underestimating it in warmer regions.

Thirdly, the estimates of NPP reduction in Chapter 6 also depend on tree mortality and defoliation parameters derived from the data synthesised in Chapter 4. In Chapter 4, disease severity and tree mortality rates are compiled from a wide range of published studies. In addition to uncertainties arising from the performance of the text-mining classifier and the restriction to English-language literature, inconsistencies in data collection protocols across field surveys may further affect the reliability of NPP estimates in Chapter 6. In particular, subjective assessments of tree damage caused by pests and pathogens may introduce uncertainty into the defoliation curve, thereby affecting the estimated relationship between the degree of defoliation and the time elapsed since ash dieback infection.

Despite these uncertainties, this thesis makes several original contributions to understanding the large-scale ecological consequences of tree pests and pathogens, based on the available evidence. First, it projects a northward shift in the potential distributions of tree pests and pathogens. Second, it estimates that the reduction in NPP attributable to ash dieback is equivalent to 39.3% of the carbon directly removed through tree mortality. Beyond these findings, the thesis introduces a novel data product, the Tree Pests and Diseases Explorer (https://zjuhaoranwu.shinyapps.io/forestpestexplorer/), which integrates a large volume of tree pest and pathogen field survey data and provides comprehensive metrics on disease incidence, severity, and tree mortality. Developed as a Shiny application, the tool offers interactive visualisation capabilities that enable forest ecologists and forestry agency managers to explore and analyse these data.

Finally, the thesis makes a methodological contribution to the study of forest disturbances by demonstrating the potential of text mining to facilitate systematic reviews and data extraction from forestry field survey literature. Considered collectively, the three research chapters illustrate how field survey records, georeferenced occurrence data, and remote sensing datasets can be integrated into a sequential modelling framework to generate large-scale ecological inferences. This approach offers methodological insights for integrative ecology and large-scale ecosystem assessments.

7.5 Living with Tree Pests and Pathogens

While tree pests and pathogens are often framed as shocks or crises, their occurrence has become increasingly common since the 2000s. Global change—particularly shifting climate conditions—together with intensifying international transport and trade has inevitably increased the likelihood of colonisation by invasive species. Accepting change in forest composition and function is therefore essential. As pests and pathogens become a persistent feature of future forests, ecosystems may no longer return to their historical states following outbreaks. Reduced forest productivity, nonlinear declines in carbon sequestration potential, enhanced pest fitness in northern regions, the loss of vulnerable tree populations, and associated biodiversity declines may all occur within decades. Conservation and management plans must recognise pest and pathogen outbreaks as an inherent component of forest dynamics and prepare forests accordingly by improving tree species diversity, promoting resistant genotypes, and strengthening long-term monitoring and early disease detection. Forest managers should also be prepared with recovery strategies for anticipated disease outbreaks, particularly in northern and boreal forests, where many pests and pathogens currently confined to temperate regions are expected to expand their ranges.

Although tree pest and pathogen outbreaks are a global problem, responsibility for and capacity to manage these risks are unevenly distributed. International coordination should prioritise regions where pest and pathogen outbreaks severely affect forests, but where local governments lack sufficient resources and institutional capacity to respond effectively. Questions of whose forests are monitored, whose forests are actively managed, and whose losses are counted raise important ethical considerations. Clearer recognition of emerging pest risks, more transparent accounting of losses, and more coordinated management approaches that accept pest and pathogen outbreaks as a defining feature of forest ecosystems are essential for a realistic vision of future forest management.

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9. Supplementary Materials

9.1 Supplementary Materials for Chapter 4

Supplementary Table S1. List of pests and pathogens investigated in this research. The disease names were used as search queries in the Web of Science database.

Pest or Disease name	Scientific name of pest or pathogen agent
Ash dieback	*Hymenoscyphus fraxineus*
Sudden oak death	*Phytophthora ramorum*
Asian and citrus longhorn beetles	*Anoplophora glabripennis* and *Anoplophora chinensis*
Bronze birch borer	*Agrilus anxius*
Dothistroma needle blight	*Dothistroma septosporum*
Dutch elm disease	*Ophiostoma novo-ulmi*
Eight-toothed spruce bark beetle	*Ips typographus*
Elm zig-zag sawfly	*Aproceros leucopoda*
Emerald ash borer	*Agrilus planipennis*
European mountain ash ringspot-associated virus	*Emaravirus sorbi*
Great spruce bark beetle	*Dendroctonus micans*
Horse chestnut bleeding canker	*Pseudomonas syringae pv. aesculi*
Horse chestnut leaf miner	*Cameraria ohridella*
Plane wilt	*Ceratocystis platani*
Oak lace bug	*Corythucha arcuata*
Oak processionary moth	*Thaumetopoea processionea*
Oriental chestnut gall wasp	*Dryocosmus kuriphilus*
Phytophthora austrocedri	*Phytophthora austrocedri*
Phytophthora lateralis	*Phytophthora lateralis*
Pine processionary moth	*Thaumetopoea pityocampa*
Red-necked longhorn beetle	*Aromia bungii*
Sirococcus blight	*Sirococcus tsugae*
Sweet chestnut blight	*Cryphonectria parasitica*

Anthracnose of plane	*Apiognomonia veneta*
Conifer root and butt rot	*Heterobasidion annosum*
Elbow-patch crust of plane	*Fomitiporia punctata*
Elm yellows	*Candidatus Phytoplasma ulmi*
Massaria disease	*Splanchnonema platani*
Neonectria canker of fir	*Neonectria neomacrospora*
Oak wilt	*Bretziella fagacearum*
Phytophthora disease of alder	*Phytophthora alni*
Phytophthora kernoviae	*Phytophthora kernoviae*
Phytophthora pluvialis	*Phytophthora pluvialis*
Pitch canker of pine	*Fusarium circinatum*
Thousand cankers disease	*Geosmithia morbida*
Green spruce aphid	*Elatobium abietinum*
Gypsy moth	*Lymantria dispar*
Large larch bark beetle	*Ips cembrae*
Large pine weevil	*Hylobius abietis*
Oak pinhole borer	*Platypus cylindrus*
Pine wood nematode	*Bursaphelenchus xylophilus*
Siberian silk moth	*Dendrolimus sibiricus*
Two-lined chestnut borer	*Agrilus bilineatus*
Two-spotted oak buprestid	*Agrilus biguttatus*

9.2 Supplementary Materials for Chapter 5

Supplementary Table S1. Description of data sources used to collect occurrence data for forest pests and pathogens that cause substantial damage to global forests.

Pest/pathogen	Scientific name	Data source	Potentially affected area	Description
Ash Dieback	*Hymenoscyphus fraxineus*	[1] Goberville et al. (2016); [2] Forest Comission - Chalara Map; [3] GBIF; [4] EPPO	Europe (except Iceland); Russia: Northwestern; Russia: Volga;	[1] (provided by authors), [2] and [3] as the main data sources, cross validated by [4]. Points in East Asia, Oceania, and North America in the GBIF dataset was removed, as the pathogen does not cause damage on those

			Russia: Central	areas (including its native range)
Asian Longhorned Beetle	*Anoplophora glabripennis*	[1] GBIF; [2] Zhou et al. (2021); [3] Zhang et al. (2022); [4] EPPO	North America; Europe (except Iceland); Asia	[1] as the main data source, cross checked by [2]. Pest distribution in China is supplemented by [3] (points in Figure 1). While in dataset [1] there are distribution points in California and Ontario, the pest seems no longer exist in these regions anymore, according to [4].
Beech Bark Disease	*Neonectria faginata*	[1] GBIF; [2] Cale et al. (2017); [3] US Alien Forest Pest Explorer	North America	[1] as the main data source, cross checked by [2] and [3]. The disease specifically cause damage in North America. Therefore, points fall in the Europe in the dataset [2] were deleted
Beech Leaf Disease	*Litylenchus crenatae mccannii*	[1] GBIF; [2] Cleveland Metroparks (2023); [3] US Alien Forest Pest Explorer; [4] EPPO	North America	[1], [2], and [3] as main data sources, cross checked by [4]. The disease specifically cause damage in North America and, therefore, data points outside of the North America in the dataset [1] were removed
Bronze Birch Borer	*Agrilus anxius*	[1] GBIF; [2] Muilenburg and Herms (2012); [3] EPPO	North America	[1] as the main data source, cross checked by [2] and [3]. It should however be cautious that several states or provinces, such as Alaska, does not have records in database [1], but the pest presents in these areas, according to [2] and [3]. Unfortunately no fine-scale distribution data could be found except from [1]. A point located in the Atlantic in database [1] is invalid and was removed. Points located in Russia and East Asia were removed, as no evidence suggests that the pest causes extensive damage in those regions.
Brown Spruce Longhorn Beetle	*Tetropium fuscum*	[1] GBIF	Europe (except Iceland); Russia: Northwestern; Russia: Volga; Russia: Central; Russia: Urals; North America	[1] as the only source. Data points in Mexico and western Canada were deleted, as no evidence suggests that the pest causes damage in those regions
Butternut Canker	*Ophiognomonia clavigignenti-juglandacearum*	[1] Government of Canada (2017); [2] EPPO	North America	[1] as the main data source, cross checked by [2]
Dothistroma Needle Blight	*Dothistroma septosporum*	[1] Watt et al. (2009); [2] GBIF; [3] EPPO	None	[1] (points in Figure 2-7) and [2] as the main data sources, cross checked by [3]. Though source [3] reports pathogen presence in some Asian administrative units, no detailed records could be found in [1] and [2]. Also, no significant damage was reported from literature in those regions. Therefore, pathogen presence in those regions in dataset [3] was ignored.
Dutch Elm Disease	Ophiostoma ulmi and Ophiostoma novo-ulmi	[1] GBIF; [2] US Alien Forest Pest Explorer	Europe (except Iceland); Russia: Northwestern; Russia: Volga; Russia: Central; North America	European distribution is approximated by source [1]. Distribution in the United States is supplemented by [2]. Distributions in Europe and Canada may not be accurate, but unfortunately no fine-scale data sources could be found
Eight-Toothed Spruce Bark Beetle; European Spruce Bark	*Ips typographus*	[1] GBIF; [2] EPPO	Europe (except Iceland), Asia	[1] as the main data source, cross checked by [2]. Data points in North America and Africa in [1] were removed, as the pest only causes significant damage in Europe and East Asia.

Beetle; Larger Eight-toothed European Spruce Bark Beetle				For the same reason, data records outside of the Europe and East Asia in [2] were ignored
Emerald Ash Borer	*Agrilus planipennis*	[1] GBIF; [2] Meshkova et al. (2023); [3] EPPO	Europe (except Iceland); Russia: Northwestern; Russia: Volga; Russia: Central; North America	[1] as the main data source, cross checked by [2] (Table S1) and [3]. Data outside of North America and Europe was removed, as the pest cause limited damage in its native range, i.e. East Asia
Fall Webworm; American White Moth	*Hyphantria cunea*	[1] Ning et al. (2022); [2] GBIF; [3] EPPO	Europe (except Iceland); Asia	[1] and [2] as the main data source, cross checked by [3]. The pest causes much lower level of damage in its native range - North America. Thus, data points in its native range were removed
Forest Tent Caterpillar	*Malacosoma disstria*	[1] GBIF; [2] EPPO	North America	[1] as the main data source, cross checked by [2]. Removed an Indian data point in the dataset [1], as the pest does not appear to present in Eurasia according to [2]
Gypsy Moth; Spongy Moth	*Lymantria dispar*	[1] GBIF; [2] Song et al. (2022); [3] EPPO	Europe (except Iceland); Asia; North America	[1] as the main data sources, cross checked by [2] and [3]
Hemlock Woolly Adelgid	*Adelges tsugae*	[1] GBIF; [2] US Alien Forest Pest Explorer	North America	[1] as the main data source, cross checked by [2]. Removed points in Eurasia in dataset [2], as the pest does not appear to cause significant damage in its native area
Japanese Oak Wilt	*Raffaelea quercivora*	[1] Kuroda et al. (2010); [2] EPPO	Japan	[1] as the main data source, cross checked by [2]
Laurel Wilt	*Raffaelea lauricola*	[1] US Alien Forest Pest Explorer; [2] EPPO	North America	[1] as the main data source, cross checked by [2]. Although the pathogen is native to East Asia, it causes damage primarily in the United States
Mountain Pine Beetle	*Dendroctonus ponderosae*	[1] GBIF; [2] Logan and Powell (2001); [3] EPPO	North America	[1] as the main data source, cross checked by [2] and [3]. Removed a data point in Europe in the database [1], as the pest does not present in Europe
Oak Decline	*Brenneria goodwinii; Gibbsiella quercinecans*	[1] Kowsari and Karimi (2023); [2] EPPO	North America; Europe (except Iceland); Asia	[1] as the main data source, cross checked by [2]. The disease caused damage in North America, Europe, and Asia.
Oak Wilt	*Bretziella fagacearum*	[1] Pedlar et al. (2020); [2] EPPO	North America	[1] (Figure 1a) as the main data source, cross checked by [2]
Oriental Chestnut Gall Wasp; Chestnut Gall Wasp	*Dryocosmus kuriphilus*	[1] GBIF; [2] EPPO	Europe (except Iceland); Asia, North America	[1] as the main data source, cross checked by [2].
Pine Processionary Moth; Pine Caterpillar; Pine processionary Moth Caterpillar	*Thaumetopea pityocampa*	[1] GBIF; [2] Kerdelhué et al. (2009); [3] EPPO	Europe (except Iceland); Russia: Northwestern; Russia: Volga; Russia: Central	[1] as the main data source, cross checked by [2] and [3]
Pine Wood Nematode; Pine	*Bursaphelenchus*	[1] Aierken et al.	Europe (except	[1] (Figure 1) as the main data source, cross

Wilt Disease	*xylophilus*	(2024); [2] EPPO	Iceland); Asia	checked by [2]
Red Turpentine Beetle	*Dendroctonus valens*	[1] Zhou et al. (2024); [2] EPPO	China	[1] as the main data source. Since the pest does not cause great damage in its native range, North America, those data points were removed
Red-necked Longhorn Beetle	*Aromia bungii*	[1] GBIF; [2] Horrocks et al. (2024)	Russian: Far Eastern; China; Japan; North Korea; South Korea	[1] and [2] as the data sources
Spotted Lanternfly	*Lycorma delicatula*	[1] GBIF; [2] EPPO; [3] Wakie et al. (2020)	Russia: Far Eastern; China; Japan; North Korea; South Korea; North America	[1] as the main data source, cross checked by [2] and [3]
Spruce Budworm; Eastern Spruce Budworm	*Choristoneura fumiferana*	[1] GBIF; [2] Nealis (2015); [3] EPPO	North America	[1] as the main data source, cross checked by [2] and [3]
Sudden Oak Death; Ramorum Disease; Ramorum Blight, Ramorum Dieback	*Phytophthora ramorum*	[1] Ireland et al. (2013); [2] EPPO; [3] US Alien Forest Pest Explorer	Europe (except Iceland and Russia); North America	[1] as the main data source (point data in Figure 2 for the United States and Norway), cross checked by [2] and [3]. Since the pathogen the Europe, but no European distribution data points (except Norway) were available, projection should be careful
Sweet Chestnut Blight; Chestnut Blight	*Cryphonectria parasitica*	[1] GBIF; [2] EPPO	North America; Europe (except Iceland and Russia)	[1] as the main data source, cross checked by [2]. Distribution points in East Asia were removed, as the pathogen causes relatively low damage in its native range
White Pine Blister Rust	*Cronartium ribicola*	[1] GBIF; [2] EPPO	North America; Europe (except Iceland); Russia: Northwestern; Russia: Volga; Russia: Central	[1] as the main data source, cross checked by [2]. Data points outside of Europe and North America in the dataset [1] was removed, as the pathogen causes significantly lower level of damage in East Asia, where host trees show partial resistance
Xylella	*Xylella fastidiosa*	[1] Koufakis et al. (2016); [2] EPPO	North America; South America; Europe (except Iceland); Iraq; Iran; Lebanon; Israel; Taiwan, China	[1] as the main data source, cross checked by [2]

Supplementary Table S2. Explanation of 19 WorldClim bioclimatic variables.

Variable name	Meaning
bio_1	Annual Mean Temperature
bio_2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
bio_3	Isothermality (bio_2/bio_7) (×100)
bio_4	Temperature Seasonality (standard deviation ×100)

bio_5	Max Temperature of Warmest Month
bio_6	Min Temperature of Coldest Month
bio_7	Temperature Annual Range (bio_5-bio_6)
bio_8	Mean Temperature of Wettest Quarter
bio_9	Mean Temperature of Driest Quarter
bio_10	Mean Temperature of Warmest Quarter
bio_11	Mean Temperature of Coldest Quarter
bio_12	Annual Precipitation
bio_13	Precipitation of Wettest Month
bio_14	Precipitation of Driest Month
bio_15	Precipitation Seasonality (Coefficient of Variation)
bio_16	Precipitation of Wettest Quarter
bio_17	Precipitation of Driest Quarter
bio_18	Precipitation of Warmest Quarter
bio_19	Precipitation of Coldest Quarter

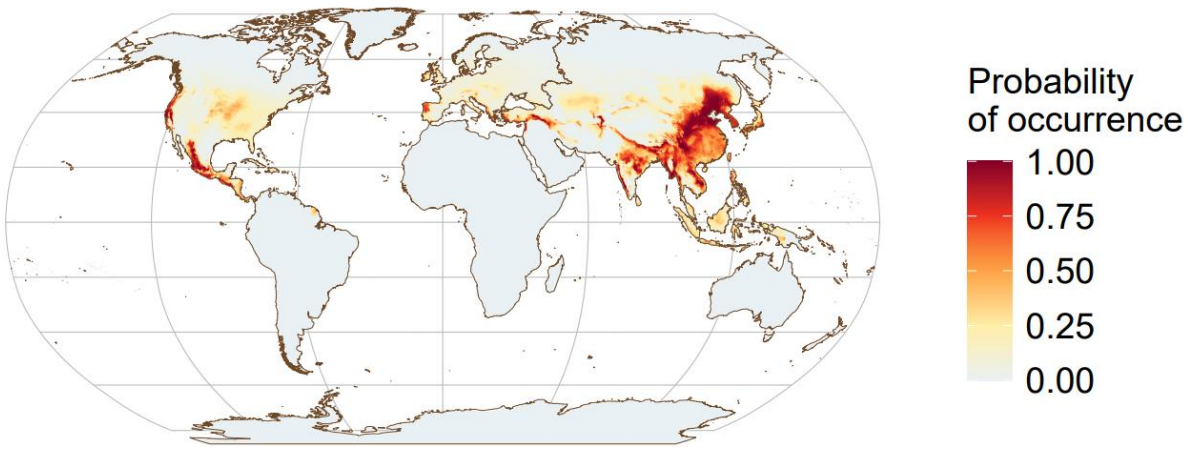
Supplementary Table S3. Area Under the Curve (AUC) values for training and testing data of MaxEnt models predicting the distribution of tree-infecting pests and pathogens. AUC (Area Under the Curve) values quantify the performance of MaxEnt models, with values ranging from 0 to 1 (higher values indicate better ability of the model to discriminate true presence). For each MaxEnt model, species presence data were split into two subsets: 75% of the data were used to train and build the model (training data), and the remaining 25% were reserved to evaluate model performance (testing data). Training data AUC reflects model performance on the data used to build the model, while testing data AUC indicates performance on independent data not used in model training. Values are provided for each pest or pathogen evaluated in the study.

Pest/pathogen	AUC on training data	AUC on testing data
Ash Dieback	0.8552	0.8621
Asian Longhorned Beetle	0.8715	0.8459
Beech Bark Disease	0.9479	0.9501
Beech Leaf Disease	0.9375	0.9441
Bronze Birch Borer	0.8495	0.8459
Brown Spruce Longhorn Beetle	0.8391	0.8348
Butternut Canker	0.8275	0.8289
Dothistroma Needle Blight	0.7975	0.7887
Dutch Elm Disease	0.6643	0.662
Eight-Toothed Spruce Bark Beetle	0.7726	0.7784
Emerald Ash Borer	0.8274	0.7784

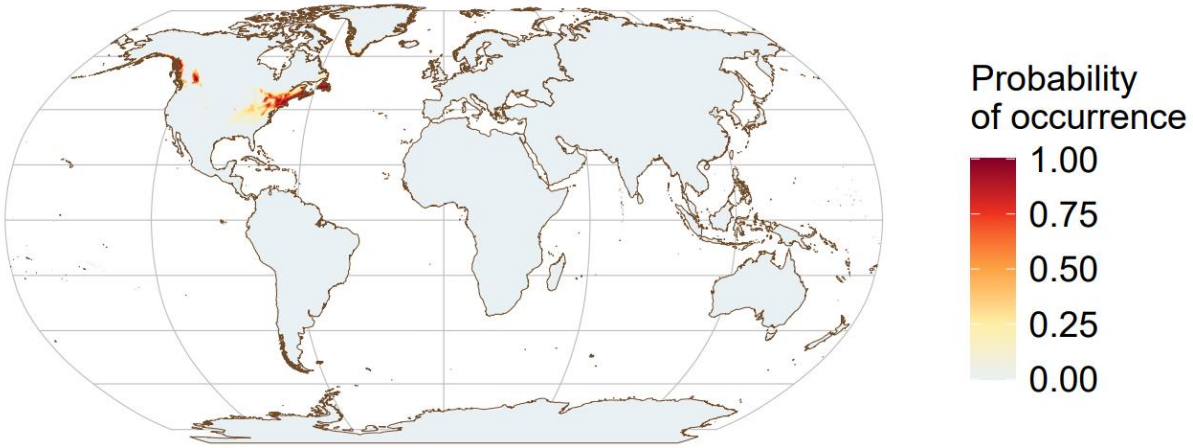
Fall Webworm	0.845	0.8547
Forest Tent Caterpillar	0.7453	0.7343
Gypsy Moth; Spongy Moth	0.6206	0.6117
Hemlock Woolly Adelgid	0.8868	0.8817
Japanese Oak Wilt	0.9897	0.9904
Laurel Wilt	0.9552	0.955
Mountain Pine Beetle	0.8277	0.8394
Oak Decline	0.6787	0.6436
Oak Wilt	0.8861	0.8764
Oriental Chestnut Gall Wasp	0.7997	0.8128
Pine Processionary Moth	0.7871	0.7947
Pine Wood Nematode	0.8267	0.8334
Red Turpentine Beetle	0.9754	0.9717
Red-necked Longhorn Beetle	0.9916	0.9903
Spotted Lanternfly	0.8822	0.8687
Spruce Budworm; Eastern Spruce Budworm	0.8703	0.8715
Sudden Oak Death	0.9283	0.9202
Sweet Chestnut Blight	0.8589	0.8658
White Pine Blister Rust	0.7771	0.7793
Xylella	0.861	0.8536



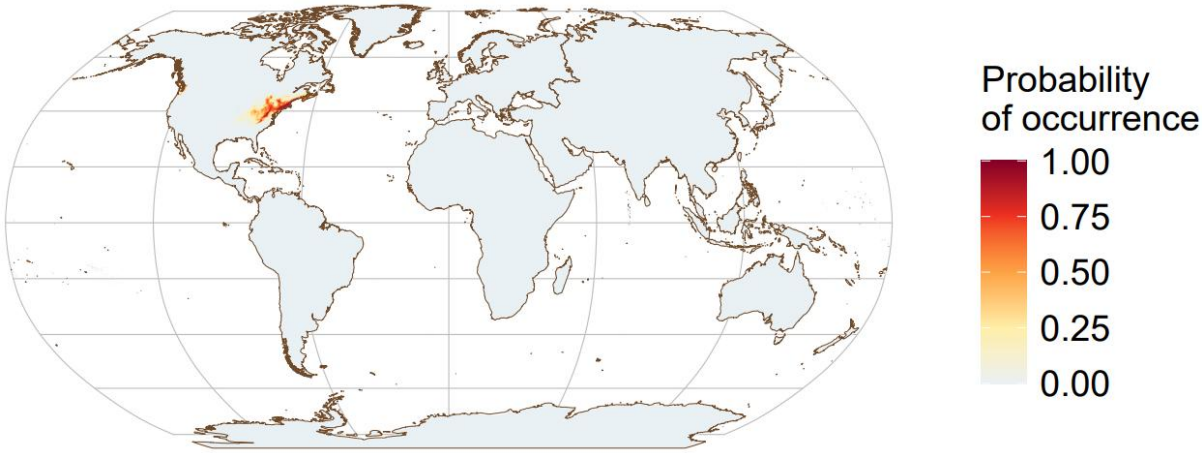
Asian Longhorned Beetle



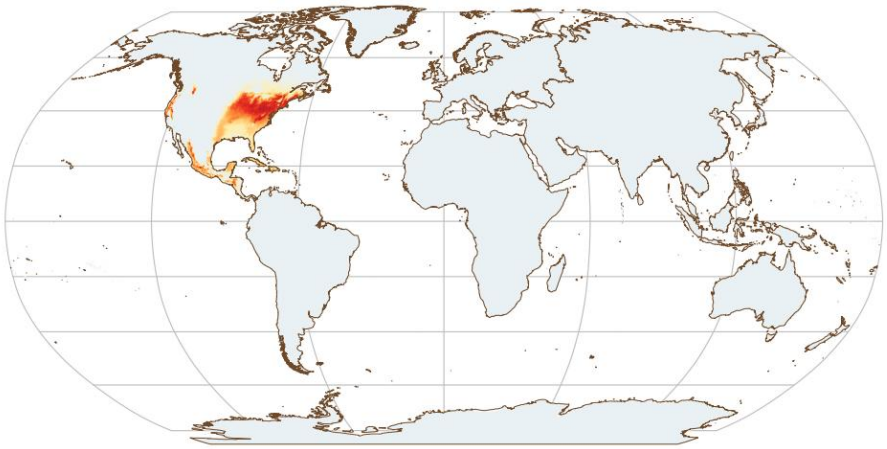
Beech Bark Disease



Beech Leaf Disease

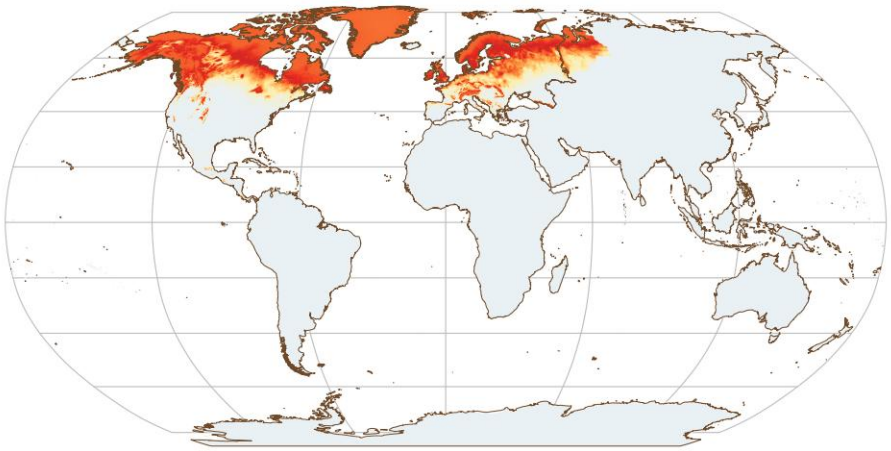


Bronze Birch Borer



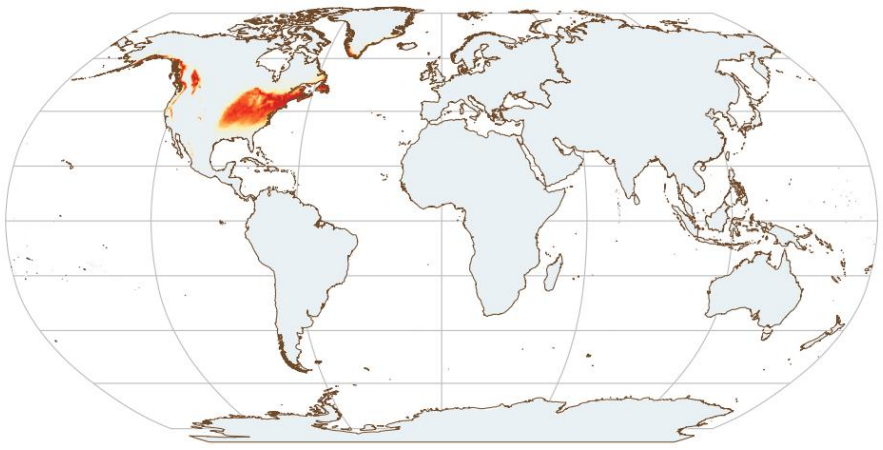
Probability of occurrence
1.00
0.75
0.50
0.25
0.00

Brown Spruce Longhorn Beetle



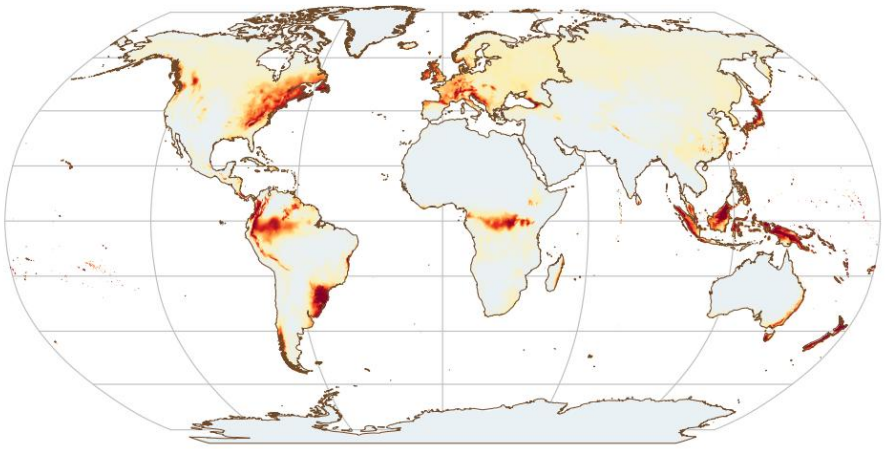
Probability of occurrence
1.00
0.75
0.50
0.25
0.00

Butternut Canker

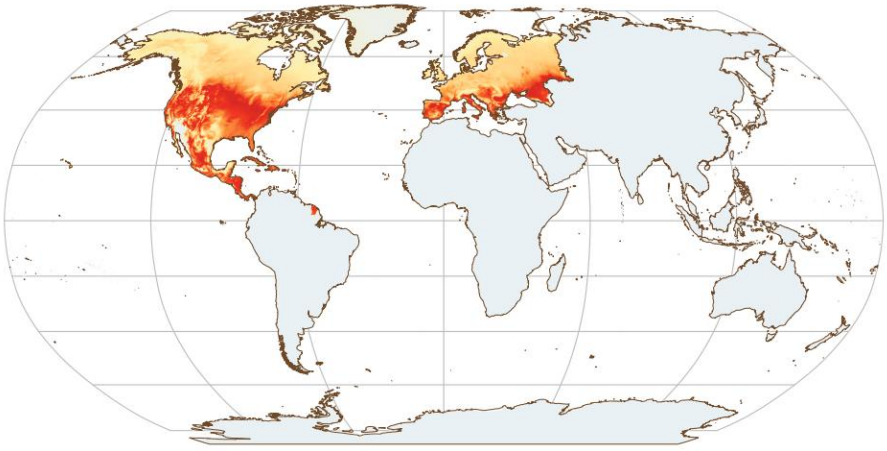


Probability of occurrence
1.00
0.75
0.50
0.25
0.00

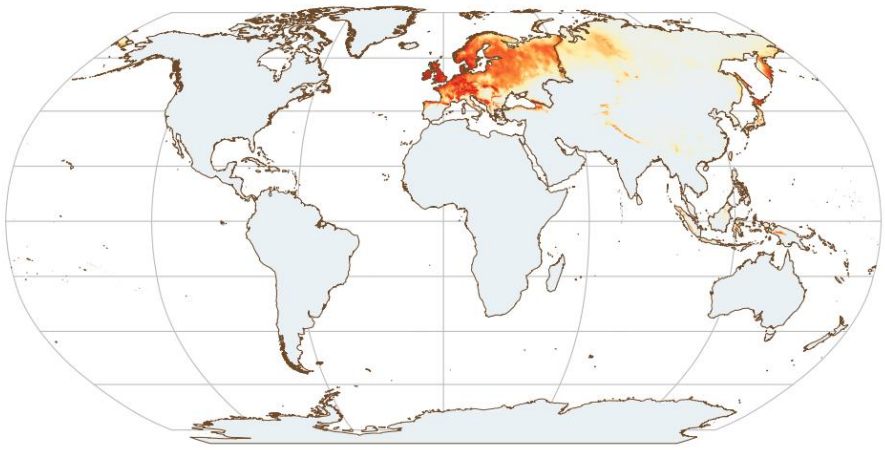
Dothistroma Needle Blight



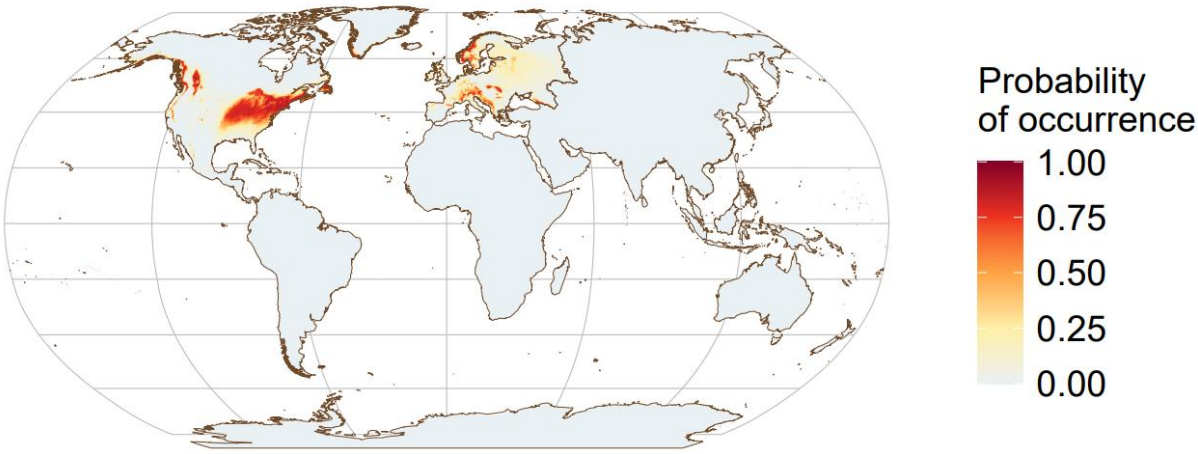
Dutch Elm Disease



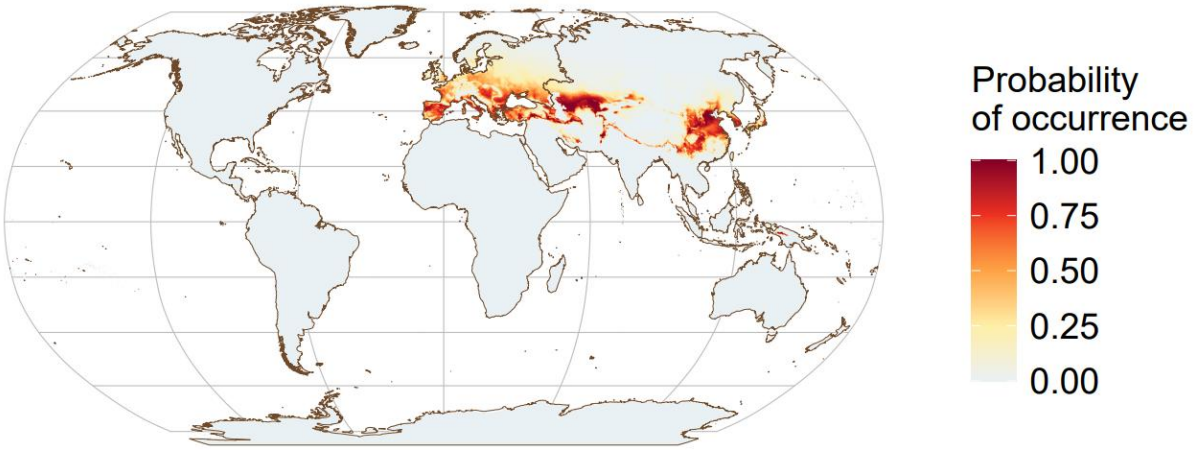
Eight−Toothed Spruce Bark Beetle



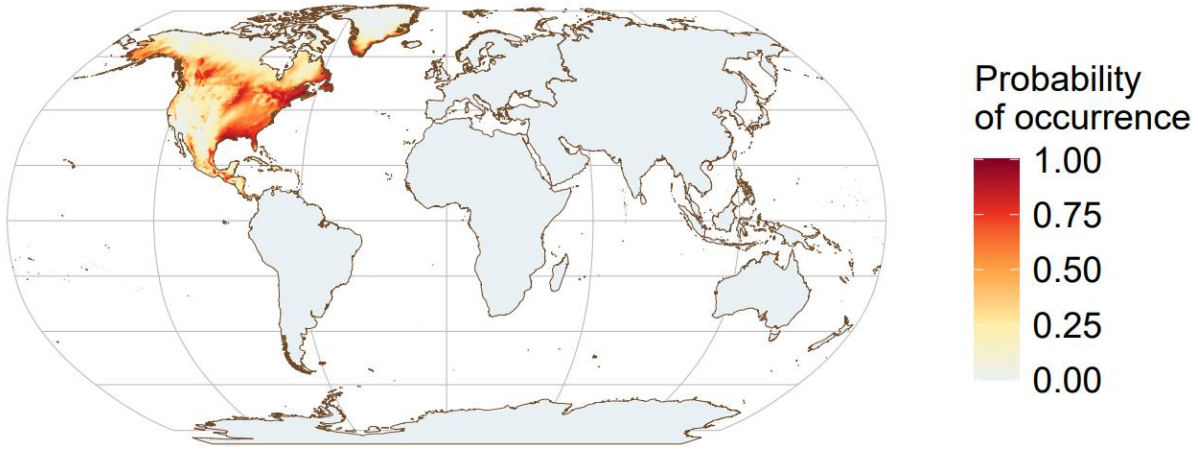
Emerald Ash Borer



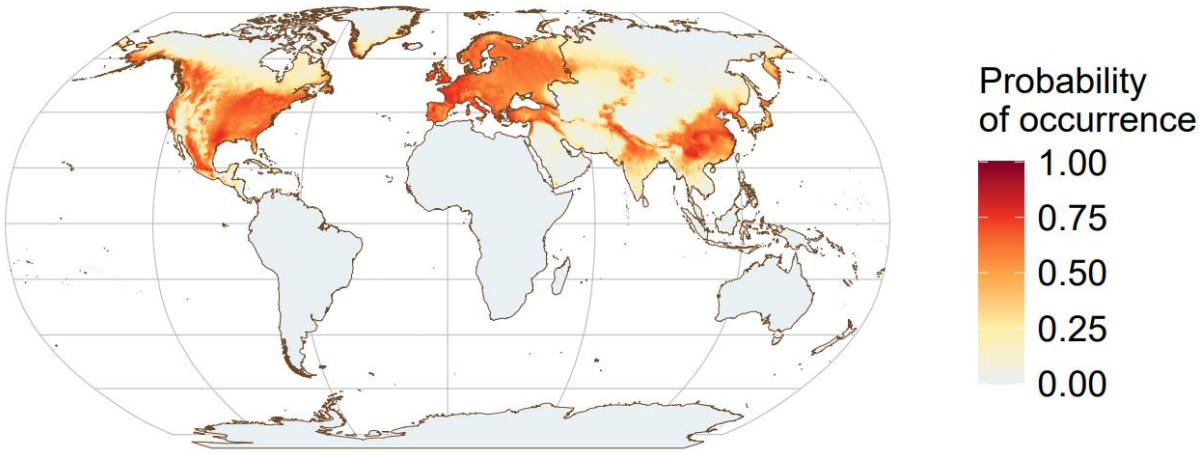
Fall Webworm



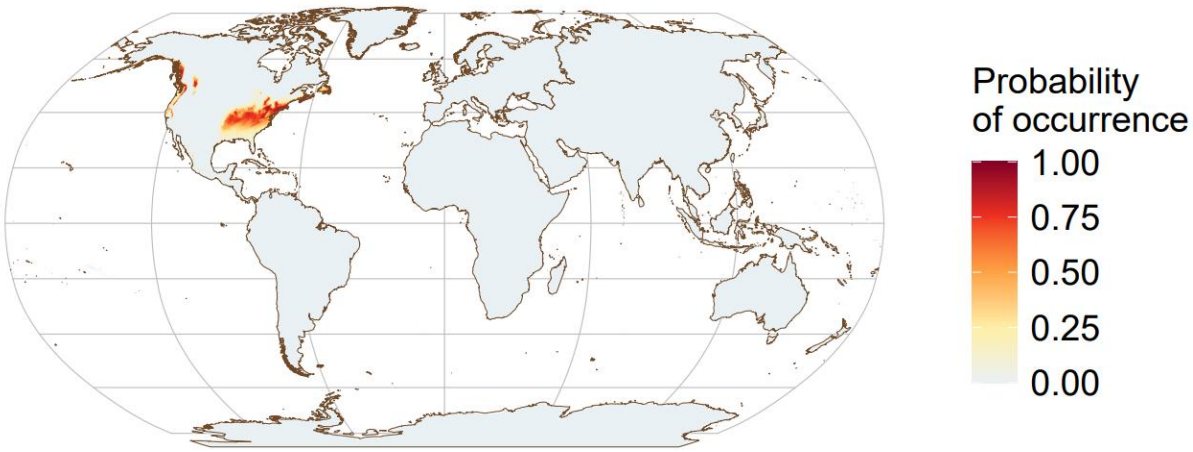
Forest Tent Caterpillar



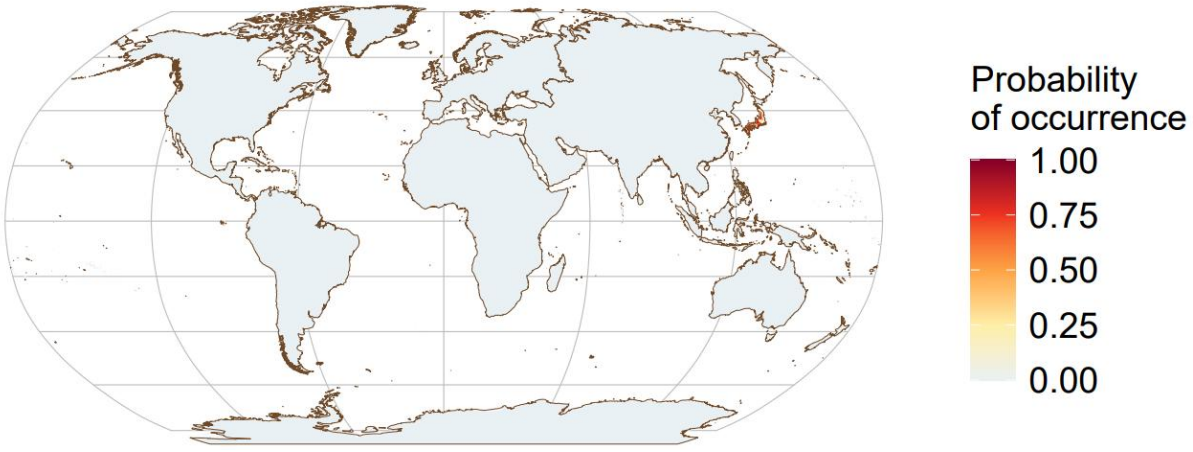
Gypsy Moth



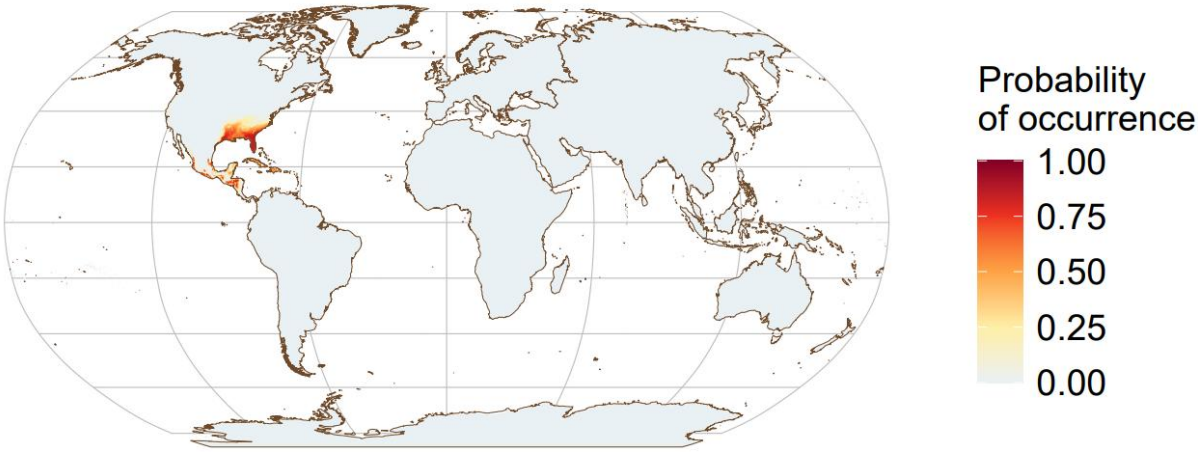
Hemlock Woolly Adelgid



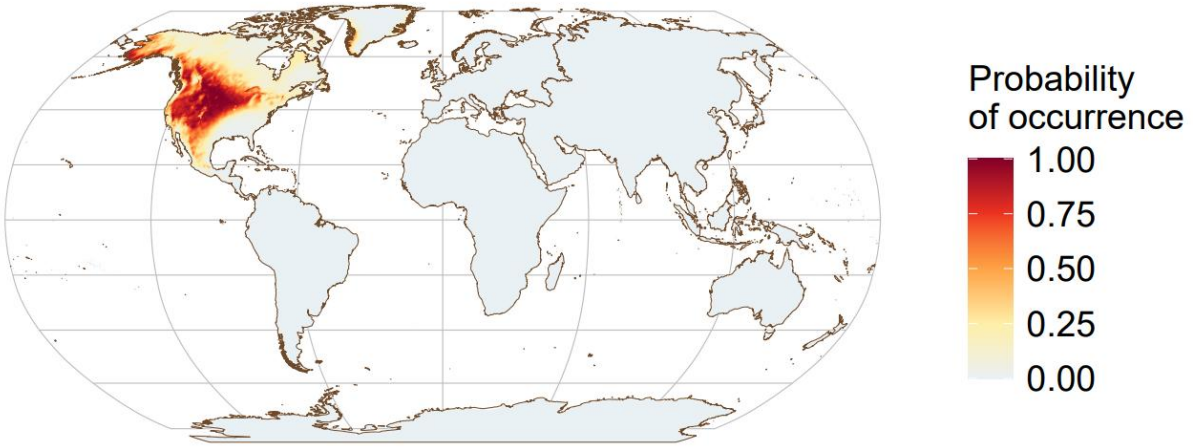
Japanese Oak Wilt



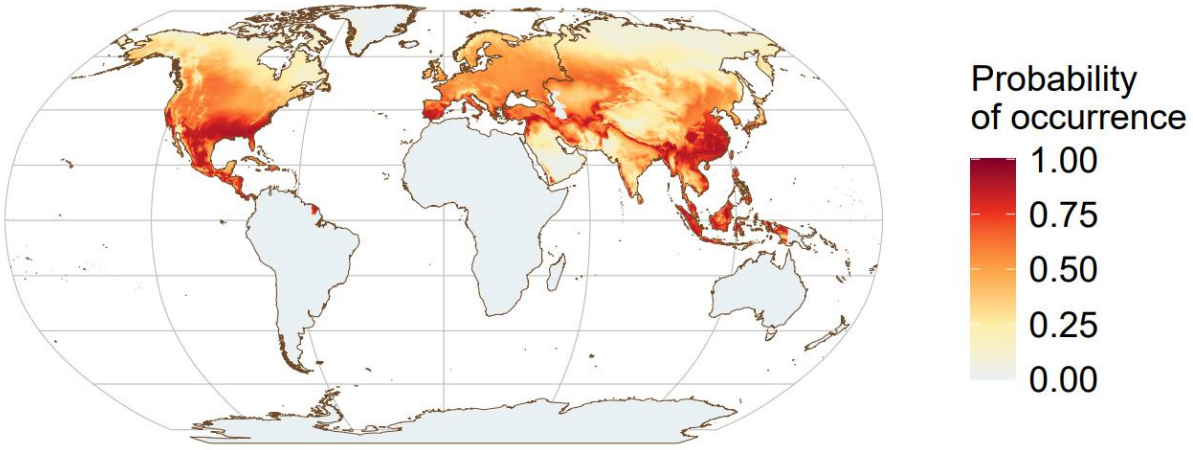
Laurel Wilt



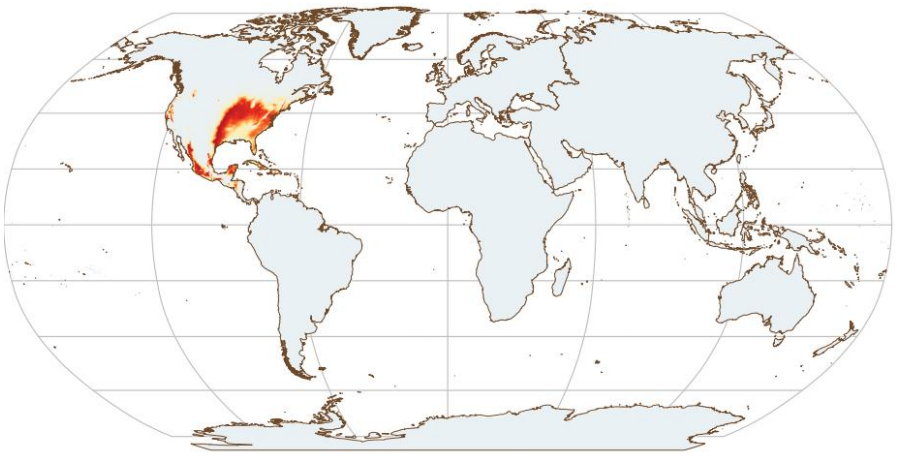
Mountain Pine Beetle



Oak Decline

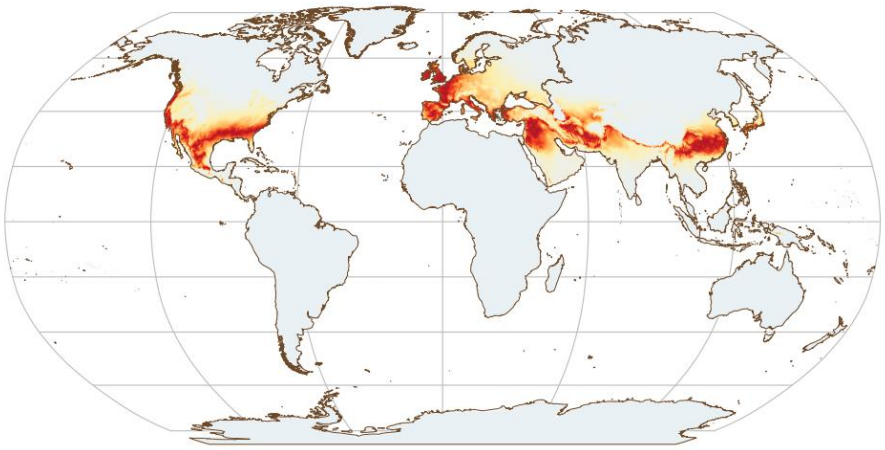


Oak Wilt



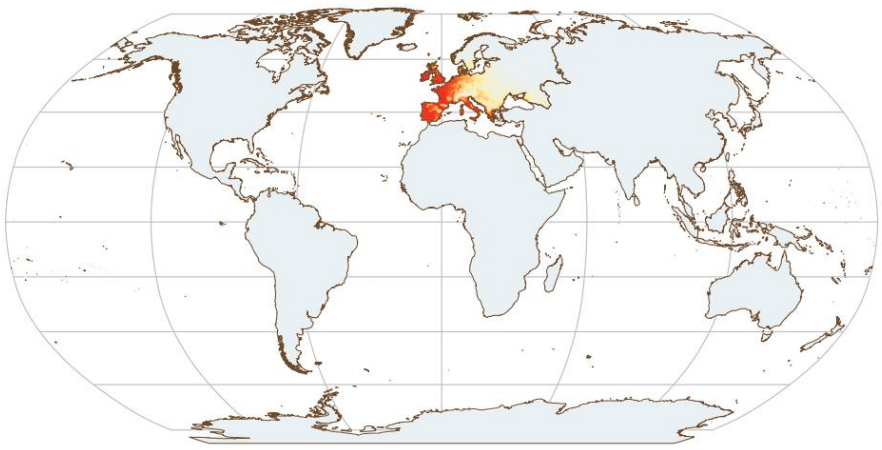
Probability of occurrence
1.00
0.75
0.50
0.25
0.00

Oriental Chestnut Gall Wasp



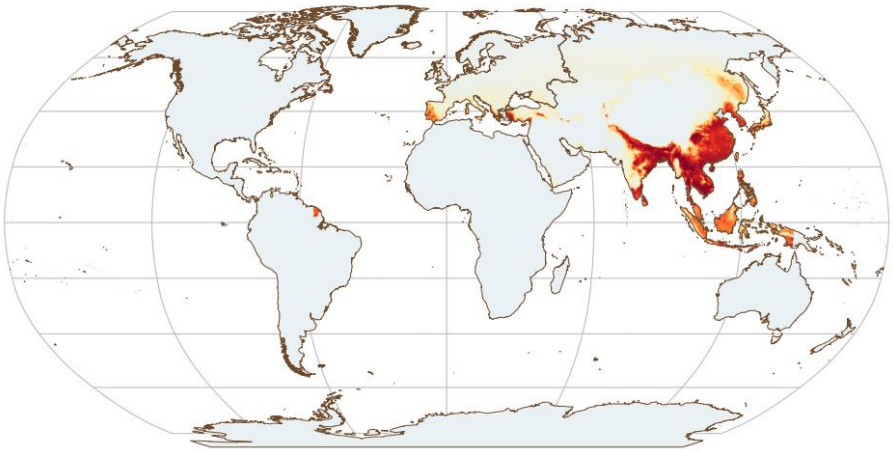
Probability of occurrence
1.00
0.75
0.50
0.25
0.00

Pine Processionary Moth

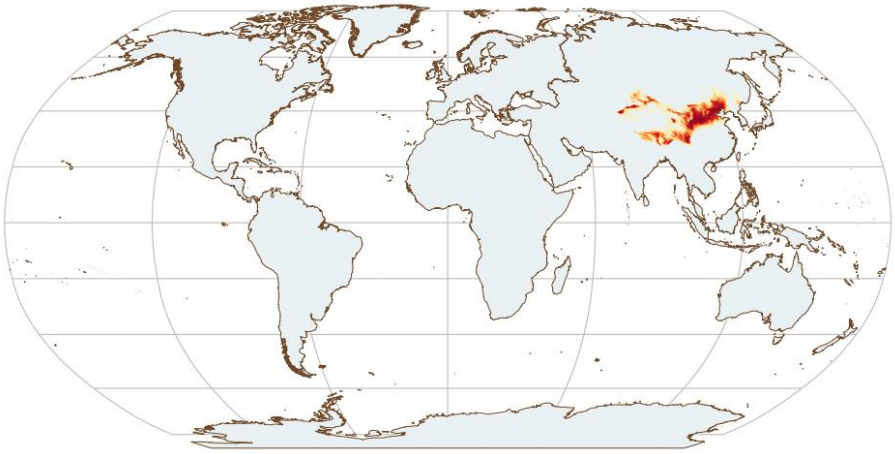


Probability of occurrence
1.00
0.75
0.50
0.25
0.00

Pine Wood Nematode



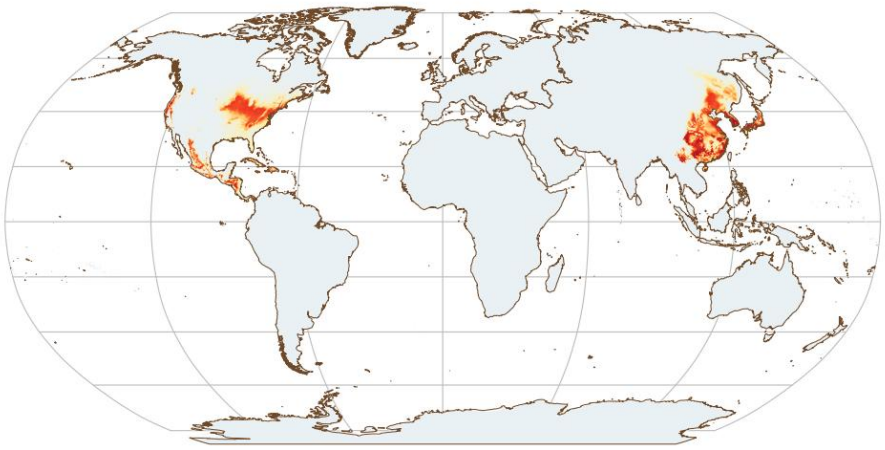
Red Turpentine Beetle



Red−necked Longhorn Beetle

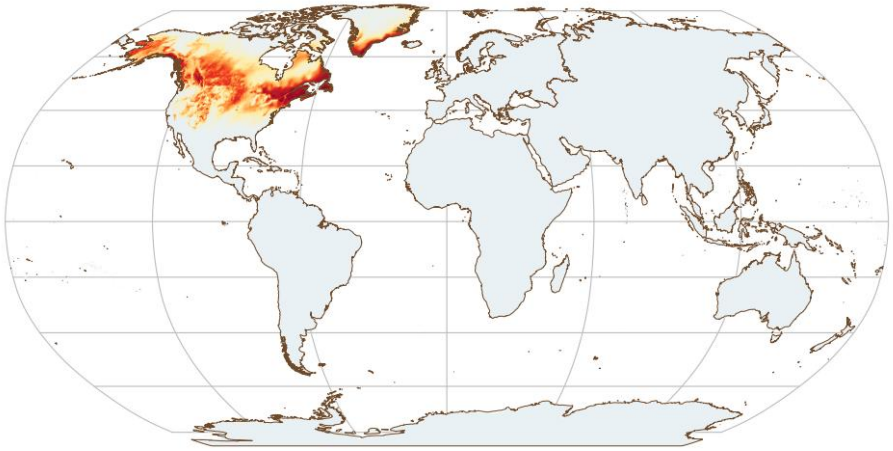


Spotted Lanternfly



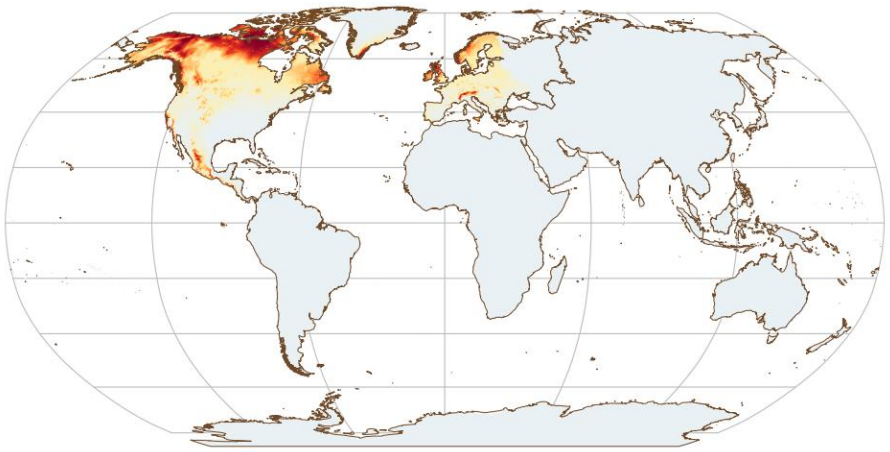
Probability of occurrence
1.00
0.75
0.50
0.25
0.00

Spruce Budworm

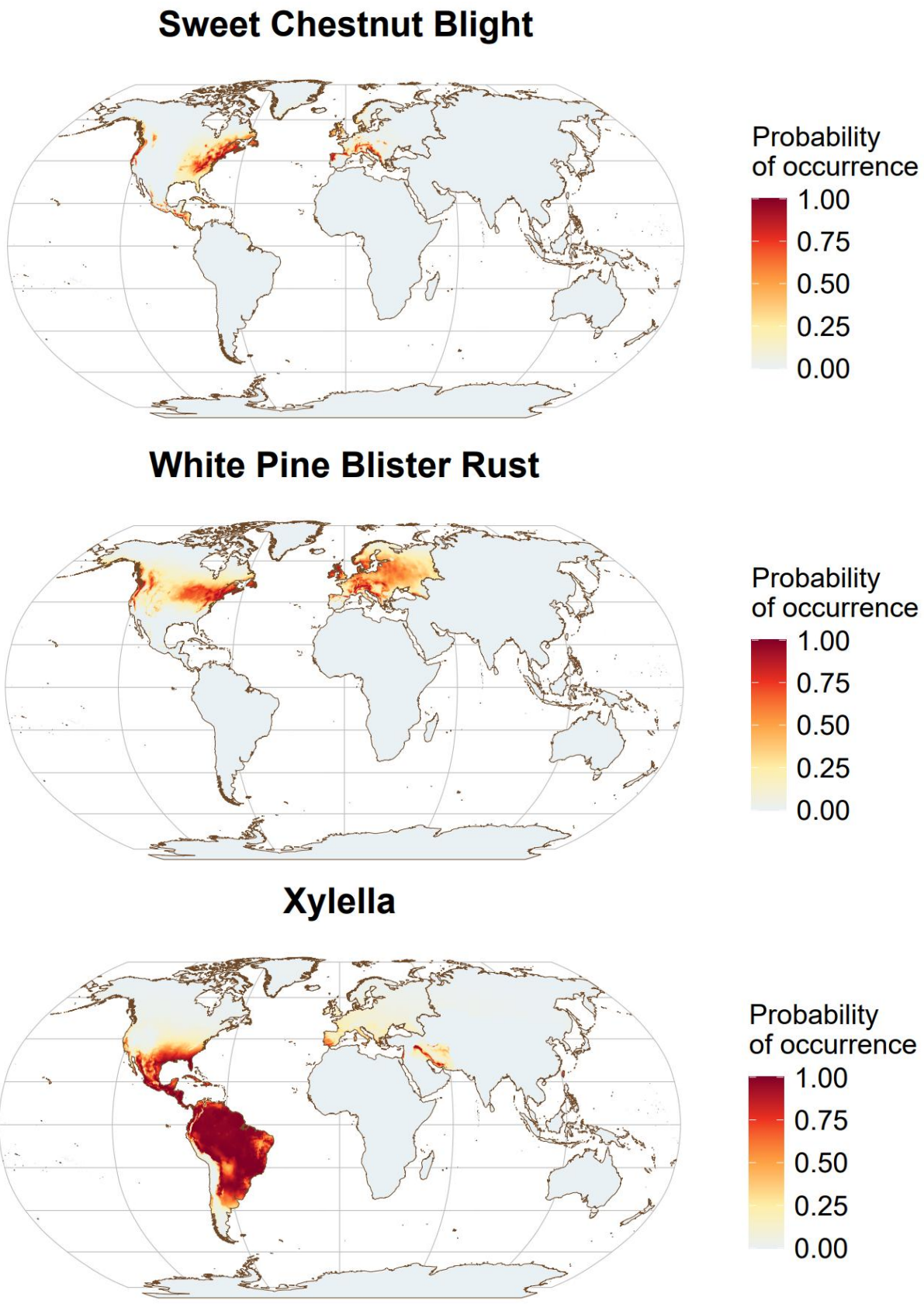


Probability of occurrence
1.00
0.75
0.50
0.25
0.00

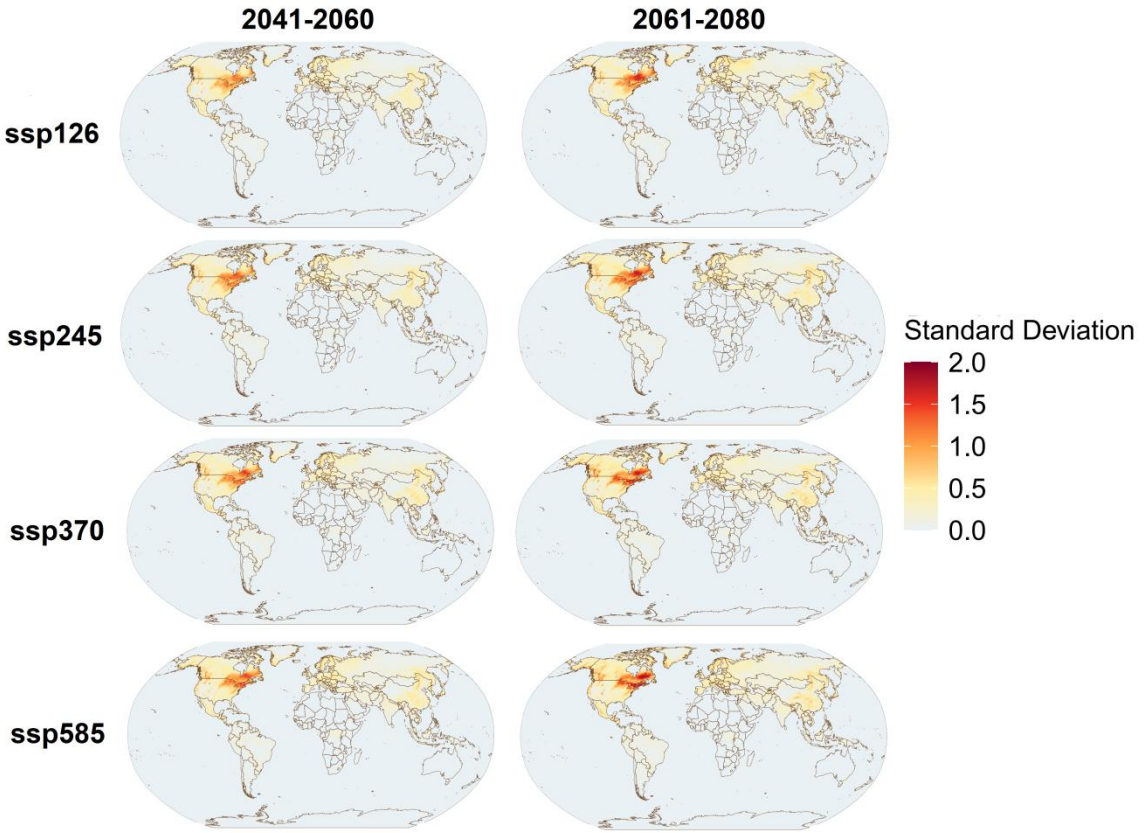
Sudden Oak Death



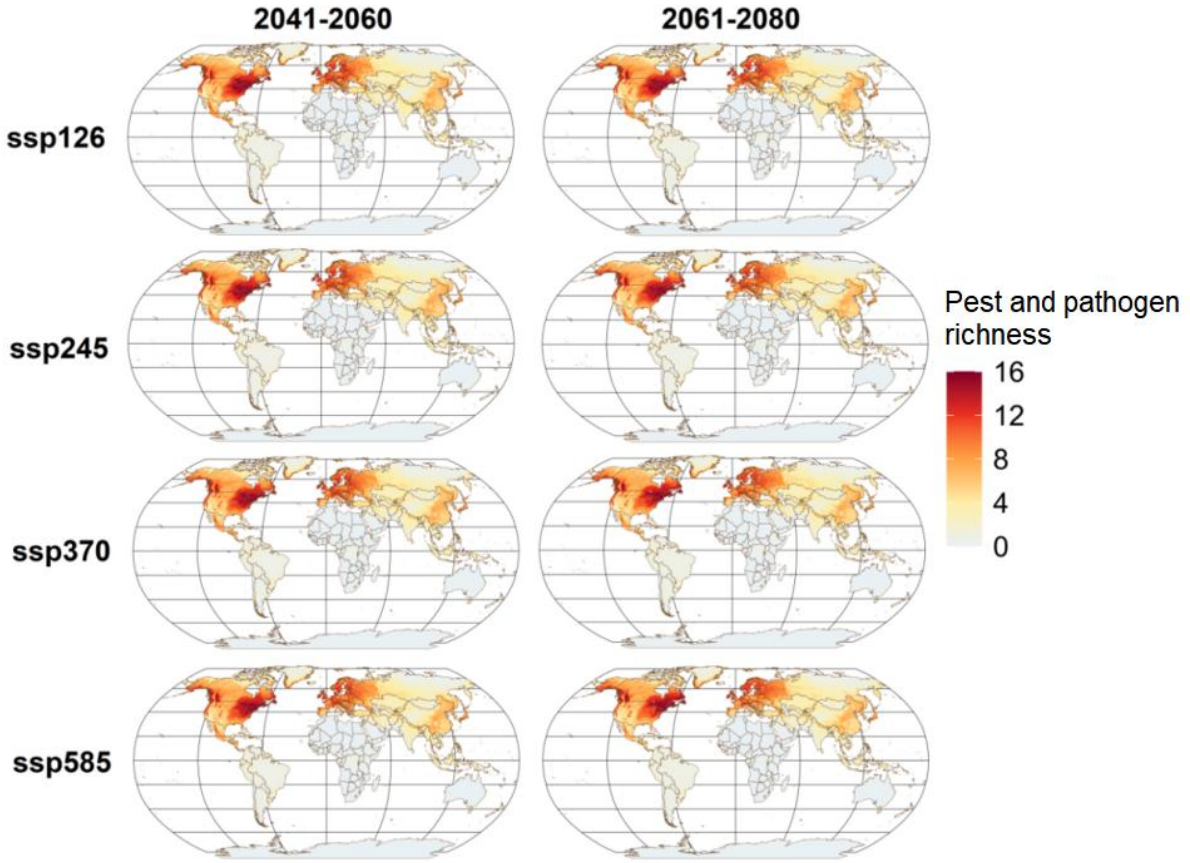
Probability of occurrence
1.00
0.75
0.50
0.25
0.00



Supplementary Figure S1. Modelled spatial distribution for 31 major forest pests and pathogens under current conditions.

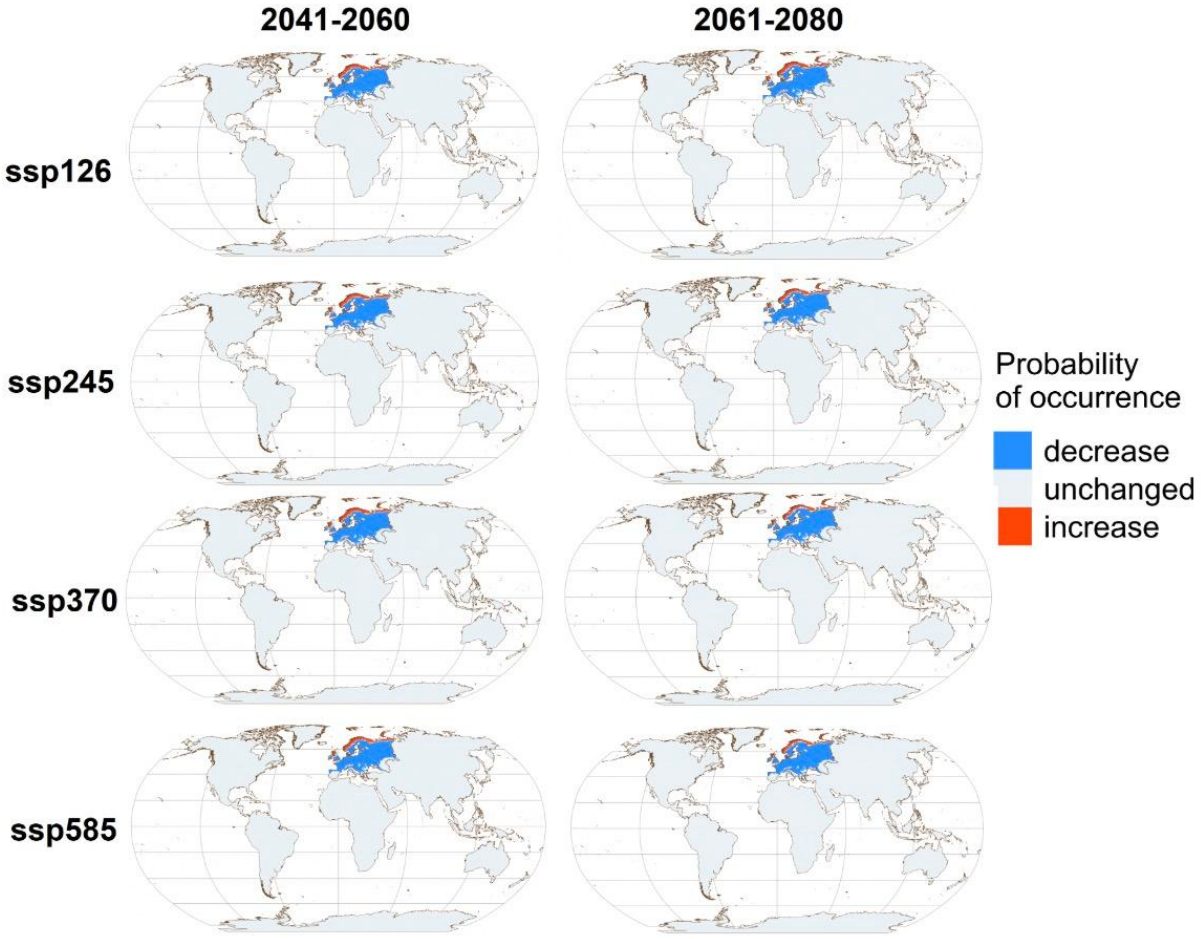


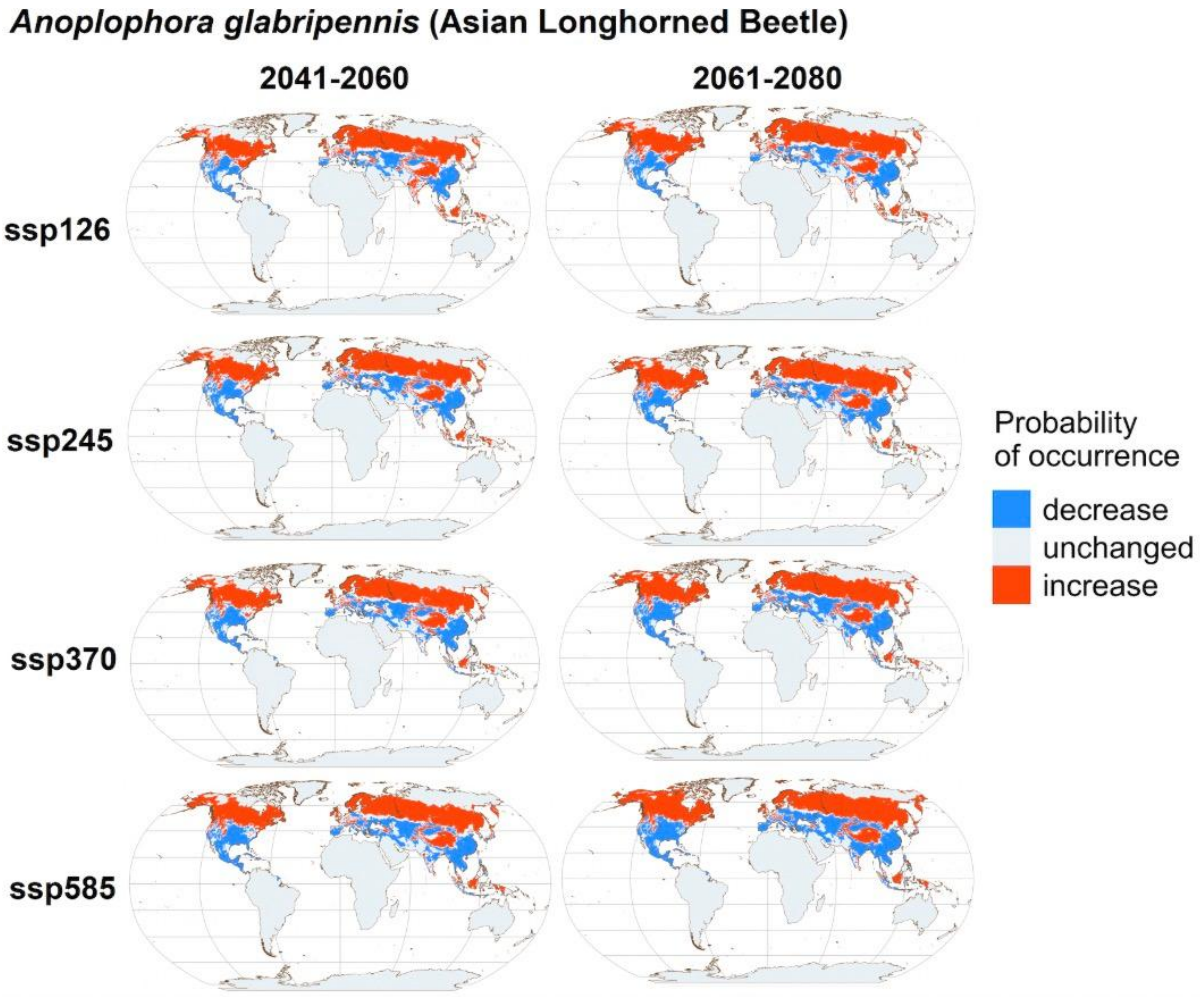
Supplementary Figure S2. Standard deviation of model projections of tree pest and pathogen richness across 11 global climate models (CGMs): ACCESS-CM2, BCC-CSM2-MR, CMCC-ESM2, EC-Earth3-Veg, GISS-E2-1-G, INM-CM5-0, IPSL-CM6A-LR, MIROC6, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL. Projections are made under four Shared Socio-economic Pathways (SSP126, SSP245, SSP370, SSP585) for two future periods (2041–2060 and 2061–2080).



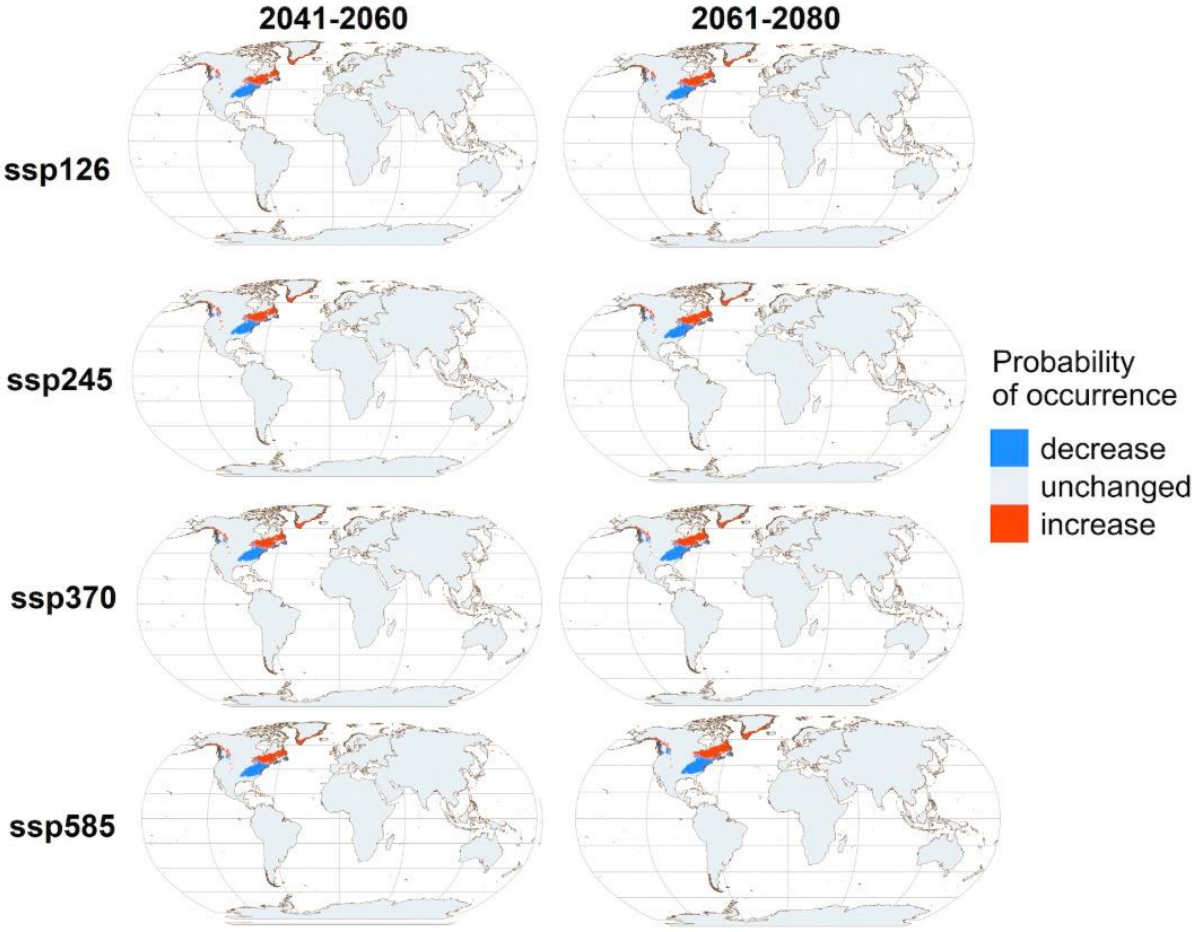
Supplementary Figure S3. Projections of tree pest and pathogen richness under four Shared Socio-economic Pathways (SSP126, SSP245, SSP370, SSP585) for two future periods (2041–2060 and 2061–2080). Color intensity represents pest and pathogen richness.

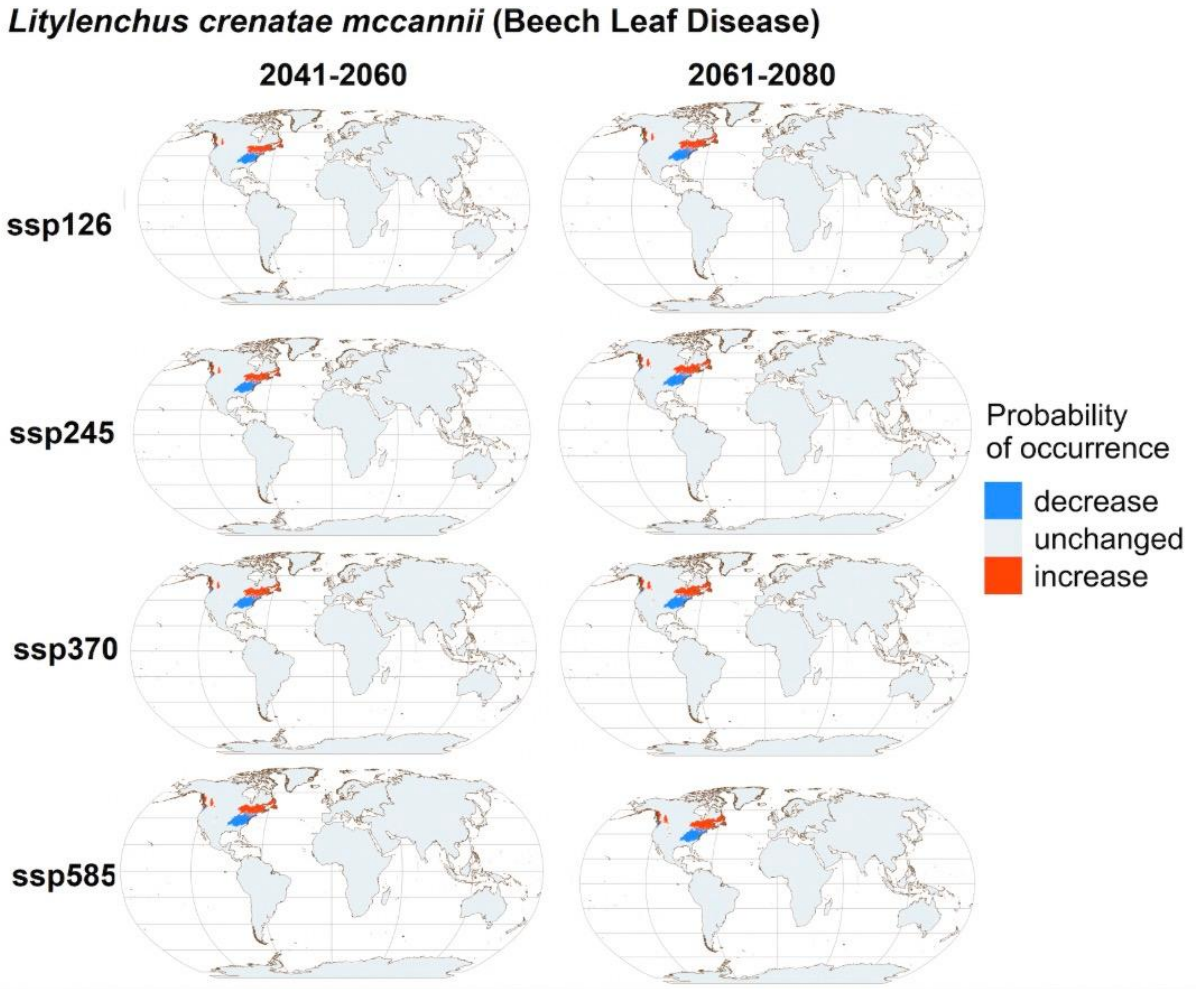
***Hymenoscyphus fraxineus* (Ash Dieback)**



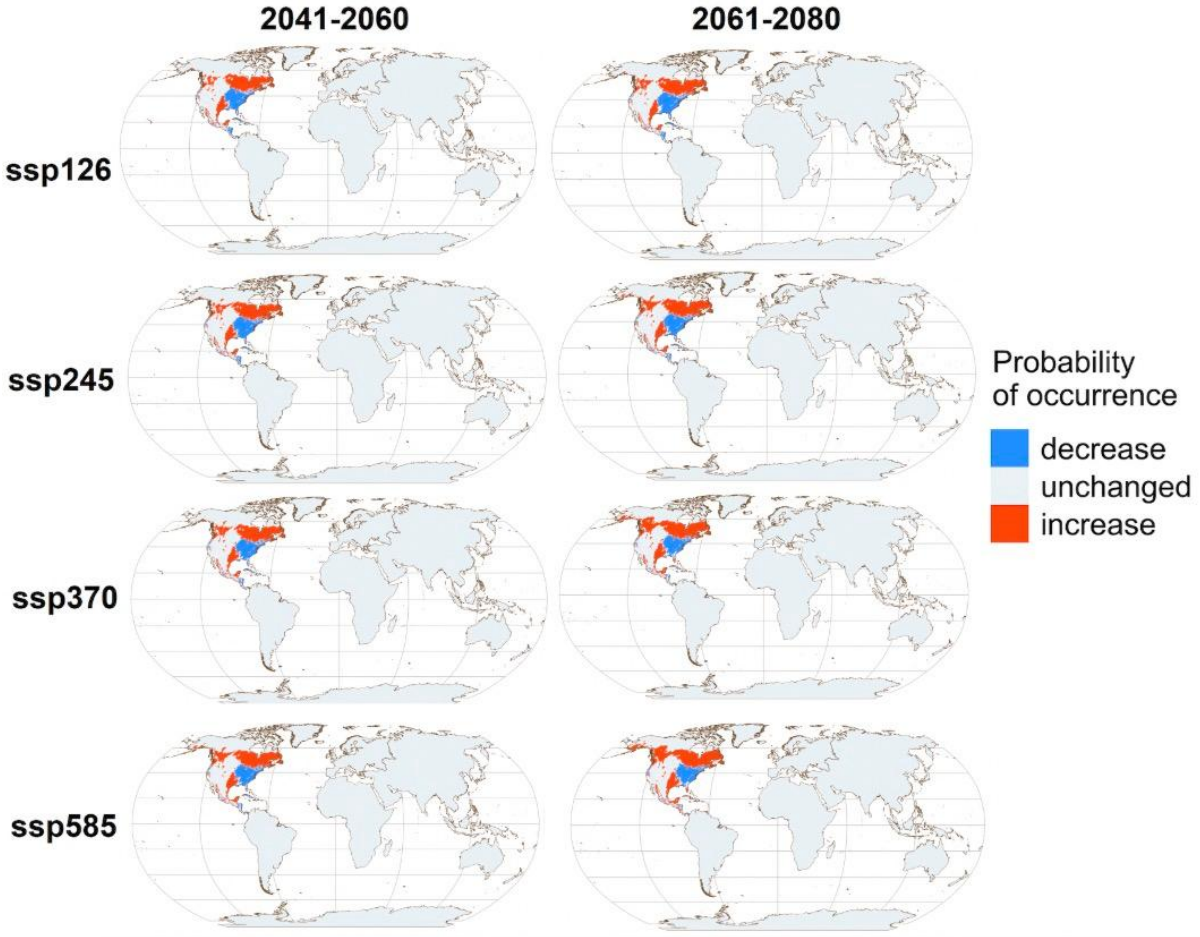

Anoplophora glabripennis (Asian Longhorned Beetle)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

***Neonectria faginata* (Beech Bark Disease)**

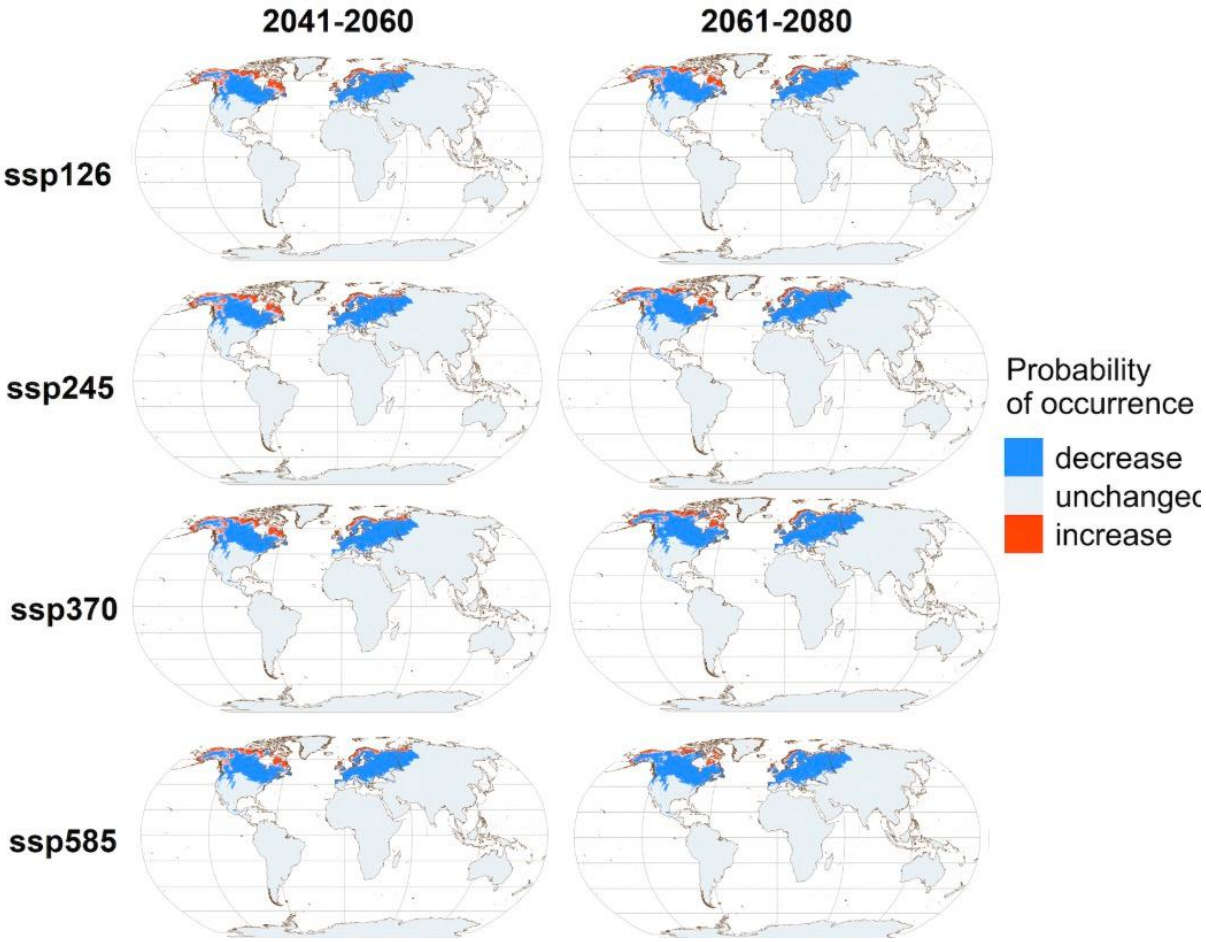



Litylenchus crenatae mccannii (Beech Leaf Disease)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

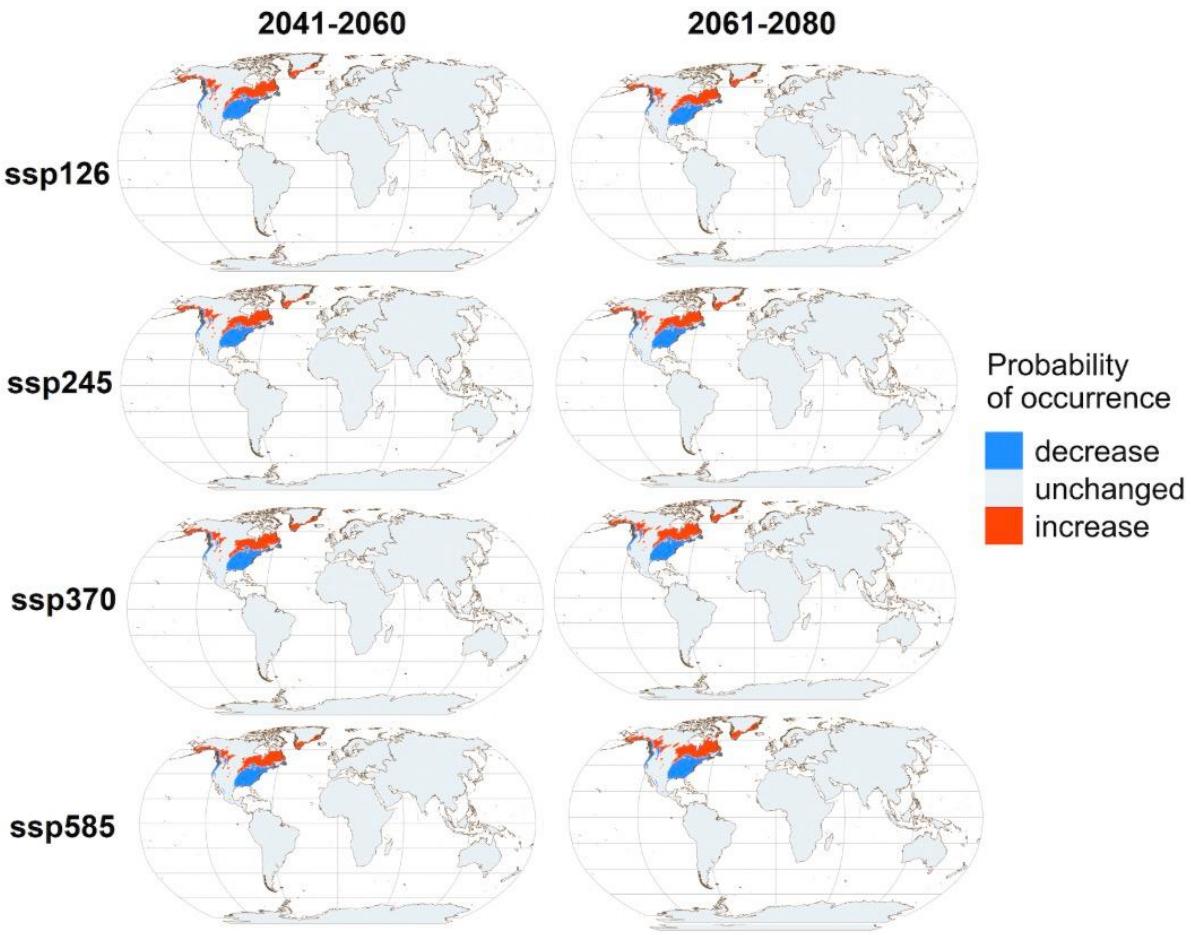
***Agrilus anxius* (Bronze Birch Borer)**

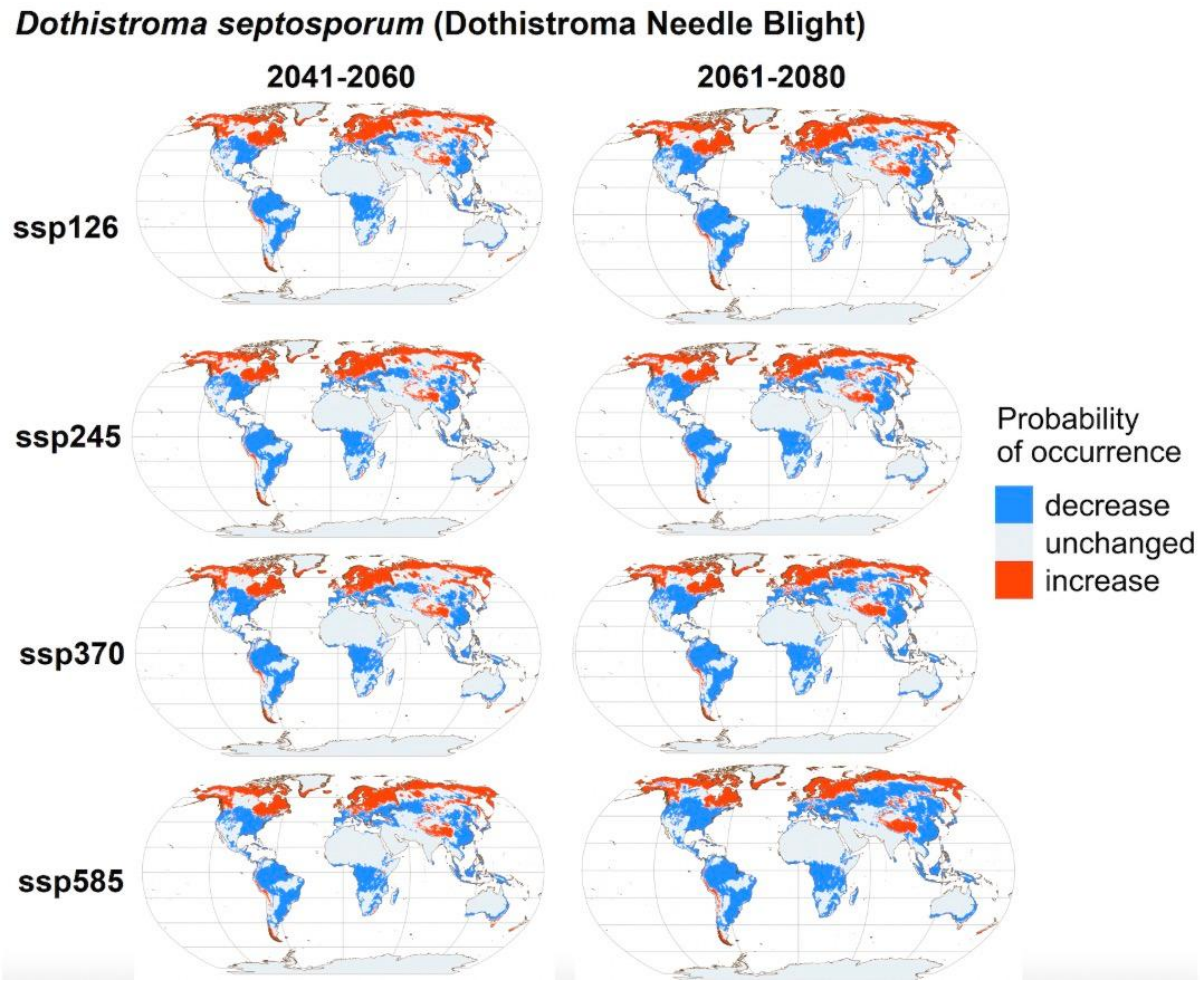


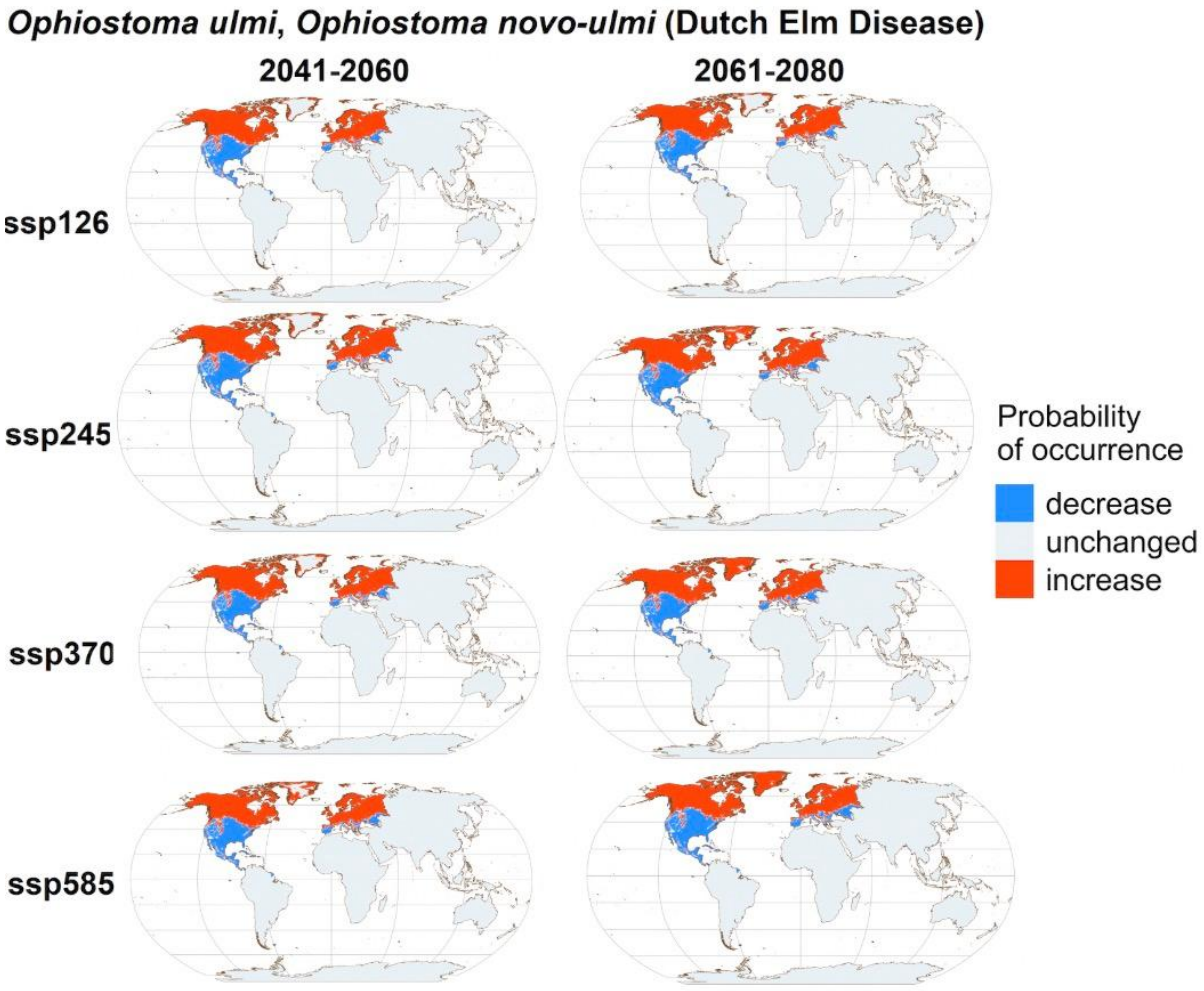
***Tetropium fuscum* (Brown Spruce Longhorn Beetle)**

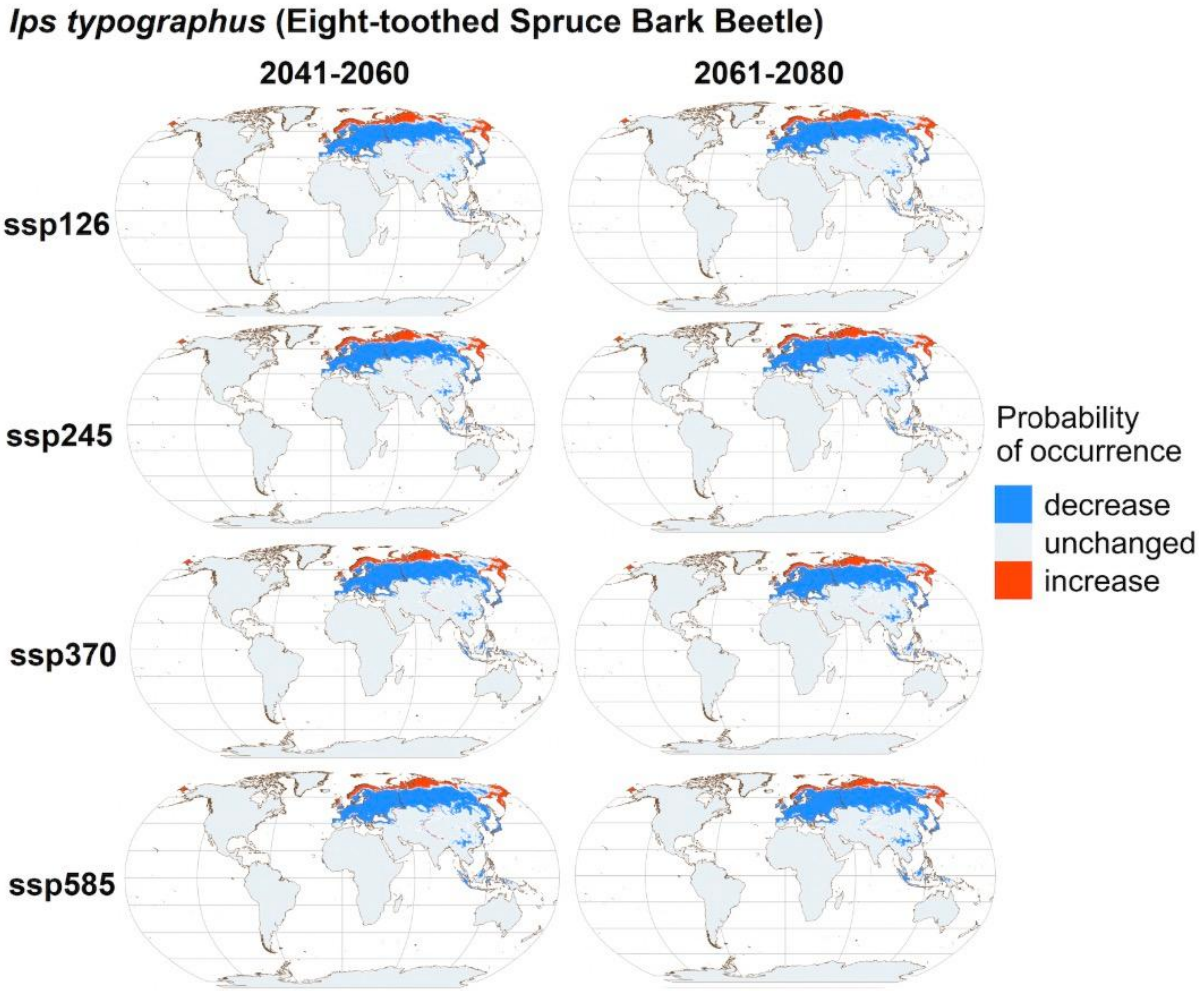


***Sirococcus clavigignenti-juglandacearum* (Butternut Canker)**

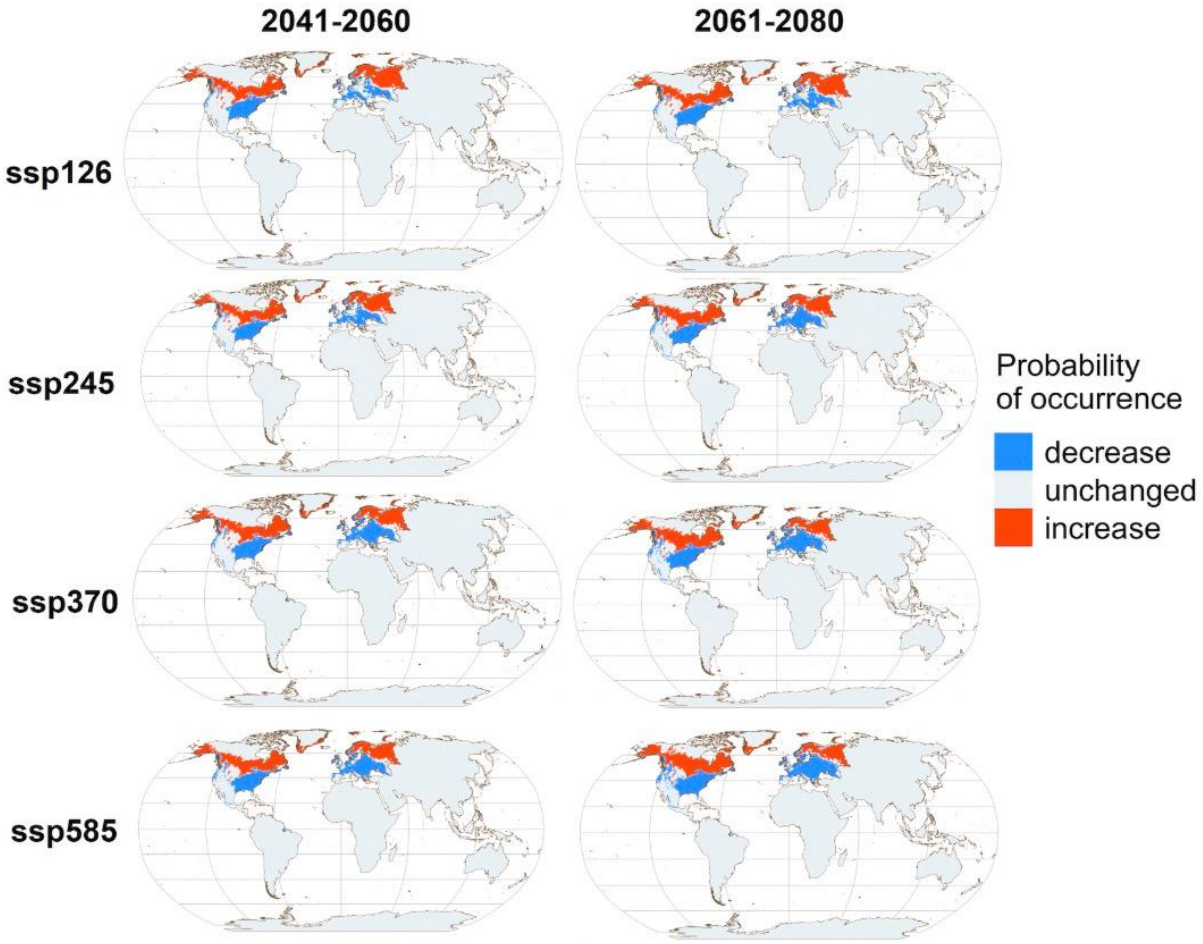


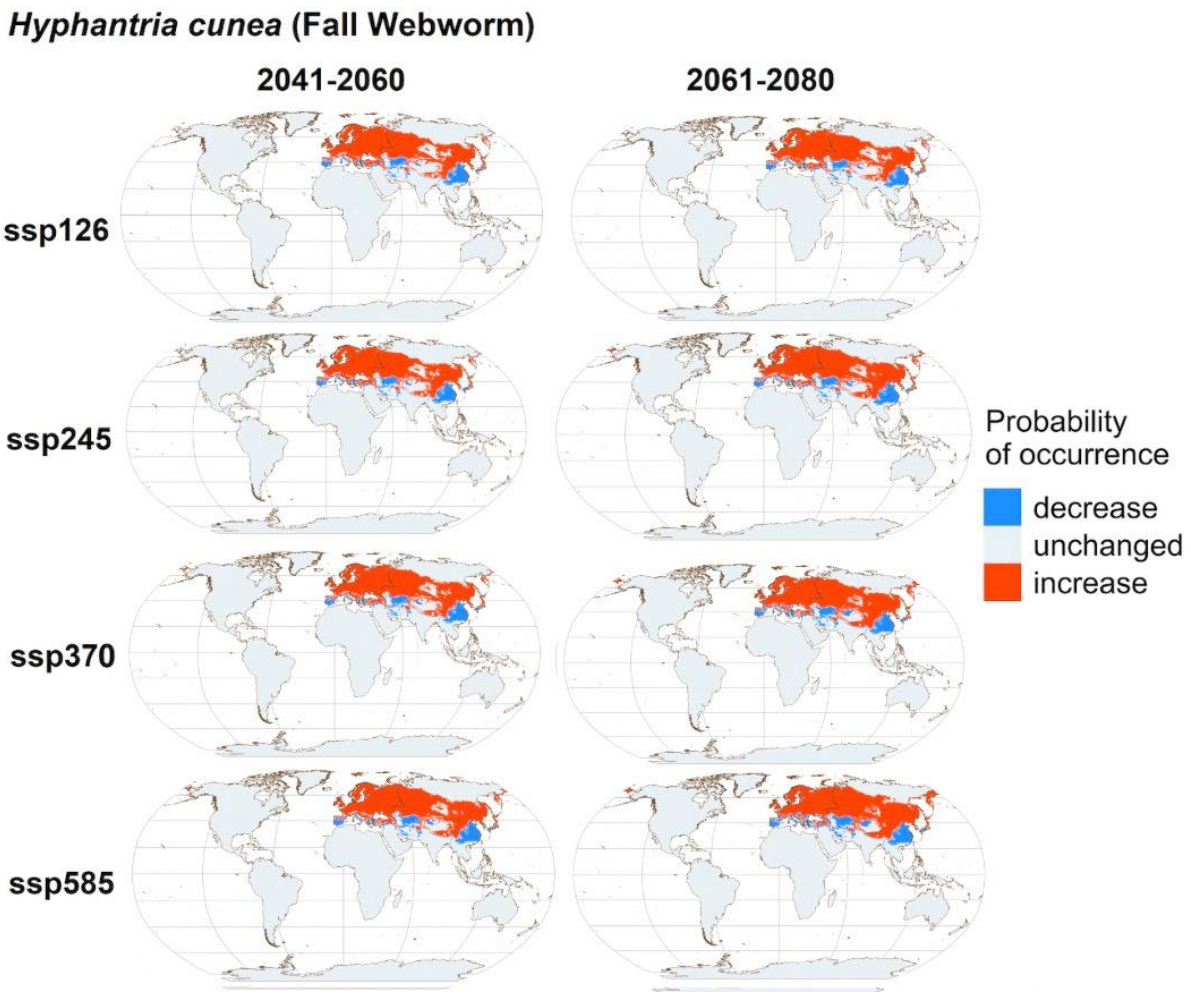

Dothistroma septosporum (Dothistroma Needle Blight)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase


Ophiostoma ulmi, *Ophiostoma novo-ulmi* (Dutch Elm Disease)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

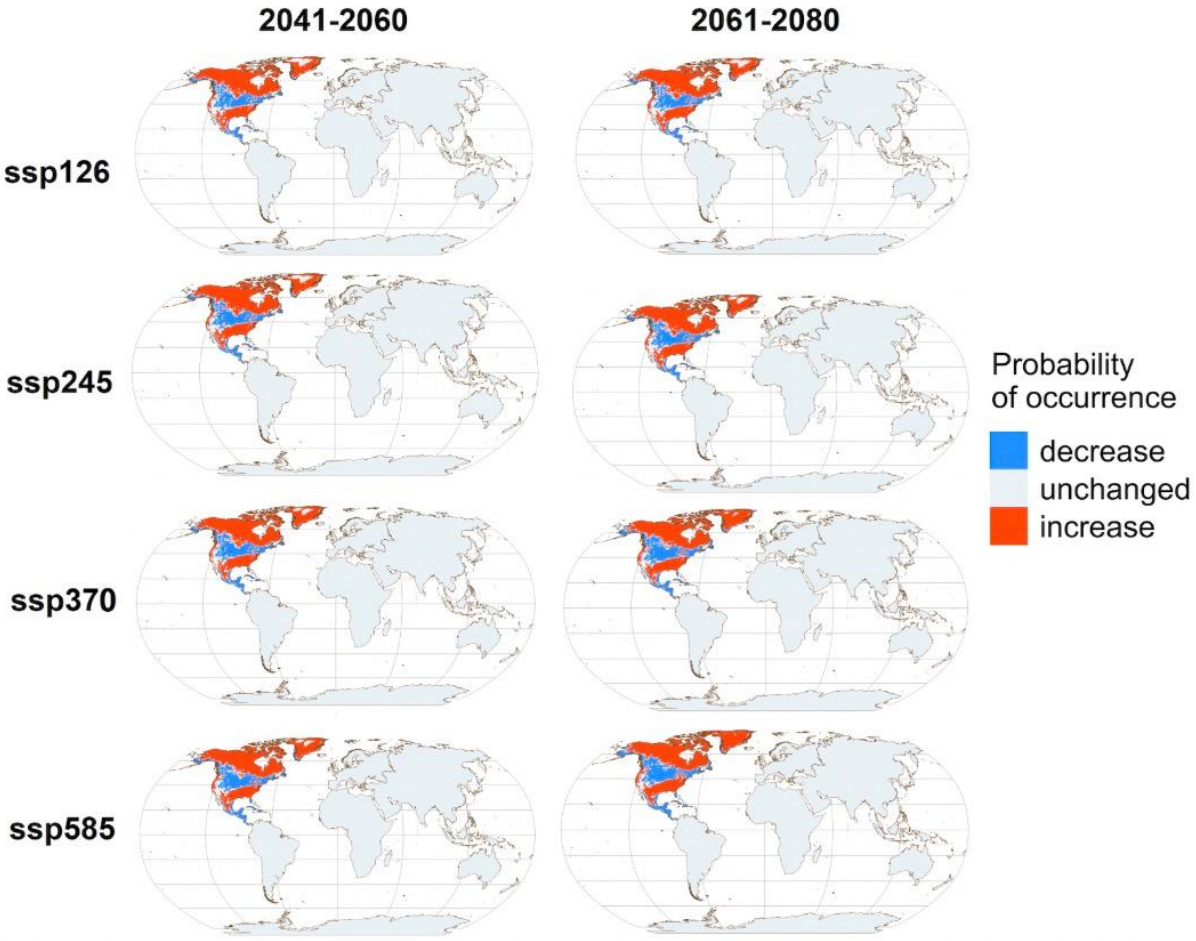

Ips typographus (Eight-toothed Spruce Bark Beetle)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

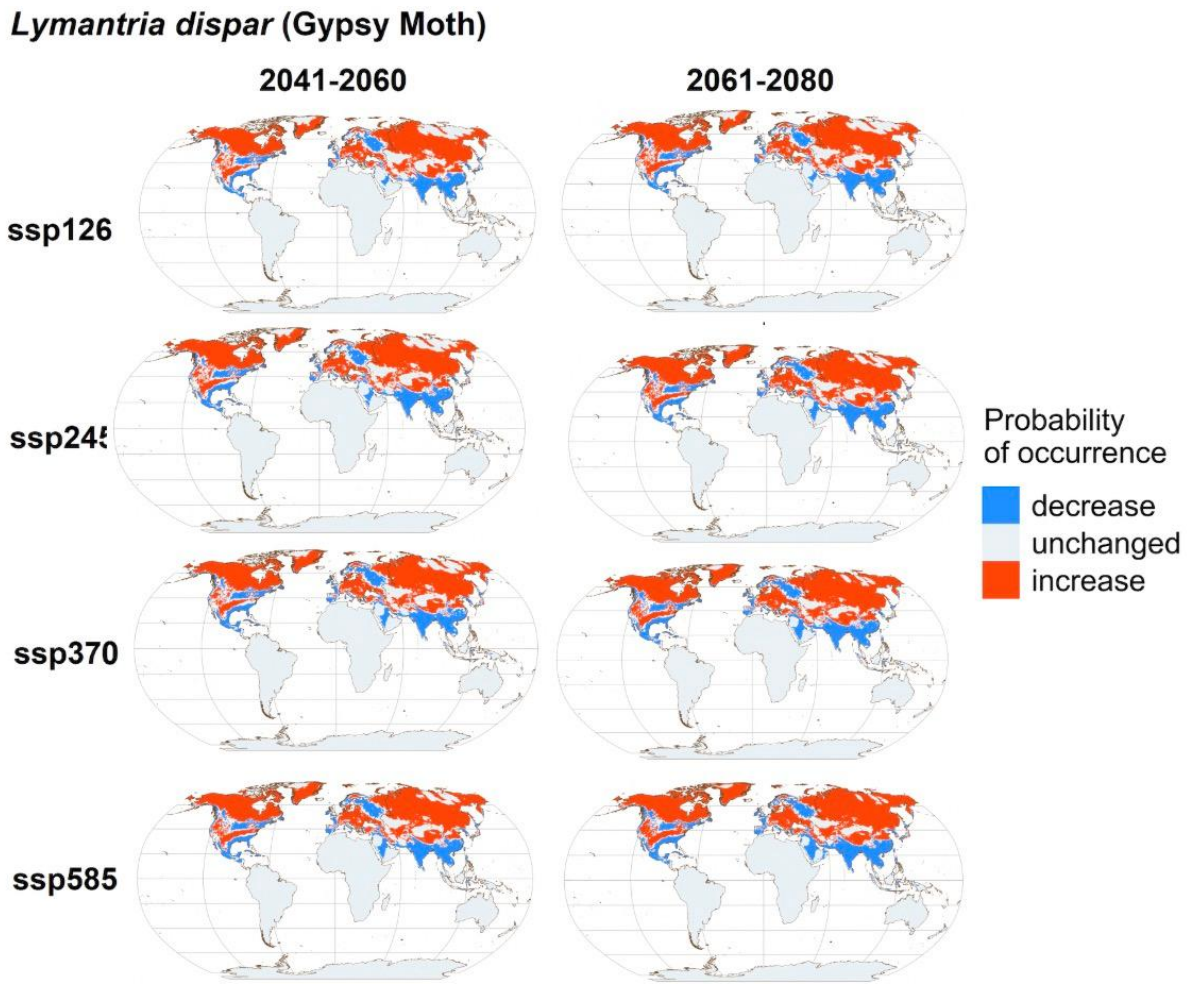
***Agrilus planipennis* (Emerald Ash Borer)**



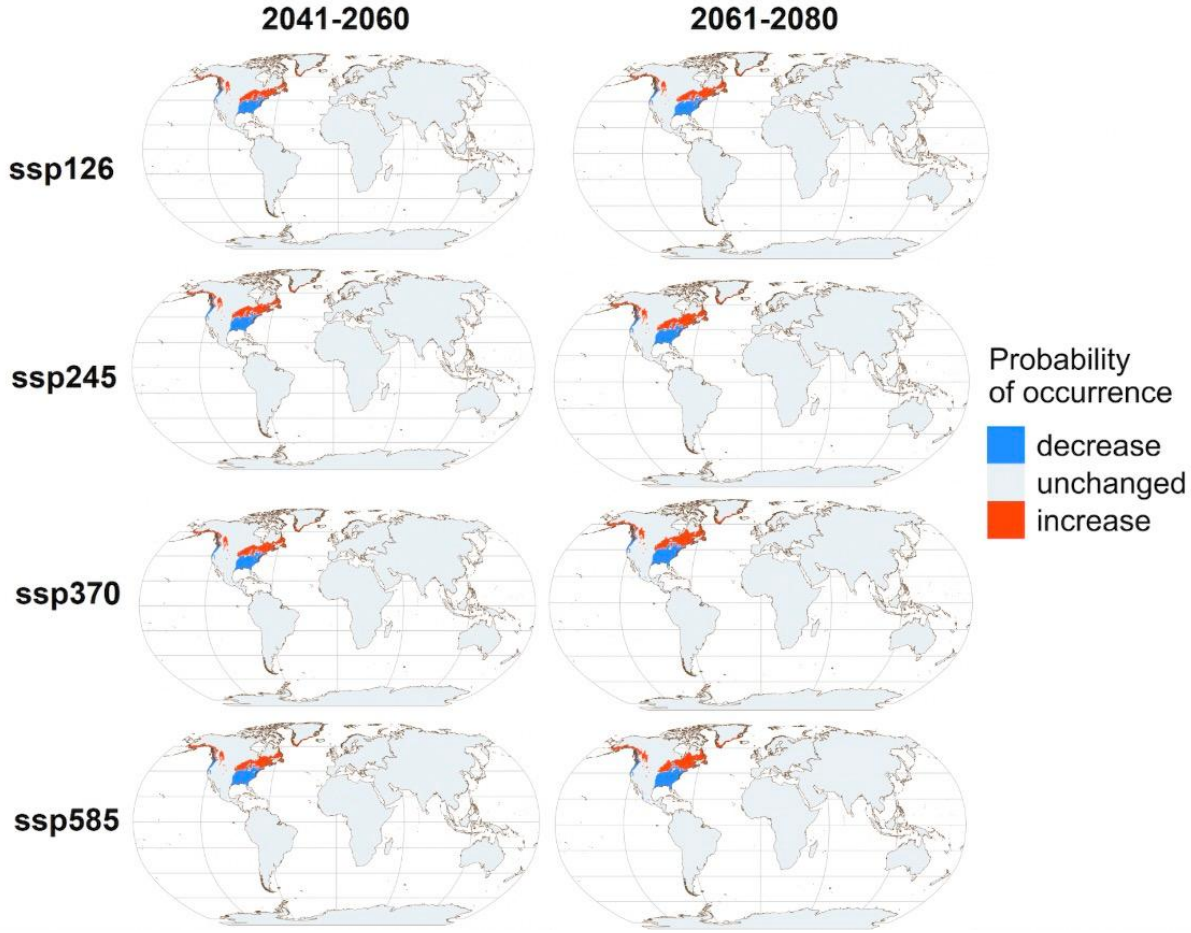

Hyphantria cunea (Fall Webworm)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

***Malacosoma disstria* (Forest Tent Caterpillar)**

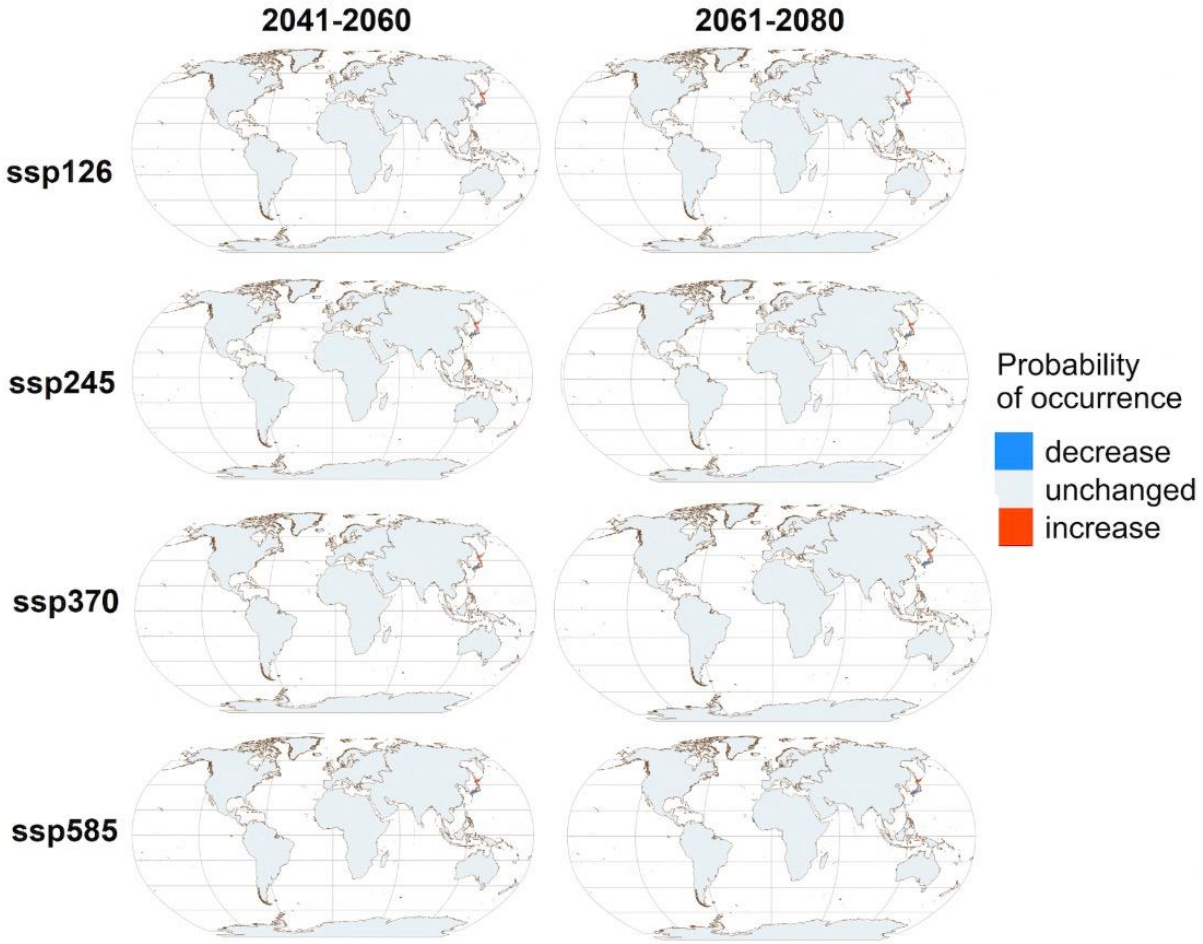


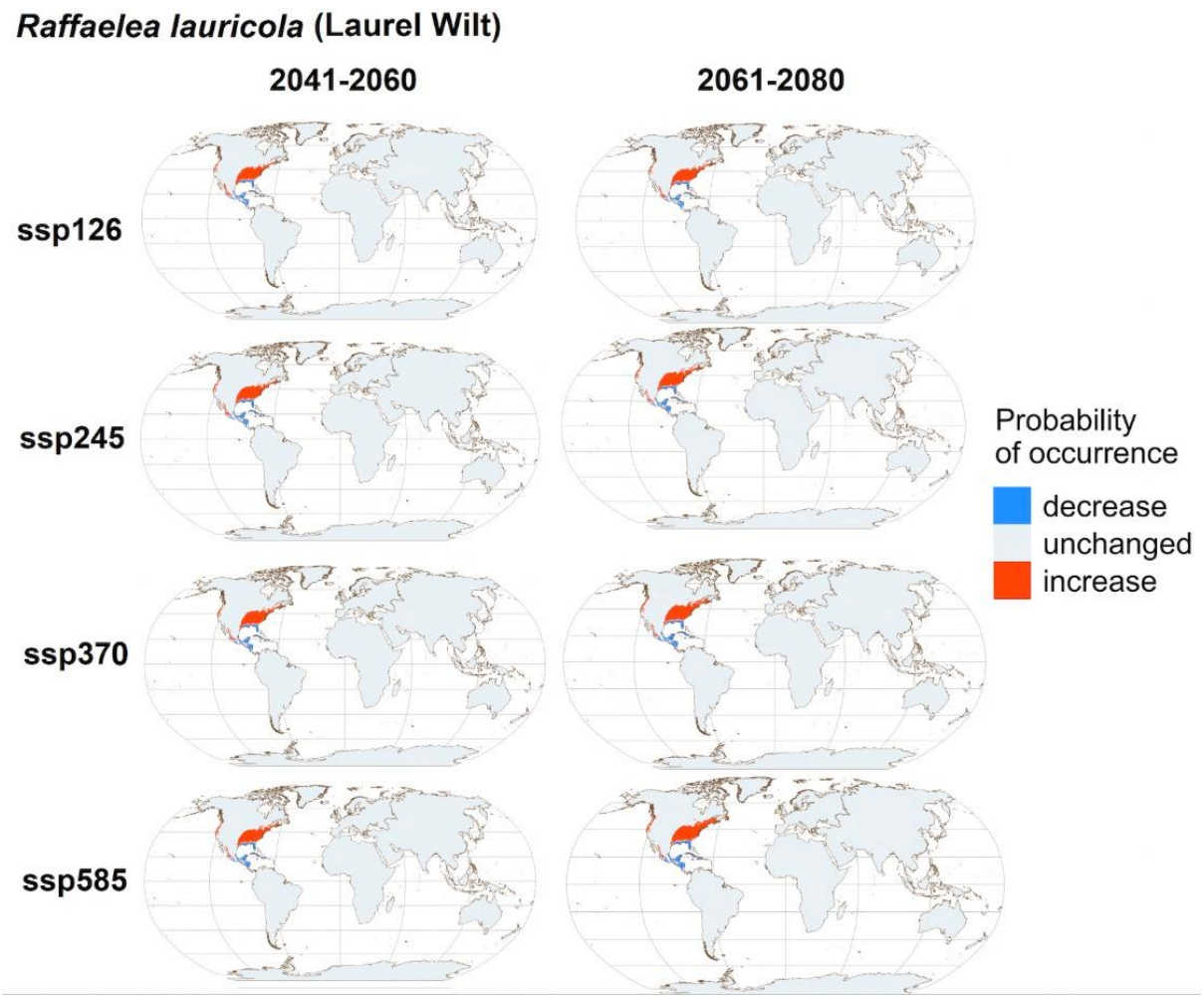

Lymantria dispar (Gypsy Moth)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

***Adelges tsugae* (Hemlock Woolly Adelgid)**

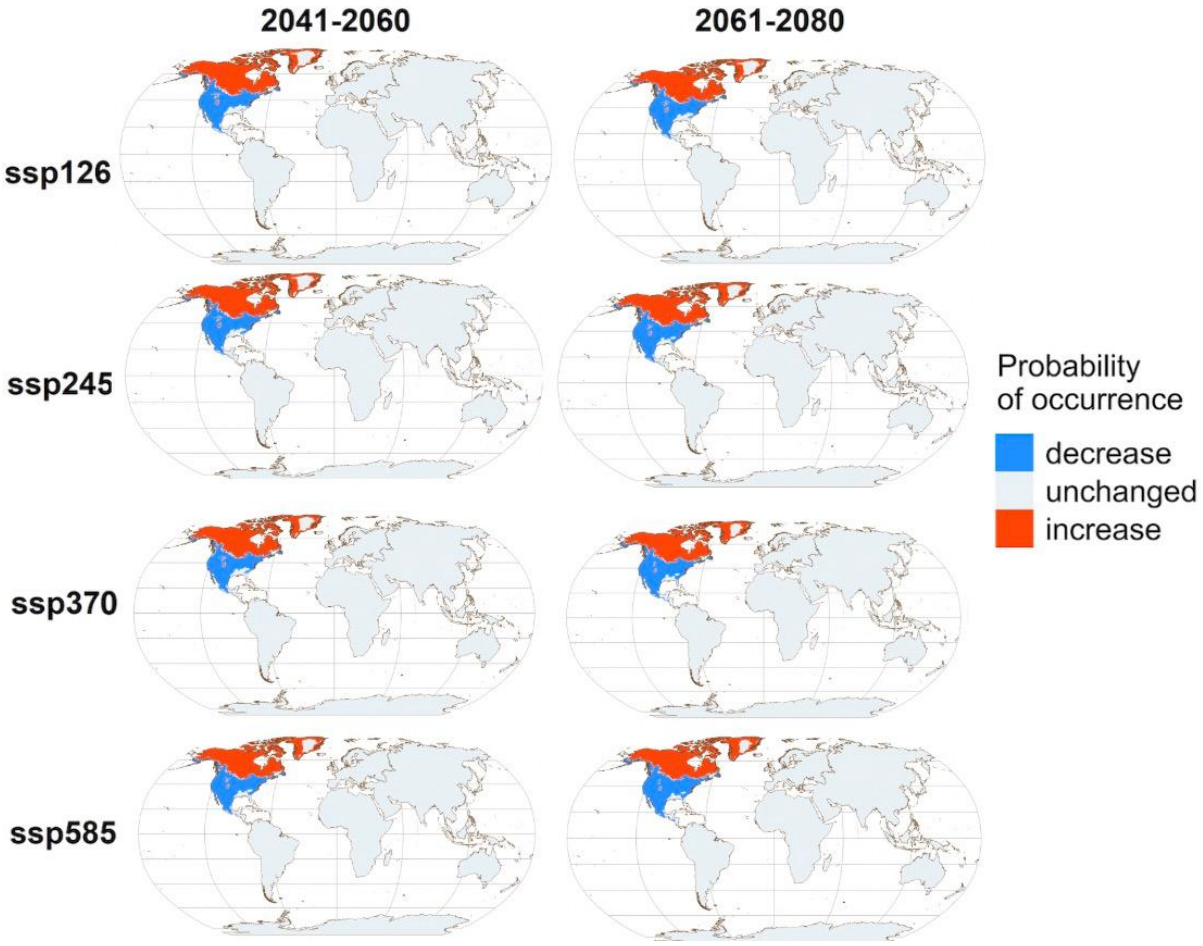


***Raffaelea quercivora* (Japanese Oak Wilt)**

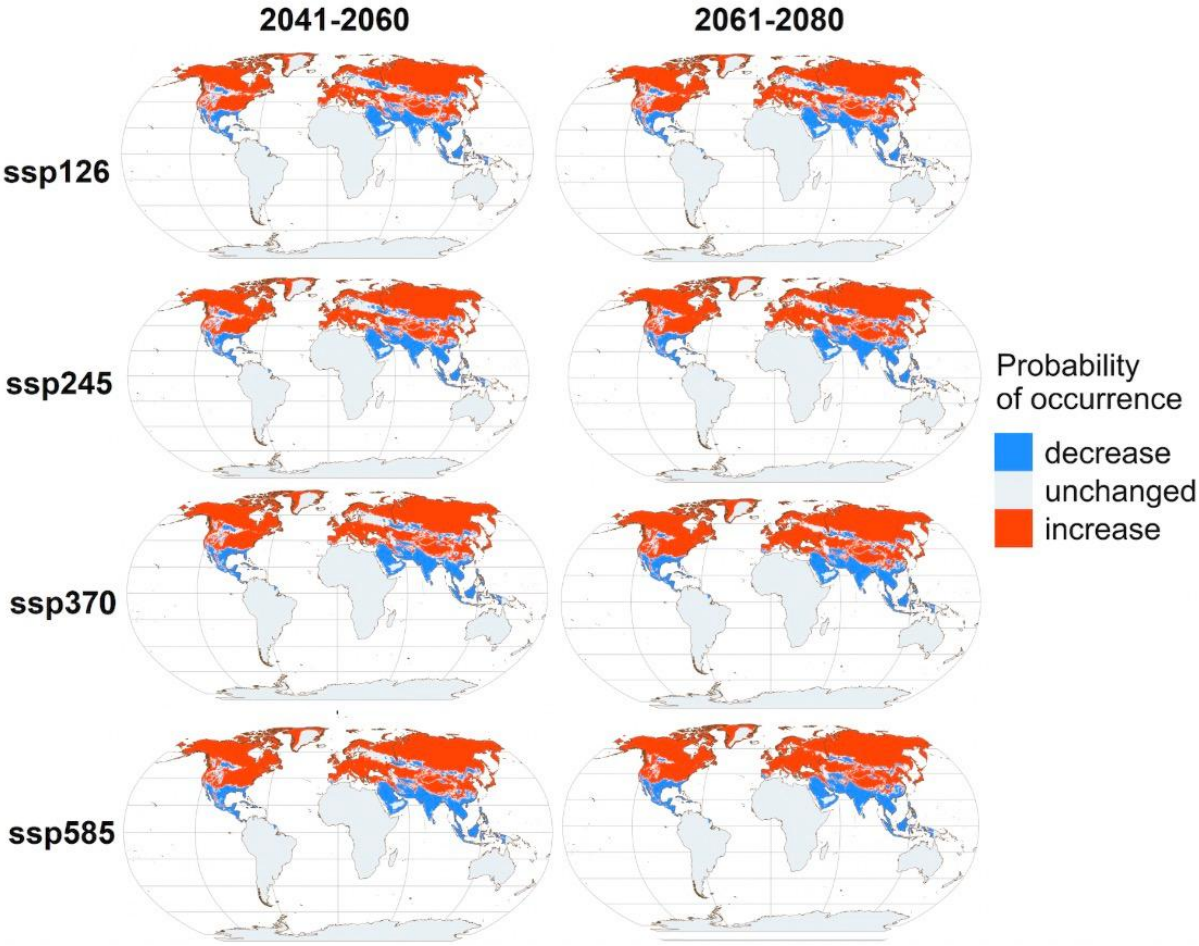



Raffaelea lauricola (Laurel Wilt)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

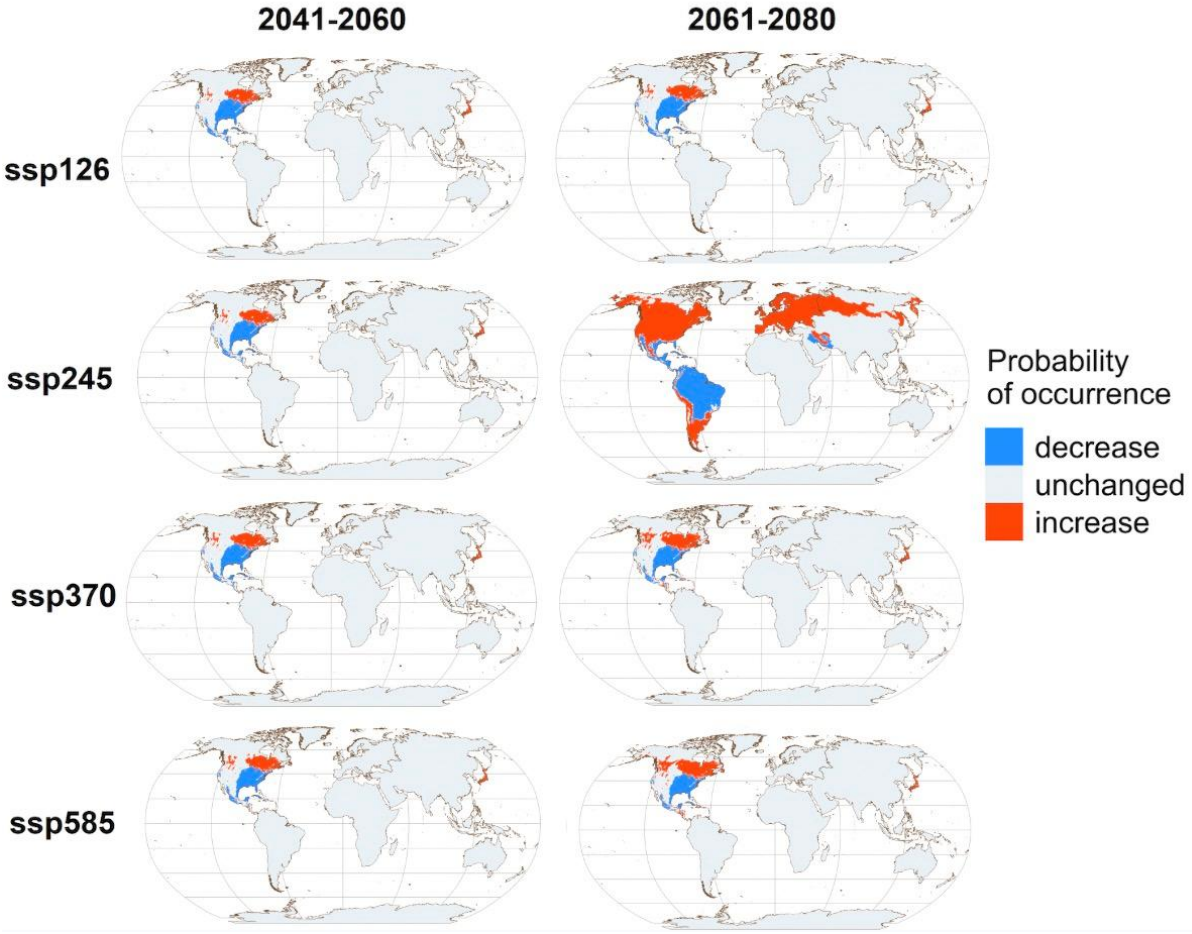
***Dendroctonus ponderosae* (Mountain Pine Beetle)**

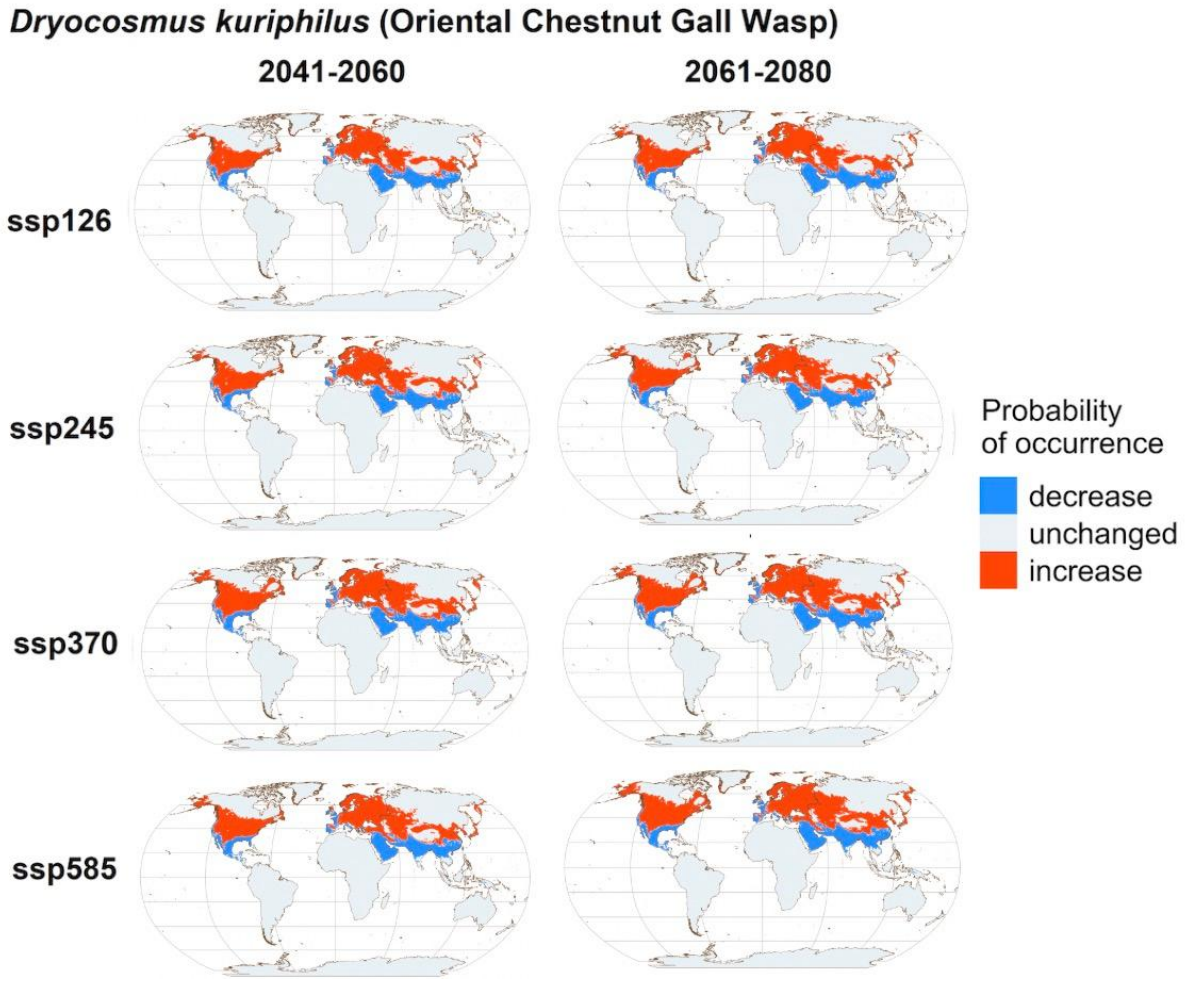


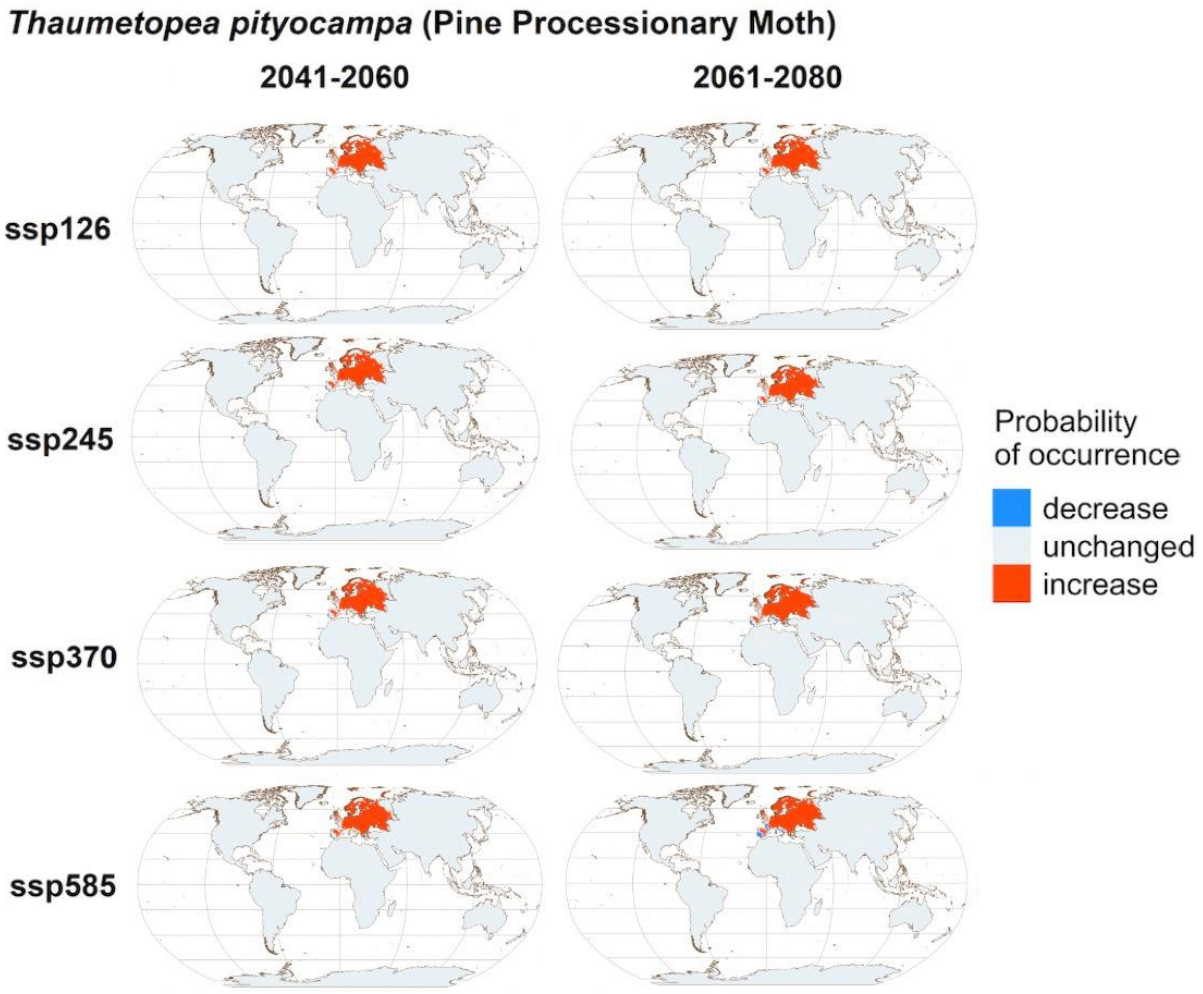
***Brenneria goodwinii, Gibbsiella quercinecans* (Oak Decline)**



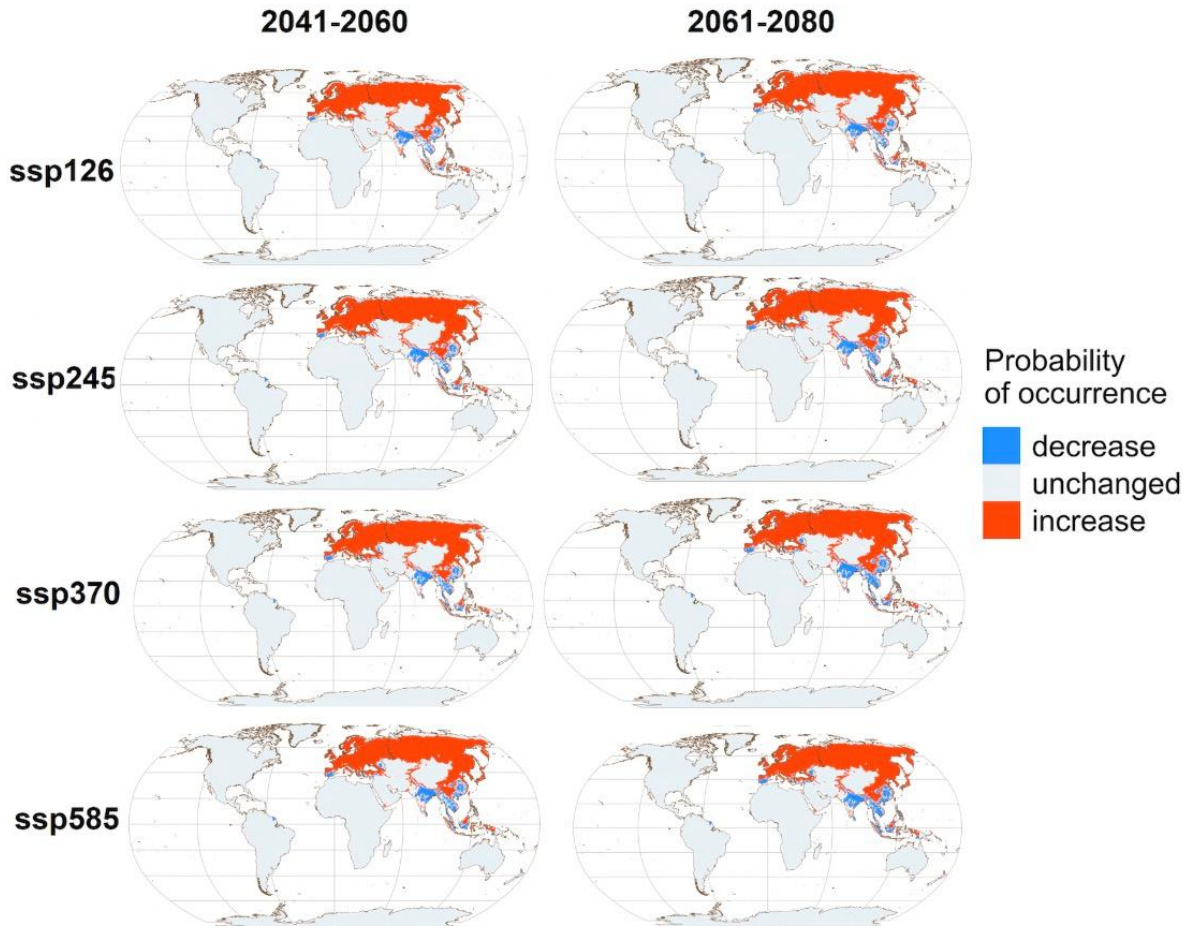
***Bretziella fagacearum* (Oak Wilt)**



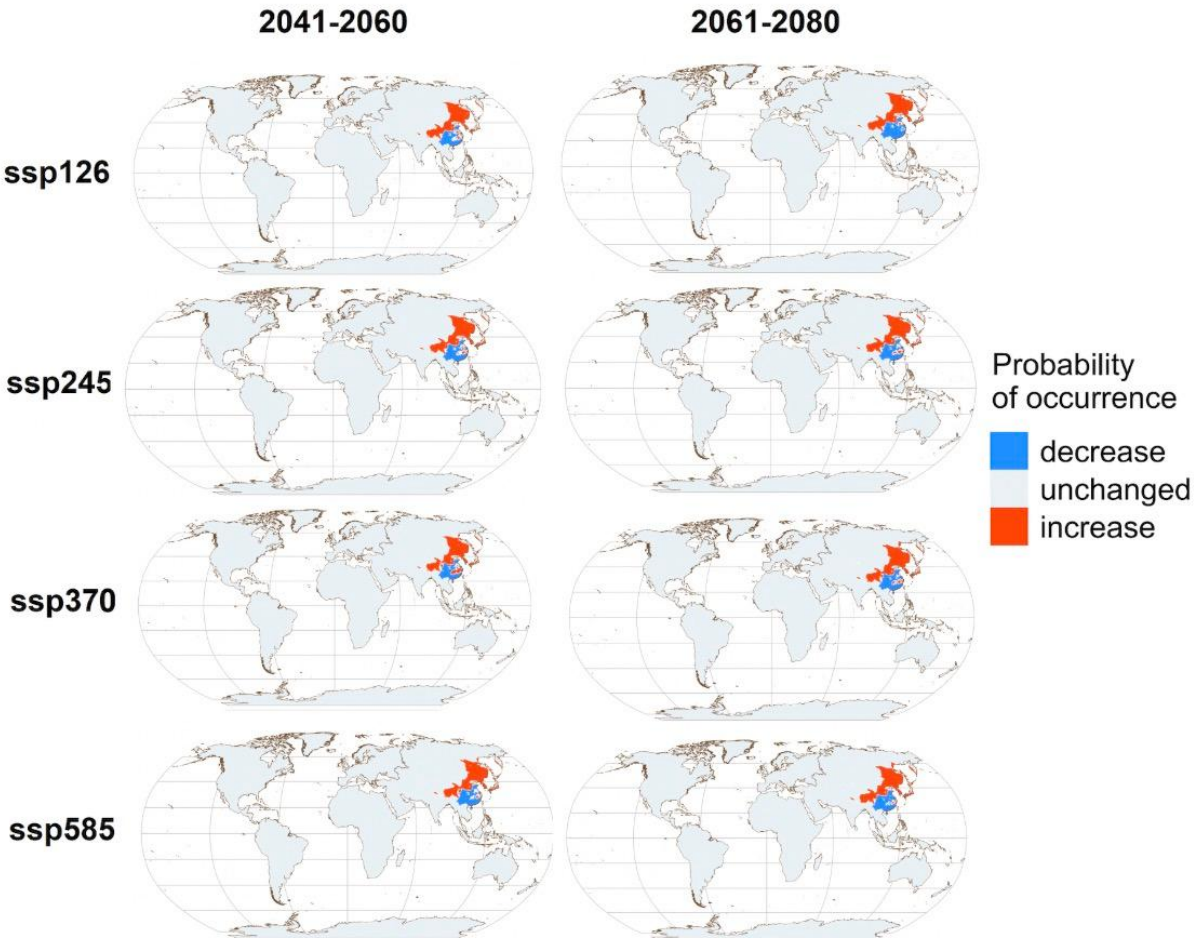

Dryocosmus kuriphilus (Oriental Chestnut Gall Wasp)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase


Thaumetopea pityocampa (Pine Processionary Moth)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

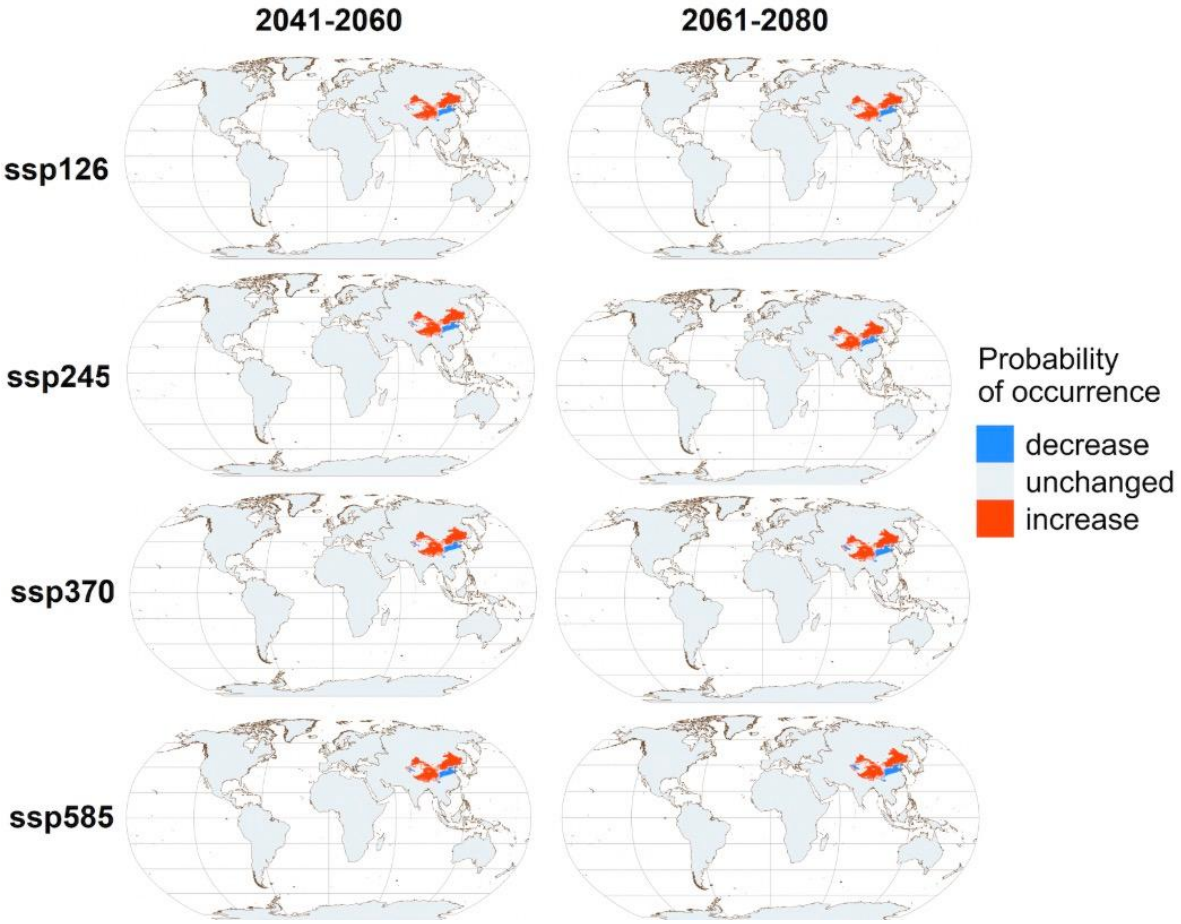
***Bursaphelenchus xylophilus* (Pine Wood Nemetode)**

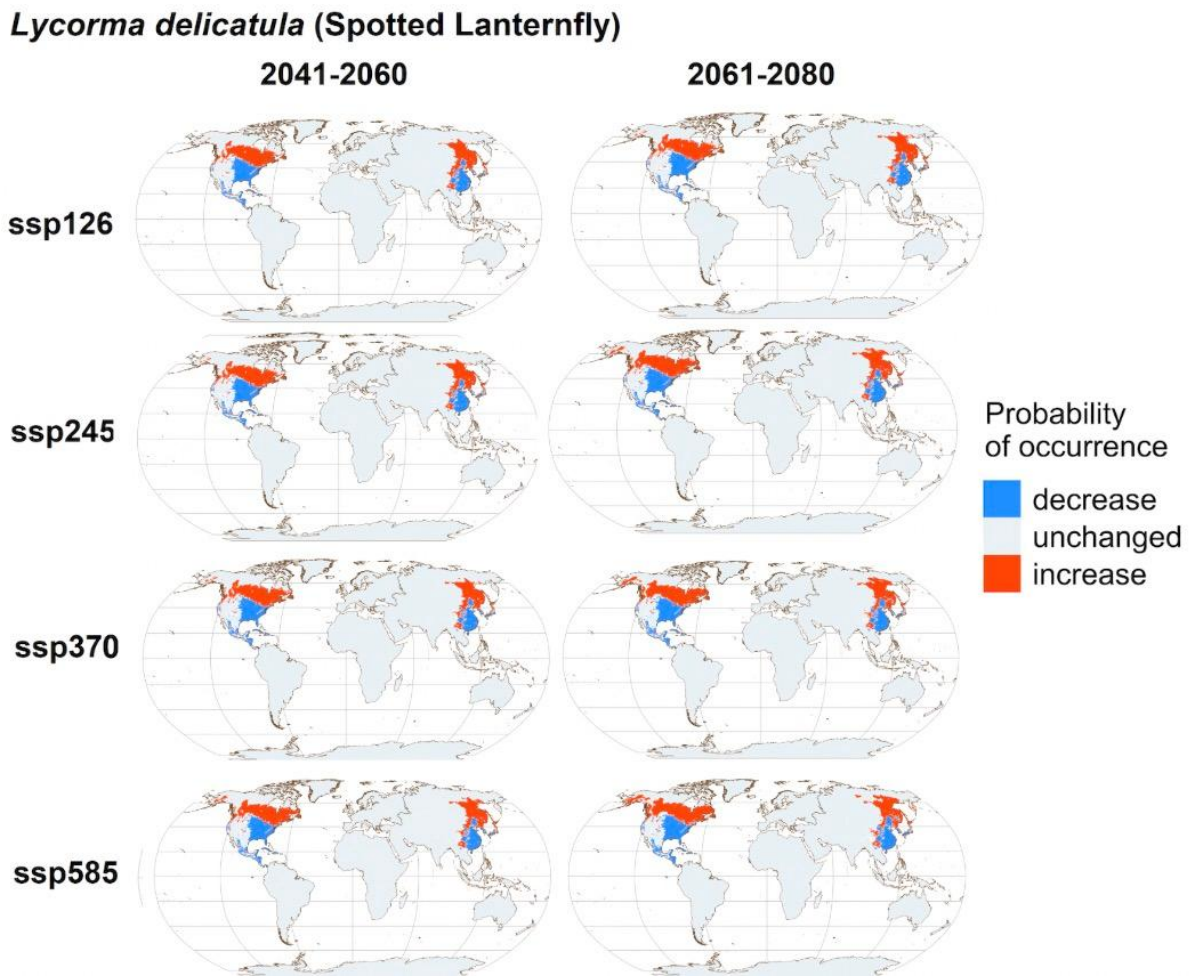


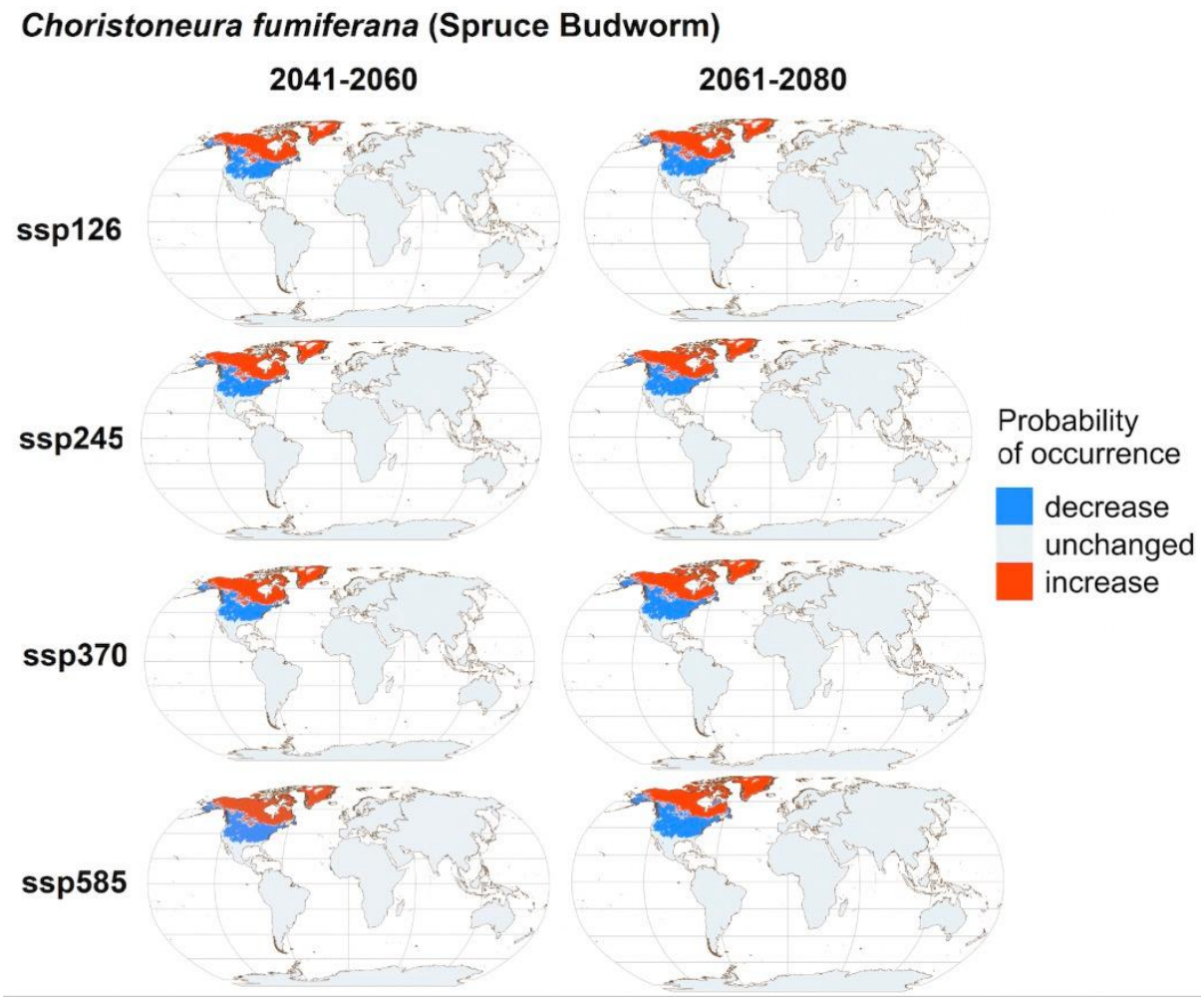
Aromia bungii (Red-necked Longhorn Beetle)

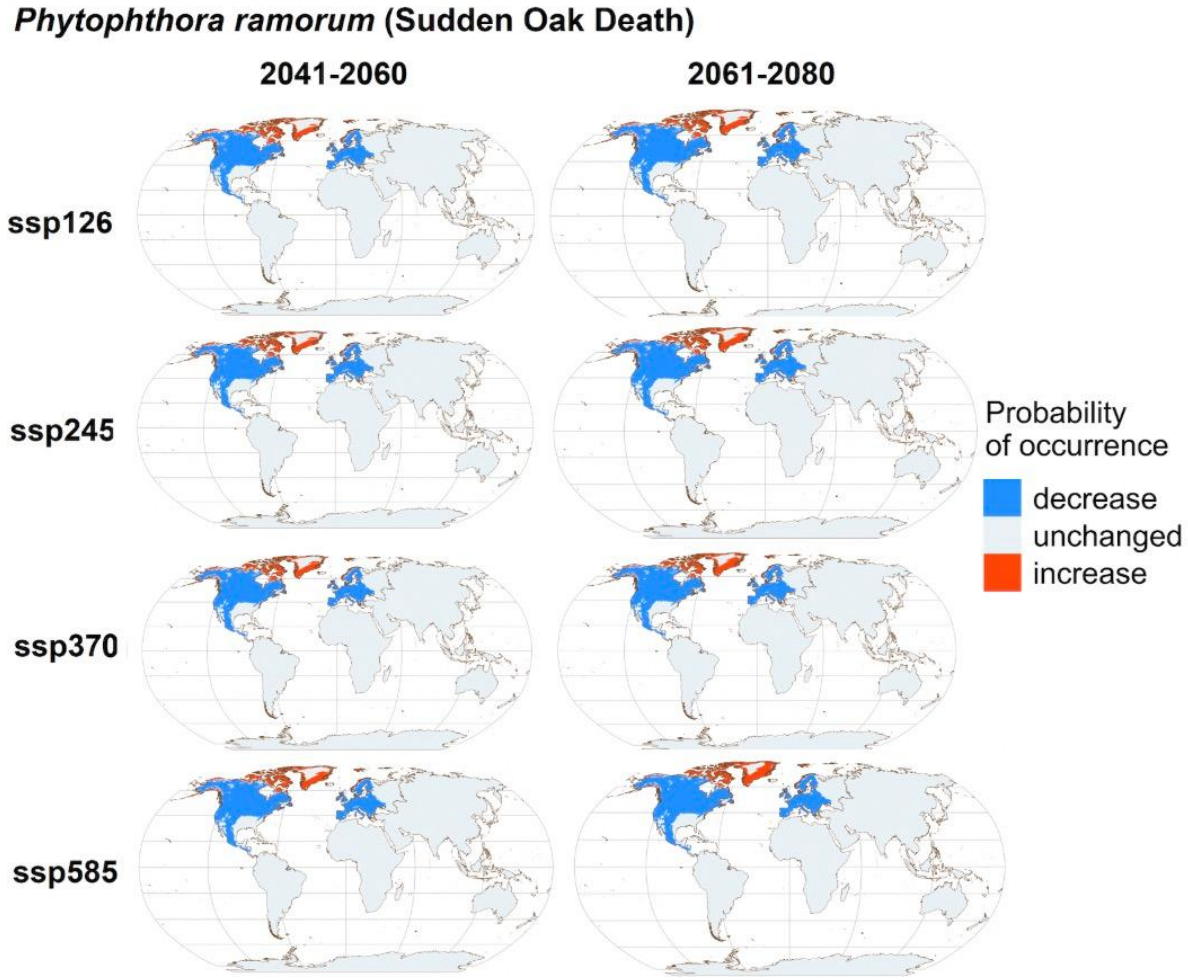


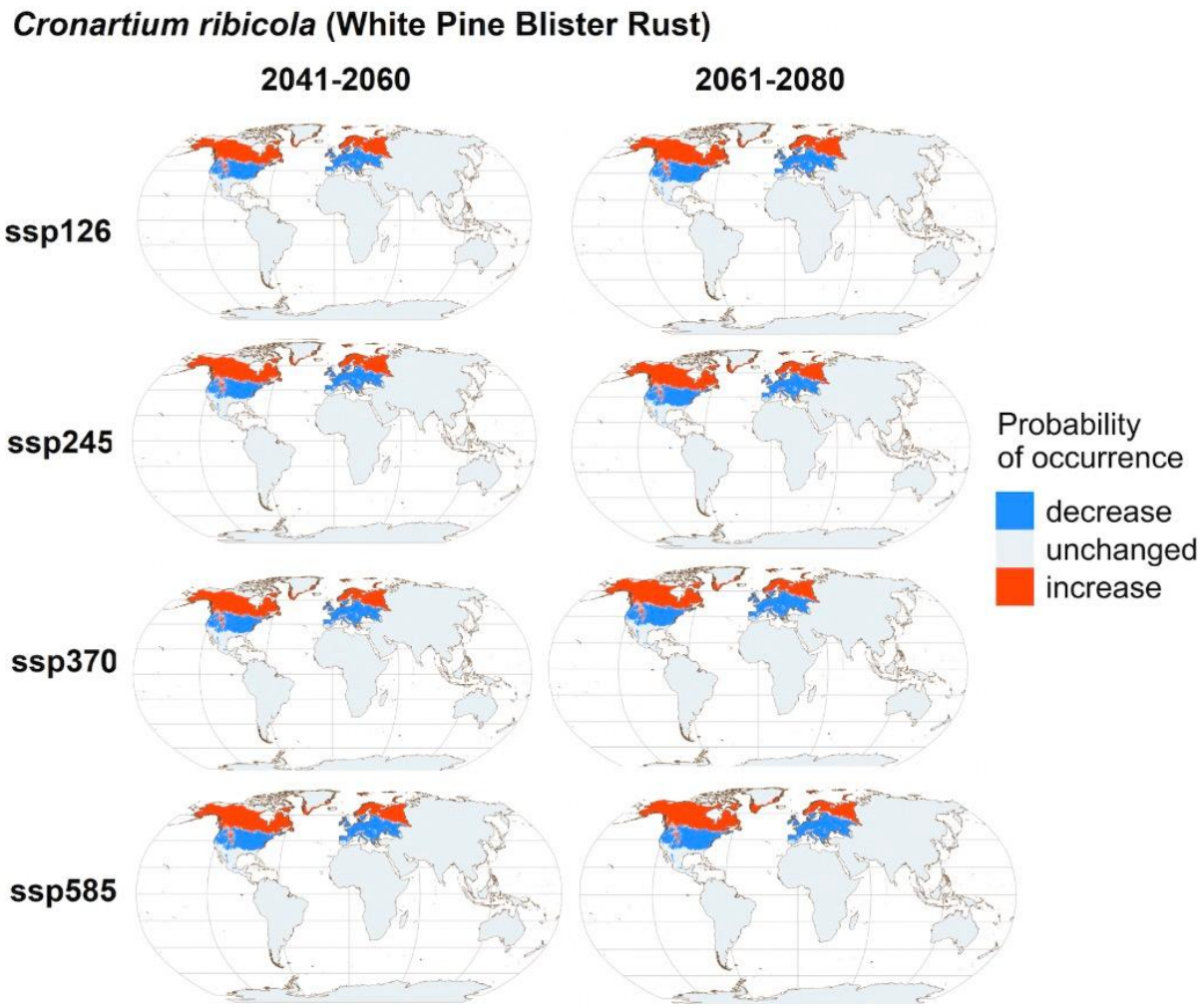
***Dendroctonus valens* (Red Turpentine Beetle)**

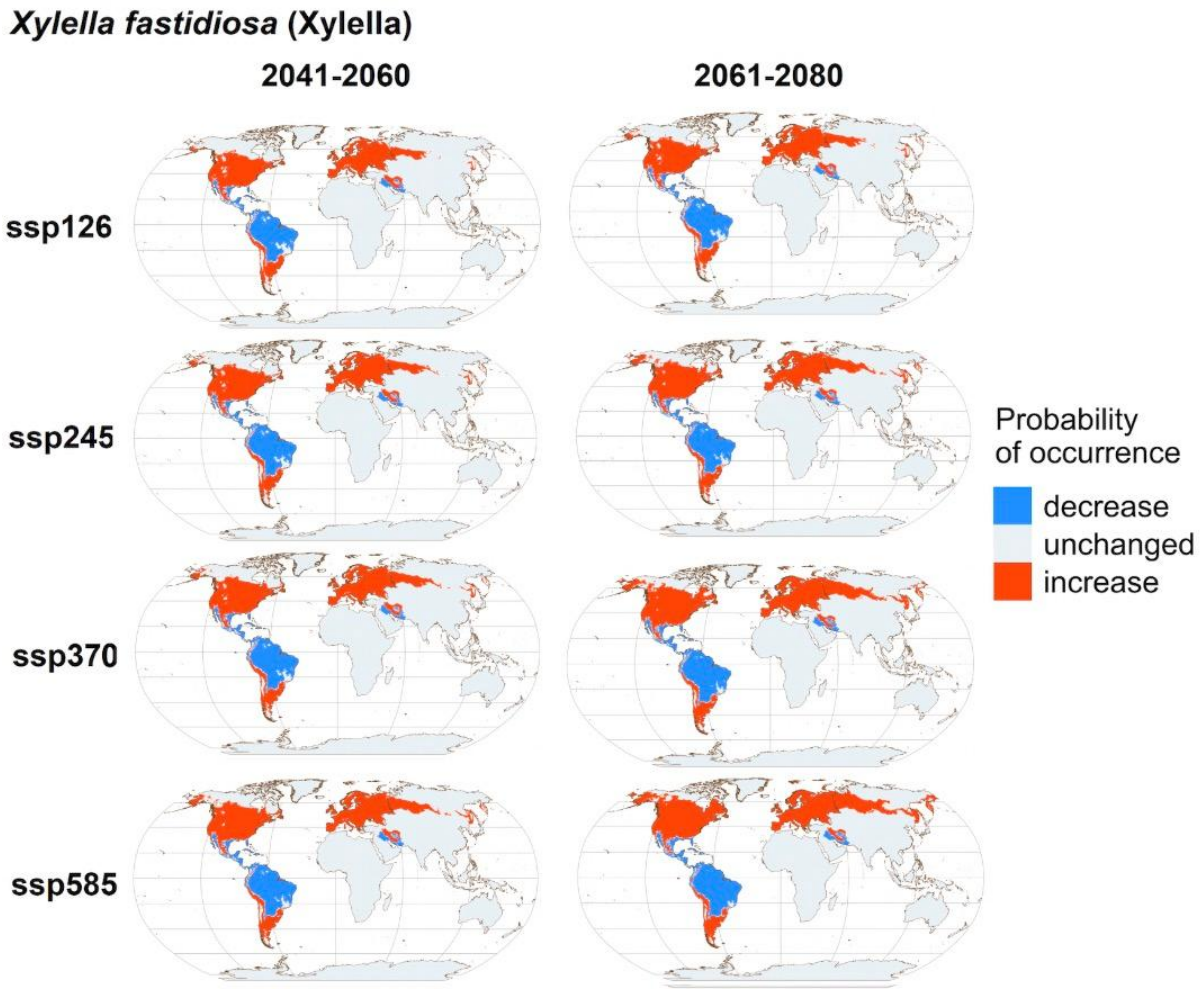



Lycorma delicatula (Spotted Lanternfly)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

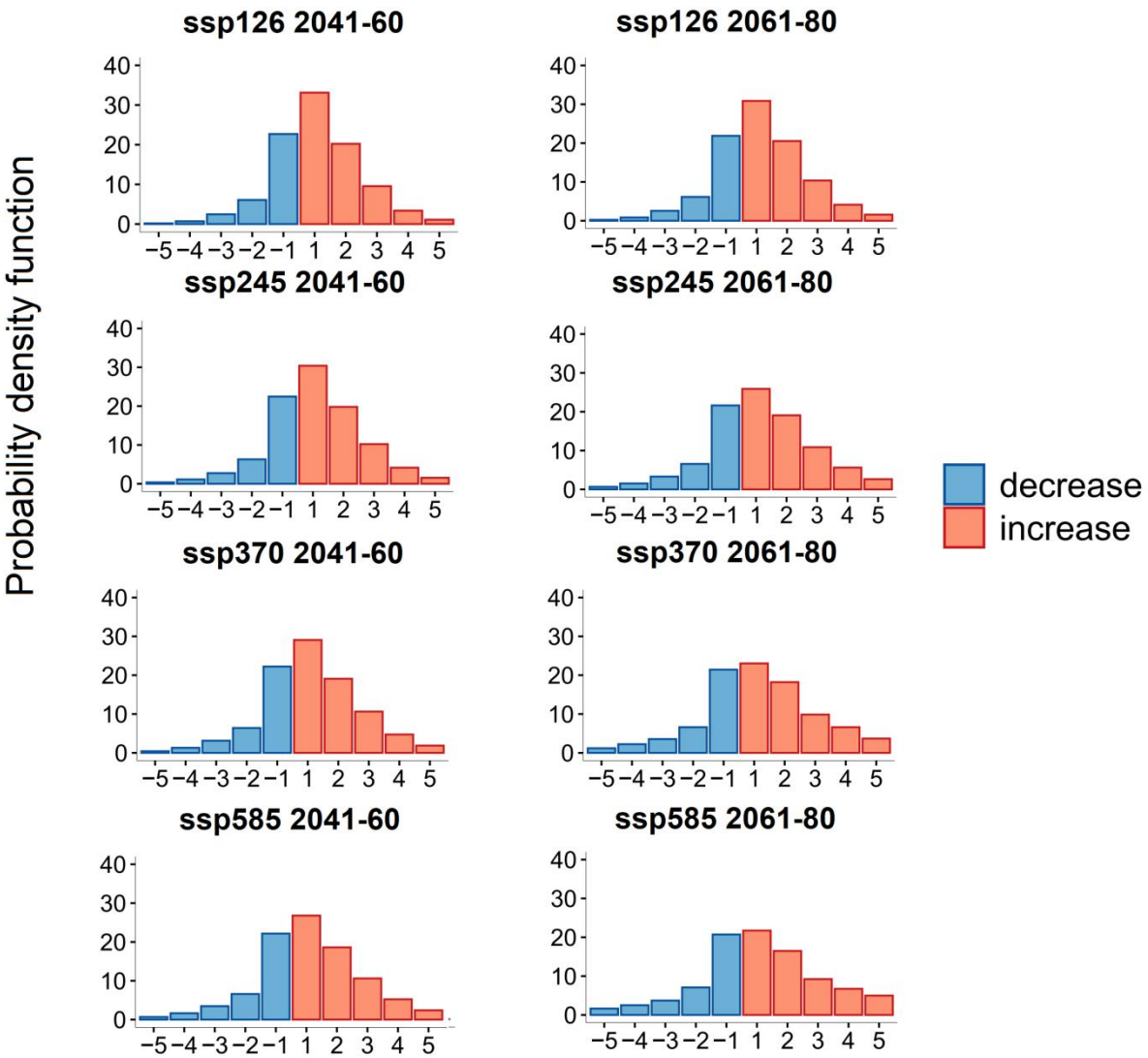

Choristoneura fumiferana (Spruce Budworm)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase


Phytophthora ramorum (Sudden Oak Death)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase


Cronartium ribicola (White Pine Blister Rust)
2041-2060
2061-2080
ssp126
ssp245
ssp370
ssp585
Probability of occurrence
decrease
unchanged
increase

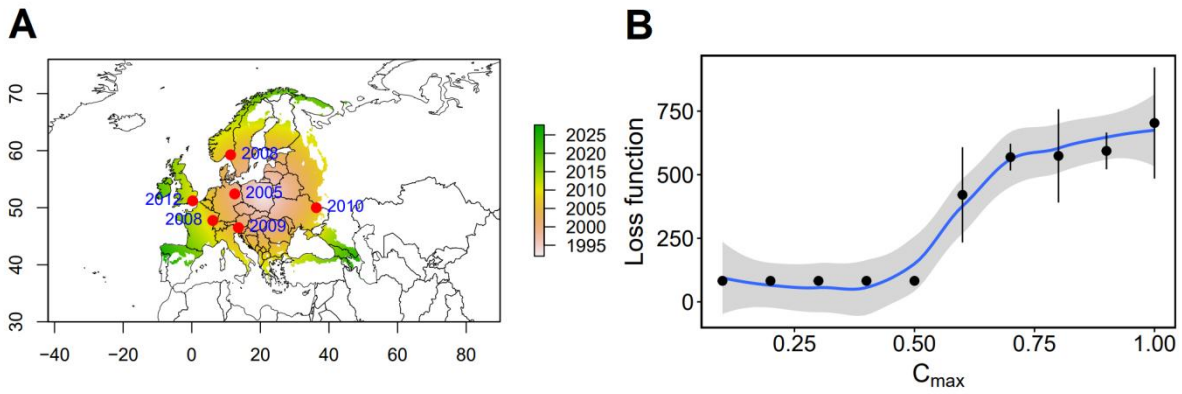


Supplementary Figure S4. Projections of changes in the probability of occurrence for 24 major forest pests and pathogens under four Shared Socio-economic Pathways (SSPs): SSP126, SSP245, SSP370, and SSP585. Regions where the change in pest or pathogen occurrence probability exceeds 0.01 are designated as “increase” (red-shaded areas), while those with a change of less than -0.01 are designated as “decrease” (blue-shaded areas). Note that the distribution maps for six major pests or pathogens (Ash Dieback, Asian Longhorned Beetle, Dutch Elm Disease, Emerald Ash Borer, Pine Wood Nematode, and Sweet Chestnut Blight) have been given in Figure 3.

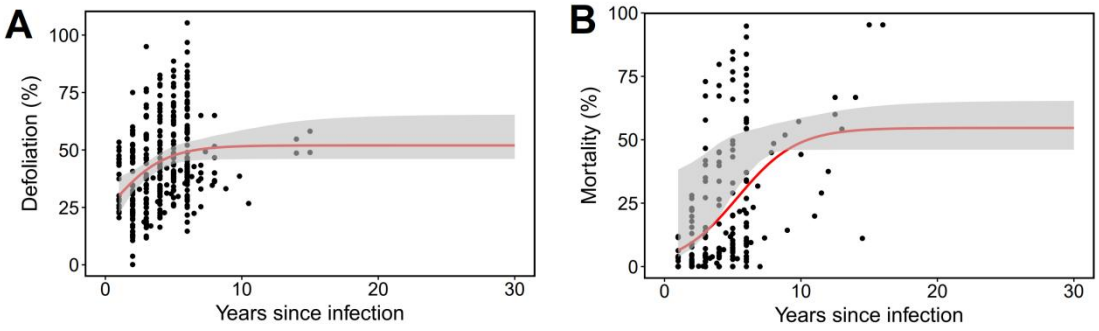


Supplementary Figure S5. Probability density functions of changes in pest and pathogen richness (number of pests and pathogens) for the years 2041–2060 and 2061–2080 under four Shared Socio-economic Pathways (SSPs): SSP126, SSP245, SSP370, and SSP585. The *y*-axis is the probability density (in percentage), indicating the relative likelihood of observing a certain change in pest and pathogen richness in an arbitrary location. Blue and red areas represent geographic regions with a decrease and increase in pest and pathogen richness, respectively. The sum of the areas of blue and red shaded regions equals to 1, the total probability, representing the complete range of possible changes in pest and pathogen richness.

9.3 Supplementary Materials for Chapter 6



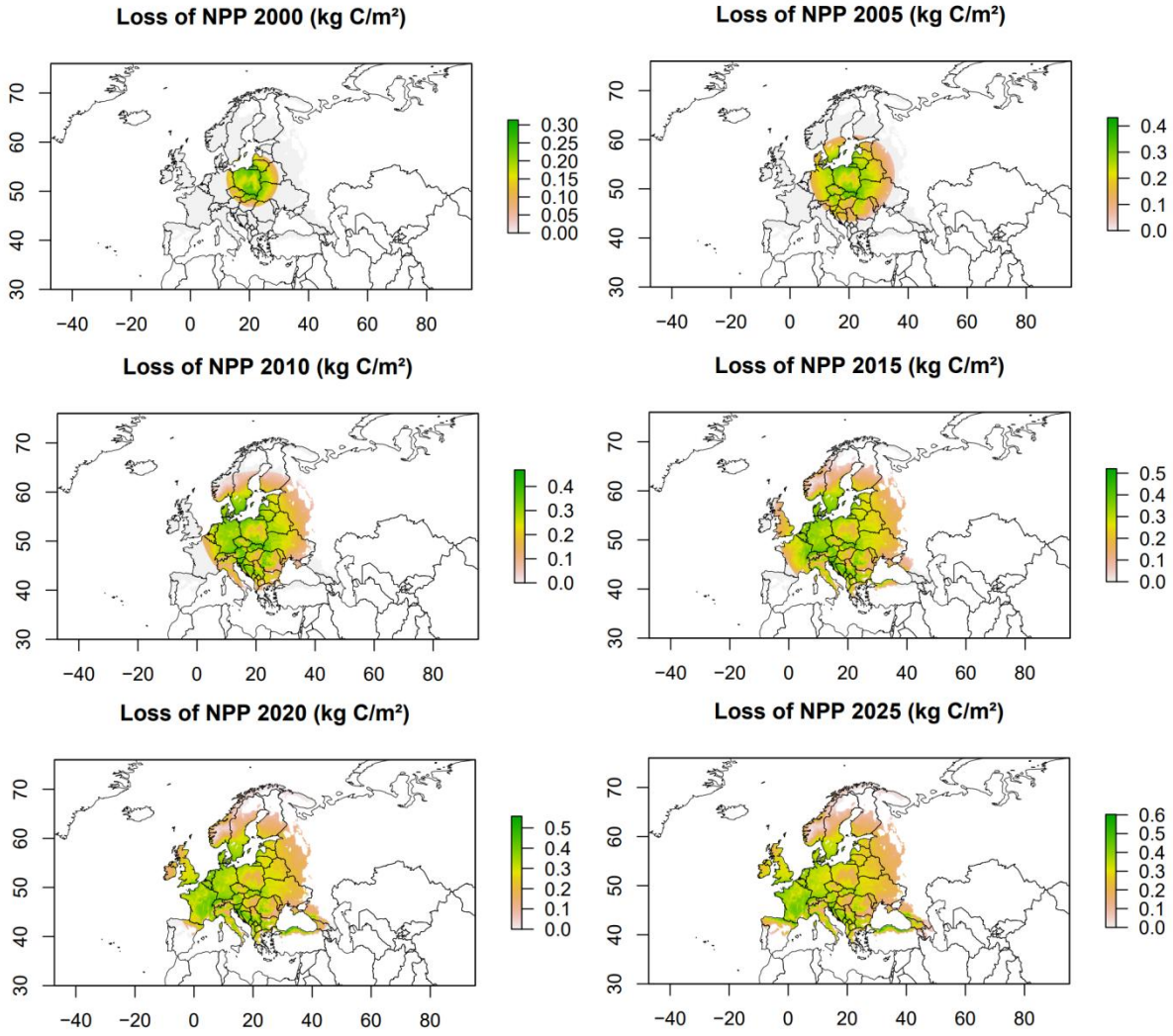
Supplementary Figure S1. Fitted model for the spread of ash dieback disease. (A) Predicted first year of disease occurrence across Europe at 0.05 × 0.05° resolution. Red points and labels indicate observed first-incidence years used for model calibration, compiled from the literature. The fitted parameter is C_{max}=0.3; (B) Loss-function values across tested C_{max} values. C_{max} (the maximum possible number of new introductions per year) is an important parameter in the ash dieback disease spread model. It characterises the intensity of long-distance dispersal of the pathogen, driven by international transports and trades. To fit the parameter, we ran the model with different C_{max} values, each repeating three times, and then evaluated the model performance using the loss function. The function was defined by the sum of squared deviations between model predicted and observed first-incidence years in several locations: Haute-Saône, France (47.7570° N, 6.1556° E, ash dieback first reported in 2008); Brandenburg, Germany (52.4125° N, 12.5316° E, first reported in 2005); South East England, United Kingdom (51.2000° N, 0.2700° E, first reported in 2012); Østfold County, Norway (59.2558° N, 11.3279° E, first reported in 2008); Kharkiv, Ukraine (50.0020° N, 36.3074° E, first reported in 2010); Fusine, Italy (46.5000° N, 13.6167° E, first reported in 2009). It can be seen that when C_{max}≤0.4, the model performs better. In this study, we choose C_{max}=0.3. In the figure, points represent the mean loss value and error bars represent mean ± SD.



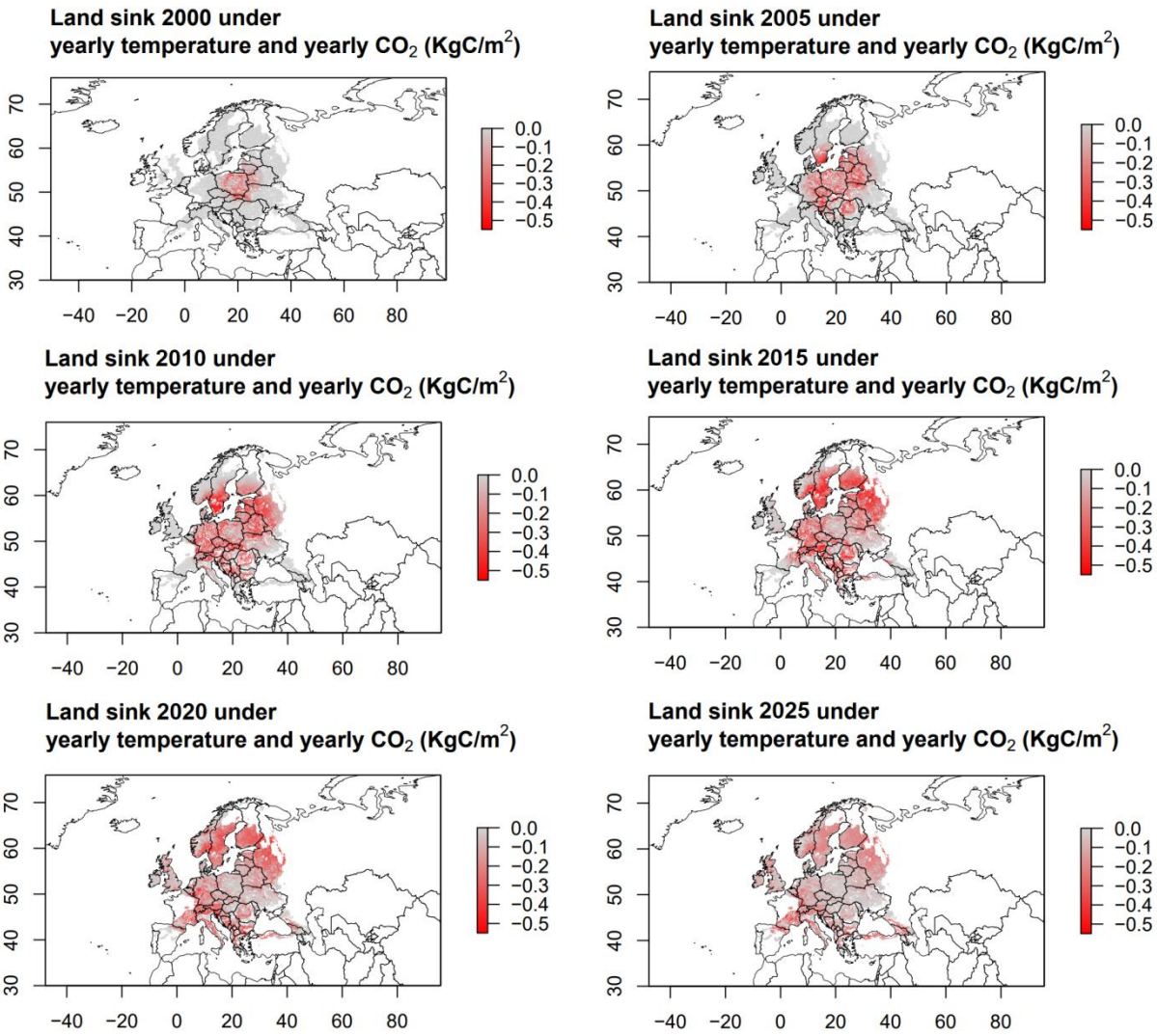
Supplementary Figure S2. Fitted logistic curves describing changes in tree defoliation and mortality following infection by *H. fraxineus*. Parameter estimates:
$A_{sym,defoliated}$=51.9778, $x_{mid,defoliated}$=0.3805, $s_{defoliated}$=1.9414, $A_{sym,death}$=54.654, $x_{mid,death}$=5.366, s_{death}=2.165

The reduction in NPP within forested areas was scaled by forest cover. Forest fraction was calculated using the MCD12Q1.061 MODIS Land Cover Type product (Friedl et al. 2010). The 500-m grid was aggregated to 0.05° resolution, with each pixel assigned the fraction of constituent cells classified as

forest (Supplementary Figure S3).



Supplementary Figure S3. Evolution of net primary production (NPP) loss as ash dieback disease spreads across Europe.



Supplementary Figure S4. Evolution of predicted net ecosystem production (NEP = NPP – soil respiration) due to the progression of ash dieback disease in the Europe.

Supplementary Table S1. Predicted reductions in forest NPP due to ash dieback disease by country.

Country	Reductions in forest NPP 2005 (kg C/m²/year)	Reductions in forest NPP 2015 (kg C/m²/year)	Reductions in forest NPP 2025 (kg C/m²/year)	Fossil fuel emission 2022 (kg C/m²/year)**
United Kingdom	NA*	0.002	0.0056	0.35
Sweden	0.016	0.035	0.037	0.023
Norway	NA	0.00064	0.00074	0.029
Germany	0.03	0.057	0.058	0.52
France	NA	0.0015	0.0024	0.13
Poland	0.046	0.049	0.049	0.28

Country	Reductions in forest NPP 2005 (kg C/m²/year)	Reductions in forest NPP 2015 (kg C/m²/year)	Reductions in forest NPP 2025 (kg C/m²/year)	Fossil fuel emission 2022 (kg C/m²/year)**
Estonia	0.038	0.062	0.063	0.07

*: Disease not predicted to arrive at the country yet.

**: Yearly fossil emission data sourced from Open climate data (https://openclimatedata.net/)

9.4 Journal submissions

At the time of viva, Chapter 4 was submitted to Biological Invasions for review. Chapter 5 was submitted to Diversity and Distributions for review. Chapter 6 was under preparation and will be soon submitted to Nature Ecology & Evolution for journal's consideration.