Potential impacts of plant pests and diseases on trees and forests in the UK

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Summary

Plant pests and diseases (PPDs) pose a serious threat to trees and forests globally. In the wake of the ash dieback epidemic, the UK Government instigated the UK Plant Health Risk Register (PHRR) to provide semi-quantitative estimates of invasion probability and impact on host plants for PPDs thought to pose a risk to the UK to help prioritize biosecurity activities. The PHRR currently contains 636 PPDs potentially affecting 74 tree species found in the UK. Of these, the genera *Prunus*, *Pinus*, *Malus*, *Pyrus* and *Quercus* have the largest number of associated PPDs. Here, we explore the implications of converting these ordinal likelihood and impact scores to quantitative estimates of invasion probabilities and losses to tree productivity, in terms of increased mortality or reduced growth, in the next 25 years. We use recent invasions, such as ash dieback and horse chestnut bleeding canker, to quantify likely losses, and generate plausible invasion probabilities from historical observations. Assuming that the expectation of loss in 25 years is the probability of invasion multiplied by the fractional loss, and that the impacts of multiple PPDs affecting the same host species are independent, we find that many tree species would suffer severe production declines under plausible invasion probability and impact estimates. Invasion probabilities and losses must be much lower than our plausible values to maintain reasonable levels of tree productivity in future. Despite several important knowledge gaps, our analysis provides a framework for projecting how trees and forests might be impacted in future and helps to highlight the risk posed by PPDs to biodiversity and ecosystem services.

Keywords

Ash dieback; disease; forest health; plant pathogens; invasive species; pest risk analysis; pest risk assessment; PRA

Introduction

Human activities have converted around one third of the world's forests to agriculture (Ellis et al., 2020). In many regions just a small fraction of the original tree cover remains, while deforestation and forest degradation, particularly in the tropics, continues apace (Hu et al., 2021). The ecosystem services provided by trees and forests have long been recognised (Ehrlich & Mooney, 1983). Forest ecosystems are among the most biodiverse and play major roles in terrestrial carbon sequestration and the water cycle. Trees provide material goods like food, fuel and fibre, along with social and cultural benefits around the world (Brander et al., 2023). Hence, numerous policies to halt and reverse forest decline have been implemented nationally (Wuepper et al., 2024) and internationally (Muthee et al., 2022). Though some mechanisms to reduce deforestation and increase forest cover have proved controversial (Cao et al., 2010; West et al., 2023), it is generally recognised that increasing tree cover remains a central goal in biodiversity protection and climate change mitigation (United Nations, 2021).

Across Europe, tree cover began to decline around 6000 BP as agriculture expanded (Roberts et al., 2018). Pollen records across the UK reveal a steep decline in deciduous woodland coupled with a rise in open and semi-open grassland starting around 4000 BP (Woodbridge et al., 2014). Tree cover in the UK fell below 5 % at the beginning of the 20th Century, growing again to around 13 % in 2018 (Forest Research, 2018). This contrasts with a European average of 39 % forest area, with the UK ahead of only Malta, Ireland and the Netherlands in terms of tree cover (Milicevic, 2023). Reforestation in the UK has primarily involved fast growing exotic conifer species, which now comprise around half of total forest area (Forest Research, 2023). Ancient woodlands, defined as areas thought to have been continuously tree-covered since 1600 and valued for their biodiversity and cultural significance, cover just 2.5 % of the UK (Spencer & Kirby, 1992). Current Government policy is to increase tree cover to 16.5 % in England by 2050 (Natural England & Forestry Commission, 2023), to 21 % of Scotland by 2032 (Scottish Government, 2017), and by 2000 ha per year in Wales (Welsh Government, 2021).

Forest is the climax vegetation type across much of the UK, and simply leaving land unmanaged and ungrazed tends to result in natural tree regeneration and succession (Harmer et al., 2011). Alternatively, tree species can be deliberately selected for planting. A central question in increasing forest cover is deciding which tree species to plant where and to what purpose (Bateman et al., 2023). The choice of species tends to be between fast growing exotic conifers (gymnosperms) and ‘native’ broadleaves (angiosperms), where the term native implies arrival in the UK by natural dispersal. Landowners are currently able to select from a wide palette of more-or-less native species such as oak (*Quercus robur*, *Q. petraea*), beech (*Fagus sylvatica*), sycamore (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*), Scot’s pine (*Pinus sylvestris*) and birch (*Betula pendula*), or exotics such as Sitka spruce (*Picea sitchensis*), Norway spruce (*P. abies*) and lodgepole pine (*P. contorta*).

Time complicates the selection of tree species for planting. Trees can live for centuries and rotations of even fast-growing exotics require many decades, meaning that projections of growth and survival of growing stands may be highly inaccurate as unexpected risk factors emerge. In an era of rapid climate change, the conditions under which a tree was planted will not be those experienced when it reaches maturity (Bateman et al., 2023). Many broadleaves are projected to become more vulnerable to heat and drought in Southeast England in particular (Yu et al., 2021). Improving models of tree responses to climate change, including extreme events like droughts and fires, will facilitate tree selection for resilient forests, extending potentially to importing non-native species better adapted to future conditions (Ennos et al., 2019).

There is another, potentially more serious, threat to future UK trees and forests than climate change. Plant pests and diseases (PPDs) can rapidly emerge and spread to devastate tree populations (Rackham, 2008; Simler-Williamson et al., 2019). International trade and transport are largely responsible for the dissemination of forest PPDs around the world (Liebhold et al., 2012; Santini et al., 2013; Simler-Williamson et al., 2019). Dozens of bacterial, fungal and oomycete pathogens and insect pests have arrived in the UK in recent decades, some with severe consequences (Bebber et al., 2024). The UK landscape changed dramatically in the 20th Century on arrival of the virulent form of Dutch elm disease (Potter et al., 2011), caused by the beetle-vectored fungus *Ophiostoma novo-ulmi*, and is changing once again as ash dieback disease, caused by the fungus *Hymenoscyphus fraxineus*, decimates one of the most common broadleaf tree species (Coker et al., 2019). Ash dieback was first noticed in Poland in the mid-1990s (Kowalski, 2006), and may have arrived in the UK as early as 2004 (Wylder et al., 2018). Given the recent and rapid emergence of ash dieback, the long-term tree mortality rate is unknown (Coker et al., 2019) but the ecosystem consequences may be severe (Hultberg et al., 2020).

Public concern over the impact of ash dieback led to the establishment of the Plant Health Risk Register (PHRR) by the UK's Department for environment food and rural affairs (Defra) in 2012 (Baker et al., 2014; Defra, 2024). The PHRR is a pest risk assessment system which aims to provide risk and impact indices for PPDs which could affect agricultural, horticultural and forestry plant species in the UK (MacLeod & Lloyd, 2020). Native and long established PPDs are usually not included. Pest risk assessment is a component of the formalized process of Pest Risk Analysis (PRA) (EPPO, 2019). Pest risk assessment activities in Europe are undertaken by national governments, the European Food Safety Authority, EFSA (Jeger et al., 2018) and the European Plant Protection Organization, EPPO (EPPO, 2019), with the purpose of advising which PPDs should be listed as quarantine organisms and identifying phytosanitary methods for preventing their spread within and across national borders. The PHRR adapts pest risk assessment methodologies, using a range of information sources and analyses to provide relative ratings for the likelihood of introduction, likelihood of spread, level of impact, and value of the resource at risk. These ratings are provided for two mitigation scenarios, an unmitigated scenario which considers only standard measures to control entry, spread and damage, and a mitigated scenario which considers the effects of co-ordinated actions. The majority PPDs in the PHRR affect agricultural crops but a substantial number affect trees.

Taken together, these risk assessments provide a qualitative overview of vulnerability of the UK's current and future trees and forests. However, PHRR risk scores have not been synthesized to gain insight into the threats faced by different plant species from the wide range of potentially-invasive pests and diseases to which they are host. Nor have the implications of multiple invasions over the long term, critical in understanding risks to long-lived tree species, been considered. Here, we analyse the PHRR relative risk and impact ratings to gain a synoptic view of potential risks of losses to tree species plantings which may form part of policy goals to increase tree cover in the UK. Since the PHRR focusses on potential invasive species, our analysis does not consider altered threats from native and long established PPDs due to climate change and other drivers.

Methods

Plant Health Risk Register data

PHRR entries were downloaded from https://planthealthportal.defra.gov.uk/pests-and-diseases/uk-plant-health-risk-register/ in June 2024 as a comma separated value (CSV) text file. Data provided for each entry include: date of entry; PPD taxonomy and common name; quarantine listing (GB, EU and EPPO); major host plants; status in the UK (present, absent, or unknown); distribution in Europe and globally; possible entry pathways (e.g. through live plant imports); likelihood, impact and value at risk scores for unmitigated and mitigated scenarios (ordinal scale, 0–5); whether statutory actions are in place; key uncertainties relating to various aspects of the risk assessment exercise; and notes on distributions and impacts. If a PPD is completely absent from the UK, the likelihood of establishment is based on estimated entry and establishment probabilities, derived primarily from source country climatic similarity to the UK and host species coverage in the UK. If the PPD is already present (in a limited part of the UK), the likelihood score is based on the estimated probability of the pest spreading to maximum extent within the next 5 years (Defra, 2021). The unmitigated risk rating assumes that no official regulatory controls are applied, for example trade restrictions on import of host species from countries where the PPD is present. The mitigated risk rating is based on current mitigations designed to reduce the risk of introduction or spread of the PPD, such as phytosanitary measures or industry certification schemes (EPPO, 2019). Where there are no mitigations, the unmitigated and mitigated scores will be the same. The PHRR is precautionary by design, and is likely to over-estimate risk where there is uncertainty.

Prior to analysis some minor errors or omissions in PHRR were corrected, e.g. where type of pest was missing. The PHRR data were filtered to extract all PPDs of forest trees. Our list of UK tree species was compiled from a range of published and online sources including tree guides (e.g. Hemery & Simblet, 2014), the Woodland Trust, Forest Research, the Forestry Commission and the Royal Forestry Society (Table S 1). We employed a broad definition of trees, to include smaller species such as juniper (*Juniperus communis*), but omitted species of purely horticultural interest (e.g. the domesticated apple, *Malus x domestica*). There are a number of rare whitebeam species native to the UK, e.g. the Devon or Broad-leaved whitebeam *Karpatiosorbus devoniensis*, which were also excluded. Where the major host of a PPD was listed as a genus, we assumed that all species within the genus are vulnerable. In 2012, the most recent year for which official data are available, the broadleaf species with the largest stocked areas were birch, oak, ash, sycamore, beech, hazel, hawthorn, willow, alder and sweet chestnut (Table S 2). The most widely grown conifers were Sitka spruce, Scots pine, larch, lodgepole pine, Norway spruce, Corsican pine, and Douglas fir (Table S 3).

Synoptic risk analysis

PPDs have the potential to reduce growth, reproduction and survival of trees by some quantity. For example, ash mortality has reached around 60 per cent in European countries where Ash dieback has been present longest, currently around 20 years (Coker et al., 2019). There are no indications that mortality has plateaued, hence in the long term the loss of ash may be complete. Ash dieback has likelihood and impact scores of 5 in the PHRR. Incidences of horse chestnut (*Aesculus hippocastanum*) bleeding canker, caused by the bacterium *Pseudomonas syringae* pv. *aesculi*, have increased dramatically in the UK since 2003 (Webber et al., 2008), and in 2007 the disease affected around half of surveyed trees in the UK (Forestry Commission, 2008). There is little published information on the impact of bleeding canker on tree growth and survival, and indeed losses of horse chestnut may be due to felling to remove diseased trees rather than the disease itself (Straw & Williams, 2013). An observational study found that trees with severe symptoms actually had more rapid growth rates than uninfected trees, suggesting that tree vigour facilitates bacterial growth (Straw & Williams, 2013). Horse chestnut bleeding canker has a PHRR likelihood score of 5 and impact score of 4. Horse chestnut leaf miner (*Cameraria ohridella*) was first recorded in the UK in 2002, and can cause severe defoliation but has little detectable influence on growth (Straw & Williams, 2013). Horse chestnut leaf miner has likelihood and impact scores of 4 and 3, respectively. Acute Oak Decline (AOD) is a bacterial syndrome putatively spread by the beetle *Agrilus biguttatus* affecting oaks. AOD was associated with the deaths of up to one quarter of affected oak trees within a 3–4 years (Brown et al., 2016). AOD has a likelihood score of 3 and impact 5. An exhaustive synthesis of growth and survival effects of PPDs is beyond the scope of this analysis, but these examples indicate the upper range of losses associated with PPDs given high PHRR impact scores.

For the purposes of modelling potential future losses of tree productivity through reduced growth or elevated mortality, we assumed that an impact score of 5 equated to a fractional loss L_5 of between 0.5

and 1 (mean 0.75), with sequentially lower impact scores halving the losses in turn (Table 1). This schema resulted in the lowest impact score having very small effect on production (mean loss 4.7 %).

Estimating arrival probabilities from historical trends

Historical invasions of forest PPDs in the UK were used to estimate annual arrival probabilities for the PHRR likelihood scores. Between 1971 and 2021, 24 new forest PPD outbreaks were recorded in the UK (Defra, 2023). Five of these occurred before the year 2000 and 19 thereafter, giving an arrival rate of around one PPD per year (Table S 4).

Let A_i be the mean annual probability of arrival for PPDs with likelihood score i, where i ranges from 1 to 5. To estimate annual arrival probabilities we made the following assumptions: A_5 is the maximum and the probability for each lower likelihood score is half of the preceding score (e.g. $A_4 = A_5/2$, $A_3 = A_5/4$, etc.); only PPDs currently listed as absent can arrive, and each can only arrive once; arrival probabilities for each PPD are independent of one another; no further PPDs are identified and added to the PHRR; historical arrivals occurred before any mitigations had been put in place. As the total number of PPDs is limited, the arrival rate should decline over time as the pool of those yet to arrive shrinks. We therefore estimated A_i to maintain a mean annual arrival rate of one PPD over the next decade.

If N_i is the number of PPDs in each likelihood category, the annualized arrival rate for all PPDs is:

$$r_a = \sum_{i=1}^{5} N_i A_i$$

Over time, r_a declines as the absent PPD pool shrinks:

$$N_{i,t} = N_i (1 - A_i)^t$$

where $N_{i,t}$ is the remaining number of species with likelihood score i after t years.

Mean $r_a = 1$ for the first 10 years means:

$$\frac{1}{10} \sum_{t=0}^{9} \left(N_{1,t} A_1 + N_{2,t} A_2 + \cdots + N_{5,t} A_5 \right) = 1.$$

Substituting $A_i = \frac{A_5}{2^{5-i}}$ and $N_{i,t} = N_i (1 - A_i)^t$, this becomes:

$$\frac{1}{10} \sum_{t=0}^{9} \sum_{i=1}^{5} N_i \left(1 - \frac{A_5}{2^{5-i}} \right)^t \frac{A_5}{2^{5-i}} = 1$$

We found the required value for A_5 using the *uniroot* function for R, which numerically solves for the root of a given continuous function within specified intervals (which were set between 10^{-6} and 1). To explore the effect of altered rates of arrival, we also calculated A for r_a values of 0.5 and 2.

Given these arrival probabilities and impacts, we can then estimate losses in the next 25 years (i.e., by around 2050) from the probability of arrival and spread in the next 25 years (assuming no changes in annual probabilities) and the expected loss of productivity through reduced growth or survival for a given annual arrival probability *A* is:

$$A_{25y} = 1 - (1 - A)^{25}$$

The number of absent PPDs in the *i*th Likelihood score category declines over time *t*:

$$N_{i,t} = N_{i,t-1}.(1 - A_i)$$

Therefore the number of new arrivals in year *t* is:

$$a_t = \sum_{i=1}^{5} N_i.(1 - A_i)^{t-1}.A_i$$

The expected loss of tree productivity (through either reduced growth or elevated mortality) per pest is:

$$E(L_{25y}) = A_{25y} \times L,$$

where *L* is the fractional loss given arrival and spread.

We assume that the effects of pests on their hosts are independent of one another, i.e. if two pests each reduce production by half, then arrival of both would reduce production by three quarters. The expected production fraction remaining (*R*) for a tree species considering the combined effect of *N* pests is then:

$$E(R) = \prod_{j=1}^{N} 1 - E(L_j),$$

where losses to pests for which the tree species is not a host are zero.

Results

Tree PPDs

The UK PHRR (obtained 11th June 2024) contained 1424 PPDs, of which 636 were listed as affecting UK tree species or genera and 339 were listed as affecting particular UK tree species (Figure 1). The majority (466) of those affecting UK tree species or genera are currently listed as absent from the UK. Of those present in the UK, 46 have a widespread distribution, 66 a limited distribution, and 33 an unknown distribution. Status in the UK is unknown for 25 PPDs. Tree species vary in the number of PPDs for which they are listed as major hosts. Bird cherry (81 PPDs), sour cherry (51), Douglas fir (36), Scots pine (35), wild pear (34), Norway spruce (27), Monterey pine (26), English oak (25) and Sitka spruce (22) were the most commonly listed major hosts, as listed specifically by species. *Prunus* (249 PPDs), *Malus* (180), *Pinus* (148), *Pyrus* (138), *Quercus* (93), *Picea* (76), *Abies* (72), *Populus*

(70), *Salix* (69) and *Acer* (66) were the most listed genera. All trees in our list were hosts for at least one PPD, the rarest being alder buckthorn (*Frangula alnus*) with a single potential PPD, *Chrysobothris mali*. This buprestid beetle, known as apple tree borer or Pacific flatheaded borer, is listed as a pest of congener *Frangula californica*, the California coffeeberry. *C. mali* has a wide host range and so it may be able to affect *F. alnus*.

The PPDs listed as affecting the most tree species were honey fungus (*Armillaria mellea,* 63 tree species), Kulsi teak borer (*Stromatium barbatum*, 51), white-marked tussock moth (*Orygia leucostigma*, 49), cottony maple scale (*Neopulvinaria innumerabilis*, 45), black timber beetle (*Xylosandrus germanus*, 44), flat-headed apple tree borer (*Chrysobothris femorata*, 40), elm spanworm or linden moth (*Ennomos subsignaria*, 40), an ambrosia beetle (*Megaplatypus mutatus*, 40), apple stem borer or city longhorn beetle (*Aeolesthes sarta*, 39) and Asian longhorn beetle (*Anoplophora glabripennis*, 39). Of these, honey fungus is widespread in the UK and the black timber bark beetle has a limited distribution, while the rest are absent. Insects, particularly weevils (Curculionidae, 69 species), long-horn beetles (Cerambycidae, 40 species), tortrix moths (Tortricidae, 33 species) and fruit flies (Tephritidae, 27 species) were the most speciose tree PPDs, though certain groups of nematodes (Longidoridae, 19 species) and bacteria (Acholeplasmataceae, 18 species) were also common tree PPDs in the PHRR.

Tree PPD risk and impact

We evaluated the risk of arrival and spread, and subsequent impact, of PPDs currently absent from the UK or with limited or unknown UK distributions and which could affect UK tree species or genera (n = 581). Of these, 508 had both mitigated and unmitigated PHRR scores. The unmitigated arrival and spread likelihood score was 3 or above for 68 % of PPDs, while the impact score was 3 or above for 60 % (Table S 5). A joint score of likelihood 3 and impact 3 was most common (20 % of PPDs), while 29 PPDs had joint scores of 4 or 5 for both risk metrics indicating high or very high risk of spread and impact on hosts. Four PPDs with very high likelihood and impact were the emerald ash borer (*Agrilus planipennis*) which affects ash, the eight-toothed spruce bark beetle (*Ips typographus*) and four-eyed fir bark beetle (*Polygraphus proximus*) which affect conifers, and the oomycete *Phytophthora ramorum* which has a very wide host range but in the UK has primarily infected larch (*Larix* spp.). *P. ramorum* is the only one of these highly dangerous PPDs listed as being present in the UK, with a distribution largely limited to wetter, western regions. A localized outbreak of *I. typographus* in Southeast England, first identified in 2018, remains under eradication (Forestry Commission, 2024).

The mitigated risk scores are, unsurprisingly, lower than the unmitigated scores, with moderate to very high (3–5) mitigated likelihood scores given for 34 % of PPDs (Table S 6). However, mitigated impact scores remain similar to unmitigated scores, with 59 % of PPDs receiving moderate to very high ratings. The most common combined mitigated rating is likelihood 2 and impact 3 (18 % of

PPDs). PPDs which retain very high mitigated likelihood or impact scores include the two-lined chestnut borer (*Agrilus bilineatus*) which affects elms and oaks, eight-toothed spruce bark beetle, *P. ramorum*, the American grapevine leafhopper (*Scaphoideus titanus*) which is a disease vector able to feed on American elm (*U. americana*), and the fungus *Sirococcus tsugae* which is able to infect cedars (*Cedrus* spp.) and hemlock (*Tsuga* spp.).

The potential impact on tree species is likely to be a function of the number of PPDs that could affect a tree, the likelihood of their arrival and spread, and the impact on growth and survival. The mitigated and umitigated risk ratings, calculated as the product of likelihood and impact scores summed across all PPDs affecting a species, were greatest in cherries, pines, apples and pears, oaks and certain exotic conifers (Figure 2). The summed risk ratings were lowest in less common species like alder buckthorn, buckthorn and giant sequoia, although several exotic conifers (*Chamaecyparis lawsoniana*, *Cupressus macrocarpa*, *C. x leylandii*, *Cedrus* spp.) also had relatively low scores. However, some trees susceptible to relatively few PPDs are at risk from some particularly damaging ones, such as *S. tsugae* affecting cedars and *P. ramorum* affecting strawberry tree (*Arbutus unedo*). It is also important to remember that the analysis excludes risks from PPDs which are currently widespread in the UK, for example honey fungus (*Armillaria* spp.), to which cedars are particularly susceptible.

Potential probabilities of spread and expectations of losses

Around one additional tree PPD has established in the UK per year since 2001 (Defra, 2023). Assuming that this trend continues for the next decade, we estimated the annual arrival probability for Likelihood score 5 as 0.007 (equivalent to once in 145 years) for the 508 PPDs currently listed as absent from the UK or with limited or unknown distributions (Table 2). This translates to a cumulative probability of arrival within 25 years of 0.15. Arrival probabilities for lower Likelihood scores were half those of the preceding higher score, following our model assumptions. If mitigations were implemented, i.e. we calculate arrivals using the probabilities associated with mitigated Likelihood scores, we would expect an average of 0.66 PPDs per year in the first decade. These rates decline slightly over time as the number of absent PPDs remaining shrinks (Figure 3). In 25 years, we would expect 24.4 PPDs to arrive under the unmitigated scenario, and 15.3 under the mitigated scenario. Changes in the first decade mean annual arrival rate have proportional effects on probabilities and long-terms rates, e.g. a rate of 2 per year would result in 47.4 arrivals after 25 years under the unmitigated scenario.

Expected remaining production per tree species in 25 years, calculated from the products of arrival probabilities and fractional production losses, varied between 0.17 and 0.99 (median 0.55, interquartile range 0.46–0.82) under the unmitigated scenario (Figure 4, Table S 1). Using the mitigated scenario Likelihood and Impact scores resulted in larger $E(R)$ values (median 0.73, interquartile range 0.67–0.88). Losses are expected to be greatest in pine, cherry, spruce, larch and oak, with less than one third of expected production remaining under the unmitigated scenario. For some of these genera, particularly spruce, larch and oak, mitigation is expected to be effective, approximately halving losses. Mitigation is less effective for pine and cherry. Most of the species with few PPDs in the PHRR are predicted to experience small productivity losses ($E(R) > 0.8$ in the unmitigated scenario).

Discussion

We have explored the implications of quantifying the ordinal invasion and impact scores for PPDs currently listed in the UK PHRR for 74 tree species found in the UK. Of 1426 PPDs, 637 are thought to be capable of affecting UK trees. The number of absent PPDs, along with their likelihood of invasion and establishment and the damage they may do, varies greatly among the 74 tree species we analysed. Using the recent historical rate of invasion by tree PPDs and plausible loss levels to quantify Likelihood and Impact scores, we estimated substantial potential production losses for many tree species in coming decades. On average, more than half of production is lost across species, with ecologically and economically important trees like oaks, pines and spruce under threat. A maximum invasion probability of just 0.007 per year was required to reach such losses, because the pool of potential invaders is so large. Under a mitigation scenario derived from the PHRR 'mitigated' Likelihood and Impact scores, and when invasion probabilities simulate lower establishment rates, losses are greatly reduced. However, we must emphasize that the purpose of this analysis was firstly to provide a synoptic overview of biotic threats to UK trees and woodlands, as revealed by the PHRR, and secondly to suggest a way by which empirical data on invasions and impacts could potentially be used to derive quantitative risks from qualitative scores.

As demonstrated by various uncertainties listed in the PHRR, much work remains to be done to fully understand the processes by which PPDs invade and the impact they have on tree health. For example, a key uncertainty for *Agrilus horni*, the aspen root girdler, is whether this pest is able to attack mature trees, while for several *Meloidogyne* nematodes the key uncertainty is whether they will be able to overwinter in UK climates. Given that our models predict severe losses to many tree species under very low invasion probabilities and production losses, we advocate urgent investment in international collaborative research, involving countries already facing these pests and those at risk of future invasions, to better understand PPD risk and mitigate future impacts (IPPC, 2021).

The global picture of tree PPD impacts does not give grounds for optimism regarding the future of forests. Invasions of forest pests and pathogens into Europe and the United States continue to grow (Aukema et al., 2010; Loehle et al., 2023; Santini et al., 2013). Recent projections for Europe suggest that 10 per cent of Europe's forest carbon is at risk from just five invasive PPDs (Seidl et al., 2018) – our analysis considers more than one hundred times that number of PDDs. The bacterium *Xylella* *fastidiosa* killed one third of Apulia's olive trees within a decade (Sabelli, 2023) while an invasive longhorn beetle *Xylotrechus chinensis* is devastating mulberry (*Morus nigra*) trees throughout southern Europe (Monteys et al., 2021). What can be done to reduce these impacts? Improved surveillance of traded goods and tree populations reduces invasion risk, as reflected in the lower risk scores of the mitigated scenarios in the PHRR. However, even small annual probabilities of arrival and establishment become near-certainties in just a few decades, well within the lifespan of many tree species. In some cases, eradication is possible if invasions are caught before widespread dispersal. In 2012, a localized invasion by Asian longhorn beetle in southern England was eradicated using a combination of tree felling, pheromone traps, sniffer dogs and public engagement in surveillance (Eyre & Barbrook, 2021). Fortunately, sub-optimal climatic conditions prevented rapid population growth and facilitated control. The felling and destruction of infected or infested trees, known as sanitation felling, is a commonly employed management method to reduce the population density of the PPD, and secondarily to reduce public health risks due to falling dead trees. Empirical studies have demonstrated that such eradication treatments do not markedly reduce PPD spread (Hansen et al., 2019) or population density (Stadelmann et al., 2013). Another approach is to remove healthy trees in a wide belt around an infested area to reduce host availability (Sun et al., 2023), known as containment felling, though models suggest that such belts must be tens of kilometres wide to be effective due to the dispersal ranges of most PPDs (de la Fuente et al., 2018; Robinet et al., 2020), and as such are technically unfeasible, environmentally undesirable and could even eradicate resistant genotypes within tree populations. Where outbreaks occur across borders, international cooperation is necessary

We assumed that the effects of multiple PPDs on tree productivity were independent, meaning that impacts accumulated multiplicatively. The combined effect of independently acting PPDs on production across the tree population could occur through impacts on tree survival (Figure 5a) or growth (Figure 5b). Several different types of interactions among PPDs are possible (Elvira-Recuenco et al., 2020): indirect antagonism, where infection by one pathogen alters overall plant susceptibility to further infection through, for example, plant defence priming (Figure 5c); direct antagonism, where infection of plant tissue by one pathogen prevents another from infecting the same tissue (Figure 5d); and synergistic interaction, where infection or infestation increases vulnerability to attack and impact on productivity by other PPDs (Figure 5e). An example of a synergistic interaction is the association between Acute Oak Decline, caused by a community of necrogenic bacteria, with the galleries of the two-spotted oak buprestid beetle *Agrilus biguttatus* (Brown et al., 2015). Conversely, infection of Ponderosa pine (*Pinus ponderosa*) by the root pathogen *Heterobasidion annosum* induces some resistance to attack by the bark beetle *Ips paraconfusus* (Eyles et al., 2010; McNee et al., 2003). In general, however, we have no information on how the PPDs in the PHRR would interact, and hence chose here to model their effects independently.

Aside from how PPDs interact, we were unable to include several other potentially-important factors in our models. We assumed no change in invasion probability over time, though it is likely that changes in climate and international trade will influence the suitability and susceptibility of UK forests to PPDs in different ways (Ramsfield et al., 2016). Warming climates will generally increase developmental rates of insect pests (Deutsch et al., 2018), but drying conditions could reduce foliar infection by fungal and oomycete pathogens (Rowlandson et al., 2014). Neither did we consider changes in trade flows which are key invasion risk (Williams et al., 2023). The PHRR is not exhaustive and cannot consider PPDs which have not yet emerged. It is also biased toward more common or commercially important tree species (Defra, pers. comm.). The current analysis is, in this way, a best-case scenario. However, we can assume that any PPDs not included are not thought to be particularly damaging or likely to invade the UK. The number of PPDs added to the PHRR has declined over time, and few have been added since 2020 (Figure 6). While it is not possible to extrapolate future PPD addition rates from these observations (Bebber et al., 2007), they give some indication that the most important PPDs have been considered. Finally, we have assumed that the impact score assigned to a PPD applies equally to all known host plants. For example, while the Sudden Oak Death pathogen has greatly reduced larch production in the UK (Dun et al., 2024), the pathogen has a very wide host range and its impact on these other tree species may not be as severe.

Despite these limitations, our analysis provides the first synoptic view of the potential combined impacts of the hundreds of PPDs that could affect UK trees in coming decades. Further research will help to refine the model framework we have developed, for example by more accurately quantifying losses of different host species to particular PPDs. The PHRR provides a wealth of information on the relative risks to plant species, including agricultural crops and forest trees, in the UK. While relative risk scores are useful in prioritizing plant biosecurity actions like live plant import inspections, quantifying invasion probabilities and potential losses provides a stark reminder that emerging PPDs pose a severe threat to trees in semi-natural woodlands, production forests, gardens and cities, and the biodiversity benefits and ecosystem services that these trees provide.

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Competing interests

The authors declare no competing interests.

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Tables

Table 1. Ranges of plausible production losses through increased mortality or reduced growth given arrival and spread of a tree PPD, for each Impact score. Mid-points of ranges are given as decimals.

Score	Range	Mid-point
1	1/32, 1/16	0.047
2	1/16, 1/8	0.094
3	1/8, 1/4	0.188
4	1/4, 1/2	0.375
5	1/2, 1	0.75

Table 2. Arrival probabilities of tree PPDs for each Likelihood score. Annualized arrival probabilities A were calculated to give a mean arrival rate r_a of 1 per year for a decade. Long term (25 year) arrival probabilities A_{25y} were used to calculate long term expected production losses.

Score	A	A_{25y}
1	0.0004	0.011
2	0.0009	0.021
3	0.0017	0.042
4	0.0034	0.083
5	0.0069	0.159

Figures

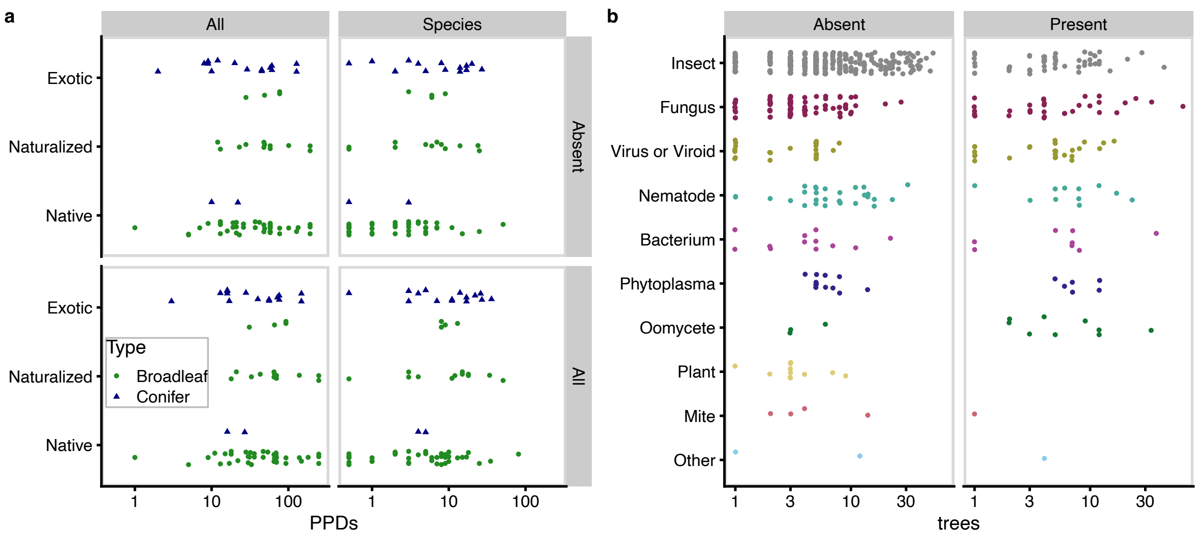

Figure 1. a) Number of PPDs per tree species. Top row shows tree PPDs currently absent from the UK (n = 466), lower row shows all PPDs of trees in the PHRR (n = 636), left column shows PPDs of trees by species or genus, right column shows PPDs of trees by species. Broadleaves shown in green, conifers in blue. PPD number scale is log-transformed, zero values shown below one. b) Number of tree hosts per PPD by pest type. PPDs absent from the UK on left, present in the UK on right. PPDs for which presence in the UK was listed as unknown (n = 25) were included in the Absent group.

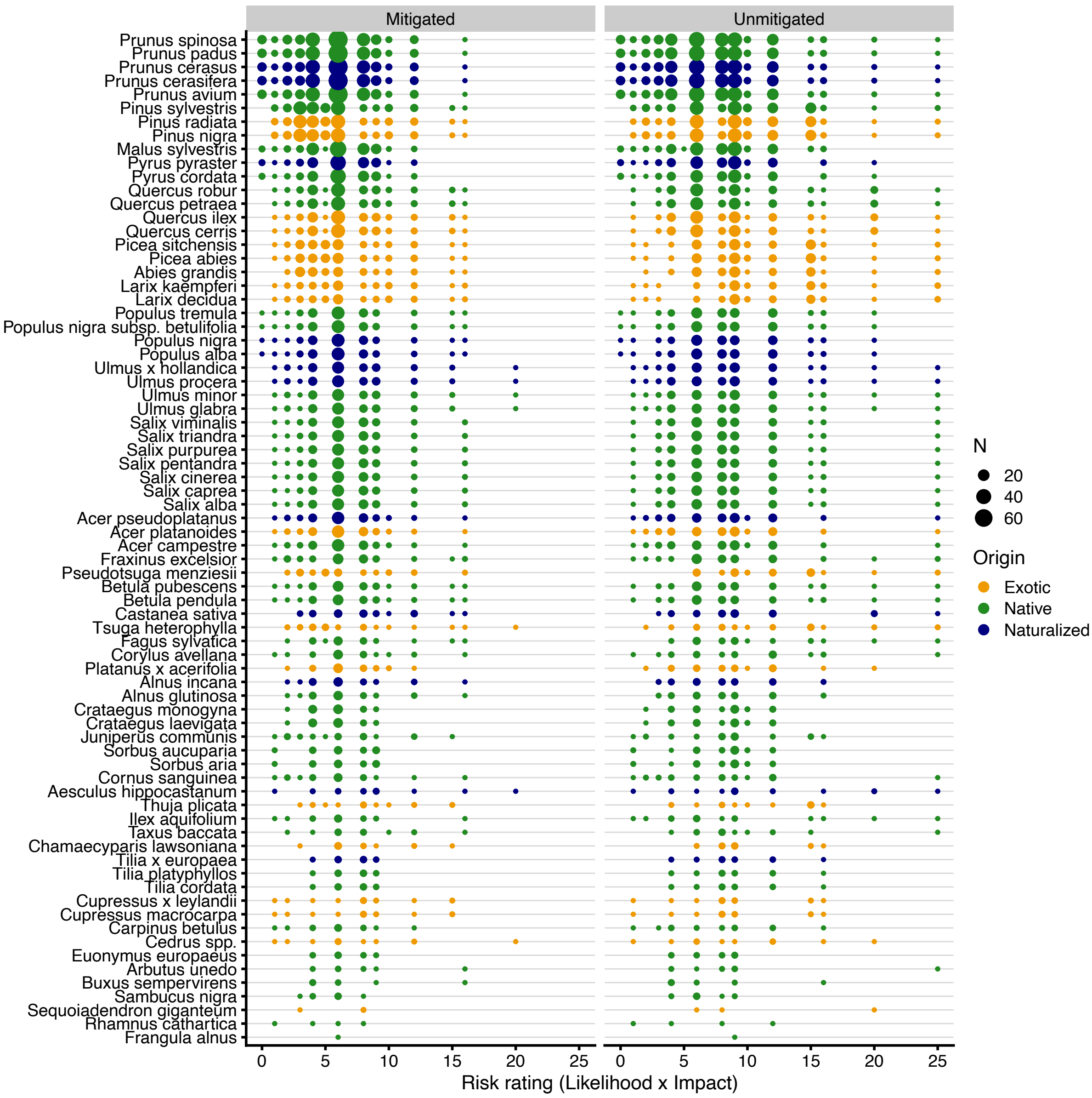

Figure 2. Risk rating by tree species. Risk rating was calculated as mitigated (left panel) and unmitigated (right panel) Likelihood × Impact. Tree species are ranked (top to bottom) by the sum of risk ratings. Size of symbols indicates the number of PPDs per species, including those which list tree genus as a major host. Colours indicate origin (native in blue, naturalized in cyan, exotic in red).

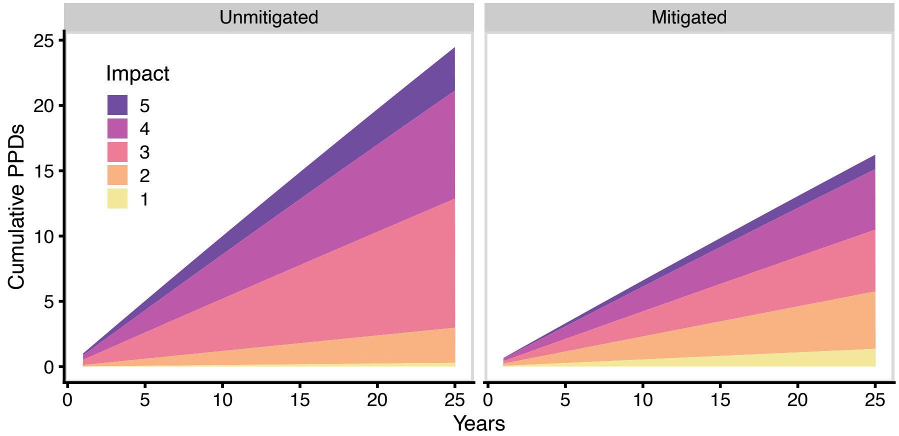

Figure 3. Potential cumulative arrival of tree PPDs over 25 years by Impact score for unmitigated and mitigated Likelihood scores. The annual arrival probability for Likelihood = 5 PPDs was 0.0068, based on mean annual arrival of 1 PPD per year for the first decade under the unmitigated scenario.

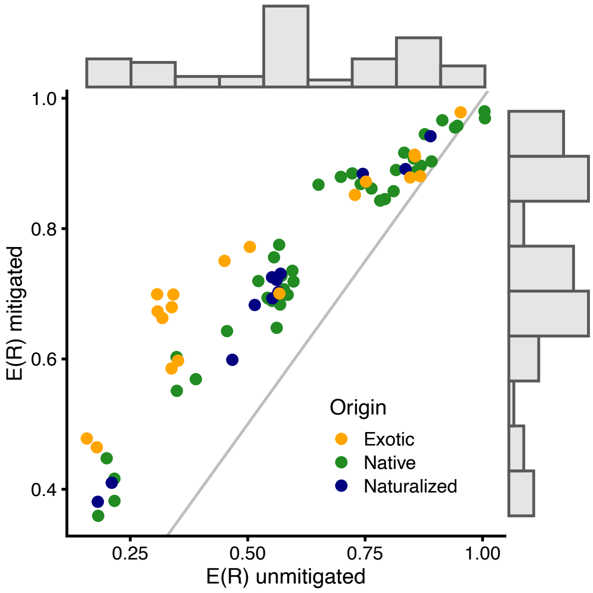

Figure 4. Expected production remaining in mitigated vs unmitigated scenarios in 25 years. *E*(*R*) was calculated from projected arrival probabilities for each Likelihood score and median loss values for each Impact score. Points show species coloured by origin. Points have been randomly shifted slightly to prevent overlaps. Marginal histograms show relative frequencies of *E*(*R*). Line of equality shown in grey.

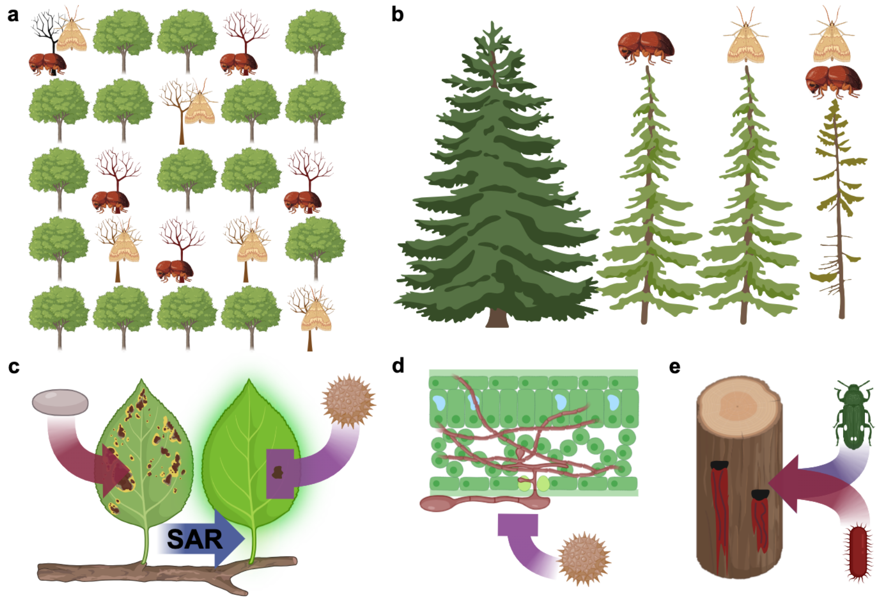

Figure 5. Combined effects of multiple PPDs. a) Independent effects of two PPDs on tree survival, each causing 20 per cent mortality. Co-incident attack has the same effect as individual attack. b) Independent effects on tree growth, where each PPD reduces growth by some fraction. c) Systemic acquired resistance (SAR) caused by one pathogen reduces infection by another. d) Infection of a leaf by one pathogen prevents colonization by another. e) Wounding by a beetle enables invasion by bacterial pathogens. Image created in Biorender.com

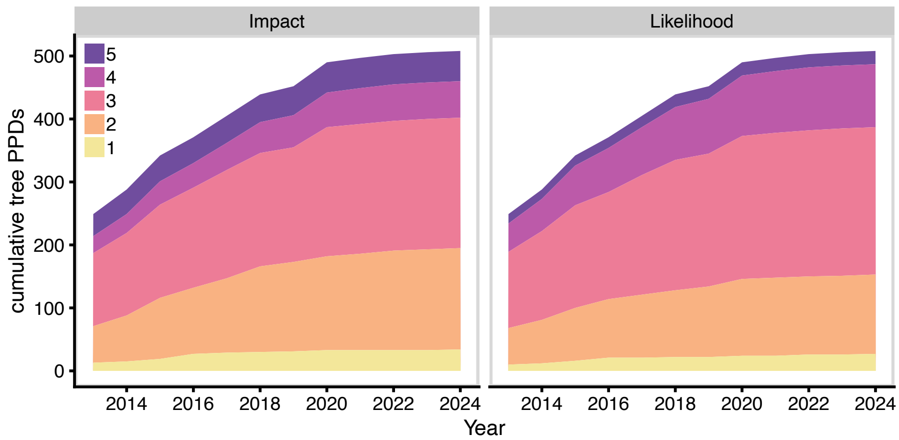

Figure 6. Accumulation of tree PPDs in the PHRR by Impact and Likelihood scores, 2013–mid-2024.

Supplementary Material

Supplementary Tables

Table S 1. Trees of the United Kingdom. Origin is based on the available literature and may be open to interpretation for certain species. Native indicates arrival in the UK by natural dispersal. Naturalized indicates human introduction with substantial natural regeneration in semi-natural habitat. $E(R_u)$ and $E(R_m)$ are the expected production fractions remaining after 25 years under the unmitigated and mitigated scenarios, respectively.

Common name	Scientific name	Origin	Type	$E(R_u)$	$E(R_m)$
Field Maple	*Acer campestre*	Native	Broadleaf	0.57	0.73
Alder	*Alnus glutinosa*	Native	Broadleaf	0.81	0.87
Strawberry Tree	*Arbutus unedo*	Native	Broadleaf	0.84	0.93
Silver Birch	*Betula pendula*	Native	Broadleaf	0.59	0.76
Downy Birch	*Betula pubescens*	Native	Broadleaf	0.59	0.76
Box	*Buxus sempervirens*	Native	Broadleaf	0.94	0.94
Hornbeam	*Carpinus betulus*	Native	Broadleaf	0.87	0.92
Common Dogwood	*Cornus sanguinea*	Native	Broadleaf	0.75	0.88
Hazel	*Corylus avellana*	Native	Broadleaf	0.71	0.86
Midland Hawthorn	*Crataegus laevigata*	Native	Broadleaf	0.82	0.89
Hawthorn	*Crataegus monogyna*	Native	Broadleaf	0.82	0.89
Spindle	*Euonymus europaeus*	Native	Broadleaf	0.93	0.94
Beech	*Fagus sylvatica*	Native	Broadleaf	0.66	0.84
Alder Buckthorn	*Frangula alnus*	Native	Broadleaf	0.99	1.00
Ash	*Fraxinus excelsior*	Native	Broadleaf	0.53	0.74
Holly	*Ilex aquifolium*	Native	Broadleaf	0.74	0.90
Crab Apple	*Malus sylvestris*	Native	Broadleaf	0.37	0.54
Black Poplar	*Populus nigra* subsp. *betulifolia*	Native	Broadleaf	0.17	0.47
Aspen	*Populus tremula*	Native	Broadleaf	0.55	0.70
Wild Cherry	*Prunus avium*	Native	Broadleaf	0.55	0.70
Bird Cherry	*Prunus padus*	Native	Broadleaf	0.20	0.39
Blackthorn	*Prunus spinosa*	Native	Broadleaf	0.20	0.39
Plymouth Pear	*Pyrus cordata*	Native	Broadleaf	0.20	0.39
Sessile Oak	*Quercus petraea*	Native	Broadleaf	0.46	0.62
Pedunculate Oak	*Quercus robur*	Native	Broadleaf	0.33	0.58
Purging Buckthorn	*Rhamnus cathartica*	Native	Broadleaf	0.33	0.58
White Willow	*Salix alba*	Native	Broadleaf	0.97	0.99
Goat Willow	*Salix caprea*	Native	Broadleaf	0.56	0.70
Grey Willow	*Salix cinerea*	Native	Broadleaf	0.56	0.70
Bay Willow	*Salix pentandra*	Native	Broadleaf	0.56	0.70
Purple Osier	*Salix purpurea*	Native	Broadleaf	0.56	0.70
Almond Willow	*Salix triandra*	Native	Broadleaf	0.56	0.70
Common Osier	*Salix viminalis*	Native	Broadleaf	0.56	0.70
Elder	*Sambucus nigra*	Native	Broadleaf	0.56	0.70
Whitebeam	*Sorbus aria*	Native	Broadleaf	0.96	0.97
Rowan	*Sorbus aucuparia*	Native	Broadleaf	0.83	0.88
Small-leaved Lime	*Tilia cordata*	Native	Broadleaf	0.83	0.88
Large-leaved Lime	*Tilia platyphyllos*	Native	Broadleaf	0.87	0.92
Wych Elm	*Ulmus glabra*	Native	Broadleaf	0.87	0.92
Field Elm	*Ulmus minor*	Native	Broadleaf	0.54	0.67
Juniper	*Juniperus communis*	Native	Conifer	0.54	0.67
Scots Pine	*Pinus sylvestris*	Native	Conifer	0.77	0.85
Yew	*Taxus baccata*	Native	Conifer	0.77	0.88
Sycamore	*Acer pseudoplatanus*	Naturalized	Broadleaf	0.57	0.73
Horse Chestnut	*Aesculus hippocastanum*	Naturalized	Broadleaf	0.75	0.91
Grey Alder	*Alnus incana*	Naturalized	Broadleaf	0.81	0.87
Sweet Chestnut	*Castanea sativa*	Naturalized	Broadleaf	0.54	0.75
White Poplar	*Populus alba*	Naturalized	Broadleaf	0.55	0.70

Black Poplar	*Populus nigra*	Naturalized	Broadleaf	0.55	0.70
Cherry Plum	*Prunus cerasifera*	Naturalized	Broadleaf	0.20	0.39
Sour Cherry	*Prunus cerasus*	Naturalized	Broadleaf	0.20	0.39
Wild Pear	*Pyrus pyraster*	Naturalized	Broadleaf	0.46	0.62
Common Lime	*Tilia x europaea*	Naturalized	Broadleaf	0.87	0.92
English Elm	*Ulmus procera*	Naturalized	Broadleaf	0.54	0.67
Huntingdon Elm	*Ulmus x hollandica*	Naturalized	Broadleaf	0.54	0.67
Norway Maple	*Acer platanoides*	Exotic	Broadleaf	0.57	0.73
London Plane	*Platanus x acerifolia*	Exotic	Broadleaf	0.74	0.85
Turkey Oak	*Quercus cerris*	Exotic	Broadleaf	0.33	0.58
Holm Oak	*Quercus ilex*	Exotic	Broadleaf	0.33	0.58
Grand Fir	*Abies grandis*	Exotic	Conifer	0.35	0.67
Cedar	*Cedrus spp.*	Exotic	Conifer	0.84	0.88
Lawson Cypress	*Chamaecyparis lawsoniana*	Exotic	Conifer	0.86	0.90
Monterey Cypress	*Cupressus macrocarpa*	Exotic	Conifer	0.86	0.88
Leyland Cypress	*Cupressus x leylandii*	Exotic	Conifer	0.86	0.88
European Larch	*Larix decidua*	Exotic	Conifer	0.33	0.67
Japanese Larch	*Larix kaempferi*	Exotic	Conifer	0.33	0.67
Norway Spruce	*Picea abies*	Exotic	Conifer	0.31	0.65
Sitka Spruce	*Picea sitchensis*	Exotic	Conifer	0.31	0.65
Black Pine	*Pinus nigra*	Exotic	Conifer	0.17	0.47
Monterey Pine	*Pinus radiata*	Exotic	Conifer	0.17	0.47
Douglas Fir	*Pseudotsuga menziesii*	Exotic	Conifer	0.45	0.76
Giant Sequoia	*Sequoiadendron giganteum*	Exotic	Conifer	0.93	0.98
Western Red Cedar	*Thuja plicata*	Exotic	Conifer	0.78	0.85
Western Hemlock	*Tsuga heterophylla*	Exotic	Conifer	0.51	0.77

Table S 2. Stocked area of broadleaves (thousands of hectares). National Forest Inventory 2012 data (Brewer, 2014a).

Species	England	Scotland	Wales	Great Britain
Birch	95.5	127.8	12.2	235.5
Oak	167.0	26.2	25.8	219.1
Ash	122.8	15.5	18.8	157.0
Sycamore	75.5	21.6	9.2	106.3
Beech	72.0	15.3	6.3	93.7
Hazel	64.6	7.9	14.3	86.8
Hawthorn	57.5	7.6	7.5	72.6
Willow	40.8	13.4	11.1	65.2
Alder	30.7	17.0	9.9	57.6
Sweet chestnut	28.5	0.0	0.4	28.9
Other	146.1	44.4	21.4	211.9
Total	902.3	297.2	137.1	1336.6

Table S 3. Stocked area of conifers (thousands of hectares). National Forest Inventory 2012 data (Brewer, 2014b).

Species	England	Scotland	Wales	Great Britain
Sitka spruce	80.5	506.8	77.3	664.6
Scots pine	61.4	153.6	3.2	218.2
Larches	40.2	65.8	19.9	126.0
Lodgepole pine	7.7	88.0	4.1	99.8
Norway spruce	27.4	25.3	7.9	60.6
Corsican pine	40.4	2.8	2.4	45.6
Douglas fir	24.6	12.5	8.6	45.6
Other conifers	23.7	10.9	5.0	39.6
Total	306.6	872.0	129.0	1307.5

Table S 4. Forest PPD arrivals since 1971 (Defra, 2023)

Year	PPD
1971	Dutch elm disease
1983	Great spruce bark beetle
1984	Phytophthora alni
1995	Gypsy moth
1997	Dothistroma needle blight
2002	Phytophthora ramorum
2002	Horse chestnut leaf miner
2003	Phytophthora kernoviae
2005	Bleeding canker of horse chestnut
2006	Oak processionary moth
2006	Phytophthora pseudosyringae
2007	Pine tree lappet moth
2010	Acute oak decline
2010	Phytophthora lateralis
2012	Ash dieback
2012	Asian longhorn beetle
2012	Sweet chestnut blight
2012	Phytophthora austrocedri
2014	Phytophthora sikiyouensis
2014	Sirococcus tsugae
2015	Oriental chestnut gall wasp
2017	Elm zigzag sawfly
2018	Eight toothed spruce bark beetle
2021	Phytophthora pluvialis

Table S 5. Number of PPDs by unmitigated likelihood and impact rating. Trees absent from the UK or with unknown or limited distributions within the UK were included.

		Impact					
		1	2	3	4	5	Total
Likelihood	1	6	11	8	2	0	27
	2	8	37	51	19	11	126
	3	13	69	107	21	24	234
	4	6	41	31	13	9	100
	5	1	3	10	3	4	21
	Total	34	161	207	58	48	508

Table S 6. Number of PPDs by mitigated likelihood and impact rating. Trees absent from the UK or with unknown or limited distributions within the UK were included.

		Impact					
		1	2	3	4	5	Total
Likelihood	1	8	20	55	17	22	122
	2	10	52	85	17	10	174
	3	6	33	26	10	3	78
	4	6	23	6	2	1	38
	5	1	2	2	0	0	5
	Total	31	130	174	46	36	508