RESEARCH ARTICLE

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Cumulative impact assessments of multiple host species loss from plant diseases show disproportionate reductions in associated biodiversity

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Abstract

1. Non-native plant pests and pathogens are increasing exponentially, causing extirpation of foundation species. The impact of large-scale declines in a single host on associated biodiversity is widely documented. However, the impact of multiple host loss on biodiversity and whether these impacts are multiplicative has not been assessed. Ecological theory suggests that systems with greater functional redundancy (alternative hosts) will be more resilient to the loss of sympatric hosts. We test this theory and show its importance in relation to pest/pathogen impact assessments.

2. We assessed the potential impact on biodiversity of the loss of two widely occurring sympatric European tree species, *Fraxinus excelsior* and *Quercus petraea/robur*, both of which are currently threatened by a range of pests and pathogens.

3. At the UK scale, the total number of associated species at risk of extirpation from plant diseases affecting these two sympatric hosts is greater than the sum of the associated species at risk from declines in either host alone. *F. excelsior* hosts 45 obligate species (species only found on that host) and *Q. petraea/robur* hosts 326. However, a decline in both these trees would impact 512 associated species, across multiple taxon groups, a 38% increase. Assessments at a local scale, 24 mixed *F. excelsior*–*Q. petraea/robur* woodlands revealed that these impacts may be even greater due to a lack of functional redundancy. Only 21% of sites were able to provide functional redundancy for *F. excelsior* and *Q. petraea/robur* associated species which can use other tree species. In most woodlands, the tree species required to provide functional redundancy were not present, although the site conditions were often suitable for them to grow.

4. *Synthesis*. Understanding of functional redundancy should be applied to assessments of pests/pathogens impact on biodiversity. In risk assessments, higher impact scores should be given to pests/pathogens affecting hosts occurring with other host plant species already impacted by pests/pathogens. Current pest/pathogen risk assessment approaches that ignore the cumulative, cascading effects shown in this study may allow an insidious, mostly overlooked, driver of biodiversity loss to continue.

KEYWORDS

biodiversity loss, cumulative impact assessment, forest, functional redundancy, pathogen, pest, resilience, risk assessment

1 | INTRODUCTION

Global biodiversity loss is occurring at unprecedented rates (Pimm et al., 2014) and the invasion of alien species, which includes non-native pests/pathogens, is one of the top five drivers of this decline (IPBES, 2019). Ecosystems with high functional redundancy are expected to maintain stability as species are lost, because other species are present within the system that fulfil similar functions (Laliberte et al., 2010; Pillar et al., 2013; Rosenfeld, 2002). Ecosystems dominated by a few foundation species, that is 'a single species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing, fundamental ecosystem processes' (Dayton, 1972), are most at risk from a lack of functional redundancy (Walker, 1992, 1995).

Many temperate-zone forests, which are typically dominated by a few foundation tree species, provide examples of ecosystems with low functional redundancy (Ellison et al., 2005). These forests are currently experiencing an exponential increase in non-native tree pests/pathogens due to increased global trade and climate change (Freer-Smith & Webber, 2017) causing substantial ecological damage and economic loss (Boyd et al., 2013; Hill et al., 2019; Roy et al., 2014). Governments and their agencies are therefore horizon scanning and developing risk assessments of potential threats, for example, the European Food Safety Authority (Jeger et al., 2012), the US Animal and Plant Health Inspection Service (USDA, 2021) and the UK Plant Health Risk Register (Defra, 2021; Spence, 2020). Such risk assessments include likelihood of pest/pathogen entry, establishment, spread and impact on tree hosts (MacLeod & Lloyd, 2020).

However, plant pest/pathogen risk assessments do not assess the potential impact of the pest/pathogen as a driver of wider biodiversity loss and their possible role in the current biodiversity crisis. Current risk assessment approaches potentially miss three important elements. First, they do not consider the cascading impacts of tree loss on associated biodiversity, species that use the tree for feeding, either directly or indirectly (eating other organisms found on the tree), or as habitat for living in (i.e.

lichens/bryophytes) or for breeding/roosting in (i.e. birds and bats; Mitchell, Beaton, Bellamy, et al., 2014). Second, the risk assessments do not include cumulative impacts, defined as the effect on biodiversity of a decline in more than one tree species within the same site or forest stand. If sympatric tree species decline, there may be cumulative impacts that cascade beyond obligate species (species requiring one tree species for their survival) to associated species that may be shared between affected tree species. Third, it is assumed there is functional redundancy, that is, that for all, but obligate species, it is assumed that the associated species could survive using alternative hosts. However, if functional redundancy is not present at an appropriate scale to support the associated species (e.g. within a site or forest stand), then the impact of tree species loss will cascade far beyond obligate species, resulting in large declines in populations, and potentially extirpations, of other associated species. There is a growing body of evidence addressing the first point, indicating that a decline in one foundation tree species may impact on many hundreds of associated species (Ellis et al., 2012; Gandhi & Herms, 2010a, 2010b; Hultberg et al., 2020; Lõhmus & Runnel, 2014; Lubek et al., 2020; Mitchell et al., 2019a). However, the cumulative impact on biodiversity of plant pests/pathogens affecting sympatric tree species, and whether a lack of functional redundancy within the ecosystem will exacerbate these impacts (points two and three above) have not previously been studied.

Although cumulative impact assessments (CIAs) of the risk of multiple diseases on a single tree species have been proposed (Davies et al., 2017), we argue the need for assessments of the cumulative impacts of diseases on associated biodiversity that occur on different trees within the same ecosystem. This would be more analogous to CIA within Environmental Impact Assessments conducted ahead of major infrastructure projects (Masden et al., 2010). Individually, a decline in any one tree species due to disease may have minor effects on biodiversity, but collectively these may be significant, potentially greater than the sum of the individual diseases acting alone. To provide a real-world context for our argument about the need for CIA, we focus on the impacts of a loss of *Fraxinus excelsior* (European ash) and

the *Quercus petraea/Q. robur* complex (sessile oak/pedunculate oak), two of the most common native trees in the United Kingdom (Rodwell, 1991), and sympatric species across much of Europe, although the principles are applicable to diseases impacting any foundation species.

Fraxinus excelsior is currently declining across Europe due to the non-native ascomycete *Hymenoscyphus fraxineus* (Kjær et al., 2012). Also, *F. excelsior* is threatened by the non-native Emerald ash borer beetle *Agrilus planipennis*, that has killed millions of *Fraxinus* sp. trees in the United States (Herms & McCullough, 2014) and has spread across the Eurasian landmass as far west as Ukraine (Orlova-Bienkowskaja et al., 2020). *Q. petraea/robur* are currently at risk from the non-native pest, oak processionary moth (Tomlinson et al., 2015), acute oak decline, caused by a native insect and bacteria (Doonan et al., 2020), exacerbated by climate change (Brown et al., 2018), as well as a variety of non-native powdery mildews (Lonsdale, 2015). In addition, *Q. petraea/robur* would be a risk of decline due to *Xylella fastidiosa* if this bacterium established in the United Kingdom (Defra, 2021).

Recent work in the United Kingdom has produced lists of the species associated with *F. excelsior* termed ash-associated species (Mitchell, Broome, Harmer, Beaton, Bellamy, Brooker, Duncan, et al., 2014) and *Q. petraea/robur* termed oak-associated species (Mitchell et al., 2019b, 2019c). When the alternative hosts to support the ash-associated biodiversity were assessed, *Q. petraea/robur* was identified as a good replacement for *F. excelsior* supporting 69% of the 955 ash-associated species, a higher proportion than 47 other potential hosts assessed (Mitchell, Beaton, Bellamy, et al., 2014; Mitchell, Broome, Harmer, Beaton, Bellamy, Brooker, Ellis, et al., 2014). Similar work for *Q. petraea/robur* identified *F. excelsior* as a good replacement supporting 28% of the 2,300 oak-associated species (the greatest proportion for any of the 30 tree species assessed; Mitchell et al., 2019a).

Given that *F. excelsior* and *Q. petraea/robur* are sympatric and can provide functional redundancy for each other in terms of supporting, many of the same associated species, we ask two questions. First, what might be the cumulative impact on associated biodiversity of a decline in both these common native tree species? Second, do native woodlands provide (through the mixture of tree species present) sufficient functional redundancy to mitigate the impact of a decline in both *F. excelsior* and *Q. petraea/robur* on biodiversity?

2 | MATERIALS AND METHODS

We study the *Q. petraea/robur* complex rather than either species individually, since there is taxonomic confusion around the two species, a situation further compounded by the occurrence of extensive interspecific hybridization and data suggesting a continuum of genetic and morphological variation between the two species (Beatty et al., 2016; Gomory et al., 2001). In addition, data on which *Quercus* species is used as a host by associated species are often unavailable

(Mitchell et al., 2019a); we therefore treat the *Q. petraea/robur* complex as one host tree 'species' throughout.

2.1 | The databases

The AshEcol database (Mitchell, Broome, Harmer, Beaton, Bellamy, Brooker, Duncan, et al., 2014) lists whether each of the 955 ash-associated species (12 birds, 58 bryophytes, 68 fungi, 241 invertebrates, 548 lichens and 28 mammals; Mitchell, Beaton, Bellamy, et al., 2014; Mitchell, Broome, Harmer, Beaton, Bellamy, Brooker, Ellis, et al., 2014) will use any of 48 alternative tree species, while the OakEcol database (Mitchell et al., 2019b) lists whether each of the 2,300 oak-associated species (38 birds, 229 bryophytes, 108 fungi, 1,178 invertebrates, 716 lichens and 31 mammals; Mitchell et al., 2019a) will use any of 30 alternative tree species (Appendix S1, Table S1). Although there is considerable overlap in the alternative tree species for which an assessment is made, these lists are not identical because *F. excelsior* grows on a greater range of soil types than *Q. petraea/robur* (Pyatt et al., 2001), resulting in a greater range of potential replacement tree species for *F. excelsior* depending on soil type (see Appendix S1, Table S1). In each case, the alternative tree species selected for assessment were those that are either currently occurring in *F. excelsior* or *Quercus* woodlands (Rodwell, 1991), or non-native species which are known to grow in the same climatic/soil conditions in which *F. excelsior* or *Q. petraea/robur* currently grow (Pyatt et al., 2001). The methods used to collate the ash- and oak-associated species lists, and to assess if these species will use each alternative tree species, are described in detail in Mitchell, Beaton, Bellamy, et al. (2014) and Mitchell et al. (2019a) respectively. Throughout the assessments below, it is noted that the number of species involved is an underestimate, as neither database includes algae, bacteria or other micro-organisms, nor do they include a complete list of all the associated fungi, only concentrating on those known fungal species with the strongest association with either *F. excelsior* or *Q. petraea/robur*.

2.2 | Cumulative assessments at the national level

The databases were queried to identify the number of species known (a) to be obligate on either *F. excelsior* or *Q. petraea/robur* (obligate-Fe/Qpr), (b) to only use *F. excelsior* and *Q. petraea/robur* (Fe&Qpr-only) and (c) to use *F. excelsior* and *Q. petraea/robur* and other tree species (Fe&Qpr&others). Combining the obligate-Fe/Qpr and Fe&Qpr-only lists provides a CIA of the species at risk of extirpation if both *F. excelsior* and *Q. petraea/robur* decline.

Of those in the obligate-Fe/Qpr and Fe&Qpr-only lists, we identified all which do not already have some form of conservation protection within the United Kingdom. The definition of conservation protection differed between taxonomic groups (as no method is systematically used across taxa) but included (a) whether the species is listed using IUCN criteria as endangered, vulnerable or near

threatened, (b) is listed in the relevant UK Red Data book or (c) is a UK Biodiversity Action Plan species or (d) a bird species listed as red or amber on the UK Birds of Conservation Concern list, see Mitchell et al. (2019a) for further details.

2.3 | Cumulative assessments at the site level

Nine *F. excelsior*-dominated woodlands that also contain *Q. petraea/robur* (termed ash-dominated woods throughout) and 15 *Q. petraea/robur*-dominated woodlands that also contain *F. excelsior* (termed oak-dominated woods throughout) were selected to be representative of either ash- or oak-dominated woodlands across Britain, where the conservation of biodiversity was a management priority (Figure 1). Sites were therefore primarily, but not always, nature reserves, or had some other form of protection [e.g. Sites of Special Scientific Interest (SSSIs) or Special Area of Conservation (SACs)].
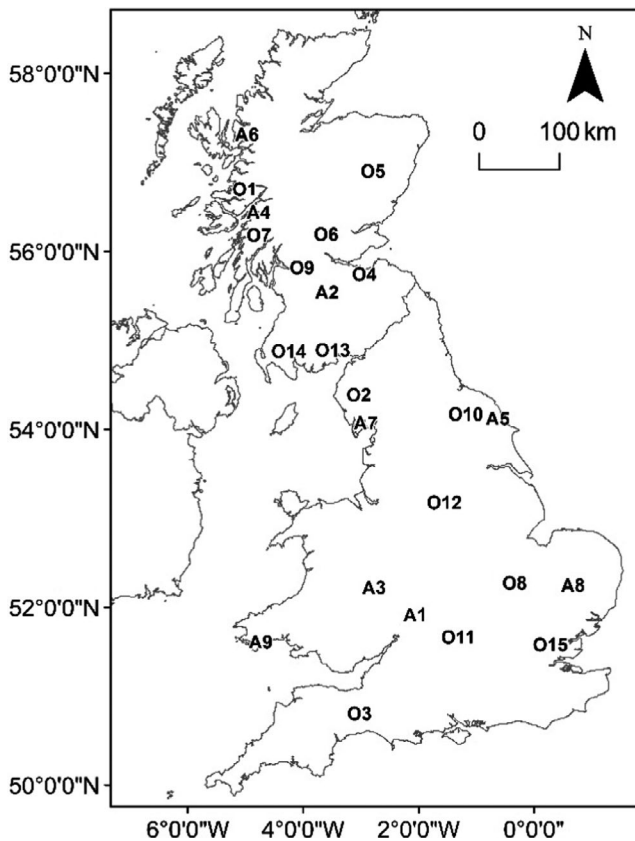
FIGURE 1 Site locations. A = *Fraxinus excelsior*-dominated woodlands with *Quercus petraea/robur* present, O = *Q. petraea/robur*-dominated woodlands with *F. excelsior* present. A1 = Bredon Hill; A2 = Cleghorn Glen; A3 = Downton George; A4 = Glasdrum; A5 = Raincliffe and Forge Valley; A6 = Rassal; A7 = Roudsea Wood; A8 = Sapiston Grove; A9 = West Williamston; O1 = Ariundle; O2 = Borrowdale; O3 = Britty Common; O4 = Dalkeith; O5 = Dinnet; O6 = Drummond Loch; O7 = Glen Nant; O8 = Monks Wood; O9 = Mugdock; O10 = Raindale; O11 = Stratfield Brake; O12 = Totley Wood; O13 = Tower Wood; O14 = Wood of Cree; O15 = Writtle

A list of the species present at each site was collated using site records and data from the UK's National Biodiversity Network Gateway (NBN, 2017). The species lists were then screened to identify any ash- or oak-associated species. This list was then split into species classed as obligate-Fe/Qpr, Fe&Qpr-only Fe&Qpr&others, using the definitions above. Combining the obligate-Fe/Qpr and Fe&Qpr-only lists provided a CIA of the species present at each site at greatest risk of extirpation if both *F. excelsior* and *Q. petraea/robur* decline.

Species at each site listed as Fe&Qpr&others may not be at risk of extirpation if other host tree species are present at the site. We split the Fe&Qpr&others list into highly associated, partially associated and cosmopolitan species. We focussed our work on the highly associated species (species rarely uses tree species other than *F. excelsior* or *Q. petraea/robur*) and partially associated species (uses *F. excelsior* or *Q. petraea/robur* more frequently than its availability) as these species will use a smaller range of alternative trees and would therefore be at greatest risk if *F. excelsior* and *Q. petraea/robur* declined. Using AshEcol and OakEcol, we identified which tree species would host the highly and partially associated species, and recorded if these tree species were present at each site. If suitable alternatives were not present, we then assessed if they could be established at the site, that is, if the trees would grow in the soils and climate at the site using the UK's Ecological Site Classification tool (Pyatt et al., 2001). Finally, we calculated the number of species currently present at the site that could not be supported by other tree species, either currently present at the site, or that could be established at the site.

To test if the number of associated species supported was influenced by the number of tree species present at the site, and whether the site being an ash- or oak-dominated wood was important, GLMs were used. The glm function within R (version 3.6.2, R Core Team, 2018) was used with a binomial distribution, with woodland type as a fixed effect and number of tree species present as a continuous variable. The binomial distribution models the proportion of species supported while taking account of the number of species present. The analysis was carried out separately for the number of highly associated species supported, and the number of partially associated species supported.

3 | RESULTS

Declines in both *F. excelsior* and *Q. petraea/robur* in the United Kingdom would result in more species being at risk than just the sum of their obligate species. There are 45 obligate ash-associated species (11 fungi, 30 invertebrates and 4 lichens) and 326 obligate oak-associated species (57 fungi, 257 invertebrates and 12 lichens) giving a total of 371 (obligate-Fe/Qpr). However, the CIA shows 512 species would be impacted due to an additional 141 species (13 bryophytes, 42 invertebrates and 86 lichens) that are not known to use trees other than *Q. petraea/robur* and *F. excelsior* (Fe&Qpr-only; Figure 2). Of the 512 species threatened by the loss of both
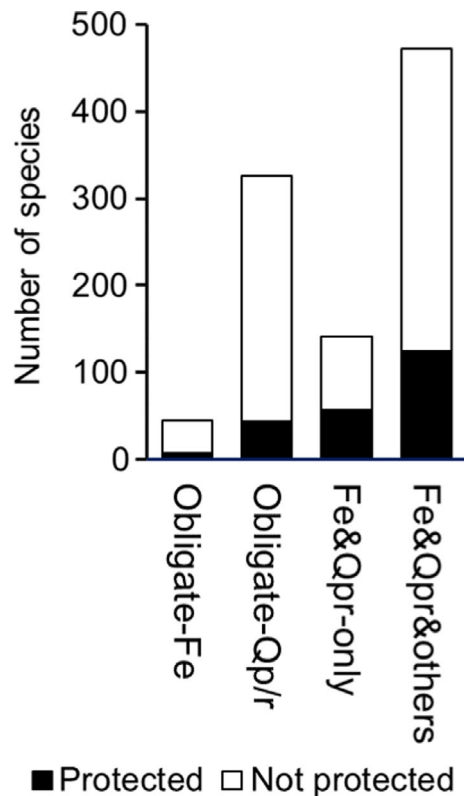
FIGURE 2 Number of species that are obligate on *Fraxinus excelsior* (Fe) and *Quercus petraea/robur* (Qp/r), only use *Fraxinus excelsior* and *Q. petraea/robur* (Fe&Qpr-only) or use *F. excelsior* and *Q. petraea/robur* and other tree species (Fe&Qpr&others) in the United Kingdom. Protected = currently has some form of conservation protection or designation. Not protected = currently does not have any form of conservation protection or designation

F. excelsior and *Q. petraea/robur*, 21% are already listed as having some form of conservation designation or protection indicating that they are already rare or are threatened by other drivers of change. However, the remaining 79% are not currently listed as being at risk (Figure 2). Thus, a decline in just these two tree species would put a further 404 species at risk of decline in the United Kingdom that are not currently identified as potentially at risk of extirpation, and therefore part of the current biodiversity crisis.

Four hundred and seventy-two species were identified that use *Q. petraea/robur* and *F. excelsior* and other tree species (Fe&Qpr&others, Figure 2). For these species, mitigation would be possible, if the relevant tree species are present, or can be established, at the site.

3.1 | Site-level cumulative impacts and assessments of functional redundancy

Of the 24 sites assessed, 21 (88%) had species that are either obligate on *F. excelsior* or on *Q. petraea/robur* (obligate-Fe/Qpr) or only use *F. excelsior* and *Q. petraea/robur* (Fe&Qpr-only), with 40 species at risk at one site, Monks Wood (Figure 3). These obligate species were from a range of taxon groups (bryophytes, fungi, invertebrates and lichens, Appendix S1, Table S2). In addition, the sites had records of many other species (range 10–306) that although using *F. excelsior* and *Q. petraea/robur* will also use other tree species (Fe&Qpr&others, Figure 4). These species included birds, bryophytes, fungi, invertebrates, lichens and mammals (Appendix S1, Table S2; Appendix S2 provide complete species lists). At 18 sites (14 oak and 4 ash woods) this included at least one species that was highly associated with either *F. excelsior* or *Q. petraea/robur* (Figure 4; Appendix S1, Tables S3 and S5; Appendix S2). Only five (28%) of these 18 sites had full functional redundancy for these highly associated species, that is they had other tree species present that would support all the highly associated species present (Figure 5a). A further five sites had limited functional redundancy, containing tree species that would support some, but not all, of the highly associated species present (Figure 5a). Although eight sites (44%) had no functional redundancy, in that there were no tree species present that would support the highly associated species occurring there, six of these sites had conditions (climate and soils) suitable for the introduction of other tree species that could support the associated species (Figure 5a). Only at two sites (11%) was there no functional redundancy and no potential to mitigate this by establishing other host trees which could grow at the site to support these species.

All sites had species that were partially associated with *F. excelsior* or *Q. petraea/robur* (range 7–137; Figure 4; Appendix S1, Tables S4 and S6; Appendix S2). Only seven (29%) of the 24 sites (six ash-dominated woods and one oak-dominated wood) had full functional redundancy, that is had tree species present that would support all the partially associated species (Figure 5b). Most sites (17 of the 24 sites, 71%) had limited functional redundancy with tree species present that would support some but not all the species present (Figure 5b). Nine (53%) of the 17 sites with limited functional redundancy had the potential to have full functional redundancy if additional tree species were established. The functional redundancy at the other eight sites could be increased by establishing additional tree species, but full functional redundancy was not possible as the tree species required to support these partially associated species would not grow at these sites (Figure 5b).

For the highly associated species, there was no significant relationship between the number of tree species present at the site, in addition to *F. excelsior* and *Q. petraea/robur*, and the number of highly associated species supported ($\chi^2(1, N = 18) = 2.35$ $p > 0.05$, Appendix S1, Figure S1a). However, there was a significant relationship between the number of tree species present at the site, in addition to *F. excelsior* and *Q. petraea/robur*, and the number of partially associated species supported ($\chi^2(1, N = 24) = 59$ $p < 0.0001$, Appendix S1, Figure S1b). There was also a significant difference between the two woodlands types ($\chi^2(1, N = 24) = 11.88$ $p < 0.0001$) but no interaction between woodland type and number of tree species for partially associated species.
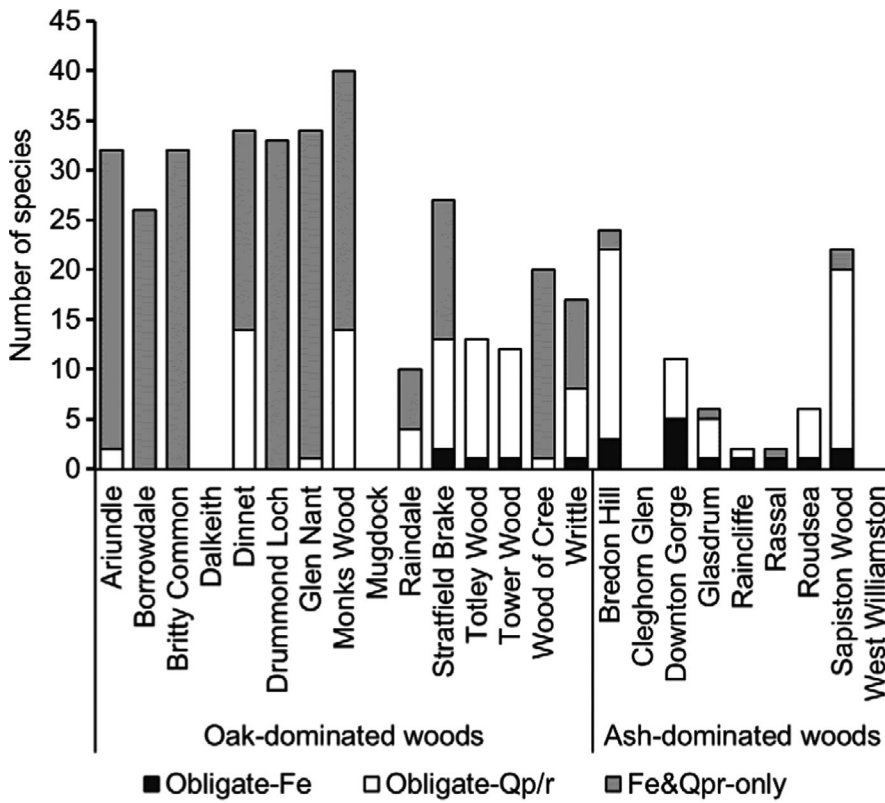
FIGURE 3 Number of species associated with *Fraxinus excelsior* and *Quercus petraea/robur* recorded at 24 mixed ash/oak woodlands in the United Kingdom that are: obligate on *F. excelsior* (Obligate-Fe), obligate on *Q. petraea/robur* (Obligate-Qp/r) or only use *F. excelsior* and *Q. petraea/robur* (Fe&Qpr-only)
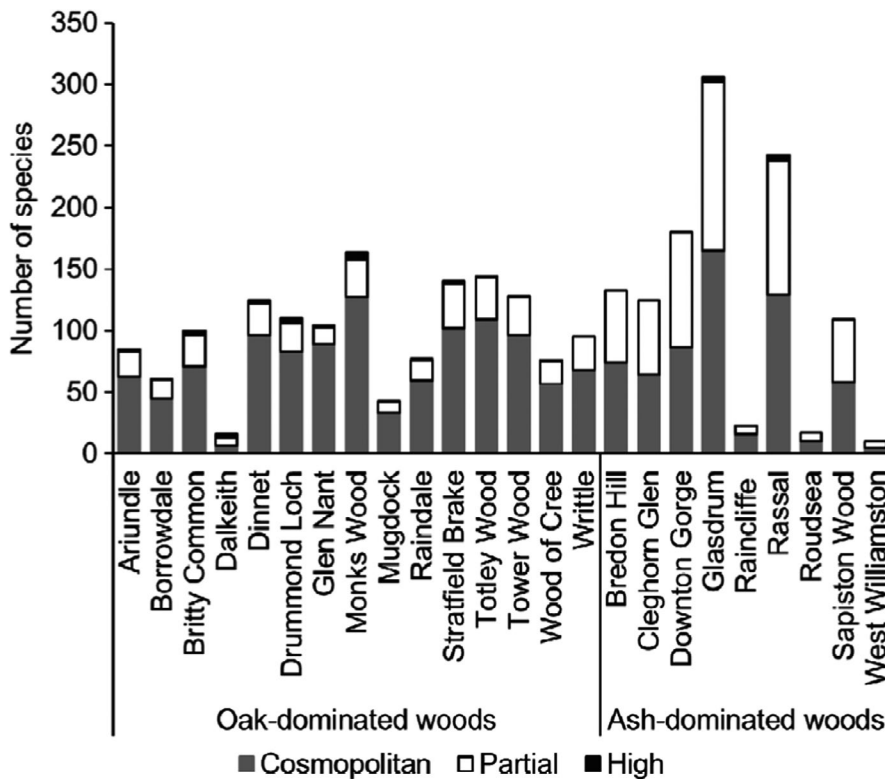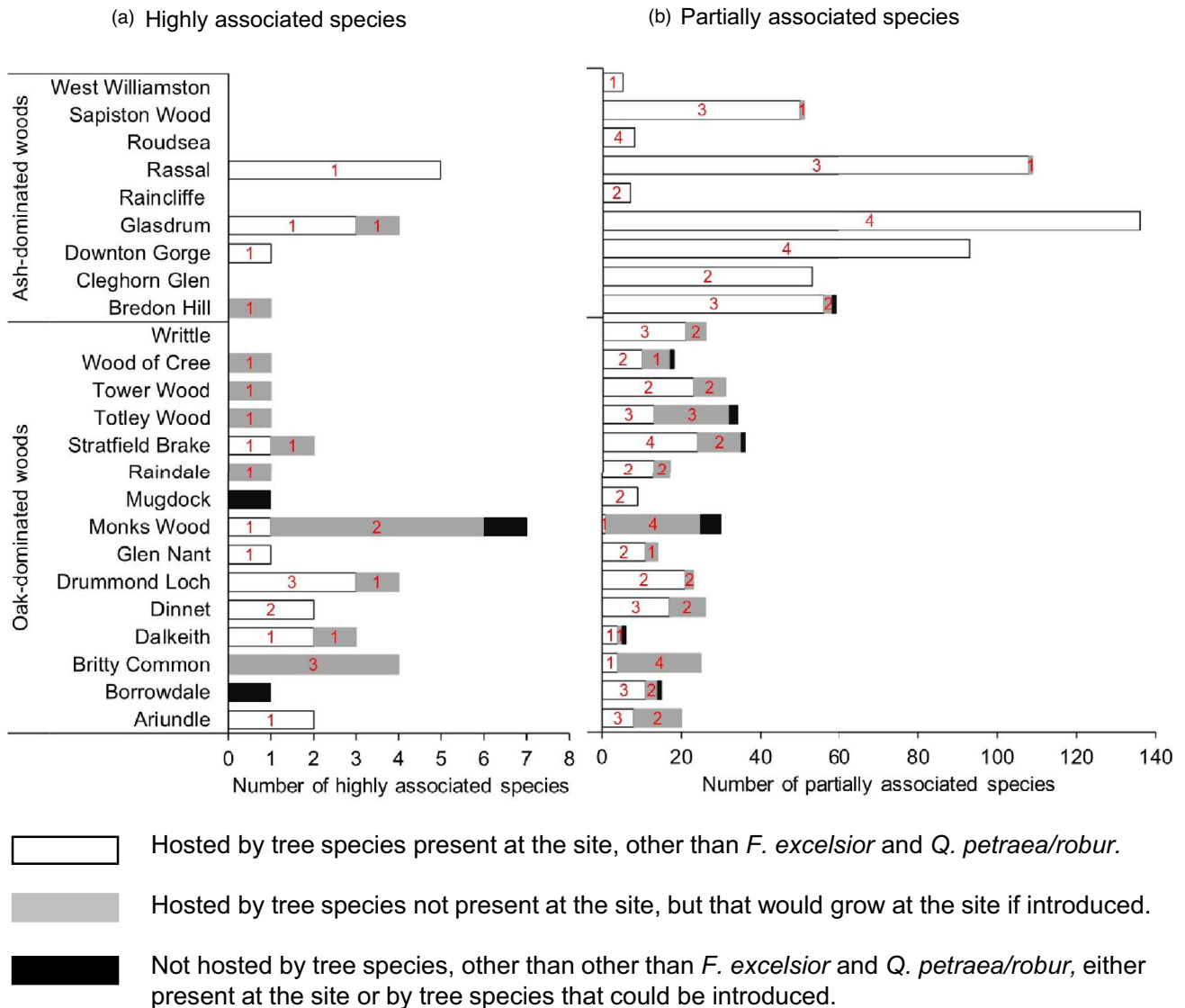

FIGURE 4 Number of species recorded at 24 mixed ash/oak woodlands in the United Kingdom that use *Fraxinus excelsior* and *Quercus petraea/robur* and other tree species (Fe&Qpr&others) and their level of association with *F. excelsior* at ash-dominated sites and *Q. petraea/robur* at oak-dominated sites. Highly associated = species rarely uses tree species other than *F. excelsior* or *Q. petraea/robur*. Partially associated = uses *F. excelsior* or *Q. petraea/robur* more frequently than its availability in the landscape. Cosmopolitan = uses *F. excelsior* or *Q. petraea/robur* as frequently or lower than their availability

4 | DISCUSSION

This study has shown that the total number of associated species at risk of extirpation from plant diseases affecting two sympatric hosts is greater than the sum of the associated species at risk from a decline in either host alone. This cumulative impact puts many hundreds of associated species at risk of extirpation, most of which are not currently rare or already viewed as directly threatened. Our work also shows that the biodiversity impacts of plant diseases on associated species cannot be fully assessed unless the functional

FIGURE 5 Functional redundancy of 24 mixed ash/oak woodlands in the United Kingdom to support ash- and oak-associated species if *Fraxinus excelsior* and *Quercus petraea/robur* were lost from the site. (a) Highly associated species and (b) Partially associated species. Data for each site show total number of associated species recorded at the site that use *F. excelsior* and *Q. petraea/robur* and other tree species (Fe&Qpr&others) and are subdivided according to whether the associated species are (i) supported by tree species, other than *F. excelsior* and *Q. petraea/robur*, currently present at the site (white part of bar), (ii) supported by tree species that are not currently present at the site but that would grow at the site if introduced (grey part of bar) or (iii) is not hosted by trees in either of the previous categories (black part of bar). The red number in the white and grey parts of the bar indicates the number of tree species involved

redundancy, or lack of, within the ecosystem affected is considered. Yet risk assessments generally do not take the impact of plant disease on associated biodiversity into account, nor do they account for these cumulative impacts. We have illustrated how this can be done at both national and site levels.

4.1 | Impact on biodiversity crisis

The direct effects of non-native plant pests and pathogens on biodiversity are already acknowledged as a major driver of biodiversity loss (IPBES, 2019). However, the indirect effects via declines

in species associated with the infected host plant are less widely acknowledged despite the growing body of evidence documenting such declines (Rabenold et al., 1998; Tingley et al., 2002; e.g. Cleavitt et al., 2008; Lõhmus & Runnel, 2014; Lubek et al., 2020). Our work is unique in that it considers the cumulative impact on biodiversity of plant pests/pathogens affecting sympatric plants, showing that the loss of two tree species is greater than sum of the associated species at risk from a decline in either host alone. As the spread of non-native tree diseases is increasing exponentially (Freer-Smith & Webber, 2017), this cumulative impact on associated biodiversity is an often overlooked driver of biodiversity loss (Jonsson & Thor, 2012).

Obligate species and species with a limited range of hosts (in this example species classed as obligate-Fe/Qpr and Fe&Qpr-only) will, by definition, be at greater risk of decline if their hosts decline. However, the site-level CIAs showed that due to a lack of functional redundancy, the impacts of a decline in just two tree species cascaded far beyond the 512 species listed as only occurring on *F. excelsior* and/or *Q. petraea/robur*. Species that should be resilient to a loss of *F. excelsior* and *Q. petraea/robur* as they could be hosted by other tree species (Fe&Qpr&others) were shown at a site level not to be resilient as the alternative hosts were absent. Only five of the 24 woods (21%) were able to provide functional redundancy for all the highly and partially associated species (Fe&Qpr&others) that are currently present. In most woodlands, the tree species required to provide full functional redundancy were not present, although the site conditions were often suitable for them to grow.

Our work provides support for a major theme in recent guidance on sustainable forestry, which advocates that species diversity of multipurpose and conservation woodlands should be increased to enhance their resilience (Barsoum et al., 2016; Forestry Commission, 2017; Bellamy et al., 2018). Previous land use (Pyles et al., 2020) and management (Bricca et al., 2020) have been shown to influence functional redundancy and hence resilience in other forests habitats. Reversing the decline in tree species diversity that has occurred in many European forests due to historical management (Ostlund et al., 1997; Paillet et al., 2010; Svenning & Skov, 2005; Urbieta et al., 2008) would increase functional redundancy and resilience. This in turn would limit the cascading impacts of plant diseases on biodiversity, ultimately helping to mitigate the biodiversity crisis.

If diversification of native woods is required, should this be limited to establishment of native species? Global guidelines for the sustainable use of non-native trees focussed on the risk of tree invasion (Brundu et al., 2020). A review of the wider benefits and dis-benefits of non-native trees (Ennos et al., 2019) concluded that 'the use of non-natives is likely to lead to an increase rather than a decrease in pest and disease problems, and to hinder rather than support the retention of threatened native tree species and their associated biodiversity'. However, this conclusion may vary at the site level, depending on the conservation status and national and global distribution of the associated species at risk. At some of the sites in this study, some associated species could only be supported by non-native trees (Appendix S1, Tables S3–S6), and the value of non-native but naturalized trees to act as alternative hosts has been shown by Mitchell, Beaton, Bellamy, et al. (2014).

4.2 | Relevance to risk assessments

In the context of the current biodiversity crisis (IPBES, 2019), current plant pest/pathogen risk assessment approaches (e.g. Defra, 2021; Spence, 2020) that ignore the cumulative, cascading effects shown in this study may allow an insidious, mostly overlooked, driver of biodiversity loss to continue. Risk assessments generally take account of likelihood of pest entry, establishment, spread and impact (MacLeod & Lloyd, 2020). However, the impact assessment is usually confined to the impact on the host(s) and consideration of impacts on the wider environment is limited to the risk of the disease spreading from commercial crops to native host plant species. The impact assessment does not include assessment of the impact on associated biodiversity which, as shown in this study, can include many hundreds of species. The European Food Safety Authority did consider including endangered species in their risk assessments, but they found a lack of effect and exposure data for the majority of endangered species (More et al., 2016). Here we show that the majority of species at risk are not currently rare or endangered, or on any conservation priority list.

Based on our study, we argue that plant pest/pathogen impact assessments should not only include the impact on associated biodiversity but also include the cumulative impact on associated biodiversity of multiple pest/pathogens on sympatric hosts and an assessment as to whether there is functional redundancy within the system. If the pest/pathogen is hosted by plants occurring in ecosystems where other foundation plant species are already impacted by disease, the pest/pathogen should be given a higher impact rating within risk assessments as the functional redundancy within the system may have already declined. In the example used here, *F. excelsior* is already declining due to the non-native fungus *Hymenoscyphus fraxineus*, therefore, risk assessments for diseases that affect *Q. petraea/robur*, such as *Xylella fastidiosa* (Defra, 2021), should take account of the cumulative impact this pest would have on associated biodiversity, in addition to the decline in *F. excelsior*.

We acknowledge that our study does not provide a complete assessment of either biodiversity loss or functional redundancy. With respect to biodiversity loss, the species data at each site will not be complete and our assessments do not account for changes in the interactions between species (e.g. parasite/pests or predator/prey) that may occur during host decline, driving further changes in species abundances. The declines in *F. excelsior* and *Q. petraea/robur* will vary both spatially and temporally, therefore extirpations of a species do not imply immediate UK wide extinctions but rather a continuing loss of diversity and abundance. With respect to functional redundancy, the presence of a particular tree species does not automatically mean it will be a suitable host tree as it may not be the correct age (Mitchell et al., 2019a), occur in the right micro-climate (Ellis et al., 2015) or be located close enough to current hosts to achieve successful colonization (Williams & Ellis, 2018). In addition, there may be other host plants beyond those tree species assessed here, such as shrubs, which may also provide functional redundancy, and the suitability of some alternative hosts to support ash- or oak-associated species is unknown (Mitchell et al., 2016). Finally, this study takes a precautionary approach in defining risk by assuming that the associated species will not adapt to new hosts, as the plasticity of most of the associated

species is unknown. However, this study does provide an example of the type of assessment that can be done using the data available, and highlights for the first time that the cumulative risks to biodiversity of multiple plant diseases is greater than the sum of individual diseases.

4.3 | Bringing ecological theory and risk assessment methodology together

This study provides the first example of the need to bring the concept of CIAs, currently used widely in Environmental Impact Assessments (e.g. Masden et al., 2010), together with ecological theory on functional redundancy. While functional redundancy is often modelled (e.g. Borrvall et al., 2000; Kaneryd et al., 2012), it is rarely measured empirically, due to the difficulty of assessing individual species' contributions (but see Pillar et al., 2013). We show the importance of understanding whether functional redundancy is present to provide a more accurate assessment of the cascading impacts of plant diseases on biodiversity, and hence their contribution to the biodiversity crisis. While the example focused on *F. excelsior* and *Q. petraea/robur* within the United Kingdom, the concepts and need for plant health risk assessments to include this type of analysis are relevant globally. In addition, this type of analysis is relevant to assessing the impact of other drivers, such as climate change, where two foundation species are both expected to decline in the future climatic conditions.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

R.J.M. conceived the idea, did the analysis and drafted the manuscript; P.E.B., C.J.E., G.R.I., N.A.L., S.N., G.P., J.A.S. and A.F.S.T. collated data on species use of ash and oak; A.B., R.L.H., R.J.M., D.R. and V.S. were involved in site assessments. All authors commented on the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data are publicly available. The AshEcol database is available at http://publications.naturalengland.org.uk/publication/5273931279761408, the OakEcol database is available at https://doi.org/10.5285/22b3d41e-7c35-4c51-9e55-0f47bb845202 and species data from the sites were downloaded from National Biodiversity Network Gateway, https://nbn.org.uk/the-national-biodiversity-network/archive-information/nbn-gateway/. The species data from the sites together with information about their level of association with *Fraxinus excelsior* and *Quercus petraea/robur* are presented in Appendix S2.

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