



Research Note

Ecological implications of oak decline in Great Britain

Alice Broome, Victoria Stokes, Ruth Mitchell and Duncan Ray

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Great Britain's native oaks (pedunculate oak, *Quercus robur* and sessile oak, *Quercus petraea*) are currently vulnerable to decline from a number of pests and pathogens, particularly in their southern British range. Stress created by extreme climatic events is likely to increase their susceptibility and this will vary in impact across Great Britain. This Research Note describes the ecological value of Great Britain's native oaks, as reflected in the biodiversity supported by the trees and ecosystem functions the trees perform. Based on 30 case studies, this Note describes the characteristics of oak woodlands in Great Britain, the consequences of oak decline for oak-associated biodiversity and suggested management actions in preparation for, or in response to, oak decline. Native oak across Great Britain supports 2300 species, of which 326 are obligate (with up to 42 obligate species being associated with certain oak sites). Oak performs ecosystem functions (e.g. leaf litter decomposition) at average rates compared with 16 other tree species that commonly occur or are capable of growing on oak sites. These results suggest that while functioning can be replicated by other tree species, filling the role that oak trees play in providing habitat for associated species is more challenging. Fewer tree species that support oak-associated biodiversity and maintain the ecological function of oak ecosystems occur, or are considered permissible, for planting in native woodlands in Scotland compared with England and Wales.

Introduction

Pedunculate oak and sessile oak are iconic species in Great Britain. Oak trees can live for many hundreds of years and England has more known ancient oak trees than other parts of Europe (Farjon, 2017), and more oak trees with a girth greater than or equal to 9 m than elsewhere in Europe. Pedunculate oak and sessile oak occur across Europe, southern Scandinavia, Turkey and southern Russia (Euforgen, 2009). Both oak species migrated north from refugia as the climate warmed following the retreat of glaciers after the last ice age. Northerly colonisation began in Great Britain about 10 000 years ago. Pedunculate oak and sessile oak now occur in 85% and 67% of 10 km grid squares in Great Britain, respectively.

Pedunculate oak is distributed more in the south and east of England, while sessile oak is more frequently found in the north and west of England, as well as in Scotland and Wales. Pedunculate and sessile oak are found on similar site types, but with subtle differences. Pedunculate oak grows better than sessile oak on warmer sites with less rainfall and on heavier, clayey soils. Both species grow best on fertile soil but can tolerate less fertile soils.

Oak is a constant or significant secondary species in seven of the native woodland communities of Great Britain (Rodwell, 1991). Four of these communities are named because of the presence of pedunculate or sessile oak in the canopy: *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). A further three are described as either ash woods (one community) or beech woods (two communities), and these National Vegetation Classification (NVC) woodland types can be diverse in species composition. Besides oak, oak woodlands can typically contain 21 other native and naturalised non-native species, some more frequently represented than others (Table 1). Species occurring frequently include beech, birches, ash and sycamore. The less frequently occurring species are often those confined to certain woodland types, W8 (*Fraxinus excelsior* – *Acer campestre* – *Mercurialis perennis* woodland) and W10 in particular. Some are forest species like hornbeam (*Carpinus betulus*), small-leaved lime (*Tilia cordata*) and sweet chestnut (*Castanea sativa*).

Oak ecosystem vulnerability

Oak trees are currently vulnerable to damage and decline from a range of pests and pathogens (Quine *et al.*, 2019) including acute oak decline, chronic oak decline, oak processionary moth

Table 1 Twenty-one typical tree species occurring in the seven woodland communities where oak is a constant or significant secondary species.

Frequency of occurrence	Native	Naturalised non-native
High-mean frequency score: >1 for the 7 communities (4 oak, 2 beech and 1 ash)	Beech (<i>Fagus sylvatica</i>) Field maple (<i>Acer campestre</i>) Silver birch (<i>Betula pendula</i>) Downy birch (<i>Betula pubescens</i>) Ash (<i>Fraxinus excelsior</i>)* Holly (<i>Ilex aquifolium</i>) Rowan (<i>Sorbus aucuparia</i>) Elm (<i>Ulmus glabra</i>)*	Sycamore (<i>Acer pseudoplatanus</i>)
Low-mean frequency score: ≤1 for the 7 communities (4 oak, 2 beech and 1 ash)	Aspen (<i>Populus tremula</i>) Alder (<i>Alnus glutinosa</i>) Wild cherry (<i>Prunus avium</i>) Small-leaved lime (<i>Tilia cordata</i>) Large-leaved lime (<i>Tilia platyphyllos</i>) Hornbeam (<i>Carpinus betulus</i>) Whitebeam (<i>Sorbus aria</i>) Yew (<i>Taxus baccata</i>) Crab apple (<i>Malus sylvestris</i>) Wild service tree (<i>Sorbus torminalis</i>)	Hybrid lime (<i>Tilia vulgaris</i>) Sweet chestnut (<i>Castanea sativa</i>)

Note: based on British National Vegetation Classification floristic tables (Rodwell, 1991). *Species widely suffering from pest and disease problems in Great Britain.

and powdery mildews. Across Europe, oak has historically under-gone periods of dieback, which was first reported in Germany in 1739–48 (Thomas, 2008). Widespread oak decline became a concern in the 20th century, particularly in Great Britain during the 1920s, then again in the 1990s. The reported mortality rates differ substantially, and the decline of an entire stand is a rare event. However, climatic extreme induced stress, particularly under climate change, is thought to increase the susceptibility of oak trees to pests and diseases. Indeed, changes in site suitability for oak as a result of UK climate change projections for 2050 are already occurring and reports of oak decline are noted from sites in England and Wales, south of a line between the Humber and Mersey rivers, with effects not likely to be seen in Scotland for several decades (PuRpOsE, 2019; Forest Research, 2020).

Oak supports a high diversity of species compared with other tree species (Southwood, 1961). Oak trees 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, 2020). It is therefore important to gain an understanding of which species are dependent on oak as well as the role of oak in woodland ecosystem functioning. Such a study will allow assessments to be made of the impact of oak declines on woodland ecosystems and for mitigation measures to be put into place.

Aims

This Research Note presents a study of the ecological value of oak based on the attributes of ecosystem functions, and the biodiversity the tree supports. The Note includes the results of case study investigations of oak woodlands, their biodiversity, management and the potential use of woodland diversification to mitigate the ecological impacts of decline in the abundance of oak. In addition, this Note aims to identify options for management of oak woodlands to sustain ecosystem functions and biodiversity. Options are considered within the context of historical oak woodland management, and changes in oak suitability and health under current and future climatic conditions.

Methods

Information was gathered as part of the three-year Protect Oak Ecosystems (PuRpOsE) project (2016–9). Literature on the biodiversity associated with oak trees, and the ecological function oak performs, were reviewed (Mitchell *et al.*, 2019). The resulting information was applied to oak woodland case study sites across Great Britain to meet an objective of sustaining local oak-associated biodiversity. The case study development followed the five-step process proposed for conservation management responses to the loss of ash from UK woodlands (Broome and Mitchell, 2017). The five steps involved were compilation of a local biodiversity list, identification of the priority species (usually the species most dependent on oak), identification of alternative tree and shrub species (which could also support oak-associated biodiversity), assessing the woodland resource and the potential to manage for oak or alternative tree species. Finally, a management approach focusing on supporting oak-associated biodiversity under a scenario of oak decline is proposed for each case study site.

Ecological value of oak

Biodiversity supported by oak trees

Oak-associated species are those that use oak trees as a food source (e.g. many insects and some mammals), a place to breed/nest (e.g. some birds), a habitat in which to live (e.g. epiphytic bryophytes and lichens) or in which to hunt for food (e.g. insects and birds that feed on other oak-associated insects). An extensive search was performed of both published and grey literature, together with unpublished information, which identified those species that use pedunculate or sessile oak (oak-associated species) in Great Britain and the nature of this association. The search was confined to six taxon groups: birds, bryophytes, invertebrates, fungi, lichens and mammals (note that algae, bacteria and other microorganisms were excluded).

The level of association of each species with pedunculate or sessile oak within Great Britain was recorded as 'obligate', 'high', 'partial', 'cosmopolitan' or 'uses', along with the age class of the oak (see Box 1 for definitions).

In total, 2300 species were found to be associated with oak, consisting of 38 bird species, 229 bryophytes, 108 fungi, 1178 invertebrates, 716 lichens and 31 mammals. Of these 2300 species, 326 were obligate species (found only on oak), consisting of 57 fungi, 257 invertebrates and 12 lichens (Figure 1). Examples of oak obligate species include the moths oak lutestring, great oak beauty and oak nycteoline; the fungi oak polypore, oak leaf blister and oak mildew; and the lichens *Arthonia byssacea*, *Calicium adpersum* and *Sclerophora farinacea*. There were 229 species classified as highly associated with oak (i.e. rarely found on other tree species), consisting of 51 fungi, 104 invertebrates and 74 lichens, for example, the beetles oak leaf-roller, cobweb beetle and twig cutter. In total, 555 obligate and highly associated species were considered to be most at risk from a decline in oak as they do not use, or rarely use, other tree species. All the information about species that use oak is available in a Microsoft Excel file called OakEcol at www.hutton.ac.uk/oak-decline.

The number of oak-associated species varies regionally, with southern England generally having the highest numbers (Figure 2). In the most species-rich sites across Great Britain, as many as 42 obligate and 113 highly oak-associated species were estimated to be present at one site in southern England, 36 and 52 at one site in Wales, 25 and 18 at one site in northern England and 38 and 9 at one site in Scotland, respectively.

All stages of oak growth, from acorn through to deadwood, support oak-associated species, but mature and veteran trees support the greatest diversity (Figure 3). Sapling, pole, mature and veteran oaks support most of the obligate species, and mature and veteran oaks support most of the highly associated species. Deadwood is also an important habitat, supporting 700 oak-associated species.

Ecosystem functions of oak

Trees influence the environment around them by casting shade, adding leaves, deadwood and roots to the woodland floor and through below-ground interactions between soil organisms and the tree roots. These processes influence litter decomposition, nutrient cycling, hydrology and the interactions between other organisms and successional processes within the woodland. Such processes are termed ecosystem functions, which help to maintain a typical set of site conditions and a community associated with that species of tree.

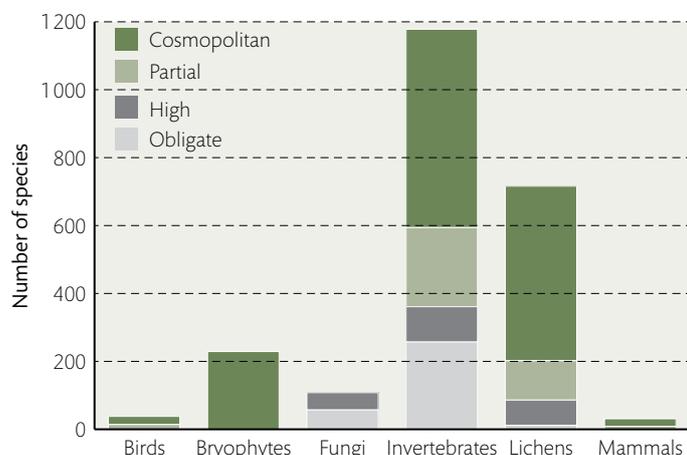
Box 1 Definitions followed in the study relating to oak (pedunculate and sessile) in Great Britain.

Species association	Use made of oak by species (includes species dependent on other species that use oak, such as parasites and some predatory insects)
Obligate	Unknown from other tree species
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

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.

Age class/growth stage	Characteristic features
Seed	Acorn
Seedling	Oak trees ≤ 1 year old
Sapling	Oak trees < 2 m in height
Pole	Oak trees > 2 m in height and < 50 years old
Mature	Oak trees > 2 m in height and < 3 m in girth. Do not have veteran tree characteristics (e.g. lots of holes, rotten wood)
Veteran	Veteran, ancient and notable trees: defined as large girth (usually > 3 m, taking into consideration environmental conditions) with at least 3 veteran attributes (e.g. deadwood in the trunk, dead branches, have fallen wood around base, rot holes, water pockets, seepage lines, hollows in trunk or major limbs)
Dead	Entirely dead oak tree, standing or fallen

Figure 1 Oak-associated species by taxon group (excluding algae, bacteria and other microorganisms) and level of association with oak.



Note: for fungi, only obligate and highly associated species were assessed.

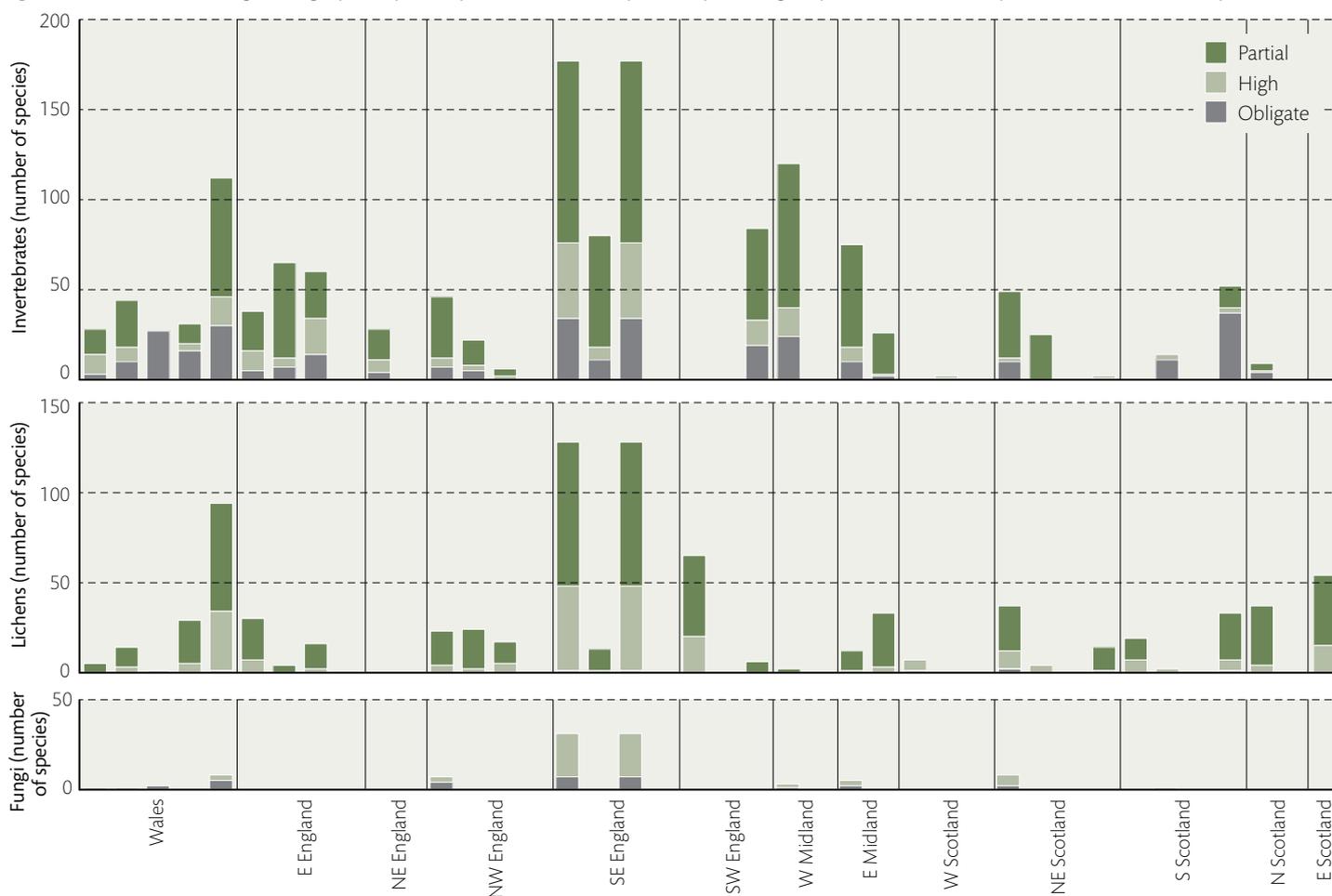
The fertility of woodland soils is partly determined by the quality of the leaf litter from tree species. A comparison has been made between oak and 16 other tree species for leaf litter decomposition (a direct measure of function) and metrics related to function (leaf litter chemistry and soil chemistry). For the functions studied, oak is in the middle of the range (Figure 4). At one end of the spectrum are species like ash, alder and sycamore, which have low levels of carbon and lignin and high levels of nitrogen in their leaf litter, leading to fast leaf litter decomposition and soils with low levels of carbon and high

levels of nitrogen. At the other end of the spectrum are species such as western hemlock and western red cedar with high levels of carbon and lignin and low levels of nitrogen in their leaf litter, leading to slow leaf litter decomposition and soils with high levels of carbon and low levels of nitrogen.

The role of other woodland trees in supporting oak biodiversity

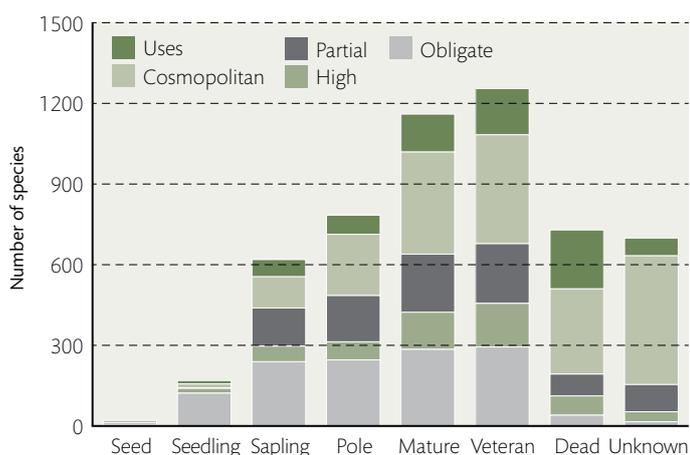
The increased use of additional tree species in mixtures to diversify woodlands is a measure proposed for the adaptation of woodlands and forests to increase resilience to environmental change. A 'solution' to reduce the ecological impact caused by the decline of oak is to encourage establishment of other, ecologically similar, tree species. A recent analysis considered how many oak-associated species were supported by other tree species (Mitchell *et al.*, 2019). This review included native and introduced trees already present in native British woodlands. Although not assessed as hosts for all oak-associated species, we know from earlier work (Broome and Mitchell, 2017) that shrubs provide habitat for many woodland species that use both oak and ash trees as habitat and we consider this partial dataset (627 of the 2300 oak-associated species) in our analysis. All the information about the use made by oak-associated species of 30 other tree species is available in the OakEcol file.

Figure 2 Numbers of obligate, highly and partially oak-associated species by taxon group considered to be present at the case study sites.



Note: The taxon groups shown (invertebrates, lichens, fungi), are the most frequently represented at the case study sites in the 14 National Forest inventory regions in Great Britain.

Figure 3 Stages of oak growth used by oak-associated species (birds, bryophytes, fungi, invertebrates, lichens and mammals, but excluding algae, bacteria and other microorganisms).



Typical tree species of oak sites

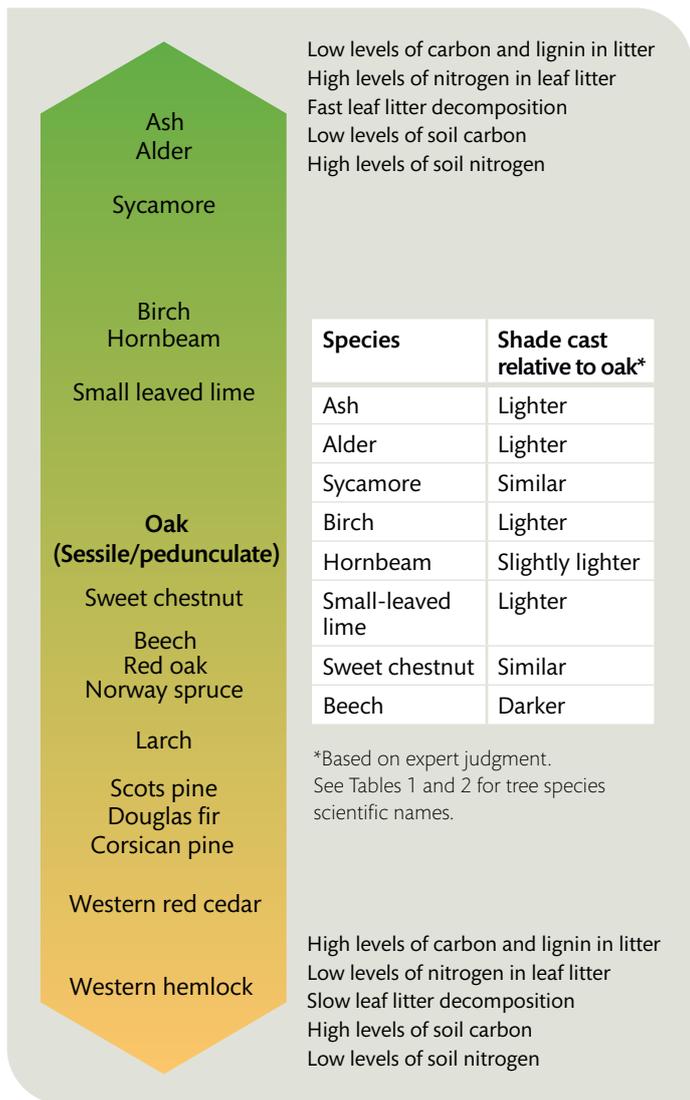
We have identified twenty-one native and long naturalized tree species other than oak (Table 1), as being suitable to establish as components of oak woodlands. Analysis showed that ash is known to support the greatest number (613) of oak-associated

species (28%) (Figure 5a). Beech had the second greatest number (347) of oak-associated species (16%), followed by sycamore (13%) then alder (11%). Of the remaining 19 tree species assessed, each is known to support less than 10% of oak-associated species. The extent of the knowledge on the use made by oak-associated species of the 21 tree species was good. For each tree species (except wild service tree), data on the use (or non-use) were available for more than 77% of the oak-associated species. Current native woodland policy would limit the planting of some of these tree species and thus reduce the options for alternative hosts for the oak-associated species. For example, only half of the tree species in this analysis are considered to be native and suitable in Scotland, whereas all (with the exception of hybrid lime) are considered native in some or all regions of England and Wales (Ditchburn *et al.*, 2020).

Woodland shrubs

Six common shrub species – hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*), elder (*Sambucus nigra*), blackthorn (*Prunus spinosa*), goat willow (*Salix caprea*) and privet (*Ligustrum vulgare*) – that appear as components of oak woodland communities are

Figure 4 The functioning of oak compared with other tree species.

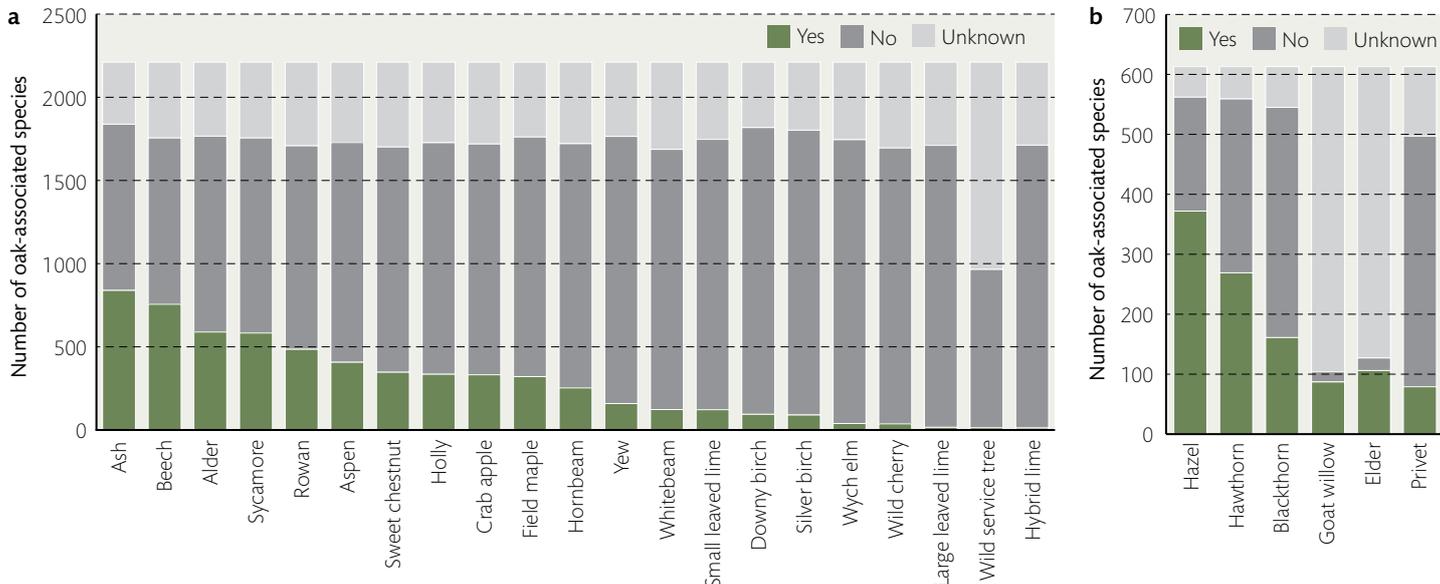


considered in this Note. Of the 613 oak-associated species for which we had data to assess, these shrubs have been shown to support 458 species. Hazel and hawthorn support the greatest number of the oak-associated species investigated (each approximately 50%) (Figure 5b). The majority of species that use shrubs as hosts are lichens, bryophytes and invertebrates. Shrubs support 26 highly and 67 partially oak-associated lichens, two highly and 28 partially oak-associated invertebrates, as well as 52 oak-associated bryophytes. The bryophytes are, along with the remaining 244 lichen and 23 invertebrates, classed as having a cosmopolitan association with oak.

Other tree species occurring on oak site types

Nine other species (non-native oaks, native conifers and non-native conifers) known to grow on oak site types, and for which there is a reasonable level of forestry management experience in Great Britain, were also considered (Table 2). Of the non-native oaks, Turkey oak is an established species in woodlands and plantations, and red oak has undergone limited trials and appears to be well suited to lighter soils. The soils associated with broad-leaved woodlands with an oak component are typically brown earths, surface water gleys and rankers and podzols in both cool-wet and warm-dry climate zones (Pyatt, Ray and Fletcher, 2001). The seven species of conifer considered in this analysis have been planted on similar sites in Great Britain; all are non-native with the exception of Scots pine. In total, nine species (Table 2) were assessed as hosts for oak-associated species. Scots pine was found to support the most oak-associated species (203; 9% of all oak-associated species) (Figure 5c), followed by Turkey oak (130; 6%) then Norway spruce (71; 3%). With the

Figure 5a-b Number of oak-associated species that are known to use (Yes) or not use (No) the 21 tree species in woodlands where oak is frequent (a) and five shrub species occurring in oak woodlands (b).



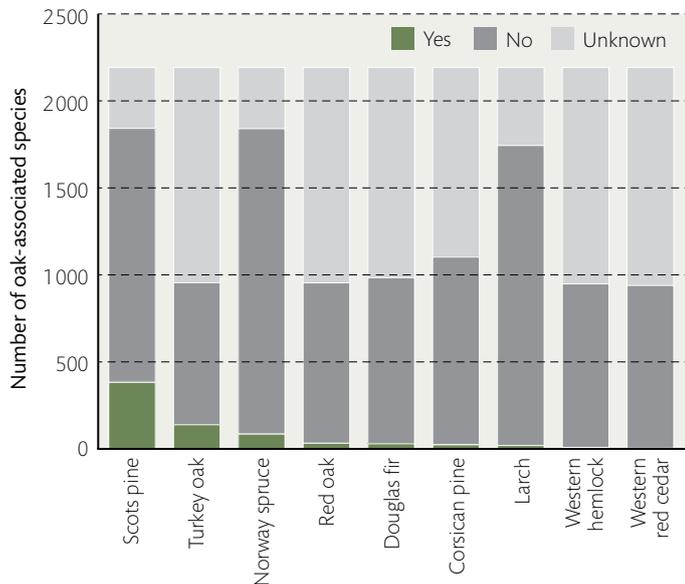
Note: 'Unknown' indicates where no data were available on a species use of the tree or shrub. For Figure 5b data are presented for a subset of 613 of the 2300 oak-associated species. See Table 1 for tree species scientific name and see text for shrub species scientific names.

Table 2 Tree species that will grow on oak site types and for which there is reasonable forest management experience in Great Britain.

Introduced conifers	Introduced oaks
Norway spruce (<i>Picea abies</i>)	Turkey oak (<i>Quercus cerris</i>)
Scots pine (<i>Pinus sylvestris</i>)	Red oak (<i>Quercus rubra</i>)
Corsican pine (<i>Pinus nigra</i> spp. <i>Laricio</i>)*	
Douglas fir (<i>Pseudotsuga menziesii</i>)	
Western red cedar (<i>Thuja plicata</i>)	
Western hemlock (<i>Tsuga heterophylla</i>)	
Larch (<i>Larix</i> spp.)*	

Note: These species have been assessed for their suitability to support oak-associated biodiversity. Scots pine is native in parts of Great Britain.
*Species widely suffering from pest and disease problems in Great Britain.

Figure 5c Number of oak-associated species that are known to use (Yes) or not use (No) the nine tree species introduced on sites that support oak.



Note: 'Unknown' indicates where no data were available on a species use of the tree. See Table 2 for tree species scientific names.

exception of Scots pine, Norway spruce and larch, knowledge of their use pertains to only half of the oak-associated species.

Oak woodland case studies

A sample of 30 oak woodlands were surveyed across Great Britain (Figure 6) to describe their composition and structure, and to consider management opportunities for maintaining conservation value. The sites had all been woodlands for more than 200 years; some were of plantation origin but others were classed as ancient semi-natural woodlands and had a longer history of ecological continuity. Sites were primarily selected as those managed for conservation, to represent a range of sizes and ownerships, and were distributed across typical site types found in Great Britain. Five of the oak woodlands were already showing decline, those located in southeast (Stratfield Brake, Island Thorns) and east England (Epping, Monks Wood and Writtle Forest).

Figure 6 Location of the 30 case study sites selected to be representative of the 14 National Forest Inventory (NFI) regions in Great Britain.



Note: for details, see individual case study reports at www.hutton.ac.uk/oak-decline.

Biodiversity present

The potential biodiversity value of the sites was assessed by identifying the pool of oak-associated species local to the site. Data were obtained from the National Biodiversity Network (NBN) Atlas (nbnatlas.org/) by searching for records of oak-associated species within defined oak woodland site boundaries or within 5 km of the woodland. Species lists from the NBN were added to other lists available in site documentation. Invertebrates, lichens and fungi make up most of the obligate, highly and partially associated species at the sites (Figure 2). Between 5% and 15% of the oak-associated species at the different sites are either highly associated with oak or obligate on oak. Maintaining a presence and continuity of oak at these sites may therefore be important for the survival of these species. Invertebrates make up most of the oak obligate species and half of the highly associated species present, with the remainder of the highly associated species at the sites being lichens.

Case study composition and structure

The survey information has been used to classify the woodlands according to six characteristic stand development structures (Broome *et al.*, 2017). The stand structures reflect the growth stages of oak trees present as well as their spatial arrangement, and the diversity and structure of co-occurring woody species.

Currently, oak makes up more than 70% of the canopy at most of the case study sites and, on the whole, canopy structures are diverse (Table 3). Most of the woodlands (60%) can be described as having a closed canopy, multiple strata stand structure (type F; Table 3), in which oak is at different growth stages. The remainder of woodlands are equally spread among three of the other characteristic stand structures: open canopy (type D), with mature and veteran oaks; open understory (type C), with mainly mature and veteran oaks; and a closed canopy, few strata stand structure (type E), with mainly pole and mature oaks (Table 3). Types A and B (shrub structures) were not present in the sample of case study woodlands. All woodlands surveyed were in the later stages of stand development (stem exclusion, understory re-initiation or old growth stand development; Table 4) (Oliver and Larson, 1996), which provides opportunities for management favouring oak.

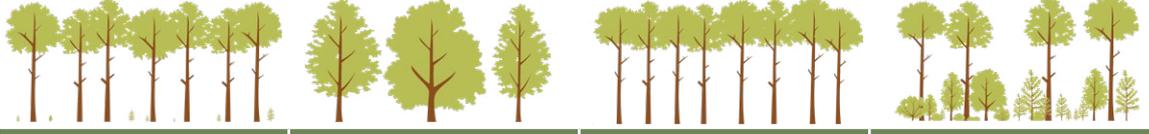
Oak dominance may not be a natural state for these woodlands. We found that all the study woodlands had been managed historically to some extent, and that management has changed the species composition of former natural woodlands.

For example, from management records dating back to the 12th century, many woodlands were coppiced to provide timber from oak standards, fuel and fencing from the coppiced poles, and also periodic grazing land four to five years after the coppicing of panels, on a twenty-year rotation. These records show a gradual change in woodland composition over the centuries with pedunculate oak becoming more dominant. This change, driven by coppice management, occurred because the higher quality standard trees of pedunculate oak chosen for timber produced much of the seed, and the proportion of oak regeneration in the stand increased relative to the other tree species.

Current management

Overall, active management of the oak component of the case study woodlands is occurring (Figure 7). Many of the woodlands with type C and E stand structure are subject to silvicultural management favouring actions for oak (e.g. thinning of the overstorey to reduce competition between tree canopies). This concurs with the stage of stand development where canopy competition is likely. Woodlands of these stand structure types are also the focus of actions to regenerate or plant the next cohort of oak, probably in response to the lack of understory structure in these woodlands. Woodlands of type E stand structure are subject to management to promote other native tree species. These woodlands generally have the least diverse overstorey composition (oak at 90% of canopy). Removal of non-native species is a widespread activity in all the woodland

Table 3 Stand characteristics and composition of case study woodlands organised by stand structure type: open understory [C], open canopy [D], closed canopy – few strata [E], closed canopy – multi strata [F].



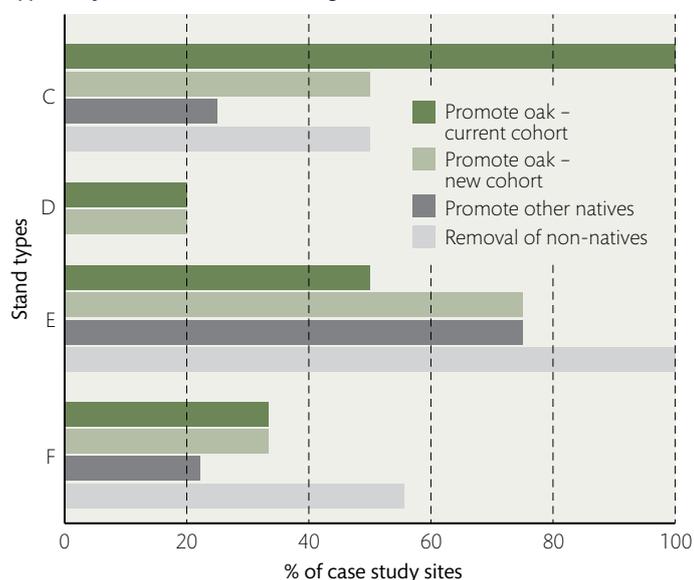
	C. Open understory structure	D. Open canopy structure	E. Closed canopy - few strata	F. Closed canopy - multiple strata
Canopy				
% of oak in canopy: median (min.–max.)	70 (60–100)	90 (70–100)	90 (80–100)	80 (30–100)
Other frequent species (number of less frequent species per site)	Ash, birch (≤ 2)	Beech, birch, nobel fir	Birch	Ash, birch (≤ 4)
Understorey				
Most frequent species (number of less frequent species per site)	Holly, hazel, rowan, ash, birch, hawthorn (≤ 1)	Holly (≤ 4)	Holly, rowan, ash (≤ 1)	Holly, hazel, birch, rowan (≤ 5)
% of sites with established oak regeneration (% of sites with oak seedlings)	50 (25)	40 (40)	0 (100)	28 (61)

Note: stand structure type A (dense low shrub layer) and B (dense high shrub layer) were not present in the sample of case study woodlands.

Table 4 Characteristics of stand types represented by the case study sites and the relationship with woodland management (Broome *et al.*, 2017).

Stand type	Stocking density		Stem exclusion	Understorey re-initiation	Old growth	Stand definition	Silvicultural notes
	Low	Medium-high					
C	✓	✓ Browsed	✓	✓	✓	Stands with no or little low shrub or woody vegetation (i.e. <5 m of the ground).	At high stocking densities, the shade cast by the overstorey will maintain the open understorey conditions, but at lower densities, grazing (or heavy browsing by deer) will be necessary. Generally has good overall canopy cover with more trees and smaller gaps between them than type D; grazed upland oak woods are a typical example of this type.
D	✓	X	X	✓	✓	Woodland with significant gaps between the crowns of individual trees. Such trees may be open-grown with spreading canopies and often have relatively high amounts of dead/decaying wood.	Typical wood pasture where grazing (or heavy browsing by, for example, deer) will be necessary to maintain open understorey conditions.
E	X	✓	✓	✓ (early)	X	Stands where the canopy layer is relatively simple; often associated with single-aged, mid-growth phases.	Is often the typical structure throughout much of the rotation for stands managed using a thin and clearfell system. Suitable management can transform these stands into others having greater variety in the shrub and understorey strata.
F	X	✓	X	✓ (late)	✓	Stands where the canopy layer is relatively complex forming several foliage strata often associated with more mature growth phases. Multiple strata could be derived from mixtures of trees of different ages or from high canopy depth within individual trees.	Such structures are likely to arise when using methods of continuous cover forestry, which create conditions allowing the development of a patchwork of shrubs and regenerating understorey trees beneath the overstorey.

Figure 7 Percentage (%) of case study sites in each stand structure type subject to woodland management.



Note: see Table 3 and Box 2 for descriptions of stand types C, D, E and F.

types, except for woodlands with type D stand structure, which are generally of low basal area or stocking density.

Oak establishing from regeneration is only reported from a subset of sites and oak seedling presence is not universal (Table 3); in many cases this may be attributable to deer browsing and other mammals.

Options to maximise biodiversity

In the future, oak in sites in southern and eastern England will be particularly impacted by climate change. In preparation for this, oak decline management options in these and other 'oak stressed' regions include maintaining native oak through thinning and regeneration (Table 5). Where forest policy allows, the planting of a more southerly oak provenance (sourced from within 2 degrees of latitude) can be considered, particularly in situations where there is a likelihood that acclimation of the local provenance will not keep pace with the rate of climate change (Whittet *et al.*, 2019). This may be the case where natural regeneration is difficult to achieve and where collecting and growing on locally sourced oak seed and seedlings for planting out is not feasible. In all cases, best practice should be followed, with appropriate site preparation, tending and pest and deer management control.

If oak were lost from woodlands, obligate oak-associated species would also be lost. We considered tree species diversification options for case study woodlands with the primary aim of providing alternative host species for the most vulnerable oak-associated species, that is, those which are highly and partially associated with oak. Thirty tree species under consideration (Tables 1 and 2) were assessed as hosts for all of the 2300 oak-associated species. Those tree species with the potential to support the suite of oak-associated

Table 5 Woodland management options for the regions in southern and eastern England selected with the primary objective of supporting oak-associated species (other objectives may influence species choice).

Region	Case study site	Crown thinning of oak	Oak regeneration*	Planting southerly oak provenance	Establish other native and naturalised species
Southwest England	Britty Common	X	✓ by natural regeneration	✓	✓ sycamore, beech, alder
Southeast England	Island Thorns	X	✓ by natural regeneration	✓	✓ sycamore, sweet chestnut
	Stratfield Brake	By ash loss	✓ by natural regeneration	X	✓ alder
	Foxhunting	✓	✓ by planting and natural regeneration	✓	✓ beech, sweet chestnut
East England	Epping	✓	✓ by natural regeneration	✓	✓ birch, sycamore
	Writtle	✓ + by ash loss	✓ by natural regeneration	X	✓ hornbeam, beech, birch, field maple, sweet chestnut, alder
	Monks wood	By ash loss	✓ by natural regeneration	X	X
East Midlands	Abbeydale	✓	✓ by natural regeneration	X	✓ birch, rowan, wych elm, alder
West Midlands	Sutton Park	X	✓ by natural regeneration	X	✓ birch, rowan, beech
	Newlands Wood	✓	✓ by planting and natural regeneration	X	✓ beech

Note: Woodland management options may not be appropriate to apply to all sites or for meeting other management objectives.

Region = National Forest Inventory region (Figure 6). *recommended in all regions with the following actions to assist oak regeneration and establishment:

- Ground preparation (e.g. ground scarification to establish a suitable seed bed for natural regeneration).
- Vegetation control (e.g. of vigorous ground vegetation that competes with young oak seedlings and saplings).
- Reducing grazing/browsing to enable natural regeneration to survive (see individual case study reports www.hutton.ac.uk/oak-decline).

species present on a site were identified. Non-natives were included, but in practice may be deemed as inappropriate in meeting national (e.g. Scottish) policies or other conservation objectives.

The tree species were first assessed using Ecological Site Classification (Pyatt, Ray and Fletcher, 2001; www.forestdss.org.uk/geoforestdss) regarding their suitability to establish and grow on the specific site (soil type, current and future climate); ash was excluded from this analysis on the basis of its current rapid decline in Great Britain. The minimum number of site-suitable species that collectively supported the greatest diversity of oak-associated species were selected. Tree species were chosen in the order from the highest to the lowest number of additional oak-associated species they supported. This process was repeated until the most suitable five or six tree species were identified, or until the addition of extra tree species would only support one additional oak-associated species. For example, in the 'oak-stressed' region of east England (sites 5, 6 and 7), diversifying the woodland by planting the following species (from most to least beneficial host species) would support at least 30% and 70% of the highly and partially oak-associated species, respectively, at each site:

- Site 5 (Epping): beech, sycamore, small-leaved lime, Turkey oak and Scots pine, alder;
- Site 6 (Monks wood): small-leaved lime, beech, sycamore, alder and Scots pine;
- Site 7 (Writtle): Turkey oak, beech, downy birch, alder and hornbeam.

We suggest planting options for case study sites in the five regions where climate projections suggest the greatest proportion of oak woodlands will be impacted and stressed by 2050 (Table 6). By planting all the beneficial tree and shrub species listed in Table 6, the same biodiversity outcomes described above for sites 5, 6 and 7 would be achieved for all sites. Introduction and management of the selected species on each site should take account of site conditions and site quality changes across the woodland. In addition, species compatibility must be taken into consideration, for example, light-demanding species should be planted in groups or patches, and not in an intimate mixture with shade-tolerant species where they would not thrive. Information about all the sites is provided online in [Supplementary Table 6s](#).

Options to maintain ecosystem functions

Identifying tree species to provide similar ecosystem functions (with respect to soil nutrient cycling) to oak is not as challenging as selecting species to support oak-associated biodiversity. Replacing oaks with trees with soil fertility and shade-casting effects like oak helps to maintain the communities associated with oak woodlands. As the nutrient and lignin composition of oak leaves in litter produces soils of average fertility, several other broadleaved trees species can substitute for oak. For example, sweet chestnut and beech are similar to oak with respect to maintaining the soil fertility, but cast more shade than oak. Small-leaved lime and hornbeam give rise to more fertile soils and cast slightly less shade (Figure 4). Where these alternative species options are considered native and therefore

Table 6 Planting options selected primarily for supporting oak-associated species in regions where oak woodland is most likely to be affected by the impacts of climate change in the next 30 years.

Region	Case study site	Species to include in the planting mixture that are beneficial for oak-associated species		ESC AT	ESC Expos.	ESC MD	ESC SMR	ESC SNR	Soil type
		Trees	Shrubs						
Southwest England	Britty Common	Alder, sycamore, Scots pine, beech	Hazel, hawthorn, blackthorn, elder, goat willow, privet	2 512	11	177	Very moist	Medium	Surface water gley
Southeast England	Island Thorns	Beech, Scots pine, small leaved lime, Turkey oak, alder, sycamore	Hazel, hawthorn, blackthorn, goat willow	2 732	10	226	Very moist	Poor	Sandy ground water gley
	Stratfield Brake	Turkey oak, beech, alder, sycamore, downy birch, hornbeam	Hazel, hawthorn, blackthorn, elder, goat willow	2 664	13	226	Very moist	Medium	Surface water gley
	Foxhunting	Beech, Scots pine, small leaved lime, Turkey oak, alder, sycamore	Hazel, hawthorn, blackthorn, elder, goat willow, privet	2 859	10	243	Very moist	Medium	Surface water gley
East England	Epping	Beech, sycamore, small leaved lime, Turkey oak, Scots pine, alder	Hazel, hawthorn, blackthorn, elder, goat willow	2 646	13	252	Very moist	Medium	Surface water gley
	Monks Wood	Small leaved lime, beech, sycamore, alder, Scots pine	Hazel, hawthorn, blackthorn	2 704	11	250	Very moist	Medium	Surface water gley
	Writtle	Turkey oak, beech, downy birch, alder, hornbeam	Hazel, hawthorn, blackthorn, elder	2 726	12	265	Very moist	Medium	Surface water gley
East Midlands	Abbeydale	Turkey oak, small leaved lime, beech, alder, sycamore, downy birch, hornbeam	Hazel, hawthorn, blackthorn, elder, goat willow	2 368	9	190	Very moist	Medium	Surface water gley
West Midlands	Sutton Park	Turkey oak, small leaved lime, beech, sweet chestnut	Hazel, hawthorn, blackthorn, elder	2 417	13	189	Slightly dry	Poor	Brown earth/podzolic brown earth
	Newlands Wood	Turkey oak, small leaved lime, beech, downy birch, aspen	Hazel, hawthorn, blackthorn, elder	2 451	12	188	Very moist	Medium	Surface water gley

Note: Beneficial trees species are matched to site type and for a projected climate of the 2050s. Beneficial tree species may not be appropriate in meeting other management objectives. Information about all sites is provided in Supplementary Table 6s.

Region = National Forest Inventory region (Figure 6). Soil type = interpreted from soilscape type, soil association and series for each location (www.landis.org.uk).

Abbreviations: AT, annual accumulated temperature >5°C; ESC, Ecological Site Classification (Pyatt, Ray and Fletcher, 2001; www.forestdss.org.uk/geoforestdss/); Expos., score of exposure or windiness of site; MD, moisture deficit; SMR, soil moisture regime; SNR, soil nutrient regime.

permissible for planting in native woodlands, only small shifts in ground flora species composition may occur. Ultimately, the impact on oak ground flora depends on the mixture of beneficial species replacing oak and, importantly, the density at which the trees are established.

Conclusions

We propose that management actions should focus on promoting oak where conserving oak-associated species is the objective to support biodiversity. Appropriate management actions are not currently being carried out on all sites, and the rate of successful regeneration is generally low. Although we highlight the promotion of oak, past management (coppice abandonment and, latterly, woodland conservation) may have contributed to a much higher abundance of oak in the canopies of ancient semi-natural woodlands than occurred in

unmanaged natural woodland stands. Plans exist for many case study sites to diversify woodlands, and sometimes these include those species that have been shown to support some oak-associated species. However, this research has shown that a wide range of beneficial tree species are needed to support even a small proportion of oak-associated species. This constraint is exacerbated by the ongoing loss of ash (ash supports 613 of the oak-associated species), and introducing ash to woodlands cannot currently be considered a realistic mitigation option. However, there is a strong indication that shrub species such as hazel, hawthorn and elder are important in supporting oak-associated biodiversity. Maintaining the broader community associated with oak woodlands (e.g. the ground flora) may not pose such a challenge as the ecosystem functions performed by oak (e.g. soil nitrogen cycling) are replicated by other broadleaved trees often found in oak woodlands.

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Enquiries relating to this research should be addressed to:

Alice Broome
Forest Research
Northern Research Station
Roslin, Midlothian, EH25 9SY

+44 (0)300 067 5915

alice.broome@forestresearch.gov.uk
www.forestresearch.gov.uk

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