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Not all trees are equal: Which tree species is more important than tree species diversity when considering provision of resilience for tree-associated biodiversity?

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Summary:
Tree species diversification is often proposed as a key mechanism to provide resilience in forests. From a biodiversity perspective, the proposed aim of diversification is the continued support of tree-associated species even if some tree species decline in abundance due to climate change or pests and pathogens. Using existing datasets on the species associated with ash (*Fraxinus excelsior*), oak (*Quercus petraea/robur*), Scots pine (*Pinus sylvestris*) and Sitka spruce (*Picea sitchensis*) in the UK, we explore the questions of how much diversity is enough and what is the relative importance of tree diversity versus the tree species composition? The work shows that while diversification does provide functional redundancy and increased resilience for tree-associated biodiversity, the level of resilience provided critically depends on which tree species are within the mix. Therefore, when planning diverse tree species mixes with the objective of supporting tree-associated biodiversity and providing resilience, it is crucial that consideration is given to which tree species are within the mix. This consideration is rarely discussed within policy documents and guidance.

Introduction

Our trees are increasingly threatened by climate change and a rapid increase in non-native tree pests and pathogens (Broadmeadow et al., 2005; Boyd et al., 2013). Yet at the same time, trees are an important component of government policies to both mitigate climate change and reverse the biodiversity crisis, in addition to the role they play in the provision of timber and other ecosystem services (Defra, 2018; HM Government, 2018; Scottish Government, 2019; The Scottish Government, 2024; Department of Agriculture, 2025). The long lifespan of trees and the lead-in time before they deliver many of these benefits presents challenges when considering the uncertainties of future environments with respect to both climate and pests and pathogens. The general advice is not to 'put all your eggs in one basket' and plant a range of tree species. Diversification of forest tree species is therefore currently viewed as key to providing resilience given all these uncertainties (Atkinson et al., 2022). The theory is that if one species declines in abundance, other tree species will fill that role in the forest, be that providing timber, recreation, or supporting biodiversity. Ecologically, when one species can fulfil the role of another, this is termed functional redundancy.

From a biodiversity perspective, trees are foundation species, supporting a range of associated species that use the tree for feeding in, either directly or indirectly, or as a place to live, such as epiphytic lichens and bryophytes, or as a breeding or roosting site for some bats and birds. The level of association between any tree-associated species and a tree species can vary from being dependent on that tree to complete its life cycle (termed obligate), to using a wide variety of other tree species (termed cosmopolitan: see Mitchell et al., 2014a). For tree-associated species that are obligate or rarely use other tree hosts, a decline in their host tree species can drive an extinction cascade with tree-associated species going locally extinct or declining in abundance (Ellis et al., 2014; Hultberg et al., 2020). For example, Lõhmus and Runnel (2014) recorded the local extinction of an epiphytic lichen due to ash dieback

in Estonia. Populations of non-obligate species may also decline if suitable alternative hosts are not nearby. For example, at Mount Collins, USA, the death of Fraser fir (*Abies fraseri*) and eastern hemlock (*Tsuga canadensis*) due to balsam woolly adelgid (*Adelges piceae*) caused 9 of 11 common forest bird species to decline by an average of 41% (Rabenold et al., 1998). While in Australia, two species of marsupial 'mouse' (*Antechinus flavipes* and *Antechinus stuartii*) declined in response to changes in forest structure caused by *Phytophthora cinnamomi* (Cahill et al., 2008). Mitchell et al. (2022) showed that in the UK, suitable alternative hosts for ash- and oak-associated species are often not present locally, even if the site is suitable for those tree species to grow, extending the impact of tree species loss on biodiversity to non-obligate species.

Thus, going forward, planting diverse tree species mixes is suggested as a mechanism for providing resilience for tree-associated species, providing 'functional redundancy'. However, is it just the diversity of tree species that matters or is the tree species composition important? We explore this by assessing the suitability of different tree species mixes to support the tree-associated species found on ash, oak, Scots pine and Sitka spruce in the UK.

Method

We utilised four datasets which had collated lists of the species that use ash (Mitchell et al., 2014b), oak (Mitchell et al., 2019b), Scots pine (Mitchell et al., 2025a) and Sitka spruce (Mitchell et al., 2026b) in the UK. These datasets are desk-based studies collating data from quality-controlled databases, peer reviewed and grey literature. The datasets list the birds, bryophytes, non-lichenised fungi, invertebrates, lichens and mammals that use each of these tree species. Due to the large number of non-lichenised fungi which would be classified as 'cosmopolitan', all of the datasets acknowledge that only those fungi that are most tightly associated with the host are included. These datasets show that across the UK, ash hosts 953 species with 44 species only found on ash trees (obligate) (Mitchell et al., 2014a), oak trees support 2,300 species of which 326 species are obligate (Mitchell et al., 2019a), Scots pine supports 1,589 species of which 227 species are obligate (Mitchell et al., 2026a) and Sitka

Table 1. The tree species assessed as alternative hosts for the biodiversity supported by ash, oak (sessile and pedunculate), Scots pine and Sitka spruce.

Alternative tree		Host tree for which assessment was made			
Common name	**Latin name**	**Ash**	**Oak**	**Scots pine**	**Sitka spruce**
European silver fir	*Abies alba*	Yes	No	Yes	No
Pacific silver fir	*Abies amabilis*	No	No	Yes	Yes
Grand fir	*Abies grandis*	No	No	Yes	Yes
Noble fir	*Abies procera*	No	No	Yes	Yes
Field maple	*Acer campestre*	Yes	Yes	No	No
Norway maple	*Acer platanoides*	Yes	No	No	No
Sycamore	*Acer pseudoplatanus*	Yes	Yes	Yes	Yes
Horse chestnut	*Aesculus hippocastanum*	Yes	No	No	No
Italian alder	*Alnus cordata*	Yes	No	No	No
Common alder	*Alnus glutinosa*	Yes	Yes	Yes	Yes
Birch (downy or silver)	*Betula pendula* or *pubescens*	Yes	Yes	Yes	Yes
Hornbeam	*Carpinus betulus*	Yes	Yes	Yes	Yes
Shagbark hickory	*Carya ovata*	Yes	No	No	No
Sweet chestnut	*Castanea sativa*	Yes	Yes	Yes	Yes
Lawson cypress	*Chamaecyparis lawsoniana*	No	No	Yes	Yes
Hazel	*Corylus avellana*	Yes	No	Yes	No
Hawthorn	*Crataegus monogyna*	Yes	No	Yes	No
Japanese red-cedar	*Cryptomeria japonica*	No	No	Yes	Yes
Leyland cypress	*Cuprocyparis leylandii*	No	No	Yes	Yes
Beech	*Fagus sylvatica*	Yes	Yes	Yes	Yes
American ash	*Fraxinus americana*	Yes	No	No	No
Common ash	*Fraxinus excelsior*	N/A	Yes	No	No
Manchurian ash	*Fraxinus mandschurica*	Yes	No	No	No
Manna ash	*Fraxinus ornus*	Yes	No	No	No
Green ash	*Fraxinus pennsylvanica*	Yes	No	No	No
Holly	*Ilex aquifolium*	Yes	Yes	Yes	No
Black walnut	*Juglans nigra*	Yes	No	No	No
English walnut	*Juglans regia*	Yes	No	No	No
Juniper	*Juniperus communis*	No	No	Yes	No
Hybrid larch	*Larix* x *marschlinsii*	No	No	Yes	Yes
European larch	*Larix decidua*	Yes	Yes	Yes	Yes
Japanese larch	*Larix kaempferi*	No	No	Yes	Yes
Private	*Ligustrum vulgare*	Yes	No	No	No
Crab apple	*Malus sylvestris*	Yes	Yes	Yes	No
Roble	*Nothofagus obliqua*	No	No	Yes	No

spruce supports 564 species including 6 obligate species (Mitchell et al., 2025b).

In each of these datasets, the associated species that were not obligate or parasitic were assessed as to whether they did or did not use between 30 to 50 other tree and shrub species, termed alternative trees (Table 1). These alternative trees were trees that would grow in the same climatic and soil conditions as the current host tree (ash, oak, Scots pine, Sitka spruce) and were recommended as alternatives for either productive timber forests or for forests where nature conservation was the primary objective. For each of the four sets of associated species, we used this information to construct hypothetical tree species mixes to assess the proportion of tree-associated biodiversity that could be supported by different mixes of alternative trees. First, we progressively added tree species to the mix according to which tree species would support the greatest additional number of associated species, i.e. support species that were not already supported by trees in the mix. Second, we created a mix of those tree species that supported the least number of tree-associated species. Tree species were again progressively added to the mix, each time adding those tree species that would bring the least support to associated species. These two hypothetical mixes showcase the 'best-' and 'worst-case' scenario mixes.

Table 1. Continued.

Alternative tree		Host tree for which assessment was made			
Common name	**Latin name**	**Ash**	**Oak**	**Scots pine**	**Sitka spruce**
European hop-hornbeam	*Ostrya carpinifolia*	Yes	No	No	No
Norway spruce	*Picea abies*	No	Yes	Yes	Yes
Sitka spruce	*Picea sitchensis*	No	No	Yes	N/A
Lutz spruce	*Picea* x *lutzii*	No	No	Yes	Yes
Lodgepole pine	*Pinus contorta*	No	No	Yes	Yes
Black pine	*Pinus nigra* ssp. *laricio*	No	Yes	No	No
Maritime pine	*Pinus pinaster*	No	No	Yes	Yes
Ponderosa pine	*Pinus ponderosa*	No	No	Yes	Yes
Radiata pine	*Pinus radiata*	No	No	Yes	Yes
Scots pine	*Pinus sylvestris*	Yes	Yes	N/A	Yes
Plane	*Platanus* x *hybrid*	Yes	No	No	No
Black poplar	*Populus nigra*	Yes	No	No	No
Aspen	*Populus tremula*	Yes	Yes	Yes	Yes
Wild cherry	*Prunus avium*	Yes	Yes	Yes	Yes
Bird cherry	*Prunus padus*	Yes	No	Yes	No
Blackthorn	*Prunus spinosa*	Yes	No	Yes	No
Douglas-fir	*Pseudotsuga menziesii*	Yes	Yes	Yes	Yes
Caucasian walnut	*Pterocarya fraxinifolia*	Yes	No	No	No
Turkey oak	*Quercus cerris*	Yes	Yes	No	No
Sessile/pendunculate oak	*Quercus petraea* or *robur*	Yes	N/A	Yes	Yes
Red oak	*Quercus rubra*	Yes	Yes	No	No
Goat willow	*Salix caprea*	Yes	No	Yes	No
Grey willow	*Salix cinerea*	Yes	No	Yes	No
Elderberry	*Sambucus nigra*	Yes	No	No	No
Coast redwood	*Sequoia sempervirens*	No	No	Yes	Yes
Giant redwood	*Sequoiadendron giganteum*	No	No	Yes	Yes
Whitebeam	*Sorbus aria*	Yes	Yes	No	No
Rowan	*Sorbus aucuparia*	Yes	Yes	Yes	Yes
Service tree	*Sorbus torminalis*	Yes	Yes	Yes	No
Yew	*Taxus baccata*	Yes	Yes	Yes	No
Western red-cedar	*Thuja plicata*	Yes	Yes	Yes	Yes
Small-leaved lime	*Tilia cordata*	Yes	Yes	Yes	Yes
Large-leaved lime	*Tilia platyphyllos*	Yes	Yes	Yes	Yes
European lime	*Tilia vulgaris*	No	Yes	No	No
Western hemlock	*Tsuga heterophylla*	No	Yes	Yes	Yes
Wych elm	*Ulmus glabra*	Yes	Yes	Yes	No

Results

For all four host species (ash, oak, Scots pine, Sitka spruce), under both the best- and worst-case scenarios, increasing the number of alternative tree species in the mix increased the percentage of tree-associated species supported and hence the resilience provided (Figure 1 and Table 2). For a given number of tree species in the mix, a lower percentage of oak-associated species were supported than for the other tree species, because oak had the highest number of tree-associated species. Conversely, in the best-case scenarios, a higher proportion of Sitka-associated species were supported for any given number of tree species in the mix because Sitka spruce had the lowest number of tree-associated species.

There was a clear difference between the

best- and worst-case scenarios (Figure 1). In the best-case scenarios, a four tree species mix supported 91% of ash, 94% of Sitka spruce, 77% of oak and 80% of Scots pine non-obligate species. In contrast, in the worst-case scenarios a four species mix supported 11% of ash, 1% of oak, 11% of Scots pine and 5% of Sitka spruce non-obligate associated species. The most diverse mixes were ten tree species. In these mixes, under the best-case scenario, 95% of ash, 82% of oak, 83% of Scots pine and 96% of Sitka spruce non-obligate species were supported. This compared to 25% of ash, 5% of oak, 37% of Scots pine and 43% of Sitka spruce non-obligate species being supported under a worst-case scenario.

Under the best-case scenario, the rate of increase in the percentage of associated species rapidly plateaus. For Sitka spruce, this is at three tree species, but for the others the rate slows after five tree species (Figure 1).

Discussion

This work shows that while diversification does provide functional redundancy and increased resilience for tree-associated biodiversity, the level of resilience provided critically depends on which tree species are within the mix. Therefore, when planning diverse tree species mixes with the objective of supporting tree-associated biodiversity and providing resilience, it is crucial that consideration is given to which tree species are within the mix. This consideration is rarely discussed within policy documents and guidance.

Government targets for forest expansion are typically expressed as hectares of trees planted. For example, Scotland's Forestry Strategy has the ambition to increase forestry and woodland creation targets to 15,000 ha per year from 2024/25 (Scottish Government, 2019), while in England, the Environment Act 2021 led to legally binding targets for at least 16.5% of land in England to be covered by woodland and trees outside woodland by the end of

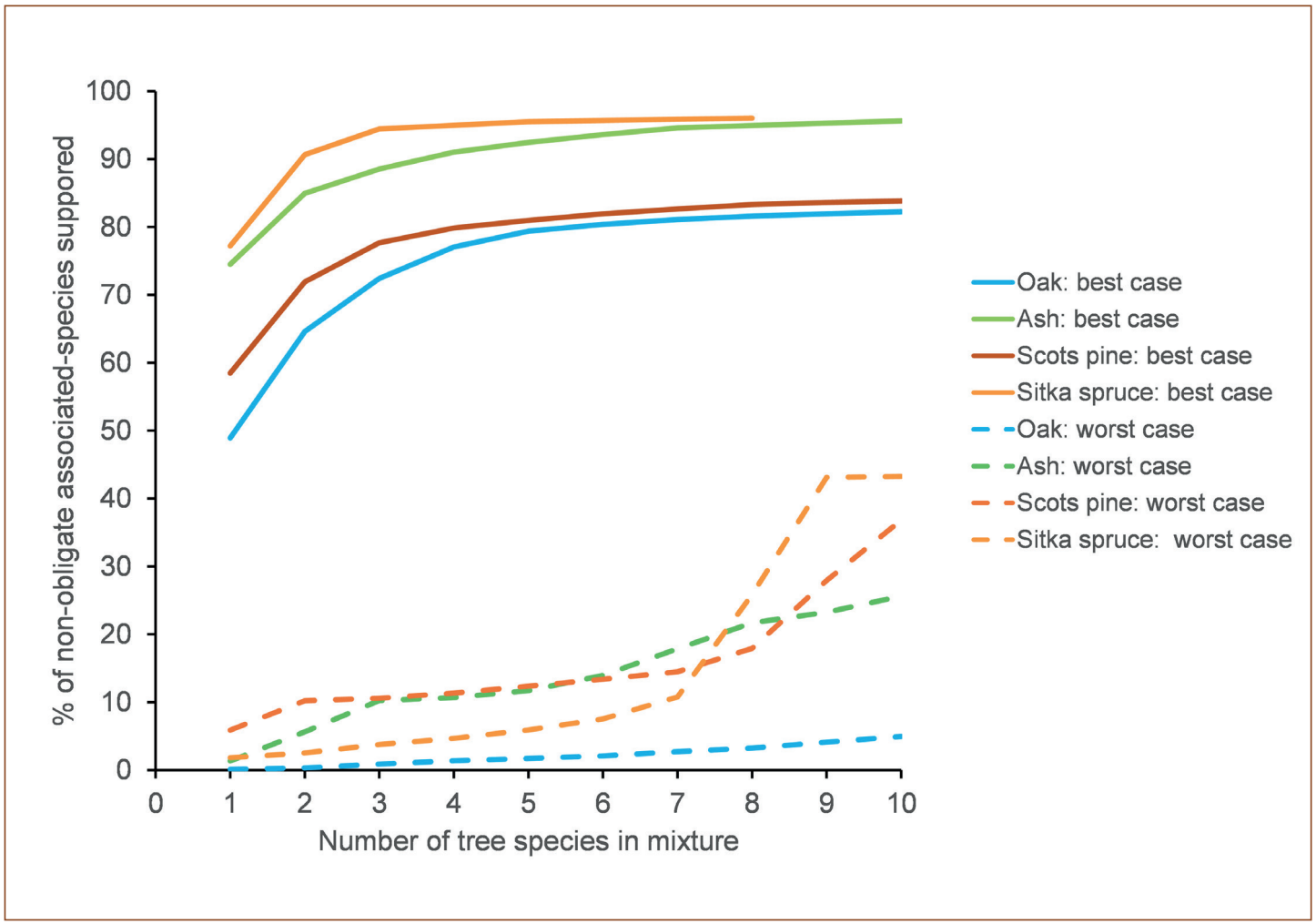


Figure 1. The percentage of non-obligate tree-associated species from ash, oak, Scots pine, and Sitka spruce supported by differing tree diversity mixes. In the best-case scenario, trees supporting the greatest number of associated species were selected, and in the worst-case scenario, trees supporting the lowest number of associated species were selected.

Table 2. The tree species and the order in which they were added to the mix to support the most (best-case scenario) and least (worst-case scenario) number of the species associated with oak, ash, Scots pine and Sitka spruce. The 'Additional species supported' is the number of additional associated species that the tree species supports by its addition to the mix, i.e. species not already supported by tree species in the mix. The numbers are just in relation to the number of oak, ash, Scots pine or Sitka spruce associated species and do not include species that may be associated with the alternative tree/shrub but are not associated with oak, ash, Scots pine or Sitka spruce.

Associated species with:	Order trees added	Best-case scenario		Worst-case scenario	
		Tree species	Additional species supported	Tree species	Additional species supported
Oak (2,064 non-obligate species)	1	Ash	940	Western red-cedar	2
	2	Birch	302	Western hemlock	4
	3	Turkey oak	150	Wild service tree	11
	4	Beech	89	Large-leaved lime	9
	5	Scots pine	45	Whitebeam	7
	6	Wych elm	19	European lime	7
	7	Common alder	14	European larch	12
	8	Aspen	9	Black pine	10
	9	Sweet chestnut	7	Red oak	17
	10	Wild cherry	6	Douglas-fir	16
Ash (909 non-obligate species)	1	Oak	663	Douglas-fir	12
	2	Wych elm	93	Western red-cedar	38
	3	Manna ash	32	Shagbark hickory	41
	4	Hazel	22	Caucasian walnut	4
	5	Beech	13	European hop-hornbeam	9
	6	Privet	10	Wild service tree	20
	7	Scots pine	9	Italian alder	35
	8	Holly	3	Norway maple	34
	9	Aspen	3	Small-leaved lime	14
	10	Blackthorn	3	Grey willow	21
Scots pine (1,362 non-obligate species)	1	Lodgepole pine	796	Roble	80
	2	Oak	183	Japanese red-cedar	59
	3	Norway spruce	78	Leyland cypress	5
	4	Sitka spruce	30	Coast redwood	10
	5	Birch	15	Lawson cypress	14
	6	Maritime pine	13	Western red-cedar	14
	7	European larch	10	Giant redwood	15
	8	Beech	9	Western hemlock	47
	9	Juniper	4	Hybrid larch	136
	10	Wych elm	3	Pacific silver fir	121
Sitka spruce (558 non-obligate species)	1	Scots pine	430	Japanese red-cedar	10
	2	Norway spruce	75	Leyland cypress	4
	3	Oak	21	Lawson cypress	7
	4	European silver fir	3	Western red-cedar	5
	5	Birch	3	Coast redwood	7
	6	European larch	1	Giant redwood	9
	7	Coast redwood	1	Western hemlock	18
	8	Rowan	1	Hybrid larch	84
	9	*		Noble fir	96
	10	*		Pacific silver fir	1

*No further tree species, of those assessed, will support additional associated species.

2050, and the Environmental Improvement Plan (EIP) sets a non-binding interim target to plant the equivalent of 34,000 ha in England by January 2028. While these targets aim to deliver a range of benefits that include not only biodiversity but also other goods and services, the implementation of these policies often assumes that all trees are equal and will deliver the same benefits. However, as illustrated by this work, what biodiversity benefits and which woodland species are supported will depend on which tree species are planted. The same area of trees may provide very different biodiversity benefits depending on the tree species composition of the forest.

Tree species diversity is just one type of diversity present within our forests that may aid resilience (Smith et al., 2025). How genetic and epigenetic diversity may influence the biodiversity supported is largely unknown. However, the diversity of monoterpenes (plant secondary metabolites) released by Scots pine trees, which show substantial genetically determined variation between individuals, has been shown to influence slug herbivory (O'Reilly-Wapstra et al., 2007) and the fungal endophyte composition (Schonrogge et al., 2022). Davies et al. (2014) showed that genotypic variation in aspen (*Populus tremula*) explained the community structure of associated epiphytes. Thus, there is also some evidence that tree genetic diversity will also influence the associated species supported.

Our analysis here is based on UK-wide data and assesses the biodiversity supported across the UK. The work shows how a diversity of trees across the UK may provide resilience for tree-associated biodiversity. Not all the species will be found at any one site nor on any one tree, and the mixes of trees in the different scenarios (Table 2) are unlikely to grow together at many sites. However, this UK-wide approach can be adapted to be implemented at a site level. When deciding which tree species to plant, one considers the soil properties at the site and which tree species will grow in the current and future climate at the site, for example through use of the Ecological Site Classification (Pyatt et al., 2001). When planting species mixes, one also needs to consider silvicultural aspects, such as which tree species will grow together in any mix (Kerr et al., 2020). This work is advocating a third step whereby, if the objective is to support local tree-associated biodiversity, one should also consider what biodiversity the proposed planting mix will support. Such considerations will increase the resilience provided to tree-associated biodiversity, rather than assume that any type of diverse woodland will benefit biodiversity and provide resilience.

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