

Scotland's Rural College

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

Mitchell, Ruth J; Bellamy, Paul E; Broome, Alice; Ellis, Chris J; Hewison, Richard L; Iason, Glen R; Littlewood, Nick A; Newey, Scott; Pozsgai, Gabor; Ray, Duncan; Stockan, Jenni A; Stokes, Victoria; Taylor, Andy FS

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31 **Abstract**

- 32 1. Non-native plant pests and pathogens are increasing exponentially, causing extirpation of  
33 foundation species. The impact of large-scale declines in a single host on associated  
34 biodiversity is widely documented. However, the impact of multiple host loss on  
35 biodiversity and whether these impacts are multiplicative has not been assessed.  
36 Ecological theory suggests that systems with greater functional redundancy (alternative  
37 hosts) will be more resilient to loss of sympatric hosts. We test this theory and show its  
38 importance in relation to pest/pathogen impact assessments.
- 39 2. We assessed the potential impact on biodiversity of the loss of two widely occurring  
40 sympatric European tree species, *Fraxinus excelsior* and *Quercus petraea/robur*, both of  
41 which are currently threatened by a range of pests and pathogens.
- 42 3. At the UK scale, the total number of associated species at risk of extirpation from plant  
43 diseases affecting these two sympatric hosts is greater than the sum of the associated  
44 species at risk from decline of either host alone. *F. excelsior* hosts 45 obligate species  
45 (species only found on that host) and *Q. petraea/robur* 326. However, a decline in both  
46 these trees would impact 512 associated species, across multiple taxon groups, a 38%  
47 increase. Assessments at a local scale, 24 mixed *F. excelsior*-*Q. petraea/robur* woodlands,  
48 revealed that these impacts may be even greater due to a lack of functional redundancy.  
49 Only 21% of sites were able to provide functional redundancy for *F. excelsior* and *Q.*  
50 *petraea/robur* associated species which can use other tree species. In most woodlands,  
51 the tree species required to provide functional redundancy were not present, although  
52 the site conditions were often suitable for them to grow.
- 53 4. *Synthesis*: Ecological understanding of functional redundancy should be applied to  
54 assessments of pests/pathogens impact on biodiversity. In risk assessments, higher  
55 impact scores should be given to pests/pathogens affecting hosts occurring with other  
56 host plant species already impacted by pest/pathogens. Current pest/pathogen risk  
57 assessment approaches that ignore the cumulative, cascading effects shown in this study  
58 may allow an insidious, mostly overlooked, driver of biodiversity loss to continue.

59 Keywords Biodiversity loss, Cumulative impact assessment, Forest, Functional redundancy,  
60 Pathogen, Pest, Resilience, Risk assessment.

Accepted Article

## 61 INTRODUCTION

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

71 Many temperate-zone forests, which are typically dominated by a few foundation tree species,  
72 provide examples of ecosystems with low functional redundancy (Ellison *et al.* 2005). These  
73 forests are currently experiencing an exponential increase in non-native tree pests/pathogens  
74 due to increased global trade and climate change (Freer-Smith & Webber 2017) causing  
75 substantial ecological damage and economic loss (Boyd *et al.* 2013; Roy *et al.* 2014; Hill *et al.*  
76 2019). Governments and their agencies are therefore horizon scanning and developing risk  
77 assessments of potential threats, for example, the European Food Safety Authority (Jeger *et al.*  
78 2012), the US Animal and Plant Health Inspection Service (USDA 2021), and the UK Plant Health  
79 Risk Register (Spence 2020; Defra 2021). Such risk assessments include likelihood of  
80 pest/pathogen entry, establishment, spread and impact on tree hosts (MacLeod & Lloyd 2020).

81 However, plant pest/pathogen risk assessments do not assess the potential impact of the  
82 pest/pathogen as a driver of wider biodiversity loss and their possible role in the current  
83 biodiversity crisis. Current risk assessment approaches potentially miss three important  
84 elements. First, they do not consider the cascading impacts of tree loss on associated  
85 biodiversity, species that use the tree for feeding, either directly, or indirectly (eating other  
86 organisms found on the tree), or as habitat for living in, (i.e.: lichens/bryophytes), or for  
87 breeding/roosting in (i.e.: birds and bats) (Mitchell *et al.* 2014a). Second, the risk assessments do  
88 not include cumulative impacts, defined as the effect on biodiversity of a decline in more than  
89 one tree species within the same site or forest stand. If sympatric tree species decline, there may

90 be cumulative impacts that cascade beyond obligate species (species requiring one tree species  
91 for their survival) to associated species that may be shared between affected tree species. Third,  
92 it is assumed there is functional redundancy i.e.: that for all, but obligate species, it is assumed  
93 that the associated species could survive using alternative hosts. However, if functional  
94 redundancy is not present at an appropriate scale to support the associated species (e.g., within  
95 a site or forest stand), then the impact of tree species loss will cascade far beyond obligate  
96 species, resulting in large declines in populations, and potentially extirpations, of other  
97 associated species. There is a growing body of evidence addressing the first point, indicating that  
98 a decline in one foundation tree species may impact on many hundreds of associated species  
99 (Gandhi & Herms 2010a; Gandhi & Herms 2010b; Ellis *et al.* 2012; Löhmus & Runnel 2014;  
100 Mitchell *et al.* 2019a; Hultberg *et al.* 2020; Lubek *et al.* 2020). However, the cumulative impact on  
101 biodiversity of plant pest/pathogens affecting sympatric tree species, and whether a lack of  
102 functional redundancy within the ecosystem will exacerbate these impacts (points two and three  
103 above) have not previously been studied.

104 Although cumulative impact assessments (CIA) of the risk of multiple diseases on a single tree  
105 species have been proposed (Davies *et al.* 2017), we argue the need for assessments of the  
106 cumulative impacts of diseases on associated biodiversity that occur on different trees within the  
107 same ecosystem. This would be more analogous to CIA within Environmental Impact  
108 Assessments conducted ahead of major infrastructure projects (Masden *et al.* 2010). Individually  
109 a decline in any one tree species due to disease, may have minor effects on biodiversity, but  
110 collectively these may be significant, potentially greater than the sum of the individual diseases  
111 acting alone. To provide a real-world context for our argument about the need for CIA we focus  
112 on the impacts of a loss of *Fraxinus excelsior* (European ash) and the *Quercus petraea*/*Q. robur*  
113 complex (sessile oak/pedunculate oak), two of the most common native trees in the UK (Rodwell  
114 1991), and sympatric species across much of Europe, although the principles are applicable to  
115 diseases impacting any foundation species.

116 *F. excelsior* is currently declining across Europe due to the non-native ascomycete  
117 *Hymenoscyphus fraxineus* (Kjær *et al.* 2012). Also, *F. excelsior* is threatened by the non-native  
118 Emerald ash borer beetle *Agrilus planipennis*, that has killed millions of *Fraxinus* sp. trees in the

119 USA (Herms & McCullough 2014), and has spread across the Eurasian landmass as far west as  
120 Ukraine (Orlova-Bienkowskaja *et al.* 2020). *Q. petraea/robur* are currently at risk from the non-  
121 native pest, Oak Processionary Moth (Tomlinson *et al.* 2015), Acute Oak Decline, caused by a  
122 native insect and bacteria (Doonan *et al.* 2020), exacerbated by climate change (Brown *et al.*  
123 2018), as well as a variety of non-native powdery mildews (Lonsdale 2015). In addition *Q.*  
124 *petraea/robur* would be a risk of decline due to *Xylella fastidiosa* if this bacterium established in  
125 the UK (Defra 2021).

126 Recent work in the UK has produced lists of the species associated with *F. excelsior* termed ash-  
127 associated species (Mitchell *et al.* 2014b) and *Q. petraea/robur* termed oak-associated species  
128 (Mitchell *et al.* 2019b; Mitchell *et al.* 2019c). When the alternative hosts to support the ash-  
129 associated biodiversity was assessed, *Q. petraea/robur* was identified as a good replacement for  
130 *F. excelsior* supporting 69% of the 955 ash-associated species, a higher proportion than 47 other  
131 potential hosts assessed (Mitchell *et al.* 2014a; Mitchell *et al.* 2014c). Similar work for *Q.*  
132 *petraea/robur* identified *F. excelsior* as a good replacement supporting 28% of the 2300 oak-  
133 associated species (the greatest proportion for any of the 30 tree species assessed) (Mitchell *et*  
134 *al.* 2019a).

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

## 141 **METHOD**

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



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

149

150 The databases

151 The AshEcol database (Mitchell *et al.* 2014b) lists whether each of the 955 ash-associated species  
152 (12 birds, 58 bryophytes, 68 fungi, 241 invertebrates, 548 lichens, 28 mammals; Mitchell *et al.*  
153 2014a; Mitchell *et al.* 2014c) will use any of 48 alternative tree species, while the OakEcol  
154 database (Mitchell *et al.* 2019b) lists whether each of the 2300 oak-associated species (38 birds,  
155 229 bryophytes, 108 fungi, 1178 invertebrates, 716 lichens, 31 mammals; Mitchell *et al.* 2019a)  
156 will use any of 30 alternative tree species (Supporting Information Appendix S1). Although there  
157 is considerable overlap in the alternative tree species for which an assessment is made, these  
158 lists are not identical because *F. excelsior* grows on a greater range of soil types than *Q.*  
159 *petraea/robur* (Pyatt *et al.* 2001), resulting in a greater range of potential replacement tree  
160 species for *F. excelsior* depending on soil type (see Appendix S1, Table S1 in Supporting  
161 Information). In each case the alternative tree species selected for assessment were those that  
162 are either currently occurring in *F. excelsior* or *Quercus* woodlands (Rodwell 1991), or non-native  
163 species which are known to grow in the same climatic/soil conditions in which *F. excelsior* or *Q.*  
164 *petraea/robur* currently grow (Pyatt, Ray & Fletcher 2001). The methods used to collate the ash-  
165 and oak-associated species lists, and to assess if these species will use each alternative tree  
166 species, are described in detail in Mitchell *et al.* (2014a) and Mitchell *et al.* (2019a), respectively.  
167 Throughout the assessments below it is noted that the number of species involved is an under-  
168 estimate, as neither database includes algae, bacteria, or other micro-organisms, nor do they  
169 include a complete list of all the associated fungi, only concentrating on those known fungal  
170 species with the strongest association with either *F. excelsior* or *Q. petraea/robur*.

171 Cumulative assessments at the national level

172 The databases were queried to identify the number of species known i) to be obligate on either  
173 *F. excelsior* or *Q. petraea/robur* (obligate-Fe/Qpr), ii) to only use *F. excelsior* and *Q. petraea/robur*  
174 (Fe&Qpr-only), iii) to use *F. excelsior* and *Q. petraea/robur* and other tree species

175 (Fe&Qpr&others). Combining the obligate-Fe/Qpr and Fe&Qpr-only lists, provides a cumulative  
176 impact assessment of the species at risk of extirpation if both *F. excelsior* and *Q. petraea/robur*  
177 decline.

178 An assessment of the increased impact of losses of both tree species make to the biodiversity  
179 crisis was made by assessing which of the species identified as 'at risk' in the cumulative impact  
180 assessment (those in the obligate-Fe/Qpr and Fe&Qpr-only lists) do not already have some form  
181 of conservation protection within the UK. The definition of conservation protection differed  
182 between taxonomic groups (as no method is systematically used across taxa) but included (i)  
183 whether the species is listed using IUCN criteria as endangered, vulnerable, or near threatened,  
184 (ii) is listed in the relevant UK Red Data book, or (iii) is a UK Biodiversity Action Plan species or (iv)  
185 a bird species listed as red or amber on the UK Birds of Conservation Concern list, see Mitchell *et*  
186 *al.* (2019a) for further details.

187 Cumulative assessments at the site level

188 Nine *F. excelsior*-dominated woodlands that also contain *Q. petraea/robur*, (termed ash-  
189 dominated woods throughout) and 15 *Q. petraea/robur*-dominated woodlands that also contain  
190 *F. excelsior*, (termed oak-dominated woods throughout) were selected to be representative of  
191 either ash- or oak-dominated woodlands across Britain, where the conservation of biodiversity  
192 was a management priority (Fig.1). Sites were therefore primarily, but not always, nature  
193 reserves, or had some other form of protection (e.g. Sites of Special Scientific Interest (SSSIs) or  
194 Special Area of Conservation (SACs)).

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

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

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

## 223 RESULTS

224 Decline of both *F. excelsior* and *Q. petraea/robur* in the UK would result in more species being at  
225 risk than just the sum of their obligate species. There are 45 obligate ash-associated species (11  
226 fungi, 30 invertebrates, 4 lichens) and 326 obligate oak-associated species (57 fungi, 257  
227 invertebrates, 12 lichens) giving a total of 371 (obligate-Fe/Qpr). However, the cumulative impact  
228 assessment shows 512 species would be impacted due to an additional 141 species (13  
229 bryophytes, 42 invertebrates, 86 lichens) that are not known to use trees other than *Q.*  
230 *petraea/robur* and *F. excelsior* (Fe&Qpr-only, Fig. 2). Of the 512 species threatened by the loss of

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

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

240 Site level cumulative impacts and assessments of functional redundancy

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

260 All sites had species that were partially associated with *F. excelsior* or *Q. petraea/robur* (range 7-  
261 137) (Fig. 4, Appendix S1 - Tables S4 and S6, Appendix S2). Only seven (29%) of the 24 sites, (six  
262 ash-dominated woods, and one oak-dominated wood) had full functional redundancy, i.e., had  
263 tree species present that would support all the partially associated species (Fig. 5b). Most sites  
264 (17 of the 24 sites, 71%) had limited functional redundancy with tree species present that would  
265 support some but not all the species present (Fig. 5b). Nine (53%) of the 17 sites with limited  
266 functional redundancy had the potential to have full functional redundancy if additional tree  
267 species were established. The functional redundancy at the other eight sites could be increased  
268 by establishing additional tree species, but full functional redundancy was not possible as the  
269 tree species required to support these partially associated species would not grow at these sites  
270 (Fig. 5b).

271 For the highly associated species there was no significant relationship between the number of  
272 tree species present at the site, in addition to *F. excelsior* and *Q. petraea/robur*, and the number  
273 of highly associated species supported ( $\chi^2(1, N=18) = 2.35 p>0.05$ , Appendix S1 - Fig. S1a).  
274 However, there was a significant relationship between the number of tree species present at the  
275 site, in addition to *F. excelsior* and *Q. petraea/robur*, and the number of partially associated  
276 species supported ( $\chi^2(1, N=24) = 59 p<0.0001$ , Appendix S1 - Fig. S1b). There was also a  
277 significant difference between the two woodlands types ( $\chi^2(1, N=24) = 11.88 p<0.0001$ ) but no  
278 interaction between woodland type and number of tree species for partially associated species.

## 279 **DISCUSSION**

280 This study has shown that the total number of associated species at risk of extirpation from plant  
281 diseases affecting two sympatric hosts is greater than the sum of the associated species at risk  
282 from decline of either host alone. This cumulative impact puts many hundreds of associated  
283 species at risk of extirpation, most of which are not currently rare or already viewed as directly  
284 threatened. Our work also shows that the biodiversity impacts of plant diseases on associated  
285 species cannot be fully assessed unless the functional redundancy, or lack of, within the  
286 ecosystem affected is considered. Yet risk assessments generally do not take the impact of plant  
287 disease on associated biodiversity into account, nor do they account for these cumulative  
288 impacts. We have illustrated how this can be done at both a national and site level.

289 **Impact on biodiversity crisis**

290 The direct effects of non-native plant pests and pathogens on biodiversity are already  
291 acknowledged as a major driver of biodiversity loss (IPBES 2019). However, the indirect effects  
292 via declines in species associated with the infected host plant are less widely acknowledged  
293 despite the growing body of evidence documenting such declines (Rabenold *et al.* 1998; Tingley  
294 *et al.* 2002; e.g. Cleavitt *et al.* 2008; Löhmus & Runnel 2014; Lubek *et al.* 2020). Our work is  
295 unique in that it considers the cumulative impact on biodiversity of plant pest/pathogens  
296 affecting sympatric plants, showing that the loss of two tree species is greater than sum of the  
297 associated species at risk from decline of either host alone. As the spread of non-native tree  
298 diseases is increasing exponentially (Freer-Smith & Webber 2017), this cumulative impact on  
299 associated biodiversity is an often overlooked driver of biodiversity loss (Jonsson & Thor 2012).

300 Obligate species and species with a limited range of hosts (in this example species classed as  
301 obligate-Fe/Qpr and Fe&Qpr-only) will, by definition, be at greater risk of decline if their hosts  
302 decline. However, the site level cumulative impact assessments showed that due to a lack of  
303 functional redundancy the impacts of a decline in just two tree species cascaded far beyond the  
304 512 species listed as only occurring on *F. excelsior* and/or *Q. petraea/robur*. Species that should  
305 be resilient to a loss of *F. excelsior* and *Q. petraea/robur* as they could be hosted by other tree  
306 species (Fe&Qpr&others) were shown at a site level not to be resilient as the alternative hosts  
307 were absent. Only 5 of the 24 woods (21%) were able to provide functional redundancy for all  
308 the highly and partially associated species (Fe&Qpr&others) that are currently present. In most  
309 woodlands, the tree species required to provide full functional redundancy were not present,  
310 although the site conditions were often suitable for them to grow.

311 Our work provides support for a major theme in recent guidance on sustainable forestry, which  
312 advocates that species diversity of multipurpose and conservation woodlands should be  
313 increased to enhance their resilience (Barsoum *et al.* 2016; Forestry Commission 2017; Bellamy  
314 *et al.* 2018). Previous land use (Pyles *et al.* 2020) and management (Bricca *et al.* 2020) have been  
315 shown to influence functional redundancy and hence resilience in other forests habitats.

316 Reversing the decline in tree species diversity that has occurred in many European forests due to  
317 historical management (Ostlund *et al.* 1997; Svenning & Skov 2005; Urbieta *et al.* 2008; Paillet *et*

318 *al.* 2010) would increase functional redundancy and resilience. This in turn would limit the  
319 cascading impacts of plant diseases on biodiversity, ultimately helping to mitigate the  
320 biodiversity crisis.

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

### 331 **Relevance to risk assessments**

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

345 Based on our study, we argue that plant pest/pathogen impact assessments should not only  
346 include the impact on associated biodiversity but also the cumulative impact on associated

347 biodiversity of multiple pest/pathogens on sympatric hosts and an assessment as to whether  
348 there is functional redundancy within the system. If the pest/pathogen is hosted by plants  
349 occurring in ecosystems where other foundation plant species are already impacted by disease,  
350 the pest/pathogen should be given a higher impact rating within risk assessments as the  
351 functional redundancy within the system may have already declined. In the example used here,  
352 *F. excelsior* is already declining due to the non-native fungus *Hymenoscyphus fraxineus*,  
353 therefore, risk assessments for diseases that affect *Q. petraea/robur*, such as *Xylella fastidiosa*  
354 (Defra 2021), should take account of the cumulative impact this pest would have on associated  
355 biodiversity, in addition to the decline in *F. excelsior*.

356 We acknowledge that our study does not provide a complete assessment of either biodiversity  
357 loss or functional redundancy. With respect to biodiversity loss the species data at each site will  
358 not be complete and our assessments do not account for changes in the interactions between  
359 species (e.g. parasite/pests or predator/prey) that may occur during host decline, driving further  
360 changes in species abundances. The declines in *F. excelsior* and *Q. petraea/robur* will vary both  
361 spatially and temporally, therefore extirpations of a species do not imply immediate UK wide  
362 extinctions but rather a continuing loss of diversity and abundance. With respect to functional  
363 redundancy, the presence of a particular tree species doesn't automatically mean it will be a  
364 suitable host tree as it may not be the correct age (Mitchell *et al.* 2019a), occur in the right  
365 micro-climate (Ellis *et al.* 2015), or be located close enough to current hosts to achieve successful  
366 colonization (Williams & Ellis 2018). In addition there may be other host plants beyond those tree  
367 species assessed here, such as shrubs, which may also provide functional redundancy and the  
368 suitability of some alternative hosts to support ash- or oak-associated species is unknown  
369 (Mitchell *et al.* 2016). Finally, this study takes a precautionary approach in defining risk by  
370 assuming that the associated species will not adapt to new hosts, as the plasticity of most of the  
371 associated species is unknown. However, this study, does provide an example of the type of  
372 assessment that can be done using the data available, and highlights for the first time that the  
373 cumulative risks to biodiversity of multiple plant diseases is greater than the sum of individual  
374 diseases.

### 375 **Bringing ecological theory and risk assessment methodology together**



376 This study provides the first example of the need to bring the concept of cumulative impact  
377 assessments, currently used widely in Environmental Impact Assessments (e.g. Masden *et al.*  
378 2010), together with ecological theory on functional redundancy. While functional redundancy is  
379 often modelled (e.g. Borrvall *et al.* 2000; Kaneryd *et al.* 2012), it is rarely measured empirically,  
380 due to the difficulty of assessing individual species' contributions (but see Pillar *et al.* 2013). We  
381 show the importance of understanding whether functional redundancy is present to provide a  
382 more accurate assessment of the cascading impacts of plant diseases on biodiversity, and hence  
383 their contribution to the biodiversity crisis. While the example focused on *F. excelsior* and *Q.*  
384 *petraea/robur* within the UK, the concepts and need for plant health risk assessments to include  
385 this type of analysis is relevant globally. In addition, this type of analysis is relevant to assessing  
386 the impact of other drivers, such as climate change, where two foundation species are both  
387 expected to decline in future climatic conditions.

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397 **AUTHOR CONTRIBUTION STATEMENT:** RJM conceived the idea, did the analysis and drafted the  
398 manuscript. PB, CJE, GRI, NAL, SN, GP, JAS, and AFST collated data on species use of ash and oak.  
399 AB, RLH, RJM, DR, and VS were involved in site assessments. All authors commented on the  
400 manuscript.

401

402 **DATA AVAILABILITY:** All data is publicly available. The AshEcol database is available at  
403 <http://publications.naturalengland.org.uk/publication/5273931279761408>, the OakEcol

404 database is available at <https://doi.org/10.5285/22b3d41e-7c35-4c51-9e55-0f47bb845202> and  
405 species data from the sites was downloaded from National Biodiversity Network Gateway,  
406 <https://nbn.org.uk/the-national-biodiversity-network/archive-information/nbn-gateway/>. The  
407 species data from the sites together with information about their level of association with  
408 *Fraxinus excelsior* and *Quercus petraea/robur* is presented in Appendix S2.

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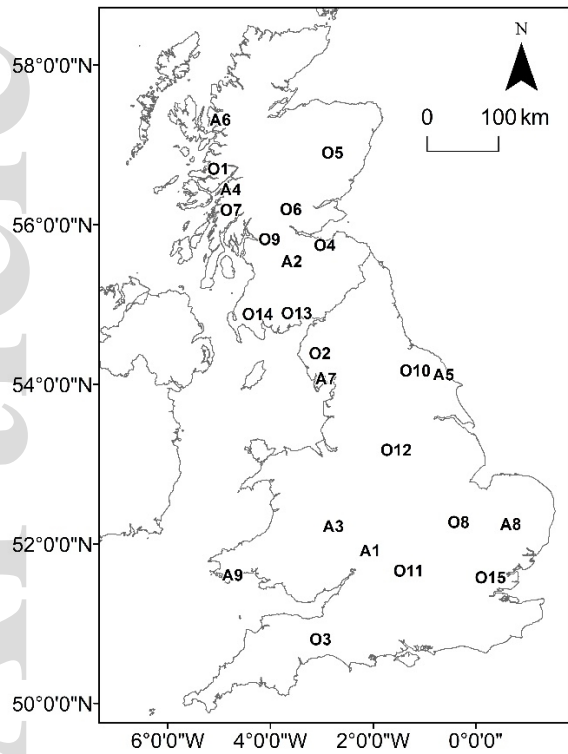


Fig 1: Site locations. A = *Fraxinus excelsior* dominated woodlands with *Quercus petraea/robur* present, O = *Q. petraea/robur* dominated woodlands with *F. excelsior* present. A1 = Bredon hill; A2 = Cleghorn Glen; A3 = Downton George; A4 = Glasdrum; A5 = Raincliffe and Forge Valley; A6 = Rassal; A7 = 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 = Totlely Wood; O13 = Tower Wood; O14 = Wood of Cree; O15 = Writtle.

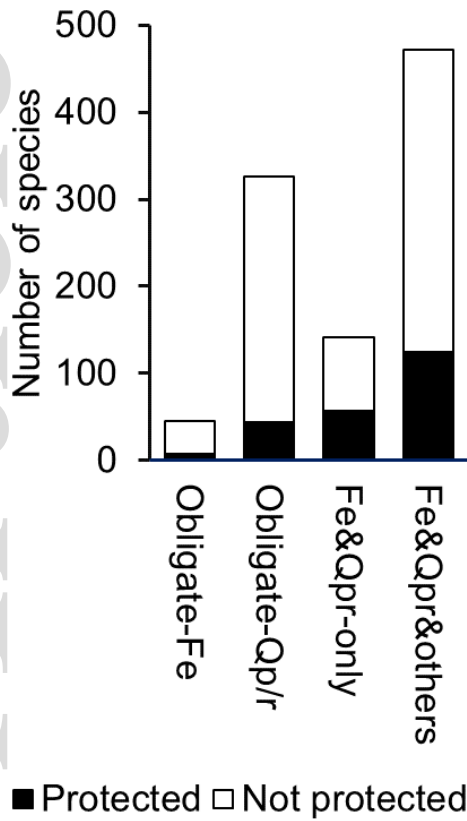
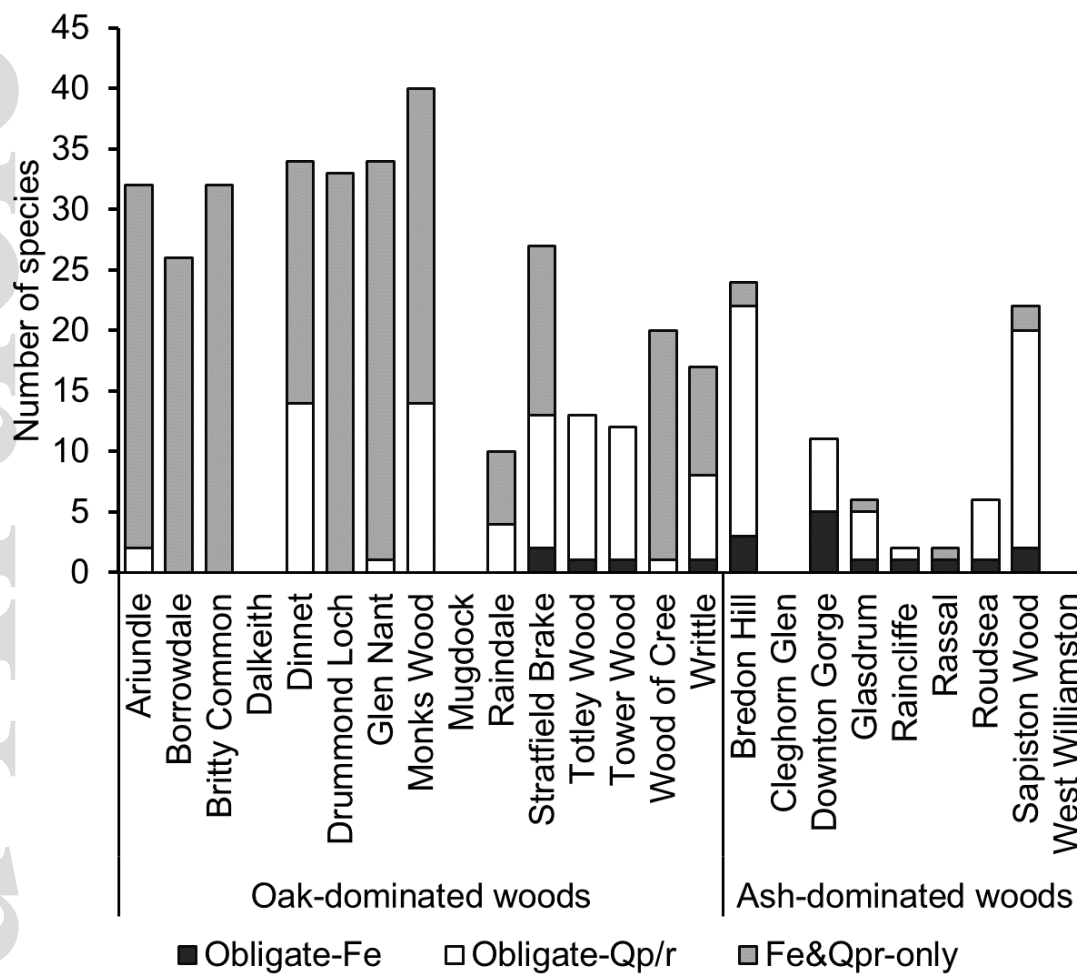
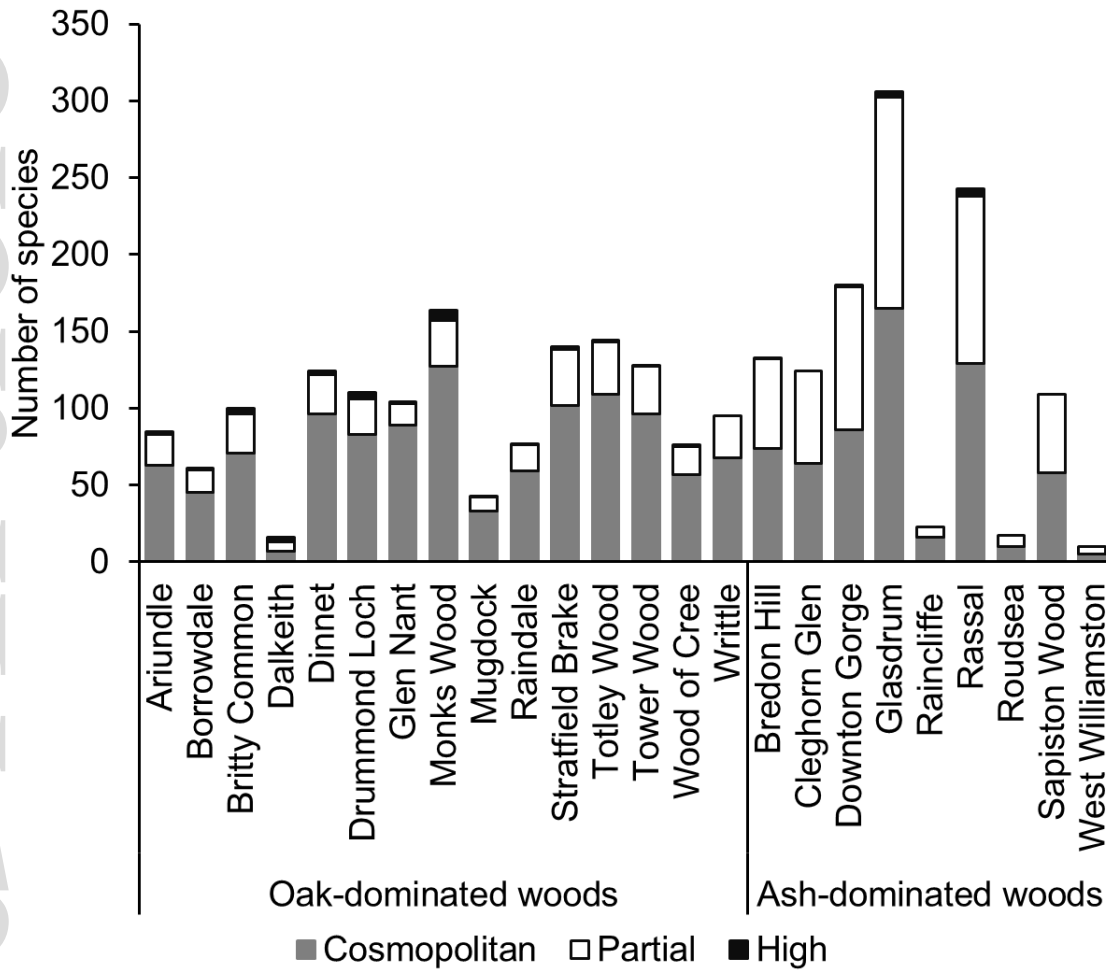


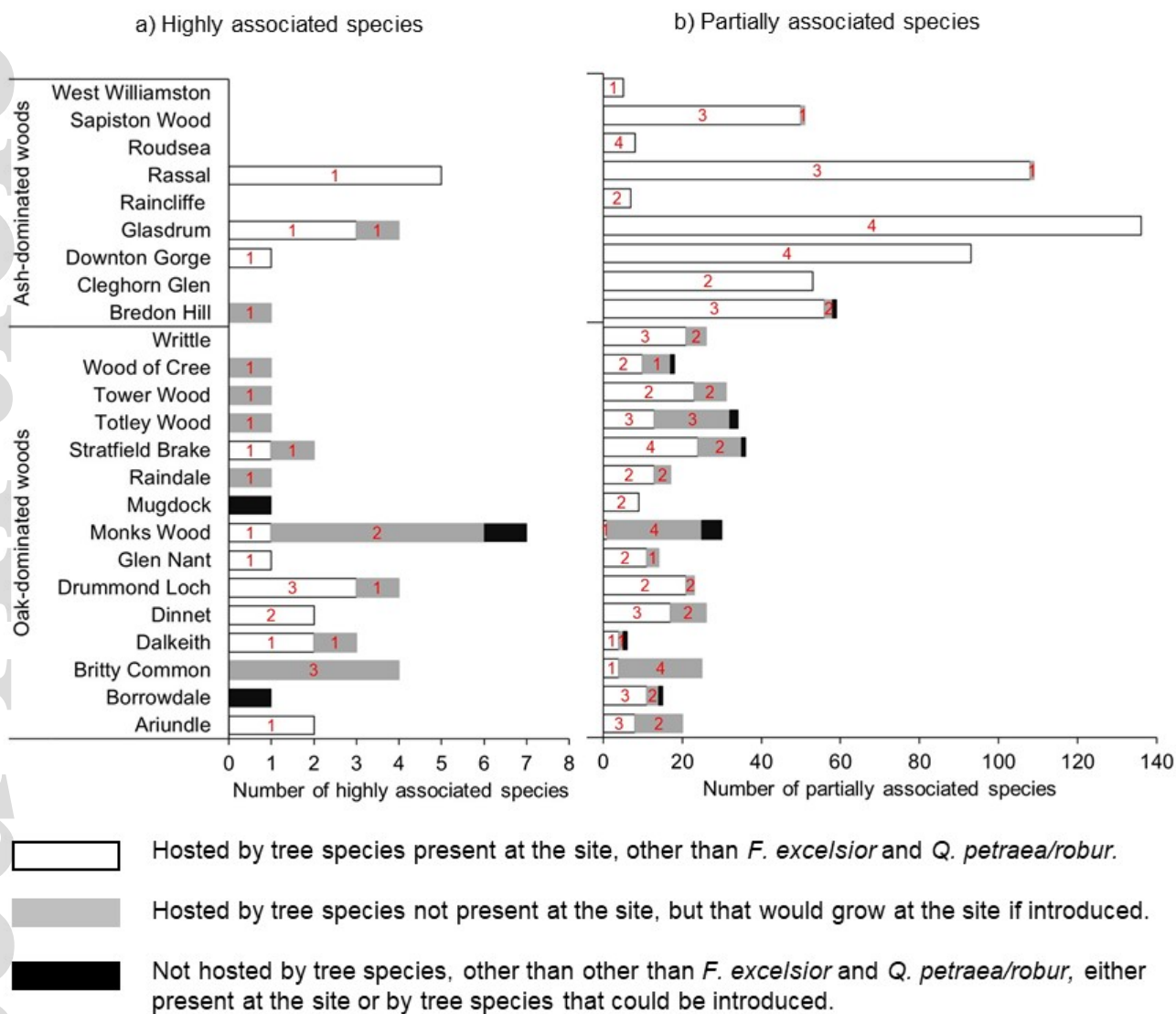
Fig. 2 Number of species that are obligate on *Fraxinus excelsior* (Fe) and *Quercus petraea/robur* (Qp/r), only use *F. excelsior* and *Q. petraea/robur* (Fe&Qpr-only) or use *F. excelsior* and *Q. petraea/robur* and other tree species (Fe&Qpr&others) in the UK. Protected = currently has some form of conservation protection or designation. Not protected = currently does not have any form of conservation protection or designation.



**Figure 3.** Number of species associated with *Fraxinus excelsior* and *Quercus petraea/robur* recorded at 24 mixed ash/oak woodlands in the UK 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 UK that use *F. excelsior* and *Q. 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.



**Figure 5.** Functional redundancy of 24 mixed ash/oak woodlands in the UK to support ash-and oak-associated species if *F. excelsior* and *Q. petraea/robur* were lost from the site. a) Highly associated species, b) Partially associated species. Data for each site shows 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 is 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.