Challenges in Assessing the Ecological Impacts of Tree Diseases and Mitigation Measures: the Case of *Hymenoscyphus fraxineus* and *Fraxinus excelsior*

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Abstract

Forests worldwide are currently threatened by a number of non-native tree diseases. Widespread death of a tree species will have ecological impacts on species that in some way depend on that tree species to complete their life-cycle. One measure to mitigate these impacts is to establish alternative tree species to replace the threatened tree species. These alternative tree species should be as similar as possible to the threatened tree species in terms of species supported, tree traits and the environmental conditions under which the tree will grow. This study assesses the availability and quality of data to assess the ecological impact of *Hymenoscyphus fraxineus* on *Fraxinus excelsior* and the suitability of 48 alternative trees to replace *F. excelsior* in the UK. To make this assessment data were collected on 1) species use (whether the 955 ash-associated species will use the alternative tree species), 2) traits (bark pH, deciduous, floral reward, fruit type, height, leaf dry matter content, leaf shape, length of flowering time, mycorrhizal association, pollen vector and specific leaf area) and 3) site requirements (occurrence within northern/southern and upland/lowland Britain, detailed climatic and soil nutrient requirements). For all three assessment methods there was lower confidence in the suitability of non-native tree species to replace *F. excelsior* due to lack of data. Different alternative tree species were ranked most suitable depending on the methods used. We conclude that no one species is suited to all the site types associated with *F. excelsior*, nor will any one tree species support a high percentage of the ash-associated species while also matching many of the traits of *F. excelsior*. Our work provides broad guidance on the suitability of the 48 alternatives but site specific information is required to refine this selection at each site. The study highlights a lack of information to make a full assessment of the suitability of many species, particularly non-native species and calls for the collation of biological records so that rapid assessments of the potential ecological impacts of the loss of any given tree species and the suitability of their alternative tree species can be made.

Keywords: adaptive forest management, ash dieback, Chalara, *Fraxinus excelsior,* diseases, *Hymenoscyphus fraxineus,* mitigation, pests

Introduction

The rate of spread of tree diseases and the number of different diseases causing serve impacts appears to have been increasing in recent years due, in part, to climate change and global trade (Woodward and Boa 2013). In North America, chestnut blight has caused near complete loss of *Castanea dentata* chestnuts (Jacobs 2007), Dutch elm disease has caused a similar loss of *Ulmus* spp. elms in Europe and North America (Potter et al. 2011) and several species of *Pinus* pine around the world are now threatened with the fungus *Gibberella circinata* which causes pine pitch canker (Wingfield et al. 2008). *Fraxinus excelsior* ash trees are currently dying in Russia and North America due to the emerald ash borer (*Agrilus planipennis*), a beetle from the Buprestid beetle family (commonly known as jewel beetles or metallic wood-boring beetles) native to China (Cappaert et al. 2005; Poland and McCullough 2006) and in Europe due to the ascomycete *Hymenoscyphus fraxineus* (Kjær et al. 2012; Baral et al. 2014) (previously called *Chalara fraxinea* and *H. pseudoalbidus*). Following common convention we call the disease caused by *Hymenoscyphus fraxineus* ash dieback throughout. The disease was first recorded in the UK in February 2012 and has since spread throughout the UK (see Clark and Webber 2017).

Tree diseases can cause severe economic and cultural impacts through loss of trade and cultural/ionic trees and/or forests (Boyd et al. 2013). However, widespread death of one tree species may also have huge environmental and ecological implications, in particular for other species that in some way depend on that species of tree to complete their life-cycle (associated-species). For species that predominately only use one species of tree, the loss of that tree species could lead to declines in populations or even extinctions (Ellis et al. 2012; Pautasso et al. 2013; Lohmus and Runnel 2014; Mitchell et al., 2014a). Wide spread loss of a tree species may also impact on ecosystem function, e.g. nutrient cycling and carbon storage (Mitchell et al. 2016) if tree species composition within a forest changes radically following the arrival of a particular disease.

One way of mitigating ecological impacts of tree diseases is to establish alternative tree species (Meason and Mason 2014, Wilson 2014), here defined as a tree species other than the one which is threatened by the disease. From an ecological view point it is critical that these alternative tree species are as similar as possible to the threatened tree species in terms of the associated species supported and the tree traits if the alternative tree is to provide successful mitigation. The ecological traits of a tree, such as height, bark pH, leaf shape, deciduous/evergreen, floral reward, pollinator and seed type will alter the environmental conditions or resources created by the tree and will influence which associated species will use the tree for feeding/breeding or as a habitat such as epiphytic species. In addition the site requirements (climate, soil type) of any alternative tree species must be similar to that of the threatened tree species to enable it to establish and grow at the site.

When identifying the most suitable alternative tree species as mitigation for production purposes there are a limited number of criteria on which to focus such as site requirements, growth rates, volume of timber produced and timber quality. However, identifying the most suitable alternative tree species as mitigation for ecological impacts is more complicated, as there are a larger number of factors to be considered, many of which interact, and this requires extensive data to be collated; specifically information on the species assemblages associated with candidate alternative species and on the traits of the trees. Our aim here is to collate information on a) species use, b) tree traits and c) site requirements for 48 tree species that are currently being considered as alternatives to replace *F. excelsior* in the UK. We aim to 1) identify the most suitable ecological alternative tree species as assessed using each of these three types of data and 2) collate information on the availability and quality of these data, as good quality data for all tree species under assessment is essential if comparisons between tree species are to be made accurately.

While this study focuses on the challenges of obtaining data to make an ecological assessment of the suitability of alternative tree species as mitigation for *Hymenoscyphus fraxineus* we aim to use this as a case study to illustrate the types of data required and generic problems that may occur with this type of assessment for any tree species. The UK is acknowledged as having excellent biological recording systems (Pocock et al. 2015) and *F. excelsior* is a common tree in the UK, occurring in 88% of 10 km grid squares (Preston et al. 2002). Thus one would expect data collation to be easier and more complete than for many other tree species or countries. With the increase in tree diseases, the need to identify the availability of this type of ecological data is critical if suitable ecological assessments of alternative tree species are to be made.

Method

Species use

Information on which species use *F. excelsior* was gathered for 6 taxon groups: birds, bryophytes, fungi, invertebrates, lichens and mammals. For each taxon group a "taxon expert" who knew the taxon group well and the available data sources (Table S1) was identified to carry out the assessment. Each taxon expert was asked to identify ash-associated species and their level of association with *F. excelsior*. The only *Fraxinus* species native and common in the UK is *F. excelsior* – thus the term ash-associated species refer to species that use *F. excelsior* in the UK. The level of association of the species with *F. excelsior* was defined as: obligate - unknown from other tree species; highly associated - rarely uses other tree species; partially associated - uses *F. excelsior* more frequently than its availability; cosmopolitan - uses *F. excelsior* as frequently as or less than its availability; uses - uses *F. excelsior* but the importance of *F. excelsior* for this species is unknown. Taxon experts were asked to note specific difficulties in identifying which species were ash-associated species.

Forty-eight alternative tree species were assessed as to whether or not the ash-associated species would also use these alternative tree species. The 48 tree species assessed included all native tree and shrub species (27 species) likely to occur on sites where *F. excelsior* is currently present in the UK and 21 non-native tree species which have been proposed as possible alternatives to *F. excelsior* where commercial production of *F. excelsior* is currently the primary objective of woodland management. The taxon experts used the same data sources as for identification of the ash-associated species but recorded the use made of the alternative tree species into one of 5 categories: yes – known to use the tree, rare – only occasional records of the species using the tree, likely – no specific information on the use of the tree species by the ash-associated species but the taxon expert suggested that the ash-associated species was likely to use that tree species, for example when the ash-associated species was known to use other tree species in the same genera and known to use a wide range of deciduous tree species; No – ash-associated species thought not to use the alternative tree species, unknown – no information on whether or not the ash-associated species will use the alternative tree species. The taxon experts also recorded the quality of the data used to assess the level of association between the ash-associated species and the alternative tree species. Data were first classed as 'expert judgement' (level of association based on 'expert knowledge' of the species habitat requirements rather than on literature, frequently used for the likely, no and unknown categories of association.) and then as 'peer-reviewed', or 'non-peer-reviewed'. 'Peer-reviewed' covered a broad range of data sources and included anything that had received some form of quality control: published text books, scientific literature and databases that were quality controlled. The 'peer-reviewed' and 'non-peer-reviewed' categories were further sub-divided depending on whether the data were based on UK information or not. This was done because there is evidence that some associated species use different tree species in the UK than in other countries. Taxon experts were asked to note specific issues with identification of use of alternative tree species by the ash-associated species.

Traits

The aim was to collect data for all 48 alternative species for the following traits: bark pH, deciduous or coniferous, floral reward, fruit type, height, leaf dry matter content (LDMC), leaf shape, length of flowering time, mycorrhizal association, pollen vector and specific leaf area (SLA). As separate trait data were available for the two *Betula* species (*B. pendula* and *B. pubescens*) and the two *Quercus* species (*Q. robur* and *Q. petraea*) this resulted in 50 assessments in total.

The primary sources of data used for the tree traits in this study were: Barkman (1958), Klotz et al. (2002), Kattge et al. 2011, Hill et al. (2004) and Kleyer et al. (2008). However, not all traits for all tree species were covered by the above sources. Gaps in the data were filled on a case-by-case basis where possible, and using a range of literature. In some cases data from congeners was used. The data sources for each tree by trait combination are listed in Tables S2 and S3. Where there were multiple values for any one tree/trait combination in a database the average value was used.

Many of the alternative tree species match *F. excelsior* when assessed by individual traits, but ideally any alternative tree species should match *F. excelsior* in a high proportion of traits. Analysis across multiple traits could be carried out using a similarity index; however the calculation of similarity indices is not possible with missing data (as is the case here). Therefore for categorical traits (deciduous, floral reward, fruit type, leaf shape, mycorrhizal association and pollen vector) the alternative trees can be classed according to whether they are the same (i.e. occur in the same category as *F. excelsior*) or dissimilar to *F. excelsior* (occur in a different category to *F. excelsior*).

For traits with continuous variables the data were standardised.

$$[1]\ \text{Standardised data} = ((\text{Fex}-\text{Alt})/\text{Fex})^2$$

Where Fex = value for *F. excelsior* and Alt = value for alternative tree.

The standardization allowed comparisons across traits measured in different units and assigned a value of zero for *F. excelsior*, with higher values indicating a greater difference between the alternative tree and *F. excelsior*. Alternative species were then classed as similar to *F. excelsior* (0-0.005); intermediate (>0.005-0.24) or dissimilar to *F. excelsior* (≥0.25). The cut-off between the different groups is essentially arbitrary but does allow species very different from *F. excelsior* to be identified. The number of traits classed as the same or similar then provided a measure of how similar the alternative was to *F. excelsior*.

Site requirements

The site requirements of the alternative trees were assessed in three different ways: 1) their occurrence within northern/southern and upland/lowland Britain, 2) detailed climatic and soil nutrient requirements and 3) natural successional processes.

The site requirements of the alternative species were first assessed using the National Vegetation Classification (NVC) for Great Britain (Rodwell 1991). Semi-natural UK broadleaved woodlands with a medium to high amount (>10% of cover and >20% frequency) of *F. excelsior* referred to here as 'ash-woodlands' were identified. The alternative species were first assessed by whether they already occurred within these ash-woodlands and an assessment of the climatic constraints was made using information on the amount and distribution of *F. excelsior* present (Forestry Commission, 2012; DARDNI, 2013) and hence the distribution of ash-woodland communities from NVC maps (Rodwell, 1991; Rodwell and Patterson, 1994). Climatic constraints were then further assessed by splitting the UK into northern (Scotland, northern England and Northern Ireland) and southern (southern England and Wales) and into upland and lowland areas. Lowland areas were defined as areas where an accumulated temperature (number of day degrees above 5 degree C) exceeded c.1200 day-degrees with 'uplands' having accumulated temperatures below this threshold. Upland and lowland areas can be found in both northern and southern parts of the UK.

For those species used for production planting in the UK, there is a greater knowledge of their site requirements (climate constraints, preferred soil conditions) from the Ecological Site Classification (ESC) for Great Britain (Pyatt et al 2001). For these species we compared their site requirements to those of *F. excelsior* in more detail. In ESC seven different climate zones have been identified in the UK based on the combined climatic factors of climatic warmth (30-year average of accumulated temperature above 5 degrees C in day degrees) and climatic wetness (30-year average of moisture deficit based on the maximum excess of potential evapotranspiration over rainfall in mm). We compare the range of climate zones in which *F. excelsior* is able to grow with the suitable range of the alternate species, using data from Pyatt et al. (2001). For forestry in the UK, soil condition is described by the availability of water (Soil Moisture Regime - SMR) and soil nutrients (including the influence of pH) for plant growth (Soil Nutrient Regime - SNR). SMR is based on soil texture, stoniness and rooting depth and is divided in to eight classes (Very Wet, Wet, Very Moist, Moist, Fresh, Slightly Dry, Moderately Dry, Very Dry). SNR is derived from lithology, soil type or ground flora composition and the gradient in SNR is arbitrarily divided in to six classes (Very Poor, Poor, Medium, Rich, Very Rich and Carbonate) (Pyatt et al. 2001). We compare the range of SNR and SMR classes suitable for *F. excelsior* with the range of suitability of each of the alternatives from (Pyatt et al. 2001).

Many of the alternative species, particularly when used for conservation purposes, would be maintained by natural regeneration. Information in the literature on the germination success of alternative species and their ability to establish from seedlings or saplings in shade, indicates how well these species may function to replace *F. excelsior* in a woodland setting. A literature review to identify the ecological function of 11 of the alternative tree species was carried out using key-word driven searches undertaken during the 6-24 January 2014 in Web of Knowledge (http://wok.mimas.ac.uk/) (see Mitchell et al. 2104b). Search terms included the Latin name of the tree species together with the keywords: succession, gaps, colonization and light. For each search the abstracts of all the extracted articles were read, and if the abstract was relevant to the project (i.e. including references to more than one tree species and so enabling comparisons to be made) the full manuscript was obtained. The papers were then used to rank the species relative to each other with respect to different successional processes (succession, gaps, colonization and light).

Results

Species use

Identification of ash-associated species

Nine hundred and fifty five species were identified which use *F. excelsior* trees. This included 45 obligate species: 4 lichen species, 11 fungi and 30 invertebrates; and 62 highly associated species: 19 fungi, 13 lichens, 6 bryophytes and 24 invertebrates (Table 1). Details of ash-associated species have already been published in Mitchell et al. (2014a, b) but that work did not report on the difficulties of identifying ash-associated species which is the focus of the results here.

Table 1. Number of species and level of association with *F. excelsior* for six taxon groups. Differences in numbers of species compared to Mitchell et al. (2014a) are due to additional records being added, see Mitchell et al (2014b) for details

Organism	Level of Association					
	Obligate	High	Partial	Cosmopolitan	Uses	Total
Birds			7	5	2	12
Mammals			1	2	25	28
Bryophytes		6	30	10	12	58
Fungi	11	19	38			68
Lichens	4	13	231	294	6	548
Invertebrates	30	24	37	19	131	241
Total	45	62	344	330	174	955

The 955 ash-associated species identified is likely to be an under-estimate of the total number of ash-associated species, due to lack of data for some taxa. Algae, soil invertebrates and micro-organisms were not included in this assessment as data on their association with tree species is lacking or hard to assess. Even for the six taxon groups that were studied our values are likely to be an under-estimate. Key issues on data availability reported by the taxon experts are summarised below.

The greatest knowledge gaps in relation to fungi associated with *F. excelsior* in the UK is the absence of data on its leaf endophytes and our limited knowledge of the fungi associated with *F. excelsior* that do not produce visible sexual or asexual structures and which are usually only detected in molecular studies. Studies on the continent (e.g. Scholtysik et al. 2012) have found high numbers of taxa from both groups associated with *F. excelsior* but so far there have been few comparable studies in the UK. In addition there are limited data on fungi associated with the below-ground structure of *F. excelsior* trees – the base and structural and feeder roots of the tree. Kubikova (1963) reported a range of common soil fungi associated with *F. excelsior* root surfaces and Summerbell (2005) also mentioned non-specialised soil fungi associated with *F. excelsior* roots.

For some invertebrate groups, in particular for saproxylic species of Diptera, Coleoptera and for Heteroptera, it is known that more species have been recorded on *F. excelsior* than those for which our literature search revealed documentation. For example, Rotheray et al. (2001) record that 69 species of saproxylic Diptera were recorded on *F. excelsior* during their fieldwork in Scotland between 1988 and 1998 but only those with a specified conservation status were named. Similarly Bernard Nau (pers. Comm.) reported finding 63 species of Heteroptera. However, many are likely to be predatory species that show no affinity to particular tree species. Identification of parasite and parasitoid invertebrate species that are associated with *F. excelsior* involved searching for species that have invertebrate hosts that were identified as having an association with *F. excelsior,* making identification of ash-associated parasitic and parasitoid species difficult. Even for the more well studied invertebrate groups, such as the Lepidoptera, there may be incomplete knowledge of plant associations for rarer species because most records are of adults and hence do not reveal information about the food plant used by the larva.

Hole nesting bird species (such as *Cyanistes caeruleus* blue tit, *Poecile palustris* marsh tit, *Sitta europaea* nuthatch, *Ficedula hypoleuca* pied flycatcher, *Dendrocopos major* and *D. minor* great and lesser spotted woodpecker) are well studied, providing quantitative assessments of tree species use compared with availability. Seed eating birds (e.g. *Pyrrhula pyrrhula* bullfinch, and *Coccothraustes coccothraustes* hawfinch) are also well studied with quantitative data on diets. Data are more limited from other bird species (e.g. *Sylvia atricapilla* blackcap, *Phylloscopus collybita* chiffchaff, *Troglodytes troglodytes* wren, and *Muscicapa striata* spotted flycatcher) that have a less direct link with tree species such as association with phytophagous invertebrate biomass or woodland structure.

Identification of use of alternative tree species by ash-associated species

In total 45840 assessments of the level of association between an ash-associated species and an alternative tree species were made (Fig. 1). Of ash-associated species 67% (640 species) are also associated with native *Quercus* species (*Q. robur* and *Q. petraea*). More than 400 ash-associated species are also associated with each of the following tree species: *Fagus sylvatica*, *Ulmus procera*, *Acer pseudoplatanus*, *Corylus avellana* and *Betula pendula*/*pubescens* (Fig. 1). Four non-native *Fraxinus* species were included in the assessment: *F. ornus*, *F. americana*, *F. pennsylvanica* and *F. mandschurica*. These species were assessed as 'likely' to support over 200 ash-associated species particularly ash-associated bird, fungi and invertebrate species. Of the non-native alternative tree species considered *Acer pseudoplatanus* (473), *Aesculus hippocastanum* (208), *Larix decidua* (166), *Juglans regia* (149), *Castanea sativa* (148) and *Juglans nigra* (126) support the greatest number of ash-associated species (number of ash-associated species supported in parentheses).

Alternative tree species are unlikely to provide a suitable mitigation measure for obligate ash-associated species, as according to our collated data obligate species only use *F. excelsior*. There may be a few species listed as 'obligate' in our data that would use other alternative species, perhaps non-native *Fraxinus* species, if they had the chance but as these alternatives are rare or not present in the UK there are no records of the obligate species using them, and hence they are classified as obligate. Alternative tree species are a potential mitigation measure for highly associated species and, after obligate species, highly associated species are most at risk from ash dieback. It is therefore important to identify which alternative tree species support the greatest number of highly associated ash species (Table 2). *Quercus robur/petraea, Corylus avellana* and *Ulmus procera/glabra* all support more than 20 highly associated ash species with *Populus tremula* and *Acer pseudoplatanus* supporting more than 15 highly associated ash species. When assessed within taxon group the alternative species that supports the greatest number of highly associated ash species varied. *Acer campestre* and *Aesculus hippocastanum* both support 5 highly associated bryophyte species. *Ulmus procera/glabra* supports 9 highly associated fungi with *Populus tremula* and *Quercus robur/petraea* supporting 7 highly associated fungi. *Fraxinus ornus* supports 6 highly associated invertebrate species and *Ligustrum vulgare* supports 4 highly associated invertebrate species. *Quercus robur/petraea* supports 10 highly associated lichen species and *Corylus avellana* and *Ulmus procera/glabra*

Table 2. Number of ash-associated species supported by 48 alternative tree species, shown for all species together and separately by the different taxon groups and their level of association with *F. excelsior* (high, partial, cosmopolitan, uses)

	All species				Bird		Bryophyte				Fungi		Invert				Lichen				Mammal		
Alternative tree species	High	Partial	Cosmopolitan	Uses	Partial	Cosmopolitan	High	Partial	Cosmopolitan	Uses	High	Partial	High	Partial	Cosmopolitan	Uses	High	Partial	Cosmopolitan	Uses	Partial	Cosmopolitan	Uses
Abies alba	1	26	38	9	2			1	1			1	1			6		22	37				3
Acer campestre	9	157	68	22	1		5	25	10	7	2	4		2	4	11	2	124	54		1		4
Acer platanoides	4	26	15	15	1	3	4	24	10	4				1	2	9							2
Acer pseudoplatanus	17	228	202	26		1	4	26	10	7	6	8		2	5	14	7	191	185	1	1	1	4
Aesculus hippocastanum	9	116	60	23	1	2	5	12	4	1	3	3		4	5	15	1	95	48		1	1	7
Alnus cordata			2	4					2							3							1
Alnus glutinosa	11	164	187	27	1	5	4	24	10	7	4	6	2	6	4	14	1	127	168				6
Betula pubescens/pendula	11	167	208	36	6	4	1	7	5	3	6	9	1	11	5	28	3	134	194				5
Carpinus betulus	7	90	57	15	1	5	4	23	10	4	2	4		2	2	8	1	60	40				3
Carya ovata				1																			1
Castanea sativa	5	61	72	10			1	1	1		4	5		1	3	7		54	68				3
Corylus avellana	21	193	186	28			4	29	10	12	6	3	3	6	6	9	8	154	169	1	1	1	6
Crataegus monogyna	9	155	117	21	1	1	4	23	10	4	3	7	1	5	3	15	1	118	102		1	1	2
Fagus sylvatica	13	222	206	64	5	2	4	25	10	6	5	14		5	5	50	4	172	188		1	1	8
Fraxinus americana	1	5	2	2								2	1	3	2	2							
Fraxinus mandschurica	1	3		2	1							2	1			2							
Fraxinus ornus	6	5	3	10								2	6	3	3	10							
Fraxinus pennsylvanica	2	5	1	2								2	2	3	1	2							
Ilex aquifolium	3	107	129	12	1	2		5	3		1	4		1	1	5	2	95	122	2	1	1	5
Juglans nigra	3	78	43	2					1				1	1	1	1	2	77	41				1
Juglans regia	7	85	50	7			2	5	6		1	1	2	2	3	5	2	77	41				2
Larix decidua		50	106	10	2	1		1		1		2		2	1	3		43	104	1			5
Ligustrum vulgare	8	61	17	6	2			1			3	3	4	9	2	4	1	46	14			1	2
Malus sylvestris	5	140	104	23			3	17	9	2	1			6	5	17	1	116	89		1	1	4
Ostrya carpinifolia		5	3	2				5	3							2							
Pinus sylvestris		60	134	22	4	2						2		2	4	14		51	127	1	1	1	7
Platanus x hybrid	2	60	34					1	2		2	1			2			58	30				
Populus nigra	4	45	17	10			1	3	1		2	2		4	4	9	1	36	12				1
Populus tremula	18	176	150	26	2	5	4	27	10	10	7	3	1	8	5	13	6	136	130				3
Prunus avium	1	48	62	5	1	1		2	5		1	1		2	8	5		42	48				
Prunus padus	2	49	41	3		1		2	5		2	1		2	4	3		44	31				
Prunus spinosa	4	76	71	15	2	2		12	7	2	3	7	1	7	4	11		47	57		1	1	2
Pseudotsuga menziesii		3	4	1		1		1	3			2											1
Pterocarya fraxinifolia			1												1								

Table 2. (Continued)

	All species				Bird		Bryophyte				Fungi		Invert				Lichen				Mammal		
Alternative tree species	High	Partial	Cosmopolitan	Uses	Partial	Cosmopolitan	High	Partial	Cosmopolitan	Uses	High	Partial	High	Partial	Cosmopolitan	Uses	High	Partial	Cosmopolitan	Uses	Partial	Cosmopolitan	Uses
Quercus cerris	3	29	21	17		3		10	6	2	3	3		5	2	13		11	10				2
Quercus robur/petraea	23	271	276	70	7	5	4	28	10	11	7	11	2	17	10	44	10	207	250		1	1	15
Quercus rubra	1	13	4	10				4	3		1	2		7	1	8							2
Salix caprea	7	44	19	35		1	4	28	10	11	3	8		8	8	17							7
Salix cinerea	4	39	17	31			4	28	10	11		4		7	7	13							7
Sambucus nigra	6	53	26	10	4	3	3	20	9	4	1	4	2		1	3		24	12		1	1	3
Sorbus aria	1	51	38	10								1		1	6	5	1	49	31			1	5
Sorbus aucuparia	9	166	192	20	3	5	3	6	7	5	2	6	1	7	4	11	3	143	176		1		4
Sorbus torminalis	2	1	1	3		1		1			2					3							
Taxus baccata		53	36			1			1			3			2			50	32				
Thuja plicata		13	1	3														13	1				3
Tilia cordata	7	37	18	22	1	5	4	23	10	4	2	6	1	7	3	15							3
Tilia platyphyllos	4	136	94	8			2	2	2			1		4	1	8	2	129	91				
Ulmus procera/glabra	21	248	183	24	2	4	4	21	10	5	9	12		15	7	16	8	197	162	2	1		1

each support 8 highly associated lichen species. No highly associated bird or mammal species were identified.

Data availability

There was more data available on ash-associated species associations with alternative tree species that are native to the UK than for those that are non-native (the unknown category in Figure 1 indicates that the data is not available to make the assessment). Most native trees had information on species use for 75% of ash-associated species. The exceptions to this were *Populus nigra*, *Salix caprea*, *Salix cinerea*, *Sambucus nigra, Sorbus torminalis* and *Tilia cordata*, which, although native to the UK, had information for less than 35% of ash-associated species. Most non-native tree species only had information for less than 35% of ash-associated species. The exceptions to this were *Acer pseudoplatanus*, *Aesculus hippocastanum*, *Castanea sativa*, *Juglans nigra, Juglans regia* and *Larix decidua*, where information was available for over 75% of ash-associated species. Thus generally, and due to a lack of data, there is lower confidence in the use made by ash-associated species of non-native tree species than native tree species.

The taxon experts also identified a number of reasons why data were lacking for the assessment of the suitability of alternative trees by ash-associated species. These can be grouped into four main issues:

Tree species not recorded:
In studies of bats and birds that use trees to roost in and/or breed in, the tree species is often not recorded. Most studies of the characteristics of bat roosts focus on the physical attributes of tree holes and their entrances (Kanuch 2005), their origins, and particularly their thermal characteristics (Jenkins et al. 1998; Ruczynski 2006; Smith and Racey 2005) without necessarily reporting the tree species involved. Birds are a well-studied taxonomic group with a wide and long established literature. If there were strong associations with *F. excelsior* for any bird species this is likely to have been noticed and remarked upon. However, most studies of both bird communities and individual species have looked at the effects of woodland structure and tree species composition, (e.g. MacArthur and MacArthur 1961, Lewis et al. 2009, Broughton et al. 2012) rather than associations with particular tree species. It is therefore often assumed that for birds and bats it is the physical attributes rather than the tree species that are important; however, this has yet to be tested with respect to using alternative trees to replace diseased tree species.

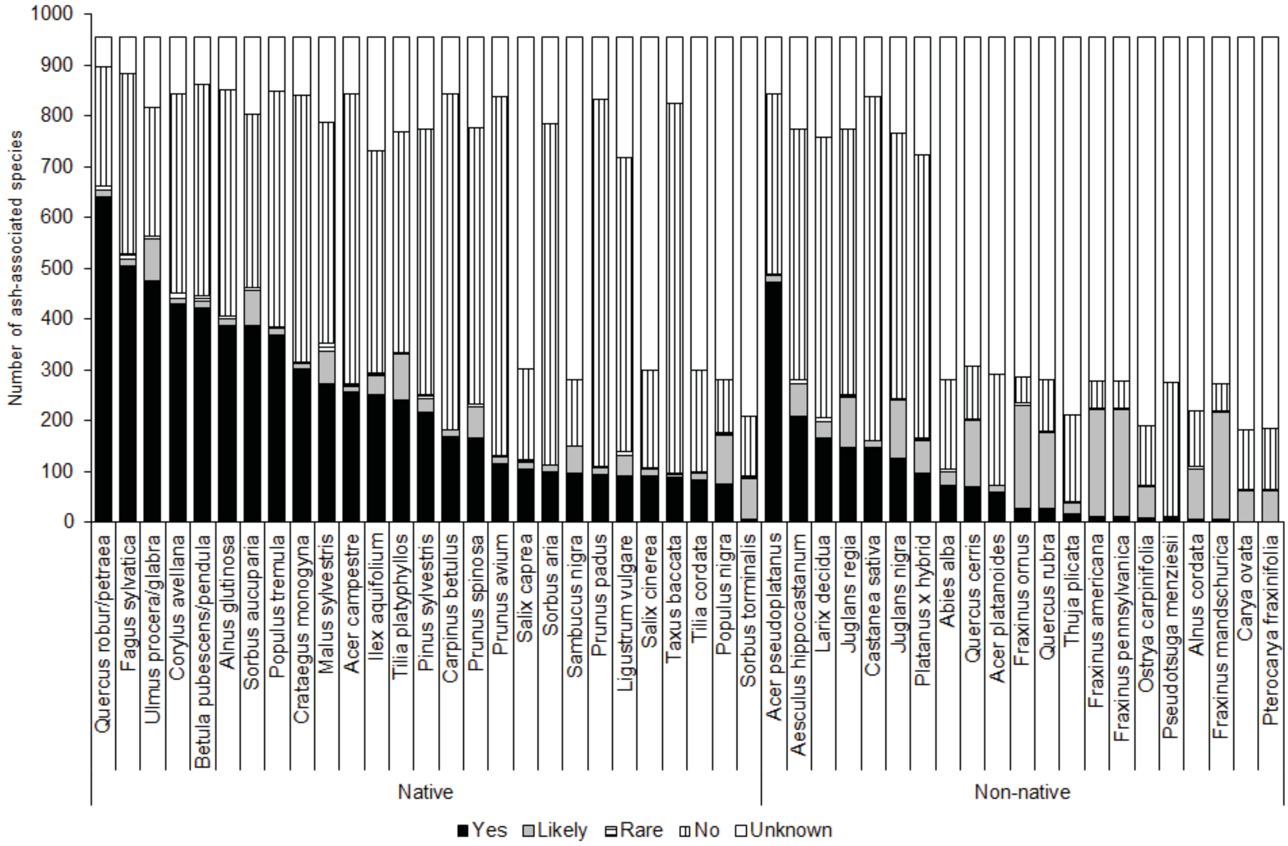

Figure 1. The use made of 48 alternative tree species by ash-associated species. Tree species ranked according to whether they are native or non-native to the UK and then by the number of ash-associated species known (yes) to use them.

Only tree genera recorded:
The lichen, bryophyte and invertebrate taxon specialists all recorded problems of only tree genera, not tree species being recorded e.g. in the British Lichen Society database the use of *Salix caprea* and *S. cinera* by ash-associated lichens was not available at the tree species level but were grouped under *Salix* spp. and records for *Tilia cordata* were only available for *Tilia* spp. (*T. cordata* and *T. platyphyllos* combined). This reduces the level of precision available when discussing which tree species may be suitable as replacements for ash.

Unclear which tree species an ash-associated species is associated with:
This problem is unique to fungi that fruit on the ground on mycelia associated with the tree roots. The Fungal Records Database of Britain and Ireland (FRDBI) records the nearest associated organism, in this case resulting in the nearest tree species being recorded. However the nearest tree may not actually be the tree whose roots the fungi is growing on. This can result in spurious associations being made between fungi and other organisms.

Unsystematic recording:
The majority of the records of species distribution in the UK are collected by volunteers, which results in unsystematic recording with the distribution of data in databases such as the FRDBI heavily weighted to those areas that have been extensively recorded. This means that when using distribution and abundance data to calculate the level of association of a species with *F. excelsior,* data from less well studied areas are likely to under represent actual species occurrence with *F. excelsior*. The data are also biased to taxa forming large obvious fruiting bodies. Information will be less complete for rare species or those that are rarely studied or documented. If there are only a small number of records of the plant species on which an invertebrate has been found, this may have the effect of making any association appear to be stronger simply through a lack of sufficient data from alternative plants. In such situations, apparent feeding preferences may be biased by the recording activity of one or a very few entomologists or may show geographic bias according to the distribution of entomological studies. The majority of records of plant-invertebrate associations are based on unsystematic observations and undoubtedly there will be many uses made of plants by invertebrate species that are not documented at all.

Data quality

Levels of association between the ash-associated species and the alternative tree species classed as 'yes' (will use the alternative tree species) generally have a high level of confidence associated with them: 91% of 'yes' records are based on peer reviewed data from the UK (Table 3). Associations that were classified as 'likely' are largely based on expert judgement (74% of likely records). These records therefore have a lower confidence associated with them, and this should be taken into account when considering which tree species to plant to promote ash-associated biodiversity, with tree species classed as 'yes' being prioritised over those classed as 'likely'. Eighty-seven percent of associations classed as 'no' were based on peer-reviewed data from within the UK, with 10% based on expert judgement. Associations classed as 'unknown' were predominantly based on expert judgement, with 70% of unknown associations in this category. Therefore, if the aim is to conserve ash-associated biodiversity, planting of alternative tree species with a level of association 'unknown' is not recommended.

Table 3. Relationship between levels of association with alternative tree species and data quality. Number of records in each class are shown. Expert judgement = level of association based on 'expert knowledge' of the species habitat requirements rather than on literature, PR = peer-reviewed data, NR = not peer-reviewed, UK = data from UK, Non-UK = data not from the UK

Data quality	Level of association					Total
	Yes	Likely	Rare	No	Unknown	
Expert judgement	94	2056	61	1755	12602	16568
NR-NonUK	87	104	1	42	117	351
NR-UK	285	377	27	283	1454	2426
PR-NonUK	279	122	16	102	164	683
PR-UK	7402	111	103	14561	3635	25812
Total	8147	2770	208	16743	17972	45840

Traits

Comparison of traits between alternative tree species

The trait values collected are available as part of the published AshEcol spreadsheets (Mitchell et al. 2014b). Table 4 ranks the alternative trees by the number of traits coded as the same or similar to *F. excelsior*. Of the eleven traits assessed, *Ulmus procera* is the most similar native tree to *F. excelsior* with eight of the traits being the same or similar; *Betula pendula* had six of the traits the same or similar. The other 27 native trees assessed had five or fewer traits the same *F. excelsior*. Twenty-four of the native trees have five or more traits classed as dissimilar with *Crataegus monogyna, Malus sylvestris, Salix cinerea* and *Tilia platyphyllos* all having six traits classed as dissimilar to *F. excelsior*. Thus when assessed by the traits most of the native tree species were not very similar to *F. excelsior*. Many of the non-native trees had similar traits to ash: *Fraxinus americana* has eight traits the same/simliar, *Juglans regia* and *F. pennsylvanica* have seven traits the same/similar and *Juglans nigra* and *Fraxinus mandschurica* have six traits the same/similar. Of the non-native trees assessed the most dissimilar species to *F. excelsior* were *Larix decidua* with seven and *Acer platanoides*, *Pseudotsuga menziesii* and *Abies alba* each with six of the eleven traits classed as dissimilar.

For the continuous variables of height, LDMC, SLA and length of flowering time the data shows that there are a large number of tree species that are intermediate in their similarity to *F. excelsior*. The niche breadth of the associated species and the mix of species that *F. excelsior* is growing with will determine the point at which the alternative species are no-longer suitable alternatives along this continuous gradient.

Data limitations

Trait data for many tree species were missing. Of the 50 tree species considered, there were only data for all 12 traits for 25 species. Despite searching international trait databases, appropriate data were unavailable for many of the non-native tree species. The proportion of traits with data for each tree species may be used as a measure of confidence in the data (Table 4). Data for all tree species were only available for the following traits: deciduous or coniferous, fruit type, height, leaf shape, mycorrhizal association and pollen vector. The number of trees out of 50 that had data for the other traits were bark pH 29, floral reward 47, LDMC 40, length of flowering time 36, SLA 38.

Relationship between tree traits and species use?

There was no correlation between the number of species supported and the number of traits that are the same as for *F. excelsior* (Table 4). Although the results may be influenced by missing data for some non-native tree species, analysis of native tree species, for which there are good data also showed no clear pattern. For example *Q. robur/petraea* supports the greatest number of ash-associated species (640) but only has four or five (*Q. robur* and *Q. petraea* respectively) of the eleven traits that are the same as for *F. excelsior*. *Ulmus procera* supports 477 ash-associated species and has eight of the eleven traits the same as for *F. excelsior,* yet *Fagus sylvatica* supports 505 ash-associated species but only has four traits the same as *F. excelsior*.

Table 4. Similarity of alternative trees to ash for 11 traits. S= traits the same or similar, I = traits intermediate, D = traits not the same or dissimilar, x = no data available. Tree species ranked according to whether they are native or non-native to the UK and then by the number of traits that are similar to *F. excelsior*. Trait confidence is the proportion of traits for which data was available. The number of ash-associated species supported is shown for comparison

Tree Species	Bark pH	Deciduous	Floral reward	Fruit type	Leaf shape	Mycorrhizal association	Pollinator	Height	LDMC	Flowering time	SLA	Trait confidence	No. ash species supported
Native species													
Ulmus procera/glabra	S	S	D	S	D	S	S	I	S	S	S	1.00	477
Betula pendula	D	S	D	S	D	D	S	S	S	S	I	1.00	423
Alnus glutinosa	D	S	D	S	D	D	S	I	S	S	I	1.00	389
Populus tremula	S	S	D	D	D	S	S	I	I	S	I	1.00	370
Betula pubescens	D	S	D	S	D	D	S	I	S	S	I	1.00	423
Sambucus nigra	S	S	D	D	S	S	D	D	I	S	D	1.00	96
Salix caprea	S	S	D	D	D	S	D	D	S	S	I	1.00	105
Carpinus betulus	D	S	D	S	D	D	S	I	S	S	D	1.00	169
Sorbus aucuparia	D	S	D	D	S	S	D	I	S	S	I	0.91	387
Tilia cordata	D	S	D	S	D	D	S	S	I	S	D	1.00	84
Prunus avium	D	S	D	D	D	S	D	S	I	S	S	1.00	116
Fagus sylvatica	D	S	D	S	D	D	S	I	I	S	I	1.00	505
Populus nigra	x	S	D	D	D	S	S	I	I	x	S	0.82	76
Prunus spinosa	x	S	D	D	D	S	D	D	I	S	S	0.91	167
Acer campestre	D	S	D	D	D	S	D	I	I	S	S	1.00	256
Salix cinerea	S	S	D	D	D	S	D	D	D	S	I	1.00	91
Corylus avellana	S	S	D	S	D	D	S	D	I	D	I	1.00	430
Ligustrum vulgare	x	S	D	D	D	S	D	D	S	S	I	0.91	92
Sorbus torminalis	x	S	D	D	D	S	D	I	S	S	D	0.91	7
Taxus baccata	D	D	S	D	D	S	S	I	S	D	I	1.00	89
Prunus padus	D	S	D	D	D	S	D	I	I	S	I	1.00	95
Malus sylvestris	x	S	D	D	D	S	D	D	S	D	I	0.91	272
Crataegus monogyna	D	S	D	D	D	S	D	D	I	S	I	1.00	302
Ilex aquifolium	x	D	D	D	D	S	D	I	S	S	I	0.91	251
Tilia platyphyllos	S	S	D	S	D	D	D	I	I	D	D	1.00	242
Quercus robur	D	S	D	S	D	D	S	I	I	D	I	1.00	640
Pinus sylvestris	x	D	S	D	D	D	S	I	D	S	x	0.82	216
Quercus petraea	D	S	D	S	D	D	S	I	I	D	I	1.00	640
Sorbus aria	D	S	D	D	D	S	D	I	I	S	I	1.00	100
Non-native													
Fraxinus americana	S	S	S	S	S	S	S	S	D	x	x	0.82	12
Juglans regia	x	S	S	D	S	S	S	S	S	D	I	0.91	149
Fraxinus pennsylvanica	x	S	S	S	S	S	S	S	x	x	D	0.73	12
Juglans nigra	x	S	S	D	S	S	S	I	S	x	x	0.73	126
Fraxinus mandschurica	x	S	S	S	S	S	S	I	x	x	x	0.64	6
Pterocarya fraxinifolia	x	S	x	S	S	S	S	I	x	x	x	0.55	1
Fraxinus ornus	x	S	D	S	S	S	S	I	x	x	I	0.73	29
Platanus x hybrid	D	S	S	S	D	S	S	D	x	x	D	0.82	96
Aesculus hippocastanum	x	S	D	D	D	S	D	I	S	S	I	0.91	208
Alnus cordata	x	S	S	S	D	D	S	I	x	x	x	0.64	6
Acer platanoides	D	S	D	D	D	S	D	I	S	S	D	1.00	60
Quercus rubra	x	S	S	S	D	D	S	I	I	x	I	0.82	28
Castanea sativa	D	S	D	S	D	D	S	I	S	D	I	1.00	148
Acer pseudoplatanus	S	S	D	D	D	S	D	I	S	D	I	1.00	473
Pseudotsuga menziesii	D	D	S	D	D	D	S	D	x	S	x	0.82	8
Ostrya carpinifolia	x	S	x	S	D	D	S	I	x	x	x	0.55	10
Carya ovata	x	S	x	D	S	D	S	I	x	x	x	0.55	1

Table 4. (Continued)

Tree Species	Bark pH	Deciduous	Floral reward	Fruit type	Leaf shape	Mycorrhizal association	Pollinator	Height	LDMC	Flowering time	SLA	Trait confidence	No. ash species supported
Quercus cerris	x	S	D	S	D	D	S	I	I	D	I	0.91	70
Thuja plicata	x	S	D	D	D	S	S	D	x	x	x	0.64	17
Abies alba	D	D	S	D	D	D	S	D	I	x	x	0.82	74
Larix decidua	x	D	S	D	D	D	S	D	D	D	x	0.82	166

Using traits to predict changes in ecosystem function

Many tree traits are linked to ecosystem functioning; thus some of the changes that would occur in ecosystem functioning if *F. excelsior* were replaced by one of the alternative tree species may be predicted. Most of the alternative trees assessed are deciduous and will therefore continue to produce a similar seasonal pattern of shading and litter fall to ash, if they replace *F. excelsior*. The exceptions to this are *Abies alba, Ilex aquifolium*, *Pinus sylvestris*, *Pseudotsuga menziesii* and *Taxus baccata*; if these tree species replace *F. excelsior* then there will be a change to a continuous canopy with heavy shade all year and a switch to a more continuous litter fall. These changes will influence nutrient cycling and ground flora species richness is likely to decline due to lack of light (Mitchell et al. 2014a).

The structure of the wood in terms of tree height will change least if *Betula pendula*, *Fraxinus americana*, *F. pennsylvanica*, *Juglans regia*, *Prunus avium* or *Tilia cordata*, replace *F. excelsior* as these tree species are generally (subject to local growing conditions) similar in height to *F. excelsior*. *Corylus avellana*, *Ligustrum vulgare* and *Prunus spinose* are generally smaller trees/shrubs than *F. excelsio*r and *Abies alba, Larix decidua, Platanus* x hybrid and *Pseudotsuga menziesii* are usually taller trees than *F. excelsior,* thus a very different woodland structure will develop if any of these species replace *F. excelsior*.

Leaf dry matter content (LDMC) is related to decomposition rates (Fortunel et al. 2009). *F. excelsior* has a low LDMC compared to most native UK trees. If *F. excelsior* is replaced by species with a high LDMC such as *Acer campestre*, *Fagus sylvatica, Prunus padus, P. avium* and *Salix cinerea* decomposition rates will be slower which in turn will increase carbon storage and slow down nutrient cycling.

Most temperate European woodland trees form ectomycorrhizal associations (ECM) with a wide range of soil fungi, whereas *F. excelsior* forms only arbuscular mycorrhizal (AM) associations with a more restricted group of fungi. Thirty of the alternative tree species assessed also form AM associations, but 20 of them form ECM. More soil carbon is stored in systems dominated by ecotomycorrhizal associations than in ecosystems dominated by AM-associated plants (Averill et al. 2014). Therefore if there was a major change to a system dominated by trees with ECM associations this would increase the amount of carbon stored in the system.

Site requirements

Occurrence within northern/southern and upland/lowland UK

Thirty-one of the alternative tree species are listed as components of ash-woodlands by Rodwell (1991) (Table 5). Twenty-eight species are native to the UK but three (*Tilia platyphyllos*, *Acer pseudoplatanus* and *Castanea sativa*) are considered non-native but regularly occur in semi-natural ash-woodlands. These 31 alternative species can all occur in ash-woodlands throughout the UK except for *Sorbus aria*, *S. torminalis* and *T. platyphyllos*, which all have a more southern distribution and are generally absent from Scotland, Northern England and Northern Ireland (Table 5). Relatively fewer of the alternative tree species are found in the upland regions. Most of the alternative species (22) occur in the lowlands of southern UK, whereas only half occur in upland areas of southern UK. Only one species (*Prunus avium*) is absent from lowland regions of southern UK. Four of the 27 alternative species which are found in northern UK are absent from the uplands of that region. Throughout the UK, 17 alternative species may be encountered in some but not all 'ash woodlands' (indicated as 'infrequent' in Table 5). For the four species which are non-native, this reflects the availability of nearby planted sites to provide a source of seed for natural regeneration of the species in semi-natural ash woodlands. For the remaining 13 species which are native to the UK, their lower frequency is often due to reduced ability to produce seed under UK climatic conditions (e.g. *Tilia cordata*) or exacting germination requirements being infrequently met (e.g. *Populus nigra*) (Pigott 1991; Cottrell 2004).

Table 5. Summary of production and distribution information available for alternative tree species. Native species: Y= species found in native ash woodlands (Rodwell 1991), N = species not generally found in native ash woods, nn = non-native species found in native woodlands, this reflects the availability of nearby planted sites to provide a source of seed for natural regeneration of the species in semi-natural woodlands. Production information: Y = species used for production and the site requirements of the species is well understood, N = species used occasionally for production but the site requirements of the species are not well understood, O = species used for amenity planting. NU = species not currently used for production in the UK. For native species distributional information is provided indicating climatic constraints to their growth based on their range in semi-natural ash-woodlands in the UK: F = a frequent species in ash woods in this region, I = species present infrequently in ash woods in this region, No = species not present in ash woods in this region. Northern = Scotland, northern England and Northern Ireland, Southern = southern England and Wales. Upland =Accumulated temperature ≤ 1200 day degrees, Lowland = Accumulated temperature >1200 day degrees. Distribution of *Ulmus* was not included due to major declines in abundance caused by Dutch Elm disease

Tree alternative	Native species?	Production information?	Distribution information					
			Northern	Upland	Lowland	Southern	Upland	Lowland
Abies alba	N	N						
Acer campestre	Y	NU	✔	No	I	✔	I	F
Acer platanoides	N	Y	✔	I	I	✔	I	I
Acer pseudoplatanus	nn	Y	✔	F	F	✔	F	F
Aesculus hippocastanum	N	O						
Alnus cordata	N	N						
Alnus glutinosa	Y	Y	✔	F	F	✔	F	I
Betula pendula	Y	Y	✔	F	F	✔	F	F
Betula pubescens	Y	Y	✔	F	F	✔	F	F
Carpinus betulus	Y	Y	✔	No	I	✔	No	F
Carya ovata	N	N						
Castanea sativa	nn	Y	✔	No	I	✔	No	F
Corylus avellana	Y	NU	✔	F	F	✔	F	F
Crataegus monogyna	Y	NU	✔	F	F	✔	F	F
Fagus sylvatica	Y	Y	✔	I	I	✔	I	F
Fraxinus americana	N	N						
Fraxinus mandschurica	N	N						
Fraxinus ornus	N	N						
Fraxinus pennsylvanica	N	N						
Ilex aquifolium	Y	NU	✔	F	F	✔	F	F
Juglans nigra	N	N						
Juglans regia	N	N						
Larix decidua	N	Y						
Ligustrum vulgare	Y	NU	✔	No	I	✔	I	F
Malus sylvestris	Y	NU	✔	I	I	✔	I	F
Ostrya carpinifolia	N	N						
Pinus sylvestris	N	Y						
Platanus x hybrid	N	O						
Populus nigra	Y	Y	✔	I	I	✔	I	I
Populus tremula	Y	NU	✔	I	I	✔	I	I
Prunus avium	Y	Y	✔	F	F	✔	F	No
Prunus padus	Y	NU	✔	I	I	✔	I	F
Prunus spinosa	Y	NU	✔	F	F	✔	F	F
Pseudotsuga menziesii	N	Y	✔	I	I	✔	I	I
Pterocarya fraxinifolia	N	N						
Quercus cerris	N	N						
Quercus petraea	Y	Y	✔	F	F	✔	F	F
Quercus robur	Y	Y	✔	F	F	✔	F	F
Quercus rubra	N	N						
Salix caprea	Y	NU	✔	F	F	✔	F	F
Salix cinerea	Y	NU	✔	F	F	✔	F	F
Sambucus nigra	Y	NU	✔	F	F	✔	F	F

Table 5. (Continued)

Tree alternative	Native species?	Production information?	Distribution information					
			Northern	Upland	Lowland	Southern	Upland	Lowland
Sorbus aria	Y	NU	✕			✔	No	F
Sorbus aucuparia	Y	NU	✔	F	F	✔	F	F
Sorbus torminalis	Y	NU	✕			✔	No	I
Taxus baccata	Y	NU	✔	I	I	✔	I	F
Thuja plicata	N	Y						
Tilia cordata	Y	Y	✕			✔	I	I
Tilia platyphyllos	nn	NU	✕			✔	No	I
Ulmus procera/glabra	Y	Y						

Table 6. Soil conditions considered suitable for the productive growth of alternative species and *F. excelsior* (Y) taken from Pyatt et al. 2001. Soil moisture regime: VW = Very Wet, W = Wet, VM = Very Moist, M = Moist, F = Fresh, SD = Slightly Dry, MD = Moderately Dry, VD = Very Dry. Soil nutrient regime: VP = Very Poor, P = Poor, M = Medium, R = Rich, VR = Very Rich, C = Carbonate

	Soil Moisture Regime								Soil Nutrient Regime					
	VW	W	VM	M	F	SD	MD	VD	VP	P	M	R	VR	C
Fraxinus excelsior		Y	Y	Y	Y	Y					Y	Y	Y	Y
Acer platanoides			Y	Y	Y	Y	Y				Y	Y	Y	Y
Acer pseudoplatanus		Y	Y	Y	Y	Y	Y			Y	Y	Y	Y	Y
Alnus glutinosa	Y	Y	Y	Y	Y					Y	Y	Y	Y	
Betula pendula		Y	Y	Y	Y	Y	Y		Y	Y	Y	Y	Y	
Betula pubescens	Y	Y	Y	Y	Y				Y	Y	Y	Y		
Carpinus betulus		Y	Y	Y	Y	Y				Y	Y	Y	Y	
Castanea sativa			Y	Y	Y	Y					Y	Y	Y	
Fagus sylvatica				Y	Y	Y	Y			Y	Y	Y	Y	Y
Larix decidua			Y	Y	Y	Y	Y			Y	Y	Y	Y	Y
Pinus sylvestris			Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	
Populus nigra		Y	Y	Y	Y						Y	Y	Y	
Populus tremula		Y	Y	Y	Y	Y				Y	Y	Y	Y	
Prunus avium			Y	Y	Y	Y					Y	Y	Y	Y
Pseudotsuga menziesii				Y	Y	Y	Y	Y		Y	Y	Y	Y	
Quercus petraea			Y	Y	Y	Y	Y			Y	Y	Y	Y	
Quercus robur		Y	Y	Y	Y	Y				Y	Y	Y	Y	
Thuja plicata		Y	Y	Y	Y	Y	Y			Y	Y	Y	Y	Y
Tilia cordata			Y	Y	Y	Y					Y	Y	Y	Y
Ulmus glabra		Y	Y	Y	Y	Y				Y	Y	Y	Y	

Detailed climatic and soil nutrient requirements

Site requirements (climatic constraints, soil moisture and soil nutrient regime) were available for nineteen of the alternative species; these were compared to the requirements of *F. excelsior* (Table 6).

Climate:
F. excelsior is ecologically suitable in five of the seven climate zones identified in the UK (Pyatt et al. 2001). Only one of the alternative species (*Betula pubescens*) is suitable in a broader range of climatic conditions than *F. excelsior* as it can still be productive where climatic warmth is as low as c.475 day degrees.

Soil conditions:
F. excelsior will grow productively where the SMR is 'Wet' through all the intervening classes up to and including 'Slightly Dry'. While 11 of the alternative species can be productive in as wet or wetter soil conditions than *F. excelsior*, and 17 species can grow well on soils as dry or with drier soil conditions, only seven species are suitable to grow on the same range of SMR classes as *F. excelsior*. *F. excelsior* is ecologically suitable where the SNR is 'Medium' to 'Very Rich' and also 'Carbonate soils', which typically occurs with rendzina soils on limestone and chalk lithologies. There is a better match between the soil nutrient requirements that are suitable for the growth of *F. excelsior*

and the alternative species. All of the 19 alternative species can tolerate 'Medium' or poorer soils and all but one species (*Betula pendula)* are ecologically suitable on sites with a 'Very Rich' SNR. However, only seven species are suitable on soils classed as 'Carbonate'. When both the SNR and the SMR requirements of the alternative species are considered, only two species, *Acer pseudoplatanus* and *Thuja plicata*, are suited to sites with the same range of soil conditions as those required by *F. excelsior*.

Natural successional processes

Information on natural successional processes is available for *F. excelsior* and eleven of the alternative species. *F. excelsior* germinates well and shows a medium to good ability to grow at the seedling or sapling stage in shade (Table S4-S6). *A. pseudoplatanus, F. sylvatica*, *P. avium* and *T. cordata* are reported to germinate well in shade and along with *Quercus petraea/robur* to grow well in shady conditions. Providing conditions were suitable for natural regeneration (e.g. available seed bed and low browsing pressure) these six species could be managed to replace *F. excelsior* in woodlands by natural regeneration. *Alnus glutinosa, Populus tremula* and *B. pubesens/pendula* all require higher light levels for seed germination and for early stage of tree growth compared to *F. excelsior* and would therefore not be as easy to manage by natural regeneration in place of *F. excelsior*.

Two further alternative species, both of which are non-native in the UK, were included by Mitchell et al. (2014b) due to their possible role in supporting ash-associated species. None of these species are considered as having production potential: *Aesculus hippocastanum* is threatened by disease (Laue et al. 2014) and *Platanus x hybrid* although being present as part of amenity planting for nearly a century has never been adopted by mainstream forestry in the UK.

The 13 remaining alternative species have been suggested for use on sites which currently support *F. excelsior*. However we have little experience of these species growing in UK conditions.

Discussion

Methods to assess the suitability of alternative trees

An awareness of the potential ecological impact of tree diseases is increasing with both predicted and actual declines in species populations now documented (Boyd et al. 2013, Ellis et al. 2012; Pautasso et al. 2013; Lohmus and Runnel 2014; Mitchell et al., 2014a). Once the potential species at risk due to tree loss are identified the next stage is to identify mitigation measures such as possible alternative trees. Here we have assessed the suitability of 48 alternative tree species to *F. excelsior* by three different methods, a far greater number than previously assessed by Mitchell et al. (2014a, 2016) where only 22 and 11 species were assessed. Our results show that it is possible to begin to make an assessment of the suitability of alternative trees based on their associated species, their traits and their site requirements. However there are a number of challenges with these approaches. When such ecological assessments are made it is important that these limitations are taken into account and where possible, additional data collected to fill the knowledge gaps.

The methods attempt to compare alternative tree species using ash-associated species, their traits and their site requirements. Ideally an alternative tree species should be similar to *F. excelsior* in all three of these categories, however different tree species were shown as most or least similar to *F. excelsior* depending on the method used (Table 7). This issue was identified by Mitchell et al. (2016) when comparing species use and ecosystem function for 11 tree species. Which ranking of alternative tree species is used may depend on the site objectives. If the aim is to conserve ash-associated biodiversity then using associated species to assess the most suitable alternative tree species will be most acceptable. However, if the aim is to preserve the visual attributes of the forest, or the ecosystem function then ranking by traits may be more useful. Finally if timber production is the objective, then site suitability may be the over-arching factor to consider. Ideally methods such as that proposed by Mitchell et al. (2016) to combine multiple types of assessment should be used.

Autoecological knowledge of species suggests that the phenotypic characteristics of a tree (traits) will influence the suite of associated species. In theory it should therefore be possible to use the phenotypic traits to predict if an ash-associated species will use any given alternative tree species. Ideally one would wish to find a correlation between certain traits and the number of ash-associated species supported. This might allow the prediction of which alternative trees would support the greatest number of ash-associated species. However, our data did not show any simple relationship between the number of traits that were the same as *F. excelsior* and the number of associated species supported. Thus while the traits of trees may be useful for assessing the use by individual ash-associated species, or groups of species (e.g. the relationship between bryophytes and lichens with that of bark pH); at the moment it is not possible to make broad generalizations about traits and the number of ash-associated species supported. This may be due to lack of data on traits for some tree species or traits other than those assessed being important in determining which ash-associated species use the alternative trees. In addition it may be the presence or absence of a few traits that determine the number of ash-associated species supported, rather than the overall number of traits that are the same.

Table 7. The 5 most suitable and 5 least suitable native and non-native tree species as alternatives to *F. excelsior* out of 48 assessed as assessed by species, traits and site requirements. ? = many species of intermediate similarity and difficult to rank them

Alternative tree species	Species use	Traits	Site requirements
Native species			
Most suitable	*Quercus robur/petraea*	*Ulmus glabra/procera*	*Quercus robur/petraea*
	Fagus sylvatica	*Betula pendula*	*Populus tremula*
	Ulmus procera/glabra	?	*Betula pendula*
	Corylus avellana	?	*Ulmus glabra/procera*
	Betula pubescens/pendula	?	*Carpinus betulus*
	Salix cinerea	?	*Fagus sylvatica*
	Taxus baccata	*Crataegus monogyna*	*Alnus glutinosa*
	tilia cordata	*Malus sylvestris*	*Populus nigra*
	Populus nigra	*Salix cinerea*	*Pinus sylvatica*
Least suitable	*Sorbus torminalis*	*Tilia platyphyllos*	*Betula pubescens*
Non-native species			
Most suitable	*Acer pseudoplatanus*	*Fraxinus americana*	*Acer pseudoplatanus*
	Aesculus hippocastanum	*Juglans regia*	*Thuja plicata*
	Larix decidua	*Fraxinus pennsylvanica*	*Acer platanoides*
	Juglans regia	*Juglans nigra*	*Larix decidua*
	Castanea sativa	*Fraxinus mandschurica*	?
	Pseudotsuga menziesii		?
	Alnus cordata	*Acer platonoides*	?
	Fraxinus mandschurica	*Pseudotsuga menziesii*	?
	Carya ovata	*Abies alba*	*Castanea sativa*
Least suitable	*Pterocarya fraxinifolia*	*Larix decidua*	*Pseudotsuga menziesii*

Limitations of approaches

In the final ranking of tree species (Table 7) all ash-associated species are treated equally and all traits are treated equally. However as shown in the results which alternative tree species are considered the most suitable does depend on how the tree species are ranked – whether by all ash-associated species, just by highly associated species or by individual taxon groups. Similarly, some traits maybe more important than others in maintaining ash-associated species or ecosystem functioning similar to *F. excelsior* and these traits could be prioritised in the assessment. However further work is needed to identify which traits would be prioritised. Some traits are known to have greater intra-specific variation influenced by environmental conditions e.g. specific leaf area. Therefore the similarity of tree species to *F. excelsior* when assessed by such traits may vary depending on the environmental conditions. All three approaches are essentially based on a ranking of species which takes no account of the quality of the data or the amount of missing data. Ideally someway of combining the quality/availability of data together with the ranking would represent an improvement.

Some of the traits were used to indicate how ecosystem functioning might change if there was a change to that alternative tree species. An alternative method to using traits is to use direct measurements of ecosystem functions such as litter quality, decomposition, soil chemistry taken from a literature review. However, when this was done by Mitchell et al. (2016) for 11 alternative tree species knowledge gaps were still a major problem with data missing for many tree species/function combinations.

Data availability and quality

Data availability was a major issue for all three types of assessment, particularly in relation to the assessment of the suitability of non-native tree species. There is a statistical basis with the more widespread and abundant alternative tree species being more likely to have had ash-associated species recorded using them when using data from volunteer recording rather systematic comparisons. Lack of data means there is a risk that an alternative tree species may be wrongly classed as ecologically inappropriate due to lack of data, but if planted without an appropriate assessment there is the potential to initiate large changes in species composition and a precautionary principal is advised. Data limitation also resulted in the data being collated at two different scales. Species composition used data that was predominantly collated from the UK (although for some invertebrates their use of non-native alternatives was assessed using non-UK data) while the trait data was collected from international datasets. As mentioned earlier some traits may change with site characteristics with the potential for traits collected from outside the UK to be invalid.

The concept of alternative tree species raises questions over the role of non-native species. If the objective is to climate-proof our forests, in addition to making them more resistant to diseases, then in some countries/regions the ecological suitability of non-native tree species will have to be considered. Non-natives may provide the best alternatives which will ultimately ensure the sustainability of our woodlands and forests. However for many non-native tree species there is insufficient data to make an accurate assessment of their suitability as alternatives.

It is unlikely that we will ever have all the ecological data one would require to make a full ecological assessment of the most appropriate alternative tree species. However recording the species found in association with non-native trees in parks/gardens/arboreta would fill some of the knowledge gaps identified above and provide a better understanding of the potential of these species as alternative trees. The collecting and sharing of information on trait data is a growing area of study and it is likely that many of the gaps in our knowledge of traits may be filled in the next few years. Studying the growth requirements of non-native tree species in their native countries may help fill gaps related to growing conditions.

Data quality seemed to be less of an issue than data availability although the issue of recorder bias was raised. Recorder bias is almost inevitable when using volunteer recording schemes although recent studies are addressing this problem (e.g. Isaac and Pocock 2015). In terms of this study, while acknowledging that the biases are present, the data from volunteer recording schemes provides an invaluable data source for making such assessments, particular since these data are not available from other sources.

Conclusion

In relation to *F. excelsior,* our study shows that no one species is suited to all the site types associated with *F. excelsior*, nor will any one tree species support a high percentage of the ash-associated species while also matching many of the *F. excelsior* traits. The approaches used here can provide broad guidance on the suitability of alternative tree species to replace *F. excelsior* but when making decisions at individual sites, a site based approach such as that used by Broome et al. (2014) is required, taking into account the ash-associated species present at the site, the site management approaches and which tree species will grow productively a site (site requirements – climate and soils). Compromises will have to be made during the selection of alternative tree species concerning whether to replicate traits/species use or to compromise on the site requirements and perhaps accept tree species that are less productive.

The methods applied here to identify species associated with a particular tree species and then the suitability of alternative trees via an assessment of species use and traits could be applied to any other tree/tree disease combination. However, one of the main aims of this work was to collate information on the quality and availability of data. This study involved data from a country (the UK) with a global reputation for high quality biological records associated with a common tree species yet we still had issues associated with lack of data. Such issues are likely to be even more prevalent in countries with less well documented biological records and/or less common tree species.

When new diseases arrive in a region/country, there is often a requirement for a rapid assessment of the potential impact and the suitability of alternative tree species. The issues outlined above in terms of data availability need to be made clear to politicians and policy makers, particularly when such rapid assessments are required. In the longer-term, this case study highlights the need for the collation of biological records, that document the use of tree species so that rapid assessments of the potential ecological impacts of the loss of any given tree species and the suitability of their alternative tree species can be made.

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Data accessibility

This work synthesised existing data. All trait data and the species use data are summarised in an Microsoft Excel file available from Natural England called AshEcol: http://publications.naturalengland.o rg.uk/publication/5273931279761408.

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Supplementary material

Table S1. Methods used to asess level of species associated with *F. excelsior* and alternative tree species.

Species group	Data sources and criteria used to assess association
Lichens	For all lichen species which had been confirmed as recorded on *F. excelsior* within the British Lichen Society database (1960-2010), the number of times that each species had been recorded on *F. excelsior* as a proportion of the total number of all records across all substrata (including corticolous, terricolous and saxicolous records, etc) was calculated. The 'level of association' for a species was considered *obligate* if 100% of records were from *F. excelsior*, *high* if >50% of records were from *F. excelsior*, *partial* if >11.16% of records are from *F. excelsior*, and *cosmopolitan* if the number of records from *F. excelsior* trees <11.16%.
Bryophytes	The British Bryological Society (BBS) records and the bryophyte atlases (Hill et al., 1991, 1992 and 1994).
Fungi	The species assessed was limited to the fungal taxa in The Fungal Records Database of Britain and Ireland (FRDBI) http://www.fieldmycology.net/FRDBI/FRDBI.asp which matched the criteria: more than 10 records with an associated organism of which 25% or more were with *F. excelsior*, or had a species epithet suggesting a strong affinity with *F. excelsior*. The degree of association with *F. excelsior* of these taxa falling within this criterium was assessed as: obligate – 95% or more of the records were with *F. excelsior*; highly dependent – 50-95% records were with *F. excelsior*, the remaining taxa were considered to be partially dependent on *F. excelsior*.
Invertebrates	Initial species selection was guided by Stubbs (2012) together with reference to the Database of Insects and their Food Plants (http://www.brc.ac.uk/DBIF/homepage.aspx). Some species were discounted where the association with *F. excelsior* was from old references and this association had not been repeated in more recent and comprehensive reviews of the species. References to use of *F. excelsior* solely in captive rearing situations were also discounted. The initial list of invertebrate species identified was then supplemented from a wider literature search and consultation with some species group experts.
Mammals	The Handbook of British Mammals (Harris and Yalden, 2008). Retrieved from http://books.google.co.uk/books?id=w_UJNAAACAAJ was used as the main information source regarding the association of mammals with *F. excelsior*, supplemented with additional literature searches, and accessing websites of interested groups and societies for natural-history information.
Birds	The assessment of birds associated with *F. excelsior* trees was primarily based on online searches of peer reviewed literature. Further information was sought from unpublished reviews on the habitat associations and requirements for woodland birds.

Table S2. Data sources for tree traits. Numbers refer to the numbered references listed in Table S3

Tree alternative	Bark pH	Deciduous	Floral reward	Fruit type	Height	LDMC	Leaf shape	Leaf size	Duration of flowering	Mycorrhizal association	Pollen vector	SLA
Abies alba	16	7	5	10	9	4	7			1	5	
Aesculus hippocastanum		4	4	4	6	3	4	3	4	1	4	3
Alnus cordata		7	11	11	9		7			1	11	
Carya ovata		7		12	8		7			1	11	
Fraxinus americana	17	8	11	11	8	5	7			1	5	
Fraxinus mandschurica		8	11	11	15		8			1	11	
Fraxinus ornus		8	5	11	9		8			1	5	3
Fraxinus pennsylvanica		8	11	11	8		10			1	11	3
Ilex aquifolium		4	4	4	6	3	4	3	4	1	4	3
Juglans nigra		8	11	11	8	11	13			1	11	
Juglans regia		4	5	4	6	3	4	3	4	1	4	3
Larix decidua		4	5	4	6	5	4		4	1	4	
Ligustrum vulgare		4	4	4	6	3	4	3	4	1	4	3
Malus sylvestris		4	4	4	6	3	4	3	4	1	4	3

Table S2. (Continued)

Tree alternative	Bark pH	Deciduous	Floral reward	Fruit type	Height	LDMC	Leaf shape	Leaf size	Duration of flowering	Mycorrhizal association	Pollen vector	SLA
Ostrya carpinifolia		8		10	8		10			1	5	
Pinus sylvestris		4	5	4	6	5	4		4	1	4	
Platanus x hybrid	17	8	5	10	9		10			1	5	3
Populus nigra		4	4	4	6	3	4	3		1	4	3
Prunus spinosa		4	4	4	6		4	3	4	1	4	3
Pterocarya fraxinifolia		8		10	9		14			1	4	
Quercus cerris	18	4	4	4	6	3	4	3	4	1	4	3
Quercus rubra		8	5	11	9	3	5	3		1	11	3
Sambucus nigra	19	4	4	4	6	3	4	3	4	1	4	3
Sorbus aucuparia	20	4	4	4	6	3	4	3	3	1	4	3
Sorbus torminalis		4	3	4	6	3	4	3	4	1	4	3
Thuja plicata		4	4	10	6		10			1	5	
Tilia platyphyllos	21	8	5	4	6	3	4	3	4	1	4	3
Ulmus procera/glabra	22	4	4	4	6	3	4	3	4	1	4	3
Acer campestre	2	4	4	4	6	3	4	3	4	1	4	3
Acer platanoides	2	4	4	4	6	3	4	3	4	1	4	3
Acer pseudoplatanus	2	4	4	4	6	3	4	3	4	1	4	3
Alnus glutinosa	2	4	4	4	6	3	4	3	4	1	4	3
Betula pendula	2	4	4	4	6	3	4	3	4	1	4	3
Betula pubescens	2	4	4	4	6	3	4	3	4	1	4	3
Carpinus betulus	2	4	4	4	6	3	4	3	4	1	4	3
Castanea sativa	2	4	4	4	6	3	4	3	4	1	4	3
Corylus avellana	2	4	4	4	6	3	4	3	4	1	4	3
Crataegus monogyna	2	4	4	4	6	3	4	3	4	1	4	3
Fagus sylvatica	2	4	4	4	6	3	4	3	4	1	4	3
Fraxinus excelsior	2	4	4	4	6	3	4	3	4	1	4	3
Populus tremula	2	4	4	4	6	3	4	3	4	1	4	3
Prunus avium	2	4	4	4	6	3	4	3	4	1	4	3
Prunus padus	2	4	4	4	6	3	4	3	4	1	4	3
Pseudotsuga menziesii	2	4	4	4	6		4		4	1	4	
Quercus petraea	2	4	4	4	6	3	4	3	4	1	4	3
Quercus robur	2	4	4	4	6	3	4	3	4	1	4	3
Salix caprea	2	4	4	4	6	3	4	3	4	1	4	3
Salix cinerea	2	4	4	4	6	3	4	3	4	1	4	3
Sorbus aria	2	4	4	4	6	3	4	3	4	1	4	3
Taxus baccata	2	4	4	4	6	3	4	3	4	1	4	3
Tilia cordata	2	4	4	4	6	3	4	3	4	1	4	3

Table S3. Details of references used to obtain trait information for alternative tree species. No. refers to the trait by tree combination number listed in Table S1.

No	Reference
1	Harley, J.L. & Harley, E.L. 1987. A check-list of mycorrhiza in the British flora. *The New Phytologist*, 105 (2 Supplement), 1–102.
2	Barkman, J.J. 1958. *Phytosociology and Ecology of Cryptogamic Epiphytes*. Netherlands: Van Gorcum & Co., 628 pp.
3	LEDA trait database: Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P, Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimes, L., Klimesová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A-K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B. (2008): The LEDA Traitbase: A database of life-history traits of Northwest European flora. Journal of Ecology 96: 1266-1274. http://www.leda-traitbase.org/LEDAportal/
4	Bioflora database: Derived from Klotz, S., Kühn, I. & Durka, W. 2002. BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde 38. Bonn: Budesamt für Naturschutz. http://www2.ufz.de/biolflor/index.jsp
5	Try database: Kattge, J., S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bönisch, E. Garnier, M., Westoby, P. B. Reich, I. J. Wright, J. H. C. Cornelissen, C. Violle, S. P. Harrison, P., M. v. Bodegom, M. Reichstein, B. J. Enquist, N. A. Soudzilovskaia, D. D. Ackerly, M., Anand, O. Atkin, M. Bahn, T. R. Baker, D. Baldocchi, R. Bekker, C. Blanco, B., Blonder, W. J. Bond, R. Bradstock, D. E. Bunker, F. Casanoves, J. Cavender-Bares,, J. Q. Chambers, F. S. Chapin, J. Chave, D. Coomes, W. K. Cornwell, J. M. Craine,, B. H. Dobrin, L. Duarte, W. Durka, J. Elser, G. Esser, M. Estiarte, W. F. Fagan, J., Fang, F. Fernández-Méndez, A. Fidelis, B. Finegan, O. Flores, H. Ford, D. Frank, G., T. Freschet, N. M. Fyllas, R. V. Gallagher, W. A. Green, A. G. Gutierrez, T. Hickler,, S. Higgins, J. G. Hodgson, A. Jalili, S. Jansen, C. Joly, A. J. Kerkhoff, D. Kirkup, K., Kitajima, M. Kleyer, S. Klotz, J. M. H. Knops, K. Kramer, I. Kühn, H. Kurokawa, D., Laughlin, T. D. Lee, M. Leishman, F. Lens, T. Lenz, S. L. Lewis, J. Lloyd, J. Llusià, F., Louault, S. Ma, M. D. Mahecha, P. Manning, T. Massad, B. Medlyn, J. Messier, A. T., Moles, S. C. Müller, K. Nadrowski, S. Naeem, Ü. Niinemets, S. Nöllert, A. Nüske, R., Ogaya, J. Oleksyn, V. G. Onipchenko, Y. Onoda, J. Ordoñez, G. Overbeck, W. A., Ozinga, S. Patiño, S. Paula, J. G. Pausas, J. Peñuelas, O. L. Phillips, V. Pillar, H., Poorter, L. Poorter, P. Poschlod, A. Prinzing, R. Proulx, A. Rammig, S. Reinsch, B., Reu, L. Sack, B. Salgado-Negret, J. Sardans, S. Shiodera, B. Shipley, A. Siefert, E., Sosinski, J.-F. Soussana, E. Swaine, N. Swenson, K. Thompson, P. Thornton, M., Waldram, E. Weiher, M. White, S. White, S. J. Wright, B. Yguel, S. Zaehle, A. E., Zanne, C. Wirth. 2011. TRY – a global database of plant traits. Global Change, Biology, 17:2905–2935.
6	Hill, M.O., Preston, C.D. & Roy, D.B. 2004. *PLANTATT - attributes of British and Irish Plants: status, size, life history, geography and habitats*. Abbots Ripton: Centre for Ecology and Hydrology.
7	Mitchell, A. (1974) A field guide to the trees of Britain and Northern Europe. Collins, Glasgow
8	Mitchell, A. Wilkinson, J. (1982) The trees of Britain and Northern Europe. Collins, London
9	Stace C.A. (1995) New Flora of the British Isles.Cambridge University Press
10	Based on descriptions of leaf shape or fruit and then categorised using Bioflora categories (expert judgement)
11	Data based on data from species in same genus due to lack of data from this species
12	http://en.wikipedia.org/wiki/Carya_ovata accessed 3/2/14
13	http://apps.rhs.org.uk/plantselector/plant?plantid=6235 accessed 3/2/2014
14	http://en.wikipedia.org/wiki/Pterocarya_fraxinifolia accessed 3/2/14
15	http://en.wikipedia.org/wiki/Fraxinus_mandshurica accessed 3/2/14
16	Legrand I, Asta J, Goudard Y (1996) Variations in bark acidity and conductivity over the trunk length of silver fir and norway spruce. Trees-Structure and Function, 11, 54-58.
17	Everhart SE, Keller HW, Ely JS (2008) Influence of bark ph on the occurrence and distribution of tree canopy myxomycete species. *Mycologia*, 100, 191-204.
18	Ozturk S, Oran S (2011) Investigations on the bark ph and epiphytic lichen diversity of quercus taxa found in marmara region. *Journal of Applied Biological Sciences*, 5, 27-33.
19	Atkinson, M.D. & Atkinson, E. (2002) Biological Flora of the British Isles. Sambucus nigra L. Journal of Ecology, 90, 895-923
20	Raspe,O., Findlay, C., Jacquemart, A.L. (2000) Biological Flora of the British Isles. *Sorbus aucuparia* L. Journal of Ecology, 88, 910-930
21	Loppi S, Frati L (2004) Influence of tree substrate on the diversity of epiphytic lichens: Comparison between tilia platyphyllos and quercus ilex (central italy). *Bryologist*, 107, 340-344.
22	Juriado I, Liira J, Paal J (2009) Diversity of epiphytic lichens in boreo-nemoral forests on the north-estonian limestone escarpment: The effect of tree level factors and local environmental conditions. *Lichenologist*, 41, 81-96.

Table S4. Species names and codes used in Tables S5 and S6

Latin	English	Code for species
Fraxinus excelsior	Ash	Fe
Sorbus aucuparia	Rowan	Sau
Betula pubescens /pendula	Birch, silver or downy.	Bp/p
Acer campestre	Field Maple	Aca
Acer pseudoplatanus	Sycamore	Aps
Populus tremula	Aspen	Ptr
Quercus petraea/robur	Oak, pedunculate or sessile	Qr/p
Fagus sylvatica	Beech	Fsy
Tilia cordata	Lime	Tco
Alnus glutinosa	Alder	Agl
Juglans nigra/regia	Walnut, black or common	Jn/r
Prunus avium	Wild cherry	Pav

Table S5. Details of references used to obtain hierarchy of the ability of the alternative trees to germinate in shade. Tree species aligned between studies where possible.

Poor					Good	Reference
Bp/p						Atkinson 1992
Bp/p					Fsy	Muys et al 1988
Bp=Ptr=Sau=Agl		Qr		Tco		Bobiec 2007
				Sau		Raspe et al 2000
Ptr						Vehmas et al 2009
Ptr						Myking et al 2011
	Aca1			Aca2		1.Mathey 1924 (in Jones 1945); 2. Jones 1945
		Sau				Raspe et al 2000
		Agl				Mcvean 1953
			Pav			Petrokas 2010
			Jr			Taugourdeau et al 2010
			Aps		Fsy	Nagel et al 2010
			Fsy	Fe	Aps	Jones 1945
					Tco	Pigott 1991
					Fsy=Aps	Collet et al 2008
					Qp	Brezina & Dobrovolny 2011
				Qp/r	Fsy	Packham et al 2012
					Qp/r	Jones 1959
					Fe=Fsy	Peltier et al 1997
					Fsy	Szwagrzyk et al 2001
					Fe=Fsy	Emborg 1998
					Fsy	Jarcuska 2009

Species codes are shown in Table S4 and references listed below:

Atkinson, M.D. 1992. *Betula-pendula* Roth (*B-verrucosa* Ehrh) and *B-pubescens* Ehrh. *Journal of Ecology*, 80, 837-870.

Bobiec, A. 2007. The influence of gaps on tree regeneration: A case study of the mixed lime-hornbeam (*Tilio-Carpinetum* Tracz. 1962) communities in the Bialowieza primeval forest. *Polish Journal of Ecology*, 55, 441-455.

Brezina, I., Dobrovolny, L. 2011. Natural regeneration of sessile oak under different light conditions. *Journal of Forest Science*, 57, 359-368.

Collet, C., Piboule, A., Leroy, O., Frochot, H. 2008. Advance *Fagus sylvatica* and *Acer pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-standards forest. *Forestry*, 81, 135-150.

Emborg, J. 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, 106, 83-95.
Jarcuska, B. 2009. Growth, survival, density, biomass partitioning and morphological adaptations of natural regeneration in fagus sylvatica. A review. *Dendrobiology*, 61, 3-11.
Jones, E.W. 1945a. *Acer campestre* L. *Journal of Ecology*, 32, 239-252.
Jones, E.W. 1959. Biological flora of the British-Isles *Quercus* L. *Journal of Ecology*, 47, 169-222.
Mcvean, D.N. 1953. *Alnus-glutinosa* (l) gaertn (a rotundifolia stokes). *Journal of Ecology*, 41, 447-466.
Muys, B., Berge, K., Roskams, P., Maddelein, D., Meyen, S. 1988. Analysis of natural regeneration in a 200 years old beech stand. *Silva Gandavensis*, 61-81.
Myking, T., Bohler, F., Austrheim, G., Solberg, E.J. 2011. Life history strategies of aspen *(Populus tremula* L.) and browsing effects: A literature review. *Forestry*, 84, 61-71.
Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J. 2010. Gap regeneration and replacement patterns in an old-growth *Fagus-abies* forest of Bosnia-Herzegovina. *Plant Ecology*, 208, 307-318.
Packham, J.R., Thomas, P.A., Atkinson, M.D., Degen, T. 2012. Biological flora of the British Isles: *Fagus sylvatica*. *Journal of Ecology*, 100, 1557-1608.
Peltier, A., Touzet, M.C., Armengaud, C., Ponge, J.F. 1997. Establishment of *Fagus sylvatica* and *Fraxinus excelsior* in an old-growth beech forest. *Journal of Vegetation Science*, 8, 13-20.
Petrokas, R. 2010. Prerequisites for the reproduction of wild cherry (*Prunus avium* L.). *Baltic Forestry*, 16, 139-153.
Pigott, C.D. 1991. *Tilia-cordata* miller. *Journal of Ecology*, 79, 1147-1207.
Raspe, O., Findlay, C., Jacquemart, A.L. 2000. *Sorbus aucuparia* L. *Journal of Ecology*, 88, 910-930.
Szwagrzyk, J., Szewczyk, J., Bodziarczyk, J. 2001. Dynamics of seedling banks in beech forest: Results of a 10-year study on germination, growth and survival. *Forest Ecology and Management*, 141, 237-250.
Taugourdeau, O., Sabatier, S. 2010. Limited plasticity of shoot preformation in response to light by understorey saplings of common walnut (*Juglans regia*). *Aob Plants*, 110, 1-8. doi:10.1093/aobpla/plq022
Vehmas, M., Kouki, J., Eerikainen, K. 2009. Long-term spatio-temporal dynamics and historical continuity of European aspen (*Populus tremula* L.) stands in the Koli national park, Eastern Finland. *Forestry*, 82, 135-148.

Table S6. Details of references used to obtain hierarchy of seedlings/saplings of alternative trees to grow in shade. Tree species aligned between studies where possible

Low						High	Reference
Agl							McVean 1953
Agl							Ogilvy et al 2006
Bp/p							Atkinson 1992
Pav				Pav*			Petrokas 2010 * may persist into older forest due to its suckering abilities.
Bp			Aca=Aps=Fe		Qp/r=Fsy		Van Couwenberghe et al 2010
Bp		Ptr		Qr			Portsmuth & Niinemets 2007
	Ptr*						Raspe et al 2000. *But evidence of regeneration in old growth forest so must manage with small gaps… not well studied (Vehmas et al 2009)
		Ptr					Myking et al 2011
		Ptr				Fsy	Wittmann et al 2001
		Jr					Taugourdeau et al 2010
			Sau				Raspe et al 2000
			Aca			Fsy	Diaci et al 2012
				Aps			Hein et al 2009
					Aca		Jones 1945a
					Aps		Jones 1945b
						Aps	Hein et al 2009
				Aps	Qp	Fsy	Kazda et al 2004
				Aps	Fe	Fsy	Petritan et al 2007
				Qp	Tco	Fsy	Pigott 1991
				Qp/r			Jones 1959
				Qp		Fsy	Ligot et al 2013
				Qr		Fsy	Mountford et al 1999

Table S6. (Continued)

Low			High	Reference
	Qp			Brezina & Dobrovolny 2011
	Qr		Fsy	Rozas 2003
	Qp		Fsy	Petritan et al 2013
		Qp/r		Von Lupke 1998
		Qr	Fsy	Welander & Otterson 1998
	Fe=Fsy			Peltier et al 1997
	Fsy			Szwagrzyk et al 2001
			Fsy	Packham et al 2012
			Fsy	Jarcuska 2009

Species codes are shown in Table S4 and references listed below

Atkinson, M.D. 1992. *Betula-pendula* Roth (*B-verrucosa* Ehrh) and *B-pubescens* Ehrh. *Journal of Ecology*, 80, 837-870.

Brezina, I., Dobrovolny, L. 2011. Natural regeneration of sessile oak under different light conditions. *Journal of Forest Science*, 57, 359-368.

Diaci, J., Adamic, T., Rozman, A. 2012. Gap recruitment and partitioning in an old-growth beech forest of the dinaric mountains: Influences of light regime, herb competition and browsing. *Forest Ecology and Management*, 285, 20-28.

Hein, S., Collet, C., Ammer, C., Le Goff, N., Skovsgaard, J.P., Savill, P. 2009. A review of growth and stand dynamics of *Acer pseudoplatanus* L. In Europe: Implications for silviculture. *Forestry*, 82, 361-385.

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Ligot, G., Balandier, P., Fayolle, A., Lejeune, P., Claessens, H. 2013. Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. *Forest Ecology and Management*, 304, 391-398.

Mcvean, D.N. 1953. *Alnus-glutinosa* (l) gaertn (a rotundifolia stokes). *Journal of Ecology*, 41, 447-466.

Mountford, E., Peterken, G., Edwards, P., Manners, J. 1999. Long-term change in growth, mortality and regeneration of trees in denny wood, an old-growth wood-pasture in the new forest (UK). *Perspectives in Plant Ecology, Evolution and Systematics*, 2, 223-272.

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Peltier, A., Touzet, M.C., Armengaud, C., Ponge, J.F. 1997. Establishment of *Fagus sylvatica* and *Fraxinus excelsior* in an old-growth beech forest. *Journal of Vegetation Science*, 8, 13-20.

Petritan, A., Nuske, R., Petritan, I., Tudose, N. 2013. Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.) - European beech (*Fagus sylvatica* L.) forest remnant in the carpathian mountains, Romania. *Forest Ecology and Management*, 308, 67-75.

Petritan, A.M., Von Luepke, B., Petritan, I.C. 2007. Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. *Forestry*, 80, 397-412.

Petrokas, R. 2010. Prerequisites for the reproduction of wild cherry (*Prunus avium* L.). *Baltic Forestry*, 16, 139-153.

Pigott, C.D. 1991. *Tilia-cordata* miller. *Journal of Ecology*, 79, 1147-1207.

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