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Review

Collapsing foundations: The ecology of the British oak, implications of its decline and mitigation options

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ABSTRACT

Oak (*Quercus* spp.) is declining globally due to a variety of pests, pathogens and climate change. Assessments of the impact of losing keystone species such as oak, should include the impact on associated biodiversity and ecosystem functioning, and consider mitigation options. Here, we assess the potential ecological implications of a decline in *Quercus petraea/robur* within the UK. We collated a database of 2300 species associated with *Q. petraea/robur* of which 326 were found to be obligate associates (only found on *Q. petraea/robur*).

One potential mitigating measure for lessening the impact of oak decline on associated biodiversity would be establishing alternative tree species. However, of 30 alternative tree species assessed, none supported a high proportion of the oak-associated species (maximum 28% by *Fraxinus excelsior* ash, which is currently declining due to *Hymenoscyphus fraxineus*, a fungus). However, the functioning of oak (leaf litter/soil chemistry and decomposition) was potentially replicable owing to its similarities with other tree species.

The impact on the four main oak woodland communities within the UK, of a theoretical 50% decline in oak on ecosystem functioning and associated species was explored for five scenarios, that differed in the selection of replacement tree species. The most resilient woodland communities (in all the aspects assessed) were those capable of supporting the greatest diversity of tree species and when the currently occurring tree species replaced oak. The greatest change was predicted where *F. excelsior* was lost in addition to a decline in oak, and if only one species, particularly *Acer pseudoplantanus* sycamore, filled the canopy gaps.

1. Introduction

Plant pests/pathogens, particularly those affecting keystone species such as trees, are becoming major drivers of declines in biodiversity (Harvell et al., 2002). For managers with a biodiversity conservation remit the management of diseased trees, both in woodland and outside woodlands, needs to go beyond that aimed at stopping or reducing the spread of the pest/pathogen and limiting timber losses. They need to understand and respond to the cascading effects of the loss or decline of individual tree species on the other species that use that tree (termed associated species), the woodland ground flora, the remaining tree canopy composition and the functioning of the ecosystem. While the potential biodiversity impacts of tree diseases are widely acknowledged (Boyd et al., 2013), detailed recommendations for tree specific diseases are often lacking (but see Broome et al., 2014; Mitchell et al., 2014).

Oaks (*Quercus* spp.) are iconic trees with over 600 species worldwide (The Plant List, 2013). Since the 1980's there has been increasing concern about the deterioration in the health of oak trees globally due to a variety of biotic and abiotic factors (Denman et al., 2014; Denman and Webber, 2009; Thomas et al., 2002) with evidence of a decline in many countries (e.g. USA: Brady et al., 2014; Transylvania: Covrig et al., 2017; UK: Denman et al., 2014; Italy: Franceschini et al., 1999; Spain: Gallego et al., 1999; Missouri: Kabrick et al., 2007; Romania: Moldovan et al., 2015b; Russia: Oleksyn and Przybyl, 1987). The causes of the oak decline syndrome are varied and still the subject of much ongoing research but include Acute Oak Decline (Brady et al., 2017; Brown et al., 2015; Denman et al., 2018), Chronic Oak Decline (Camilo-Alves et al., 2017), Oak Processionary Moth *Thaumetopoea processionea*

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(Klug, 2013; Wagenhoff et al., 2014), powdery mildews (Bert et al., 2016; Topalidou and Shaw, 2016), *Phytophthora ramorum* (Rizzo and Garbelotto, 2003) and *Phytophthora cinnamomic* (Camilo-Alves et al., 2013; Frisullo et al., 2018). In addition, changes in site climatic conditions, either drought or excessive soil moisture, are thought to stress oak trees providing an additional cause of decline (Besson et al., 2014; Bussotti et al., 1995; Moldovan et al., 2015a; Perkins et al., 2018) that may act synergistically with pests/pathogens (Brown et al., 2018; Csoka et al., 2018; Marcais and Desprez-Loustau, 2014). While pathologists, entomologists and foresters are still researching the casual agents of oak decline, conservationists urgently require knowledge of the impact of oak decline on associated biodiversity and ecosystem functioning so that mitigation strategies can be implemented.

In the UK oak trees are currently affected by Acute Oak Decline (Denman et al., 2014), Chronic Oak Decline (Denman and Webber, 2009), Oak Processionary Moth (Tomlinson et al., 2015), and a variety of powdery mildews (Lonsdale, 2015). In some locations in the UK 80% of trees show symptoms of Acute Oak Decline and high levels of oak tree mortality have been reported (Denman and Webber, 2009). More typically the oak pests/pathogens within the UK cause a decline in the health of the tree rather than imminent death, however a slow decline in health over many decades will have a cumulative impact on oak tree survival and changes in climate may decrease their survival rates (Denman and Webber, 2009).

The native oaks in the UK are *Quercus petraea* and *Q. robur*. *Quercus robur* occurs in 85% of 10 km grid squares in Great Britain and *Q. petraea* in 67%. Oak trees can live for many hundreds of years and England has more known ancient oak trees than the rest of Europe (Farjon, 2017). Oak trees in the UK are a major feature of internationally important habitats, such as the Atlantic rainforests of the west coast which are renowned for their bryophyte and lichen flora (JNCC, 2014).

The non-woodland tree canopy is estimated to cover 11% of the urban land area and 3% of the rural land area in Britain (National Forest Inventory, 2017) and *Quercus petraea/robur* is the second most common non-woodland tree after *Fraxinus excelsior* (7.7% vs 10.3%) (Forestry Commission, 2001). Half of the ancient oak trees recorded in The UK Ancient Tree Inventory (The Woodland Trust, Undated) are in non-woodland ecosystems. Thus, oak trees outside woodlands form an important feature of the UK landscape.

Oak has long had a reputation of supporting a high diversity of species compared to other tree species but this is largely based on Southwood (1961) who found more invertebrate species on *Q. petraea/robur* than other tree species. More recently the importance of oak, particularly ancient oak trees, for lichens and fungi has also been highlighted (Farjon, 2017). However, we still lack a comprehensive list of oak-associated biodiversity coupled with an assessment of their level of association, i.e. how dependent they are on oaks. This knowledge is required to identify which associated species are most at risk of population decline with a reduced abundance of oaks.

If extant oak trees die, then the canopy gaps will be filled by other tree species. When the canopy gaps are small they will be filled by the surrounding canopy; if the gaps are larger new trees will establish. Which tree species establish will depend on whether the establishment happens via natural regeneration (in which case it will be driven by available seed source) or if the wood is managed and tree species are planted. If the management objective is to conserve oak-associated biodiversity then it is important that the tree species replacing oak support as many of the oak-associated species as possible. However, knowledge about the suitability of alternative tree species to support this oak-associated diversity is currently lacking.

Tree species differ in terms of their role in ecosystem functioning. If oak declines in abundance within woodlands this will have cascading effects on the ecosystem functioning of the wood if other tree species with different functional properties fill the canopy gaps. It is therefore important to understand how similar other tree species are to oak, in order to assess the magnitude of any change in ecosystem function due to an oak decline.

In order to fill these knowledge gaps this review had four objectives: 1) identify the species associated with oak in the UK and their level of association; 2) assess the ability of alternative tree species to support oak-associated species; 3) assess how similar other tree species are to oak in terms of their ecosystem functioning and 4) use the data collated in Objectives 1–3 to model how oak-associated species and ecosystem functioning may change in different scenarios of oak decline in the main oak woodland communities (Rodwell, 1991) in Britain.

We confine our review to the two species of oak native to UK: *Q. petraea* and *Q. robur* (Jones, 1959) and their hybrids, referring to all three taxa as *Q. petreaea/robur*. We hope that this review will show how this approach can be used to aid conservation managers in undertaking mitigation work in the face of the decline of a tree species.

2. Methods

2.1. Identification of biodiversity supported by oak

A literature review was conducted in 2016/17 using an extensive search of both published and grey literature, together with unpublished information, in order to identify as comprehensively as possible those species that use *Q. petraea/robur* (oak-associated species) in the UK and the nature of this association. We confined ourselves to six taxon groups: birds, bryophytes, invertebrates, fungi, lichens and mammals, and did not attempt to include algae, bacteria or other micro-organisms. All data were collected under a pre-defined common structure and collated into a relational database (OakEcol).

The level of association of each species with *Q. petraea/robur* within the UK was recorded as 'obligate', 'high', 'partial', 'cosmopolitan' or 'uses' (Table 1). For some guilds it was possible to define these categories based on the number of records of a species occurring on *Q. petraea/robur* as opposed to other tree species. For other guilds a more subjective assessment was made based on the available literature (Table S1). We also recorded if the use of oak was for just *Q. robur* or *Q. petraea*, for both species, or if the data did not distinguish between the two tree species. The quality of the data used to make the assessment of the level of association of the species with oak was recorded with the categories based on whether the literature was peer reviewed/the database quality controlled and if the data were from the UK or not (Table

Table 1
Criteria used to assess the use of *Quercus robur/petraea* in the UK. This includes species dependent on other species that use *Q. robur/petraea*, such as parasites and some of the predatory insects.

Association with oak in UK	Definition
Obligate	Unknown from other tree species. NOTE: when dealing with parasites the following criteria were used: obligate host + obligate parasite = obligate; obligate host + parasite with multiple hosts = uses; highly associated host + obligate parasite = highly associated; highly associated host + parasite with multiple hosts = uses
High	Rarely uses other tree species
Partial	Uses oak more frequently than its availability
Cosmopolitan	Uses oak as frequently or lower than availability
Uses	Uses oak but the importance of oak for this species is unknown

S2).

Information on the conservation status of associated species was recorded; this was broadly grouped as to whether the species was known to have some form of conservation protection, as different taxon groups have different measures of conservation protection. Where relevant, according to taxon group, additional information was collated on the IUCN status of the species, if the species was on a UK Red Data book list, a Biodiversity Action Plan species or on the priority species list of any of the four countries within the UK. Birds species were also recorded as red, amber or green on the UK Birds of Conservation Concern list. Further details of these measures of conservation status within the UK and how they were recorded within the database are provided in Table S3.

Information on the ecology of the oak-associated species was collated. How the species used the tree was recorded: feeding directly (i.e. eating part of the tree), feeding indirectly (i.e. eating another organism found on the tree) or for use as living space such as nesting or roosting for birds and bats or living space for epiphytic plants and fungi. The part of the tree used (bark, canopy, dead wood, flowers, leaves, limbs/branches/twigs, roots, seeds, shoots, trunk), age of tree (seed, seedling, sapling, pole, mature, veteran, dead), and tree form (natural, coppice or pollard) was also recorded where possible. The woodland type used by associated species was recorded as ancient woodland, recent woodland, wood pasture, plantation or non-woodland. Definitions for all these aspects of the ecology of the oak-associated species are given in Table S4.

2.2. Identification of oak associated species for conservation

To identify those species most at risk of a decline in oak a scoring system based on level of association with oak and conservation status was developed. Associated species were given a RED-code if they were either: (a) obligate on *Q. petraea/robur* or (b) highly associated with *Q. petraea/robur* trees and were either of "conservation concern-protected", "conservation concern-unprotected" or "unknown" (Table S3) (this takes the precautionary approach as it is currently unknown whether or not these species are of conservation concern).

Species were given an AMBER-code if they were defined as highly associated with *Q. petraea/robur* but currently of no conservation concern, or only partially associated with *Q. petraea/robur* but already of conservation concern. These species may be at moderate risk following the decline of *Q. petraea/robur*. We have also included those species that use *Q. petraea/robur* but whose level of association is unknown (i.e. uses) and are either of conservation concern or of unknown conservation concern (this again takes a precautionary approach).

Species coded YELLOW were defined as those of no current conservation concern and whose level of association with *Q. petraea/robur* was either 'partial' or 'uses'; the risk to these species of a decline in *Q. petraea/robur* is likely to be low. Species coded GREEN were defined as those species that are cosmopolitan in their use of *Q. petraea/robur* and they are considered unlikely to be impacted by the decline in *Q. petraea/robur*.

2.3. Use of alternative tree species

Two broad categories of tree species can be considered as candidate replacement trees on sites presently classified as oak dominated. Firstly, replacement with native and long-naturalised (archaeophyte) species that are already a component of oak woodlands that could increase in abundance in response to loss of oaks either through natural demographic processes or by management interventions such as planting or encouraging natural regeneration. Nineteen native tree species (*Acer campestre* field maple, *Alnus glutinosa* alder, *Betula pendula* silver birch, *Betula pubescens* downy birch, *Carpinus betulus* hornbeam, *Fagus sylvatica* beech, *Fraxinus excelsior* common ash, *Ilex aquifolium* holly, *Malus sylvestris* crab apple, *Pinus sylvestris* Scots pine, *Populus tremula* aspen, *Prunus avium* wild cherry, *Sorbus aria* whitebeam, *S. aucuparia* rowan, *S. torminalis* wild service tree, *Taxus baccata* yew, *Tilia cordata* small leaved lime, *T. platyphyllos* large leaved lime, *Ulmus glabra* wych elm) and three non-native naturalised species (*Acer pseudoplatanus* sycamore, *Castanea sativa* sweet chestnut, *Tilia vulgaris* hybrid lime) were identified as currently being present in the main oak woodland communities within Britain (Rodwell, 1991) in addition to *Quercus petraea/robur*. Secondly *Q. petraea/robur* could be replaced by introduced non-native species, such as productive conifers (where timber production is a priority) or by other exotic broadleaved species including other non-native oak species. The soils associated with oak communities in Britain are typically brown earths, surface water gleys, and rankers and podzols in both cool-wet and warm-dry climate zones. Conifers that have been planted on similar sites in Britain include: *Larix* spp., *Picea abies*, *Pinus nigra* ssp. *laricio*, *P. sylvestris, Pseudotsuga menziesii, Thuja plicata* and *Tsuga heterophylla* (Pyatt et al., 2001), all of which are non-native accept for *P. sylvestris*. However, planting of *Pinus nigra* ssp. *laricio* is restricted due to *Dothistroma* needle blight and the planting of *Larix* spp. by *Phytophthora ramorum.* If an oak disease outbreak is confined to native oak species, then other introduced oak species could be considered. Most exotic *Quercus* species in Britain are only known as ornamental trees. *Quercus cerris* Turkey oak is an established species in woodlands and plantations and belongs to a different taxonomic section (Sect. *Cerris*) of the genus *Quercus* compared to the British native oaks (Sect. *Quercus*) and so may be resistant or tolerant to diseases affecting native oaks. Most of the other European oak species have not been tested sufficiently to make confident recommendations for use in Britain. Of the N. American oaks, *Quercus rubra* red oak has undergone limited trials and could be a suitable alternative to native oaks, particularly on lighter soils. *Quercus rubra* also belongs to a different section (Sect. *Lobatae*) from native oaks species. Thus, the seven conifer species mentioned above and two non-native *Quercus* species were added to the list of 21 native broad-leaved and archaeophyte species to give a list of 30 potential replacement tree species.

The literature was searched in the same manner as that used to identify oak-associated species to collate evidence of whether the oak-associated species did or did not use these 30 alternative tree species. The level of use of the alternative tree species was categorised according to whether the species was known to use that particular tree species, or just that genus of tree and if the species regularly used the tree species or only rarely (Table 2). In addition, there were categories to record whether the oak-associated species was known not to use the tree in question, if information was unavailable or if only expert judgement drawing on ecological knowledge could be used (Table 2). Again, the quality of the data used to make the assessment (Table S2) and references used were recorded. All the data were collated into the OakEcol database. Of the 2300 oak-associated species, 89 were parasites (species known to parasitise hosts that are oak-associated species). Assessments of the use of alternative trees by parasite hosts were beyond the scope of this work. Thus, assessments of use of alternative tree species was made for 2211 associated species, with the category parasite recorded against 89 species (Table 2).

2.4. Ecosystem functioning

The 'ecosystem function of a tree species' covers a wide range of processes. We limited the functional characteristics and ecosystem processes studied to a direct measure of function (leaf litter decomposition) and metrics related to function (leaf litter chemistry and soil chemistry). For brevity, both types of measurement are called 'ecosystem function' throughout.

A literature review to identify the decomposition, leaf litter chemistry and soil chemistry of the 30 alternative tree species (see Section 2.3) and *Q. petraea/robur* was carried out using key-word driven searches undertaken between 24th July and 17th August 2017 in Web of Knowledge (http://wok.mimas.ac.uk/). Two Boolean searches were

Table 2
Definitions of criteria used to assess association of oak-associated species with 30 alternative tree species.

Association	Definition
No	Known not to use this tree species.
Parasite	Species is a parasite, so no assessment of alternative tree species made
Probable	Based on ecological knowledge of the species the oak-associated species is thought likely or probable to use this tree species but there are no records of the species using this particular tree species. For example, the species is known to use a wide range of deciduous tree species, thus it is probable that it will also occur on other deciduous tree species, even if no records of its occurrence on this tree species exist.
Rarely_Gen	The oak-associated species has very occasionally been recorded on this genus but there is no information on if it will occasionally use this species. Unlikely to be a good alternative tree species
Rarely_Sp	The oak-associated species has very occasionally been recorded on this tree species but very rarely, so unlikely to be a good alternative tree species
Unknown	The use (or otherwise) of this tree is unknown
Yes_Gen	Known to use this genus but no information on if it will use this species
Yes_Sp	Known to use this tree species.

conducted for each tree species: {[Latin name of the tree species] and carbon or nutrient cycling or nitrogen}; {[Latin name of the tree species] and litter or decomposition}. For *Pinus nigra* ssp. *laricio* the search was conducted with and without the subspecies included in the search string.

For each search, the abstracts of all the extracted articles were read and, if the abstract referred to more than one of the 31 tree species, relevant data were extracted, with the aim of producing a matrix of functional data versus tree species for further analysis. The following chemical data were collated for the litter: C, C:N, Ca, K, Lignin, Lignin:N, Mg, N, P and for the soil: C, C:N, Ca, K, Mg, N, P and pH. In addition data on leaf litter decomposition rates were also collated. No information for either search string was found for *Ilex aquifolium, Malus sylvestris, Quercus cerris, Sorbus aria, Sorbus torminalis, Taxus baccata*, and *Tilia vulgaris*. An additional six tree species were also deleted from the analysis due to lack of data (fewer than 3 references): *Acer campestre, Populus tremula, Prunus avium, Sorbus aucuparia, Tilia platyphyllos* and *Ulmus glabra*. Data for *Betula pendula* and *B. pubescens* were combined as it was not always clear which tree species was involved.

As the data were collected in different units they were first converted so that data for any function were in the same units. Decomposition data were all converted, where necessary, to provide values for the decomposition rate constant 'k'. The soil and litter chemistry data were converted into mg g^{-1} for concentrations and a log ratio for litter and soil C:N and litter lignin:N.

In most cases there were multiple values for each tree/function combination obtained from a variety of different references. The mean value for each tree-function combination were calculated using restricted maximum likelihood (REML) with a fixed factor of tree species and a random factor of 'reference identity' using Genstat (ver. 16.1.0.10916, VSN International, 2013). If there were multiple study sites within one reference, then these were nested within reference as a random factor within the analysis. There were data for all combinations of tree/function other than for soil C and soil C:N for *Castanea sativa.* The missMDA (Husson and Josse, 2010) function in the statistical programme R (ver. 2.12.1, R Development Core Team, 2010) was used to impute these two missing values in the matrix. The matrix was then analysed using PCA in FactoMineR (Husson et al., 2011) with the total weight of decomposition set to 1, total weight of soil variables set to 1 and total weight of litter set to 1.

2.5. Predicting changes in species and functioning of British oak woodland communities

The current pests/pathogens impacting *Q. petraea/robur* in the UK, while causing a decline in tree health and abundance, are not predicted to cause the complete disappearance of *Q. petraea/robur* from British woodlands (Denman and Webber, 2009). Therefore, rather than model the impact of the complete loss of *Q. petraea/robur*, which is unrealistic, we modelled the impact of a 50% decline in *Q. petraea/robur* on ecosystem function and oak-associated biodiversity. In Britain there are four main woodland types where *Quercus petraea/robur* is dominant: *Quercus robur-Pteridium aquilinum-Rubus fruticosus* woodland (W10), *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland (W11), *Quercus* spp.-*Betula* spp.-*Deschampsia flexuosa* woodland (W16) and *Quercus petraea-Betula pubescens-Dicranum majus* woodland (W17) (Rodwell, 1991). We assumed a 50% loss of both *Q. petraea* and *Q robur* (and any hybrids) and the five scenarios differ in which tree species fill the canopy gaps left. In Scenario 1 the other tree species increase in abundance in proportion to their current abundance to fill the gap left by *Q. petraea/robur*. In Scenario 2 *Fraxinus excelsior* is lost due to ash dieback by *Hymenoscyphus fraxineus* in addition to the decline in *Q. petraea/robur* and the other tree species increase in abundance in proportion to their current abundance. Scenario 2 was not carried out for W16 as *Fraxinus excelsior* is not present in this community. In Scenario 3 the 50% decline in *Q. petraea/robur* is replaced by *Acer pseudoplatanus*. For woodland types W10, W16 and W17 this represents *Acer pseudoplatanus*, which is already present in the woodland, increasing in dominance; for W11 this scenario represents *Acer pseudoplatanus* colonising and rapidly establishing within the woodland. In Scenario 4 the *Q. petraea/robur* that are lost are replaced by *Q. rubra*. This species is not currently present in any of the woodland types and represents a major replanting effort to replace the British native oaks with a non-native oak species. In Scenario 5 the *Q. petraea/robur* that are lost are replaced by *Fagus sylvatica*. This species is already present in all four woodland types but increases in abundance under this scenario.

The British National Vegetation Classification (NVC, Rodwell, 1991) describes species composition in terms of frequency (how often a species is found on moving from one quadrat to another) and cover (how much of a species is present). Tree species composition for each scenario was calculated using the frequency and abundance data from Rodwell (1991) for W10, W11, W16 and W17. In order to take account of both abundance and frequency, a weighted abundance was calculated for each tree species by multiplying the abundance data by the frequency data. The proportional cover data for each tree species was then calculated as the weighted abundance data for an individual tree species divided by the total weighted abundance for all tree species in the community. Thus, the total tree cover within the community always equalled one. The proportional cover of each tree was then calculated for each of the five scenarios for each of the four communities (Table S5a–d).

Change in ecosystem function for each scenario was investigated by assuming that the biomass ratio hypothesis (Grime, 1998) applies: i.e. that the average ecosystem function would be the average of the ecosystem function for the individual tree species weighted by their abundance. The proportional cover data was multiplied by the functional score for each species for each of the four oak-dominated communities and the 19 scenario communities. The functional score was derived from the first axis of the PCA analysis of function (Section 2.4) rescaled to run from zero to one. A functional score was unavailable for some tree species (Section 2.4) but these were generally minor components of the community (Table S5a–d) and were therefore thought unlikely to be major drivers of ecosystem functioning.

The impact on oak associated species due to changes in woodland tree composition was investigated by calculating the number of oak-associated species that would not be supported by any of the non-oak tree species present within the woodland. As *Q. petraea/robur* continues to be present in all the scenarios modelled, the number of oak-associated species present may not decline, instead those species only supported by *Q. petraea/robur* and not by other tree species within the community may be described as being 'at risk of decline' as their suitable habitat/food will decline with oak. An oak-associated species was only assumed to be supported if one of the trees in the community was known to support that species (Yes_Species, Table 2). We assumed that all oak-associated species were present in the current woodland community which we acknowledge is an over simplification but is the only practical way to make an assessment unless it were carried out on a site by site basis. The number of oak-associated species at risk was then graphed on the Y-axis against ecosystem functioning on the X-axis.

3. Results

3.1. How important is Quercus for UK biodiversity?

In total 2300 species were found to occur on oak (Table 3). This consisted of 38 bird species, 229 bryophytes, 108 fungi, 1178 invertebrates, 716 lichens and 31 mammals. This included 587 species which only used the tree for feeding indirectly (predatory invertebrates, some birds and bats) but did not include species which may occasionally use oak woodland habitat, but which had no specific association with the oak trees such Red Fox *Vulpes vulpes*, Western Hedgehog *Erinaceus europaeus*, European Mole *Talpa europaea* or Wild Cat *Felis silvestris*.

Of these 2300 species, 326 were obligate species consisting of 57 fungi, 257 invertebrates and 12 lichens, while 229 species were classified as highly associated with oak consisting of 51 fungi, 104 invertebrates and 74 lichens. These 555 species were considered most at risk from a decline in oak health. Although there were 229 bryophytes recorded on oak none of them have a particular association with oak, hence they were all recorded as cosmopolitan. For the majority of species (1626) the data showed that they used native British oak trees (*Quercus petraea/robur*) but it did not distinguish between the two species. For 313 species it was possible to specifically state that the species used both *Q. robur* and *Q. petraea*. For 358 species there were data to show that the species used *Q. robur* but use of *Q. petraea* had not been specifically recorded and for 3 species there were data to show the species used *Q. petraea* but use of *Q. robur* had not specifically been recorded. Given the lack of data on species use for the two different native British oaks, all analysis was done for *Q. petraea/robur* combined, without distinguishing between the two tree species.

In total 610 different data sources were consulted to collate the list of oak-associated species (see reference list in OakEcol database). There was a high level of confidence in the level of association of the species with oak, particularly for obligate species where 94% of data came from peer reviewed literature using UK data and for highly associated species where 99% came from peer reviewed literature using UK data (Fig. S1).

Table 3
Oak associated species by group and their level of association with oak.

Species group	Level of association with oak					
	Obligate	High	Partial	Cosmopolitan	Uses	Total
Bird			14	24		38
Bryophyte				229		229
Fungi	57	51				108
Invertebrate	257	104	233	200	384	1178
Lichen	12	74	116	514		716
Mammal			9	22		31
Total	326	229	372	989	384	2300

Table 4
Number of species in each species group classed as red, amber, yellow and green with respect to the impact of oak decline. RED = species either obligate on *Q. robur/petraea*; or highly associated with *Q. robur/petraea* trees and either of conservation concern (protected or unprotected) or unknown conservation status; AMBER = species highly associated with *Q. robur/petraea* trees but currently of no conservation concern, or only partially associated with *Q. robur/petraea* but already of conservation concern. YELLOW = species currently of no current conservation concern and whose level of associated with *Q. robur/petraea* was either 'partial' or 'uses'; GREEN = species that are cosmopolitan in their use of *Q. robur/petraea*.

Species group	Impact of oak decline			
	RED	AMBER	YELLOW	GREEN
Bird		6	8	24
Bryophyte				229
Fungi	108			
Invertebrate	314	258	406	200
Lichen	55	73	74	514
Mammal		13	7	4

3.2. Prioritisation of oak associated species for conservation

The prioritisation of oak associated species for conservation identified 477 RED-coded species: 108 fungi, 314 invertebrates and 55 lichens (Table 4, see Table S6 for the complete list). These RED-coded species are considered to be most at risk if there is a major decline in the abundance of *Q. petraea/robur*. Of these 477 species, 145 already have some conservation status (Table S7), but the remaining 332 species currently have no measure of conservation protection. A total of 343 species were identified AMBER-coded ('medium risk') in relation to oak decline, 491 YELLOW-coded ('low risk') species and 989 GREEN-coded ('no risk') species (Table 4).

3.3. Tree part and age used by oak-associated species

The greatest number of oak associated species is found on the bark of oak trees, followed by dead wood, leaves and limbs/branches/twigs (Fig. S2a). Obligate species occurred in all parts of the tree (Fig. S2a) but the greatest number utilise the leaves. Although fewer species use the roots, seeds and shoots of oak, a greater proportion of these species were obligate. Unsurprisingly the part of the tree used differed between species groups with bryophytes and lichens being more associated with the trunk and bark, fungi and invertebrates with the leaves.

Although information on the age of tree used was lacking for 699 species, the information that was available showed that the greatest number of species is found on veteran trees. The number of obligate species was similar across pole, mature and veteran trees (246, 285, 294 respectively) but the number of highly associated species was more than twice as high in mature and veteran trees (138 and 162 respectively) as in pole aged trees (67 species). There was little information on the age of tree used by many lichen species (Fig. S3b). All fungi and over 90% of bryophyte species used both mature and veteran trees. Mature and veteran trees were used by the greatest proportion of bryophytes, fungi, invertebrates and mammals (Fig. S3b). The pattern differed slightly for birds where pole aged and mature trees were the most commonly used (Fig. S3b). This could stem from the fact that much of the information for birds was assessed at the stand scale rather than the individual tree scale (except nest holes), and stands of mature or pole stage are more likely than stands of veteran trees.

3.4. Effect of woodland and tree type

Information on woodland type (Fig. S2c) showed the importance of oak trees in not only woodland situations but also non-woodlands (single trees, trees in gardens, parks, hedges) and wood pastures. Of the 1699 species for which there was information on the woodland type used, 116 species were found in non-woodland/wood pasture situations but not in woodlands and 331 species were found in woodland situations but not non-woodland/wood pasture situations.

Of the 2172 species for which information was available on the tree form used (coppice, pollard or natural), fewer species were known to use coppice or pollarded growth forms (Fig. S2d). This was largely due to more cosmopolitan species using the natural growth form and may be due to lack of recording of cosmopolitan species on coppice or pollarded growth forms. Coppice and pollarded trees were very important for bryophytes (Fig. S3d), with nearly all bryophyte species known to use these growth forms. Coppice trees were also important for oak associated birds, but pollarded trees less so. There was little information on the growth form used by lichens and fungi.

3.5. Use of alternative tree species

3.5.1. Precautionary assessment of the suitability of alternative tree species

The most precautionary assessment of suitability of the alternative trees in supporting oak-associated biodiversity uses only information with a secure knowledge that the oak-associated species will use a given tree species (Yes_Species) as opposed to using information that the species only rarely uses that tree or uses that genus (Table 2). Using this approach *Fraxinus excelsior* is shown to support the greatest number of oak-associated species, 613 species (28%) (Fig. 1). *Fagus sylvatica* supports the second greatest number of oak-associated species (347 or 16%). *Alnus glutinosa* supports 11% of the oak-associated species and the remaining 16 native tree species each support less than 10% of the oak associated-species. Of the non-natives *Acer pseudoplatanus* is known to support the greatest number of oak-associated species (292 or 13%) with *Quercus cerris* and *Castanea sativa* ranked second and third (Fig. 1).

Different alternative tree species provide higher levels of support for some taxon groups than others (Fig. 2). For taxon groups such as birds and mammals, which contain many cosmopolitan species, single alternative tree species such as *F. sylvatica*, or *F. excelsior* can support a higher proportion (c. 40%) of the associated species than for taxon groups containing many specialists. No tree supported a high proportion of the oak-associated invertebrates; *F. sylvatica* supporting 15% was the highest. Of the non-native trees *A. pseudoplatanus* is important for oak-associated birds, bryophytes and mammals, supporting over 30% of the species within each of these groups.

As obligate species will not be supported by any alternative trees, it could be argued that the most suitable alternative tree species will be those that support the greatest number of highly and partially associated species (Fig. 3). Thus, for native trees a similar pattern of suitability to that for all oak-associated species emerges, with *F. excelsor, F. sylvatica* and *A. glutinosa* ranked as the top three. However, the results for the non-native trees show that *Q. cerris* is known to support as many highly associated and partially associated species as *A. pseudoplatanus*.

An alternative way of ranking the alternative tree species is by the number of RED-coded and AMBER-coded species they support. Once again *F. excelsior* and *F. sylvatica* are the most suitable native alternatives followed by *Alnus glutinosa*. For the non-native trees *Qurcus cerris* supports nearly twice as many RED and AMBER coded species as does *Acer pseudoplatanus* (78 v 41 species, Fig. 4) which was ranked highly under the previous methods (Figs. 2 & 4).

3.5.2. Optimistic assessment of the suitability of alternative tree species

The most optimistic assessment of the suitability of the alternative tree species for supporting oak-associated biodiversity includes classing all data from Yes_Species, Yes_Genera, Rarely_Species, Rarely_Genera and Probable (Table 2) as indicating that the oak-associated species may "potentially use" that tree species. Under this analysis, while *F. excelsior* still supports the greatest number of species (941), *Betula pubescens* and *B. pendula* support 918 and 915 species respectively (Fig. S4). This is due to the large number of oak associated species that are known to either regularly or rarely use the genus *Betula*. This optimistic assessment also shows the potential of the two non-native oaks, with *Q. cerris* potentially supporting 610 and *Q. rubra* 604 species. Many of the

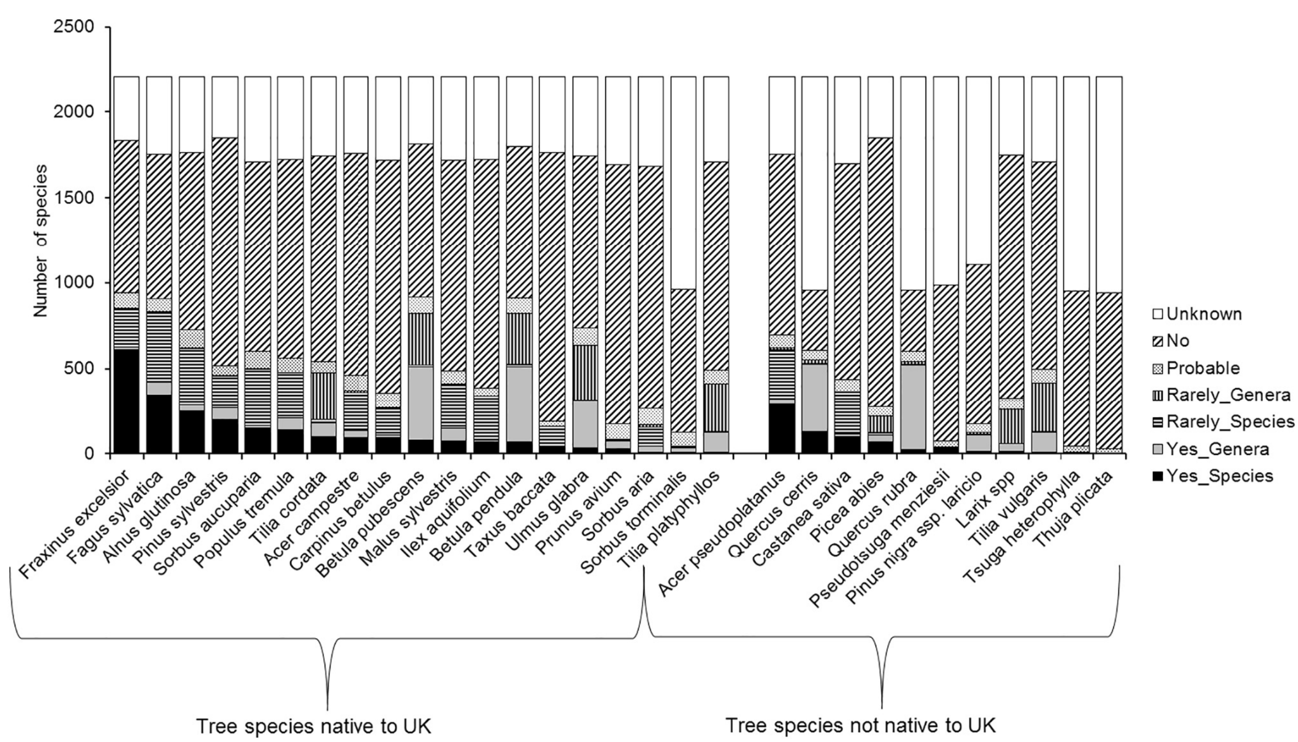

Fig. 1. Use by oak associated species of 30 alternative tree species. See Table 2 for definitions of levels of association with alternatives.

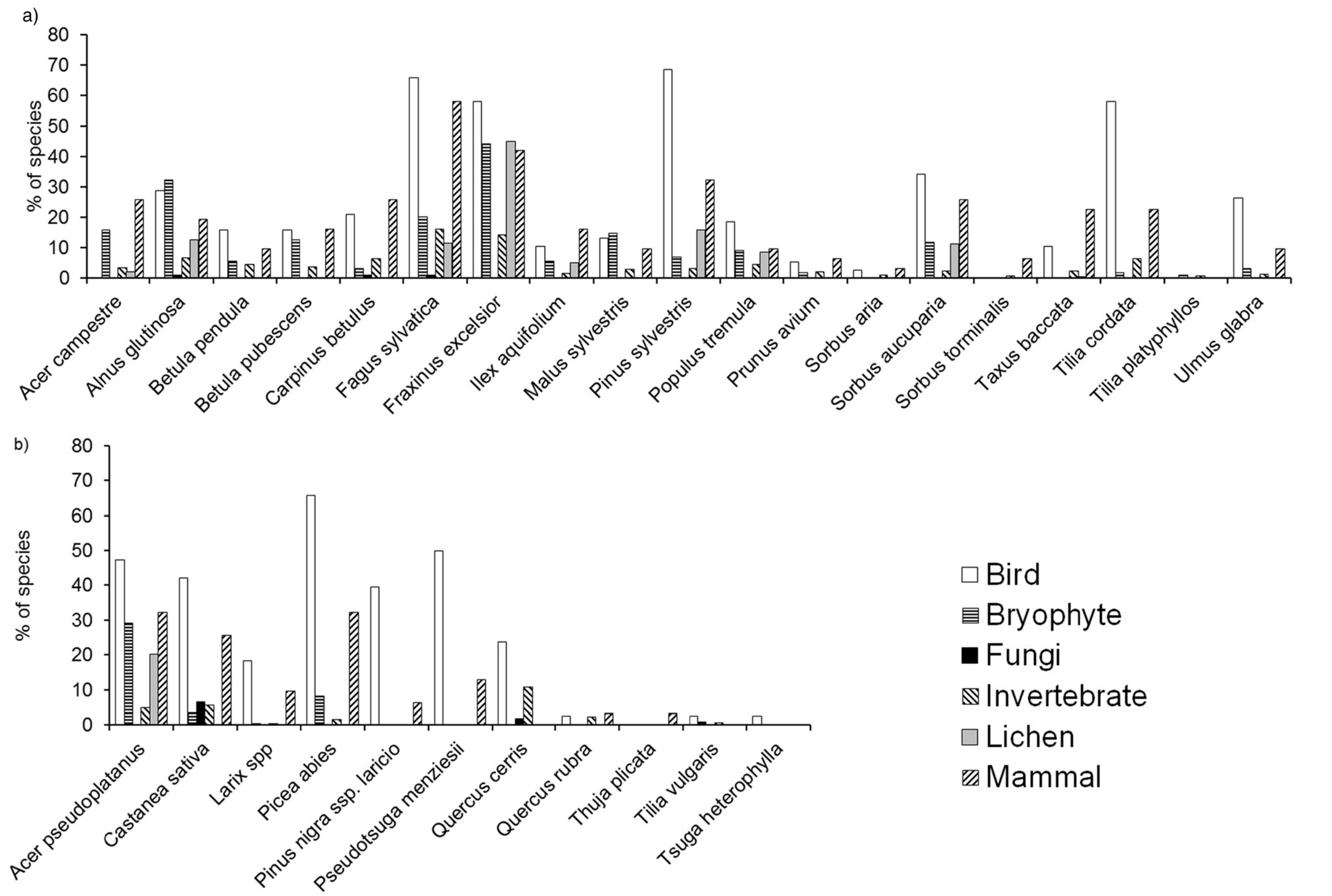

Fig. 2. Use by oak-associated species groups of a) native and b) non-native alternative tree species. Data are shown as the % of species within each species group that are known to use that tree species. Birds = 38 species, Bryophytes = 229 species, Fungi = 108 species, Invertebrates = 1089 species, Lichens = 716 species and Mammals = 31 species.

oak-associated species are known to use other *Quercus* genera, but not these specific species, thus they were classified as Yes_Genera.

3.5.3. Knowledge gaps and confidence in data

For all native tree-alternatives, except *Sorbus torminalis,* information on use was available for over 75% of oak-associated species, thus allowing an informed decision to be made about the suitability of the tree as a replacement. This level of information was available for five of the non-native tree species, but for the remaining six species, including the two non-native *Quercus* species, information was not available for over 50% of associated species, giving low confidence in their suitability. This distinction in the confidence of the data is critical; for example *Quercus cerris* and *Castanea sativa* are known to support similar numbers of oak associated species (130 and 101 respectively, Fig. S5). However, we have data for over 75% of species for *C. sativa* (Fig. S4) and we know that 1266 species (57% of species) will not use *C. sativa*; this compares with *Q. cerris* were we only have data for 43% of species and we know that 350 species (16%) will not use this tree species.

3.6. Comparison of species functioning

One hundred and two references were used to construct a matrix of litter decomposition rates and soil and litter chemical variables for 16 of the alternative trees plus *Q. petraea/robur*. Table S8 lists the number of data points for each tree/variable combination and Table S9 lists all the references used.

The first axis of the PCA explained 48% of the variation and separated species with high soil and litter N concentrations and fast decomposition: *Fraxinus excelsior, Acer pseudoplatanus, Betula pubescen/pendula, Carpinus betulus, Tilia cordata* and *Alnus glutinosa*, from tree species with high soil C concentrations and high C:N ratios and litter with high lignin and C concentrations and high lignin:N ratios: *Thuja plicata, Tsuga heterophylla, Pinus nigra* ssp. *laricio, Pseudotsuga menziesii* and *Pinus sylvestris* (Fig. 5). *Q. petraea/robur* occurred in the middle of the ordination.

3.7. Scenarios of change in abundance of oak-associated species and ecosystem functioning

Across all woodland types, about half of the oak-associated species were at risk if *Q. petraea/robur* declined (c. 1000 species) (Fig. 6). This is because no one alternative tree species found in the woodlands supports a high proportion of the oak-associated species. Community W10, which has a greater diversity of tree species present than the other three communities, had a smaller number of oak-associated species at risk (Fig. 6). In all community types if *F. excelsior* was lost in addition to a decline in *Q. petraea/robur* (Scenario 2) the number of associated species at risk increased considerably more than if just *Q. petraea/robur* declined (comparison of Scenarios 1 and 2) (Fig. 6).

Across all woodland types, if all the remaining tree species within the community increased in abundance in proportion to their current abundances, then the functioning of the system remained fairly similar to the current NVC community (Fig. 6). The greatest change in functioning in all woodland types was when *Acer pseudoplatanus* filled the gaps left by *Q. petraea/robur* (Scenario 3). This resulted in faster nutrient cycling and decomposition with leaf litter and higher soil N content and lower soil C and lower leaf litter lignin content. Replacement of *Q. petraea/robur* by *Q. rubra* (Scenario 4) or *Fagus sylvatica*

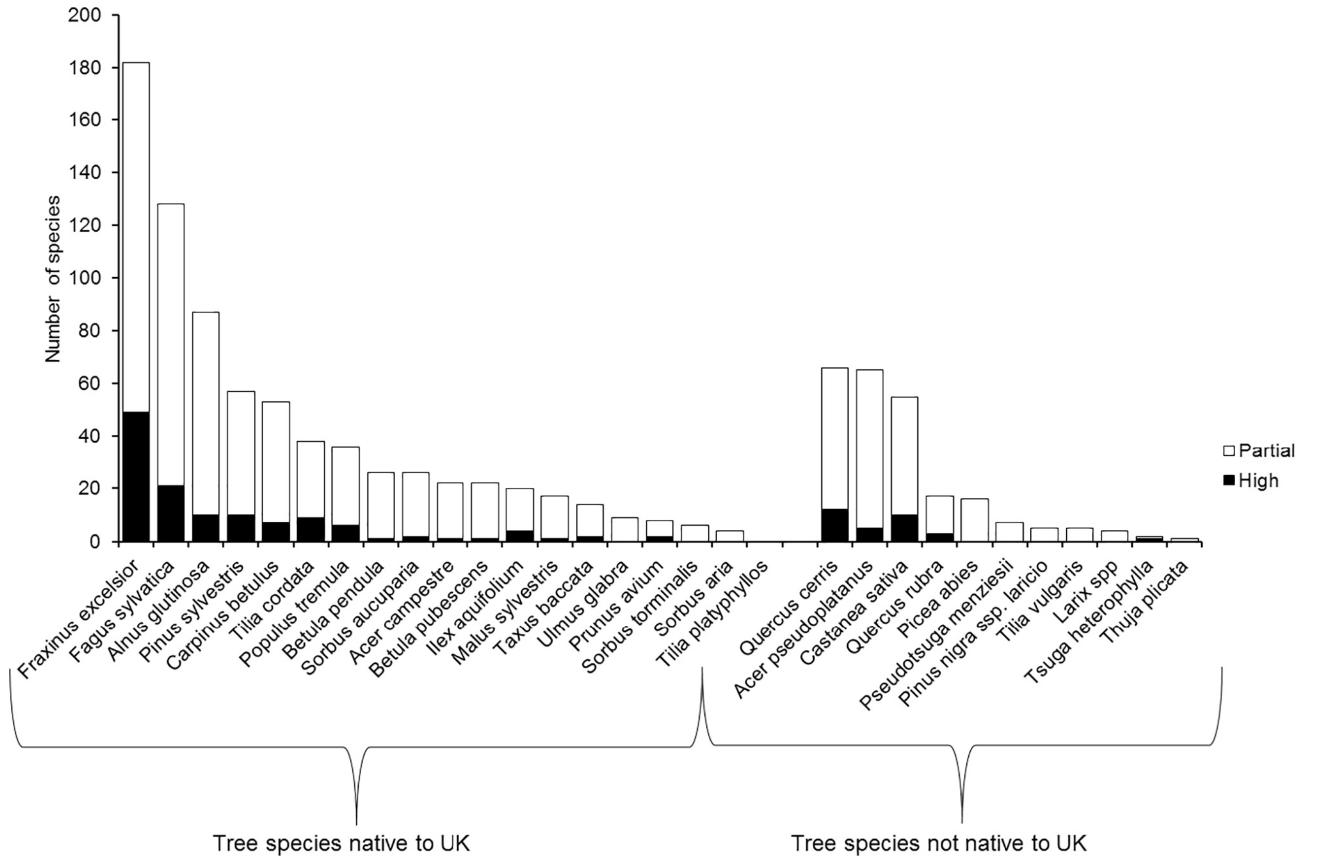

Fig. 3. Number of high and partially associated species supported by 30 alternative tree species. See Table 1 for definitions of high and partially associated species.

(Scenario 5) resulted in very little change in functioning.

4. Discussion

Quercus petraea/robur has anecdotally been known to support a large number of other species but this is the first time an empirical list of the known biodiversity has been collated across taxa to provide the evidence upon which conservation action can be built. With 477 RED-coded species, species most at risk if *Q. petraea/robur* declines, the conservation challenge is huge. In order to manage this challenge two parallel approaches can be trialled. Site specific management plans could be developed based on the data provided here and individual species lists for the site using the methodology by Broome et al. (2014). This will allow targeted management of those oak-associated species known to be present at a site. In addition, we suggest that it is these RED-coded species that conservation agencies should give the highest priority to for monitoring to assess the impact of oak decline. Second, overlying information of the predicted regions most at risk of a decline in oak health due to site conditions (e.g. predicted climate change) with areas known to be rich in oak biodiversity (particularly those sites with a high number of the RED coded species) would allow prioritisation of such sites for which management plans should be developed. As further information on the relative sensitively of oak trees of different ages and in different woodland types to the various oak pests/pathogens and climate change become available it may be possible to further prioritize management by tree age and woodland type.

Information on the part of tree used by the oak-associated biodiversity could be important if the pest/pathogen initially targeted a particular resource e.g. the leaves. This would allow further prioritisation of the species for which rapid conservation was required. Conversely species which utilise dead wood may initially increase in abundance if the decline in oak results in increased dead wood. This work has highlighted the importance of older trees for biodiversity, thus mitigation management needs to have long-term planning that thinks even a hundred years, or more, ahead.

4.1. Alternative tree species

The assessment of the suitability of alternative trees to replace oak revealed difficulties since no one tree supported a high percentage of the oak-associated species and mixtures of tree species are likely to be the only viable option to conserve oak-associated species. Similar work for *F. excelsior* in the UK showed that 68% of the ash-associated species could be supported by *Quercus petraea/robur* and five alternative trees each supported over 40% of the ash-associated species. Due to the higher number of oak-associated species compared to ash (2300 v 995), no one tree species is able to support such a high percentage of the oak associated species (max 28%). Ultimately there is unlikely to be a one size fits all approach and site specific management plans are required (Broome et al., 2014), but fewer generalizations about the suitability of alternative tree species for *Q. petraea/robur* are possible compared to *F. excelsior* owing to this lower number of species supported by any one alternative tree. While the suitability of the alternative trees may be ranked by different methods, a consistent pattern in the suitability of the native trees emerges. All the methods within the precautionary assessment show *F. excelsior* followed by *F. sylvatica* as supporting the greatest number of species with *Alnus glutinosa* ranked third. This is a concerning conclusion as *F. excelsior* is not currently a viable alternative to oak, due to the presence of *Hymenoscyphus fraxineus* (Baral et al., 2014; Kjær et al., 2012) causing ash dieback and the rapid decline of *F. excelsior* in some woods within the UK. The more optimistic assessment of the suitability of native tree species shows the potential for *Betula* species to support oak associated species, but the confidence in these data are lower. This suggests that further work on establishing the

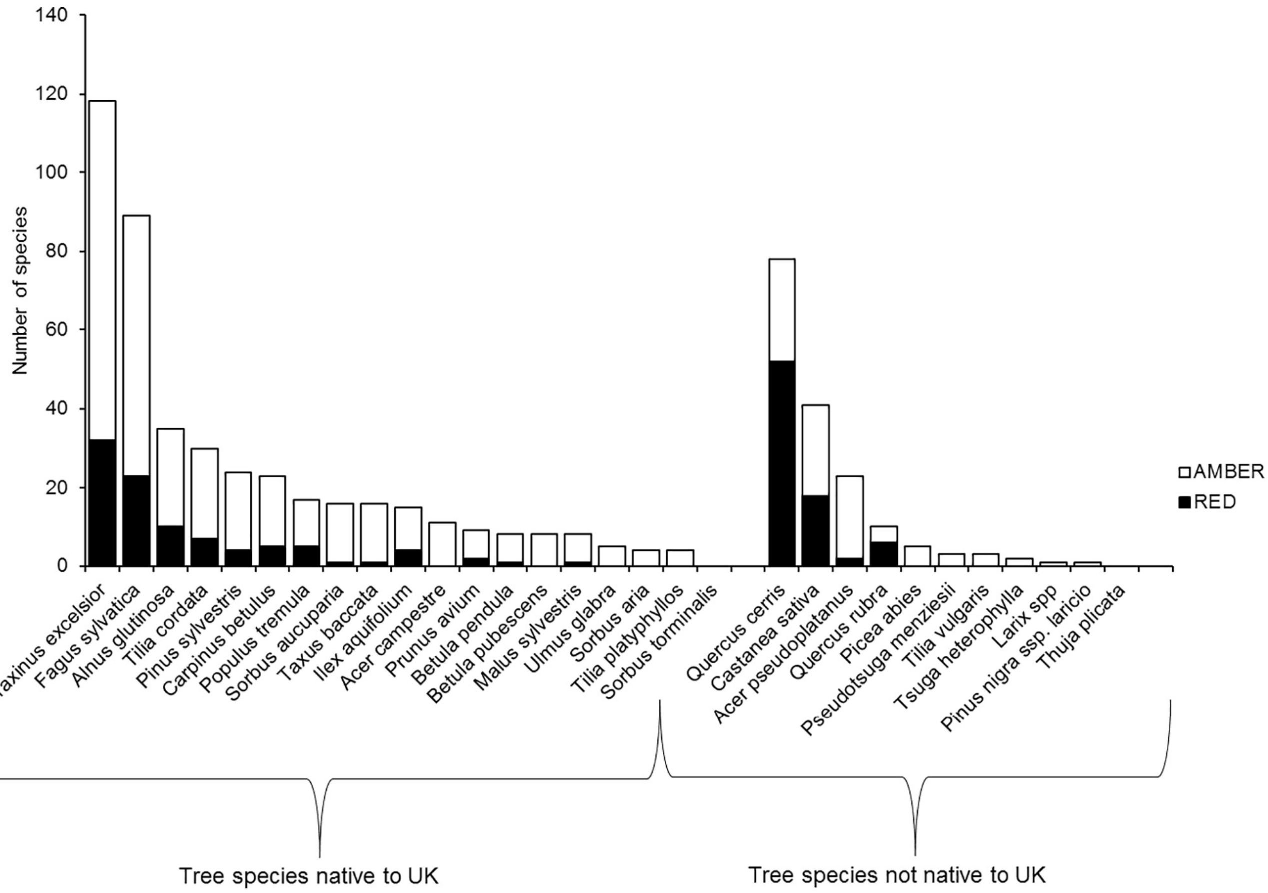

Fig. 4. Number of RED-coded and AMBER-coded species supported by 30 alternative trees species. See Table 4 for definitions

suitability of *Betula* as a potential replacement for oak is desirable as *Betula* is a widespread, early successional species within the UK which could quickly colonise sites from which oak were lost.

The different methods of ranking the alternative non-native species are consistent in showing the suitability of *Acer pseudoplatanus*, *Quercus cerris* and *Castanea sativa* but their rank order varies depending on the method of ranking. If just total oak-associated species is used then *A. pseudoplatanus* is the most suitable alternative, however, if the ranking is based on species most at risk from a decline in oak then the suitability of *Quercus cerris* and *Castanea sativa* is highlighted. Prioritising which species to manage for will influence which non-natives may be most suitable.

The functioning of *Q. petraea/robur* was shown to be in the middle of the range of species studied, suggesting that it may be possible to replace the functioning of *Q. petraea/robur* using a mixture of other trees. The analysis of change in the four main oak woodland community types also suggests that it is possible to maintain the functioning of oak woodlands through redundancy with other tree species. This contrasts with *F. excelsior* which was discovered to be at one extreme of the ecosystem functioning across a range of UK deciduous tree species and was thus identified as potentially difficult to replace (Mitchell et al., 2014; Mitchell et al., 2016).

4.2. Knowledge gaps

Western Europe, and the UK in particular, is renowned for having good biodiversity records for many taxa and this work shows how these data can be collated to provide tools (the database) and advice for conservation managers. Such knowledge continues to grow, and although specifics around individual oak-associated species may change as data accumulate, the general patterns observed here are expected to be robust. Nevertheless, despite the UK's good biodiversity records, the work highlighted a major knowledge gap about the use made of many non-native trees by our native fauna. Generally, there was more information available for non-native tree species that had been naturalised in the UK or widely planted and for those tree species whose range includes parts of Europe (i.e. overlaps with a high proportion of oak-associated species), compared to American tree species. Most species recording is for native habitats, and encourages the recording of date and location, with less emphasis placed on the tree species (as opposed to tree genera) on which the species is recorded. However, as we adapt our management to adjust to climate change and pests/pathogens, such knowledge is increasingly important and encouraging more recording of the tree species used would help fill this knowledge gap, including for non-native amenity plantings.

4.3. Resilience of UK oak woodlands and implications for management

Oak woodlands with a more diverse canopy composition (W10) were consistently shown to be more resilient to a decline in *Q. petraea/robur* in terms of species supported and functioning than those with a less diverse tree species composition (W11, W16, W17). It is acknowledged that the analysis of changes in the four main oak woodland types in the UK is a simplification. Not all oak-associated species will be present within one woodland, so the declines depicted are unlikely to be as severe at an individual site-scale. Additional non-tree species, particularly some shrubs such as *Corylus avellana* hazel will be present within woodlands and these will also support some of the oak-associated species. Thus, fewer oak-associated species may be at risk than shown. However, the scenarios illustrate five key points relevant to conservation: a) a decline in *Q. petraea/robur* is likely to have a greater impact on biodiversity than on ecosystem functioning; b) the impact on

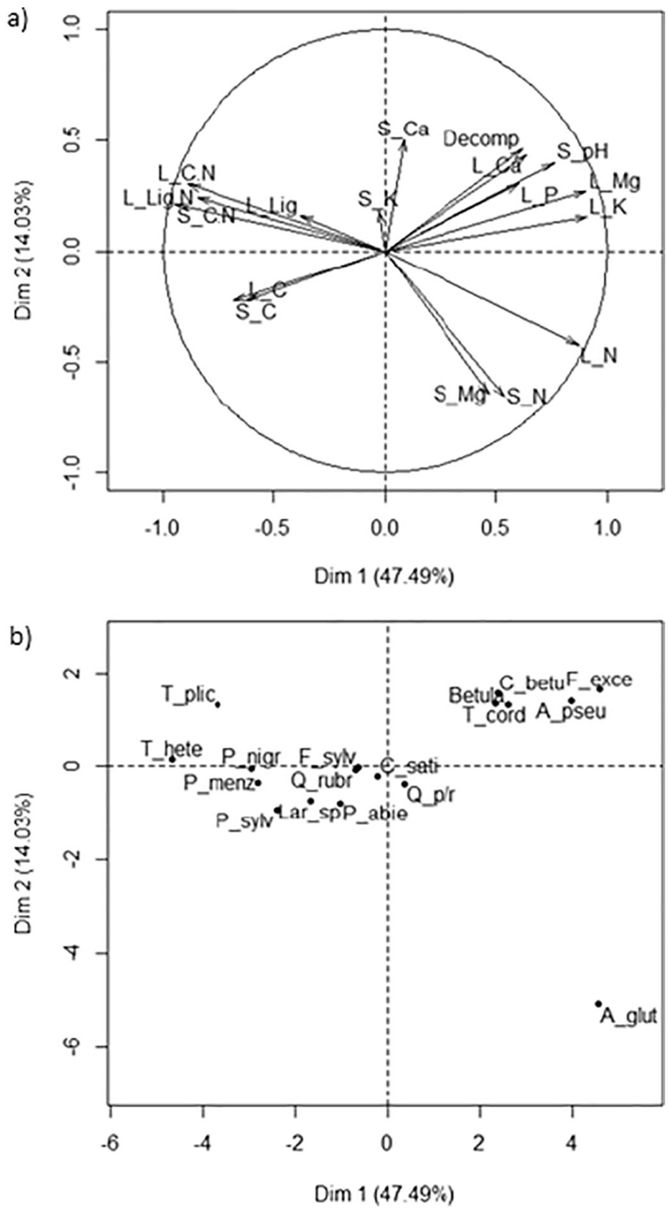

Fig. 5. Ordination diagram from PCA analysis of soil and litter chemical variables from *Q. petraea/robur* and 16 alternative tree species. a) ordination diagram of functions: L_ = litter chemistry, S_ = soil chemistry, C = carbon, C.N = carbon:nitrogen ratio, Ca = calcium, K = potassium, Lig = lignin, Lig.N = lignin:nitrogen ratio, Mg = magnesium, N = nitrogen, P = phosphorus, pH = pH, Decomp = decomposition rate of leaf litter. All data were concentration (mg g^{-1}) except for the ratios and the decomposition rate. b) Ordination diagram of tree species: A_pseu = *Acer pseudoplatanus*, A_glut = *Alnus glutinosa*, Betula = *Betula* sp., C_betu = *Carpinus betulus*, C_sati = *Castanea sativa*, F_sylv = *Fagus sylvatica*, F_exce = *Fraxinus excelsior*, Lar_sp = *Larix* spp., P_abie = *Picea abies*, P_nigr = *Pinus nigra* ssp. *laricio*, P_sylv = *P. sylvestris*, P_menz = *Pseudotsuga menziesii*, Q_p/r = *Quercus petraea/robur*, Q_rubr = *Q. rubra*, T_plic = *Thuja plicata*, T_cord = *Tilia cordata*, T_hete = *Tsuga heterophylla*.

biodiversity of a decline in oak is less in more diverse woodlands; c) a decline in oak and loss of *F. excelsior* will have a larger effect on biodiversity than just a decline in oak, highlighting the need for cumulative impact assessments of multiple tree diseases on biodiversity; d) maintaining ecosystem functioning as *Q. petraea/robur* declines can be achieved if the current tree species are allowed to increase in proportion to their current abundances; e) the greatest change in functioning will occur if naturalised but non-native *Acer pseudoplantanus* fills all the gaps left by *Q. petraea/robur*.

Making our woodlands more diverse has been advocated for increasing resilience to climate change and the direct impacts of pests and pathogens on trees. This study suggests that the cascading impacts of pests and pathogens on associated biodiversity and ecosystem functioning are also reduced, if the woodland is more diverse. While acknowledging that at some sites climate and soils will limit the diversity of tree species able to grow, British woodlands typically have low numbers of native canopy species due to historical management. The use of non-native trees to diversify woodlands remains risky due to our poor knowledge of associated species for most non-native species (Ennos et al., 2019). However, increasing the diversity of native tree species within the woodlands would be an ecologically sound step towards increasing the resilience of our oak woodlands.

4.4. Tree diseases, wider biodiversity and environmental impacts

There is ample evidence of the cascading impacts of a wide range of tree diseases on biodiversity around the world. Examples of extinctions due to tree diseases are rare but see Lohmus and Runnel (2014) who recorded the local extinction of an epiphytic lichen due to ash dieback (*Hymenoscyphus fraxineus*) in Estonia. More common are examples of severe declines in populations due to tree loss via disease. Populations of birds that are habitat specialists in Fraser fir *Abies fraseri* and eastern hemlock *Tsuga canadensis* forests declined following the death of trees caused by balsam woolly adelgid, *Adelges piceae* (Rabenold et al., 1998; Tingley et al., 2002). At Mount Collins, USA, 9 of 11 common forest bird species declined by an average of 41% - the two other species became too rare to permit mapping (Rabenold et al., 1998). In Australia species such as mardo *Antechinus flavipes* and brown antechinus *Antechinus stuartii* have been shown to decline in response to changes in forest structure caused by *Phytophthora cinnamomi* (Cahill et al., 2008). However, rarely are these potential impacts assessed across taxa at the start of a disease outbreak, as done here and for ash dieback by Mitchell et al. (2014). Such assessments, and the identification of potential mitigation options, via alternative trees needs to become common practise if tree pests/pathogens are not to become ever increasing drivers of declines in biodiversity (Harvell et al., 2002). Crucially such assessments should include not only the impacts on biodiversity but the impacts on ecological functioning. This will ensure that any mitigation measures suggested for biodiversity will not have a detrimental impact on functioning (Mitchell et al., 2016). In addition, consideration should be given to developing cumulative impact assessments for multiple tree diseases, e.g. loss of ash and decline of oak in the UK, as the impacts are likely to be greater.

5. Data access

All data on the oak associated species is available at Mitchell, R.J.; Bellamy, P.E.; Ellis, C.J.; Hewison, R.L.; Hodgetts, N.G.; Iason, G.R.; Littlewood, N.A.; Newey, S.; Stockan, J.A.; Taylor, A.F.S. (2019). Oak-associated biodiversity in the UK (OakEcol). NERC Environmental Information Data Centre. https://doi.org/10.5285/22b3d41e-7c35-4c51-9e55-0f47bb845202.

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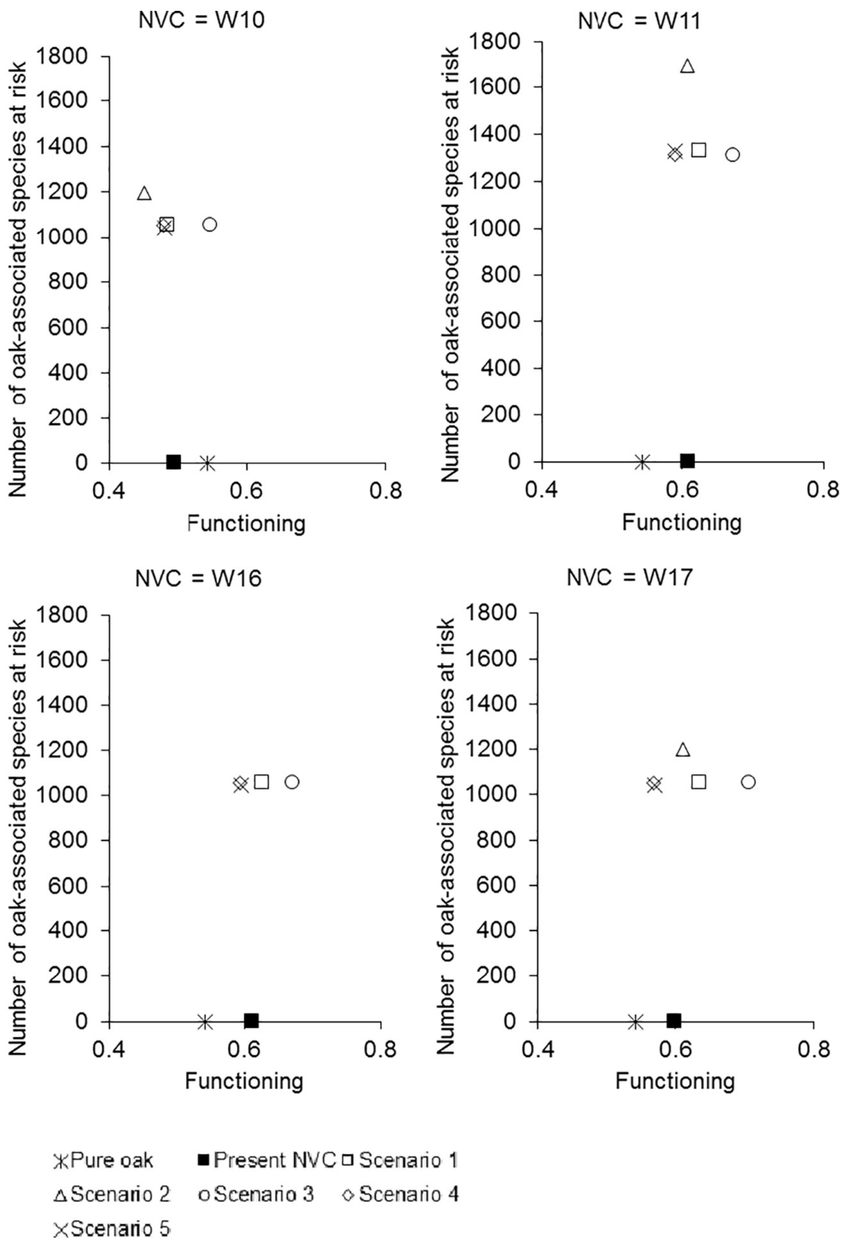

Fig. 6. The number of oak associated species at risk of declining in abundance and change in ecosystem functioning in four oak dominated woodland communities following a 50% decline in oak under different scenarios. Scenario 1: the other tree species increase relative to their current proportions. Scenario 2: *Fraxinus excelsior* is lost in addition to a 50% loss of *Q. petraea/robur* and the remaining species increase relative to their current proportions. Scenario 3: *Acer pseudoplatanus* replaces those *Q. petraea/robur* that are lost. Scenario 4: *Quercus rubra* replaces the *Q. petraea/robur* that are lost. Scenario 5: *Fagus sylvatica* replaces the *Q. petraea/robur* that are lost. Scenario 2 was not carried out for W16 as *Fraxinus excelsior* is not present in this community. The ecosystem functioning axis uses the results from the PCA analysis (Fig. 5) to calculate an overall function for the NVC community based on the proportional abundance of the tree species present. A high axis scores indicates rapid leaf litter decomposition, litter and soil with a high N content and a low C:N ratio, a low axis scores indicates slow leaf litter decomposition, litter and soil with a low N content and a high C:N ratio. See Section 2.5 for further details.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.03.040.

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