MAINTAINING ECOSYSTEM PROPERTIES AFTER LOSS OF ASH (*FRAXINUS EXCELSIOR*) IN GREAT BRITAIN

Authors:

Louise Hill*[1], Gabriel Hemery[2], Andy Hector[1] and Nick Brown[1]

1: Department of Plant Sciences, University of Oxford, South Parks Road, OX1 3RB

2: Sylva Foundation, Sylva Wood Centre, Little Wittenham Road, Long Wittenham, Oxfordshire, OX14 4QT

*Corresponding author
Email addresses:
louise.hill@plants.ox.ac.uk

Abstract

1. Acute outbreaks of pests and disease are increasingly impacting tree populations around the world, causing widespread ecological effects. In Britain, ash dieback (*Hymenoscyphus fraxineus* Baral *et al.*) is affecting common ash (*Fraxinus excelsior* L.) populations severely, and the emerald ash borer (*Agrilus planipennis* Fairmaire) is likely to add to the impact in future. This will cause significant changes to the character and functioning of many ecosystems. However, the nature of these changes and the best approach for conserving ecosystems after ash loss are not clear.

2. We present a method to locate those areas most ecologically vulnerable to loss of a major tree species (common ash), and identify the resultant damage to distinctive ecosystem properties. This method uses the functional traits of species and their distributions to map the potential degree of change in traits across space, and recommend management approaches to reduce the change. An Analytic Hierarchy Process is used to score traits according to ecological importance.

3. Our results indicate that in some areas of Britain, provision of ash-associated traits could be reduced by over 50% if all ash is lost. Certain woodland types, and trees outside woodlands, may be especially vulnerable to ash loss. However, compensatory growth by other species could halve this impact in the longer term.

4. We offer management guidance for reducing ecosystem vulnerability to ash loss, including recommending appropriate alternative tree species to encourage through planting or management in particular areas and woodland types.

5. *Synthesis and applications.* Our practical recommendations for the ash dieback outbreak in Britain could help to conserve functional traits in ecosystems affected by the loss of a key species. Furthermore, our method allows spatially-explicit assessment of species trait

conservation to be used in the restoration of ecosystems for the first time. This technique is widely applicable to a range of restoration and conservation scenarios, and represents a step forward in the use of functional traits in conservation.

Keywords: Analytic Hierarchy Process; Ash dieback; *Chalara fraxinea*; Functional traits; Ecosystem adaptation; Functional ecology; *Hymenoscyphus fraxineus*; Tree diseases

Introduction

Trees are critical components of most natural terrestrial ecosystems and provide supporting services essential for human survival, yet their long lifespans and slow reproduction and migration rates make them uniquely vulnerable to modern pressures (Rackham, 2008). In recent years, tree pests and diseases have emerged as one of the great challenges threatening ecosystems worldwide (Boyd, Freer-Smith, Gilligan, & Godfray, 2013; Ennos, 2014; Wingfield, Brockerhoff, Wingfield, & Slippers, 2015). Artificial processes such as international trade in plants and plant products, and climate change, have facilitated the introduction and spread of tree natural enemies and altered long-standing disease dynamics, causing more frequent epidemics that threaten to wipe out whole populations (Brasier, 2008; Cavers, 2014; Pautasso et al., 2010).

The current threats to common ash (*Fraxinus excelsior* L.) in Great Britain are examples of such artificial processes. *Hymenoscyphus fraxineus* (T. Kowalski) Baral et al., causing ash dieback, is an invasive fungal pathogen which is currently in an epidemic phase, showing rapid spread from centres of introduction since its initial detection in Britain in 2012 (Forestry Commission, 2017a). In parts of mainland Europe where the disease has been present for longer (the first symptoms were noticed in Eastern Europe in the early 1990s with earlier introduction likely (Sønstebø et al., 2017)), the disease has shown high rates of infection and mortality, with only between one and five percent of common ash trees showing high levels of tolerance (Kirisits & Schwanda, 2015; Kjær, McKinney, Nielsen, Hansen, & Hansen, 2011; Pautasso, Aas, Queloz, & Holdenrieder, 2013). A future severe threat comes from the recent introduction into Europe of *Agrilus planipennis* Fairmaire, the emerald ash borer (Straw, Williams, Kulinich, & Gninenko, 2013). This has been an exceptionally severe forest pest in North America where it has killed up to 100 million ash trees of various species since its discovery there in 2002 (Herms & McCullough, 2014). Emerald ash borer has the potential to spread throughout Europe, including Britain, by a mixture of natural and human-assisted spread, such as in packing wood or “hitchhiking” on vehicles (Baranchikov, Mozolevskaya, Yurchenko, & Kenis, 2008; Musolin, Selikhovkin, Shabunin, Zviagintsev, & Baranchikov, 2017; Straw et al., 2013; Thomas, 2016).

In combination, these two threats are likely to lead to a rapid decline in populations of common ash species across Europe, and conceivably extirpation from some areas (Straw et al., 2013; Thomas, 2016). However, the knock-on effects are likely to differ across the outbreak zone. In much of Europe, ash species tend to be relatively uncommon forest trees which only comprise a major component of certain characteristic ecosystems (Beck, Caudullo, Tinner, & de Rigo, 2016), although their abundance has been increasing in many areas (Hofmeister, Mihaljevič, & Hošek, 2004). In Britain, by contrast, common ash is the third most abundant broadleaved tree in woodlands (Forestry Commission, 2013), and the most common tree outside of woodlands (Brown & Fisher, 2009; Maskell, Henrys, Norton, Smart, & Wood, 2013), so these threats could lead to the loss of a major constituent of many British ecosystems. Common ash is also an ecologically distinct species, having a range of unusual traits such as high bark pH and rapidly decomposing litter (Mitchell, Bailey, et al., 2014). This means that in Britain, widespread loss of ash is likely to drive changes in the ecological properties of many ecosystems and a reduction in the occurrence of traits and functions associated with ash.

Limited options exist for control of ash dieback or emerald ash borer, although projects to identify and breed cultivars tolerant to ash dieback are ongoing (Clark, 2014). However, there may be other management options available immediately that could reduce the impact of ash loss on ecosystems, such as replanting badly-affected areas with other tree species. These measures are, however, likely to be costly for land managers, so it would be advantageous to be able to prioritise areas that are particularly vulnerable to loss of ash.

The unique ecological characteristics of ash cannot be approximated by any single species; therefore a mixture of trees will be required to replace the highest possible proportion of ash-associated traits (Mitchell, Beaton, et al., 2014). Plant functional traits are the features of plants that determine their responses to the environment and their influence over other trophic levels. They also have substantial effects on ecosystem properties and services (see Pérez-Harguindeguy *et al.* 2013 and references therein). The Mass Ratio Hypothesis states that a species' relative contribution to total ecosystem properties should be proportional to its contribution to primary productivity (Grime, 1998). Thus, we may be able to use species' proportional abundances and functional trait values to predict how the traits that occur in an ecosystem could change with the loss of a species. We can also apply this logic to produce guidance for ways in which we can manage trees and forests to minimise the effects of species loss on the traits that occur, and prioritise areas for action in real-world scenarios, such as the loss of ash.

Our novel method indicates which areas within an outbreak zone are the most ecologically vulnerable to loss of a species, defined as experiencing the greatest degree of change in average trait values. For ash loss in Britain, we use this method to identify the most vulnerable areas and woodland types, and offer management guidance for how to minimise ecological change in those areas. Changes in functional traits in ecosystems are not the only important factors in designing management responses, but they are extremely important to the functioning of ecosystems (Byrnes et al., 2014). We believe that this is the first time it has been possible to consider them directly in a geographically-targeted manner when designing management responses.

Materials and methods

Our analysis is comprised of five steps which are summarised here and in figure 1. Further details are provided in the Supplementary Methods.

Step 1. Compile data on tree abundance distributions and trait values.

Modelled abundance distributions of 20 common British tree and shrub species at 1 km^2 resolution were obtained from Hill et al. (2017), and converted into proportions of the total tree cover in each 1 km^2. The species were: *Acer campestre* L., *Acer platanoides* L., *Acer pseudoplatanus* L., *Alnus glutinosa* (L.) Gaertner, *Betula pendula* Roth, *Betula pubescens* Ehrhart, *Carpinus betulus* L., *Castanea sativa* Miller, *Corylus avellana* L., *Crataegus monogyna* von Jacquin, *Fagus sylvatica* L., *Fraxinus excelsior* L., *Prunus avium* L., *Pseudotsuga menziesii* Franco, *Quercus petraea* Lieblein, *Quercus robur* L., *Salix caprea* L., *Salix cinerea* L., *Taxus baccata* L. and *Tilia cordata* Miller. Trait values were compiled for each of the above species, and for a further six species (*Populus tremula* L., *Prunus padus* L., *Rhamnus cathartica* L., *Sorbus aria* Crantz, *Sorbus aucuparia* L. and *Ulmus glabra* Huds.) for which abundance distribution maps were not available, but which occur regularly alongside ash in woodland National Vegetation Classification (NVC) communities (for use in analysis of different woodland types).

The values of 36 functional traits (see table 1) were obtained for each species – this was every trait for which we could find information for all species. Trait data was obtained from a variety of databases (Ecoflora (2017), AshEcol (Mitchell, Broome, et al., 2014), the TRY Plant Database (Kattge et al., 2011), and Wageningen University and Research Tree Database (Goudzwaard, 2017)) and a wider literature search to fill gaps in coverage and maximise the number of useable traits, as our analysis does not permit missing values. A complete database of the trait data used, including trait values and details of the original sources used for each species and every trait, is available in the Supplementary Materials.

Step 1. Species abundances and trait values:

Species	Abundance (proportion)	Bark pH	Height (m)
Ash	0.5	Alkaline	33.8
Oak	0.3	Neutral	38.6
Rowan	0.2	Acidic	13.3

Step 2. i) Standardise trait values (1 = trait value of ash):

Species	Bark pH	Height (m)
Ash	**1**	**1**
Oak	**0.5**	**0.77**
Rowan	**0**	**0**

Step 2. ii) Multiply standardised trait values by species abundance, and sum across species:

Species	Abundance	Bark pH	Height (m)
Ash	0.5	1	1
Oak	0.3	0.5	0.77
Rowan	0.2	0	0
Average trait values		**0.65**	**0.73**

Step 2. iii) Recalculate average trait values after total ash loss:

Species	Abundance	Bark pH	Height (m)
Ash	**0**	1	1
Oak	0.3	0.5	0.77
Rowan	0.2	0	0
Average trait values		**0.15**	**0.23**

Step 3. Weight average trait values by importance, using AHP weights (see Step 3 in Methods):

	Bark pH	Height (m)
Importance (AHP weight)	**0.85**	**1.62**
Initial average trait values	0.65	0.73
Average trait values multiplied by importance	**0.55**	**1.18**
Initial overall average trait levels (a)	**0.87**	
Average trait values after ash death	0.15	0.23
Average trait values multiplied by importance	**0.13**	**0.37**
Overall average trait levels after ash death (b)	**0.25**	

Step 4. Calculate vulnerability as proportional reduction in overall average trait levels (i.e., decrease in similarity of the ecosystem to ash, because of how traits were standardised):

$$(1 - (b \div a))$$

$$= (1 - (0.25 \div 0.87)) = \mathbf{0.71}$$

Figure 1. A simplified worked example for calculating vulnerability to ash loss for a single kilometre squared, with three species and two traits. The numbered steps correspond to steps in the Methods.

Table 1. Functional traits considered (36 traits). A complete database of the traits used, including trait values and details of the sources used for each species for all traits, is available in the Supplementary Materials.

Trait name		
Annual seed production	First seed production	Litter decomposition rate
Appendages on seeds	Flowering period	Longevity
Bark pH	Fruit type	Mycchorizal type
Deciduous	Germination rate	Nitrogen fixing
Dispersal agent	Germination time	Pollination syndrome
Dispersal time	Growth rate	Pollinator reward type
Dispersule size	Height	Resprouting ability
Ellenberg Light (L)	Inflorescence type	Seedbank type (seed dormancy)
Ellenberg Moisture (F)	Leaf or leaflet area	Seed mass
Ellenberg Nitrogen (N)	Leaf dry matter content per fresh mass (LDMC)	Shade tolerance
Ellenberg Reaction (R)	Leaf lifespan	Specific leaf area (SLA)
First flowering time	Leaf shape	Wood density

Step 2. Calculate average trait values across Britain, and how this may change with loss of ash: a) for different localities (every 1 km2); and b) for different woodland types.

i) Trait values were standardised on a scale of 0 to 1, where 1 is the value of ash and 0 is the value of the most dissimilar species to ash. **ii)** The average value of the standardised traits was calculated for each 1 km^2, by multiplying the standardised trait values of each species by that species' proportional abundance, and summing across species. **iii)** The average standardised trait value was then recalculated for each 1 km^2, for four hypothetical scenarios for the loss of ash and subsequent compensatory growth of other species: 1) Total ash loss followed by no compensatory growth by other tree species; 2) Total ash loss followed by compensatory growth: all other tree species present increased in proportion to their original abundance to fill the space left by ash; 3) and 4) The same as scenarios 1) and 2) (respectively, no compensatory growth and complete compensatory growth), but with a final step where each 1 km^2 is multiplied by the proportion of forest cover present in that square, as defined by the National Forest Inventory (Forestry Commission, 2017b).

The scenarios represent the most extreme possible cases for compensatory growth, chosen for simplicity and to frame the full range of possibilities – however the true rate of compensation would be expected to be somewhere between these two extremes. Scenarios 3) and 4) represent the change that may occur in woodland ecosystems only, not including trees outside woodlands. In all scenarios, we assumed 100% ash loss. This is a simplification of the true situation as current evidence suggests that between 1% and 5% of ash trees may survive ash dieback (Vasaitis & Enderle, 2017). However, losses of 95% to 99% of ash trees would cause impacts on trait provision almost as severe as complete loss. With the additional threat from emerald ash borer, extirpation from some areas remains a possibility (Enderle et al., 2017; Straw et al., 2013; Thomas, 2016).

We carried out the same analysis for different woodland types, using species abundances from the National Vegetation Classification (NVC) floristic tables (Rodwell et al., 1991). The woodland types used were the 15 NVC woodland sub-communities where ash is a constant or frequent species (see table 2).

Step 3. Weight traits by importance for ecosystem services using Analytic Hierarchy Process (AHP).

Traits are unlikely to have equal contributions to emergent ecosystem properties, such as ecosystem services: for example, litter decomposition rate and the type of appendages on seeds were both included in our analysis, but litter decomposition rate is likely to have a far greater impact on most ecosystem services. An Analytic Hierarchy Process (AHP) (Saaty, 2008) was used to produce weights for all traits based on their relative importance for woodland ecosystem services, using the *R* package 'ahp' (Glur, 2017). For explanations of the theory and practical use of AHP, see Saaty (2008) and Glur (2017). Eight key woodland ecosystem services were considered (climate regulation, primary production, nutrient cycling, soil formation, water cycling, flood protection, pollination services and supporting biodiversity). Cultural services, which are unlikely to be adequately explained by species' traits, were not considered.

For simplicity, all ecosystem services were weighted equally to avoid arbitrarily assigning more importance to one service over another, but alternative weightings can easily be incorporated in any future analyses. All 36 traits were compared in a pairwise manner in terms of their importance to each ecosystem service. Scores were agreed between all authors, using our knowledge of woodland ecosystems and best judgement to agree scores between us. Each author scored the traits separately to avoid bias towards the opinions of senior authors, and we then discussed and resolved any disparities, which were minor. The agreed orders of trait importance and the file containing complete pairwise comparisons (in *yaml* format required for *ahp* package) are available in the Supplementary Materials. For each ecosystem service, consistency indices were calculated; these measure the internal consistency of the comparison matrices generated by AHP, to check for impossible ratings (e.g. $a > b$, $b > c$, $c > a$). All our pairwise comparisons have consistency indices ≤ 0.1, and are acceptably consistent (see Supplementary Material).

Our final trait weights were produced by averaging the weights produced for each trait across the ecosystem services. These were used to weight each trait by importance; the average trait value for each trait (produced in step 2) was multiplied by its weight, before averaging across traits. This produced overall average trait levels weighted by importance of traits, for both the initial ecosystem and the four future scenarios.

Step 4. Calculate "vulnerability": the proportion of ash-like traits lost.

Our final vulnerability scores are the proportional change in average trait values between the current scenario and the four future scenarios. This can be considered as the reduction in similarity of the average trait values to ash, because the traits are standardised according to their similarity to ash. See figure 1 for a complete simplified worked example of calculating vulnerability scores. We also projected where the greatest changes in provision of each ecosystem service might occur, by calculating vulnerability scores using the AHP weightings for each ecosystem service in turn, rather than the overall weightings for all ecosystem services combined. This analysis assumed no compensatory growth by other tree species.

Step 5. Identify recommendations for alternative tree species with the aim of stabilising average trait values after loss of ash.

Vulnerability scores were also produced for each trait separately, by calculating vulnerability as in Step 4 but without averaging across traits first. These vulnerability scores showed us which traits are most at risk in which areas, allowing us to recommend alternative species that are most similar to ash for those traits. For each of the most vulnerable areas and woodland types, the five traits with the highest vulnerability scores were identified. We then used our compiled trait database to identify the tree species with the greatest similarity to ash for those traits; these species were recommended as suitable replacements; three or four species were required in each case to ensure that all five highly vulnerable traits were provided for (see Box 1). For the NVC communities, replacement species were only chosen from the subset of species that already occur in each NVC community. This avoided species that would drastically alter these communities or be unsuitable for the growing conditions.

Results

Overall vulnerability scores and vulnerability hotspots.

Our results predict that loss of ash with no compensation could cause a large decrease in ash-like traits in ecosystems (Figure 2a). The mean value of vulnerability across Great Britain was 0.14, but the distribution of vulnerability scores was right-skewed, suggesting that a small number of areas are expected to be much more vulnerable to loss of ash than the majority. The highest decrease in overall trait similarity to ash per kilometre squared was 0.53 (where 1 means all ash-like traits are lost), *i.e.* more than half of the ash-like traits in that location are expected to be lost. However, the overall vulnerability score varies considerably across Great Britain. The largest hotspot of high vulnerability was the Yorkshire Wolds (Figure 2c), with other smaller patches of high vulnerability occurring throughout much of Britain, in both lowland and upland areas (Figure 2). Visual exploration of the distribution maps shows that these patches of high vulnerability occur where the overall proportion of ash is high and the diversity of other tree species is low, so there are few available species that may provide similar traits to ash.

In the second scenario (maximum compensation, Figure 2b), there is a strong contrast in the vulnerability scores. The effect of loss of ash is predicted to be much lower when other tree species are allowed to grow to compensate (although the geographical patterns of the most vulnerable areas remained the same). The highest vulnerability score under this scenario was 0.20, less than half of the highest score without compensation, and the average vulnerability was only 0.06, suggesting that ecosystems will be much less vulnerable if high compensation occurs.

When we restricted our analyses to consider only trees within woodlands (Figure 3a) we revealed a different geographical pattern of vulnerability, with generally a much lower vulnerability, and a more even distribution of vulnerable areas across Britain (*c.f.* Figure 2). The maximum vulnerability for this scenario was 0.15 in parts of Scotland and Wales, and in England the south, north east and East

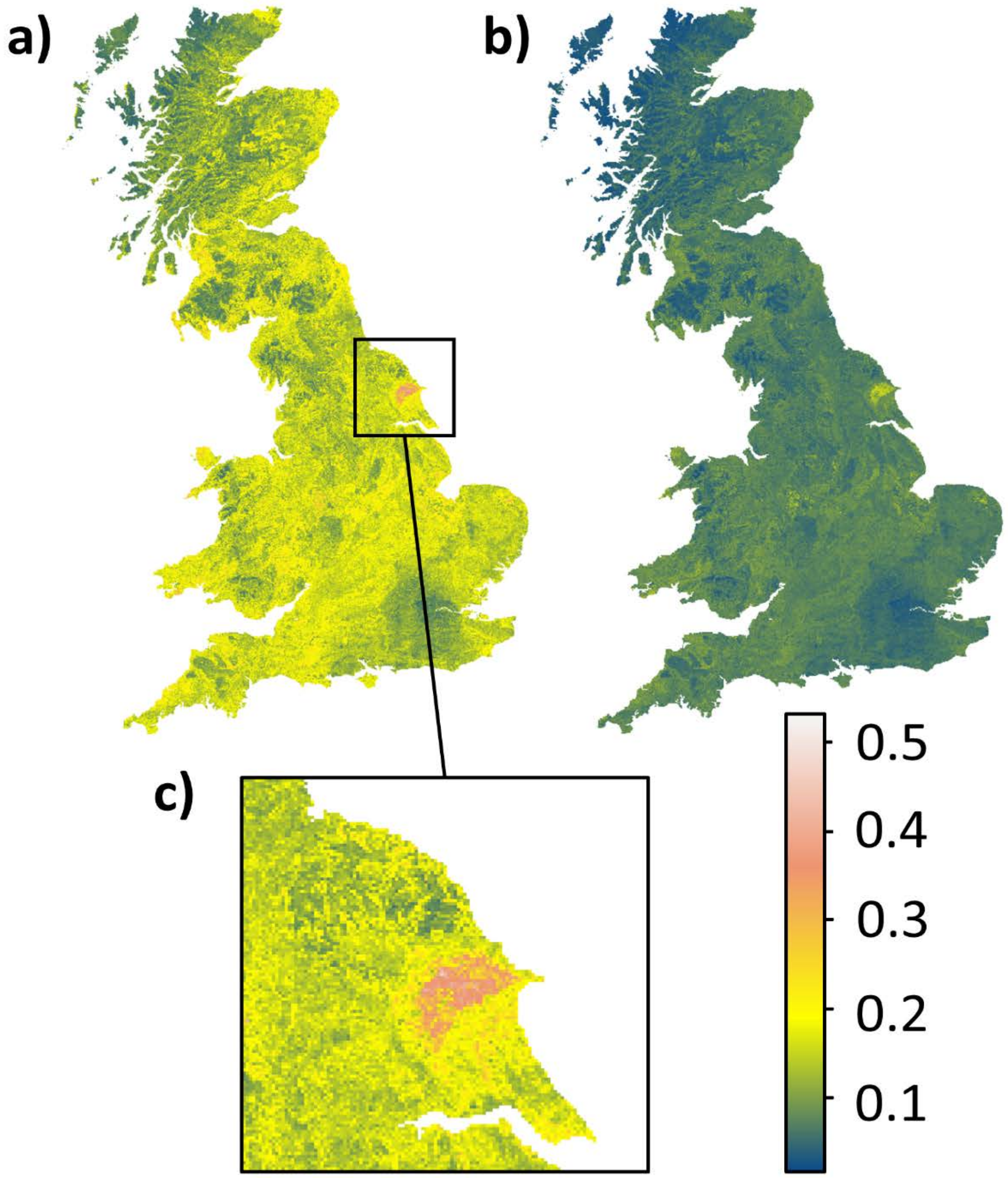

Figure 2. Vulnerability scores (reduction in average similarity to ash-like traits after 100% ash death) for two different scenarios: **a)** loss of all ash, no compensatory growth of other trees; **b)** loss of all ash, with compensatory growth of other tree species to completely fill the gaps left by ash; **c)** expanded view showing one of the most vulnerable areas (Yorkshire Wolds) with no compensatory growth. A vulnerability score of 0 means that all ash-like traits are predicted to continue to be provided at the same levels after ash death by alternative trees; a score of 1 means that all ash-like traits are predicted to be lost.

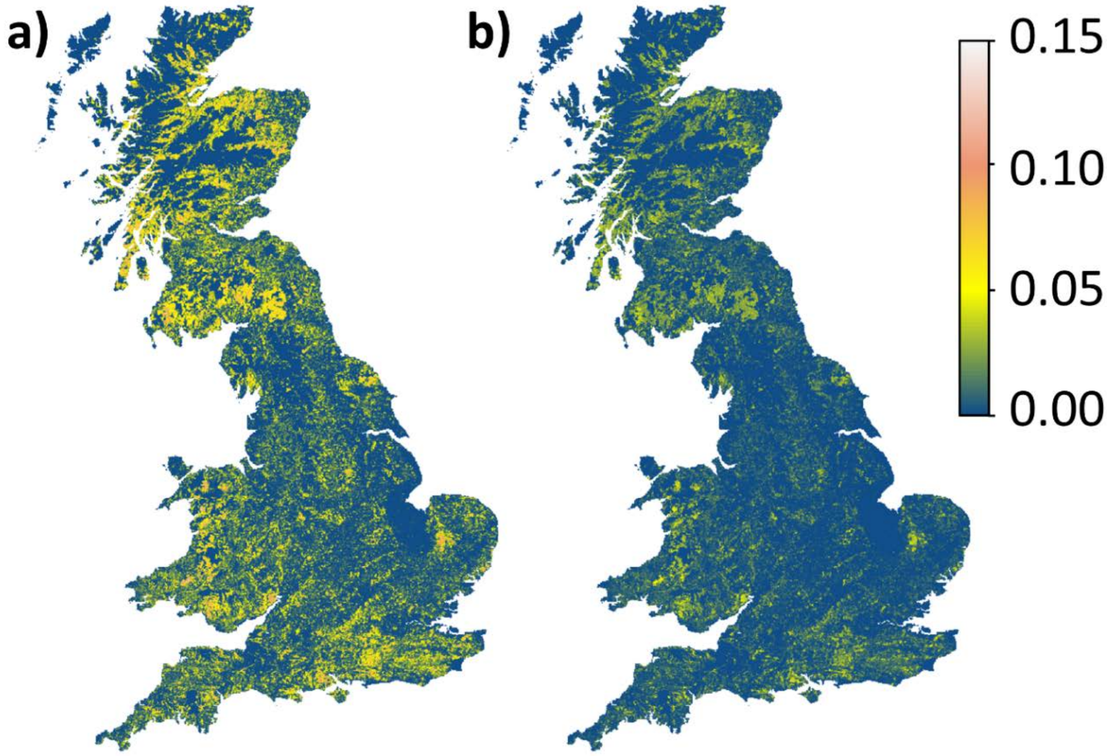

Figure 3. Vulnerability scores, for woodland trees only, for two scenarios: **a)** loss of all ash, no compensatory growth of other trees; **b)** loss of all ash, compensatory growth of other tree species to completely fill the gaps left by ash. Note that the colour scale is different from that used in Fig. 2.

Anglia. Compensatory growth also reduced vulnerability for woodlands-only (Figure 3b), with maximum vulnerability 0.07.

The effects of ash death within some woodlands are likely to be locally important. Very few 1-km squares in Britain are entirely covered in woodland and so high impacts within some woodlands will be masked by averaging within 1-km squares. For this reason, we applied our method to typical community compositions from the National Vegetation Classification (NVC). These woodland types also varied greatly in vulnerability: the classification with the highest vulnerability was W10e with a score of 0.47, and the lowest was W5b with 0.07 (see Table 2). W10e contains only *Acer pseudoplatanus* and *Corylus avellana* as frequent tree species in addition to ash, neither of which share many traits with ash.

For each NVC woodland sub-community considered, and for each of the most-vulnerable areas, we have also produced guidance for mixtures of alternative tree species which could be planted or

Table 2. Vulnerability to ash loss for NVC woodland sub-communities containing constant or frequent ash (0 indicates provision of ash-like traits by alternative trees is predicted not to change after ash loss, and 1 indicates predicted loss of all ash-like traits). As for the maps of vulnerability, vulnerability scores with and without compensatory growth by other trees that are currently present are shown. Guidance for recommended tree species mixes for each community are shown in Box 1.

NVC woodland sub-community	Vulnerability score (without compensation)	Vulnerability score (with compensation)
W10e	0.47	0.18
W7a	0.46	0.22
W8a	0.44	0.21
W8c	0.41	0.18
W8d	0.37	0.17
W8b	0.35	0.18
W8g	0.33	0.12
W12a	0.33	0.15
W8e	0.29	0.1
W8f	0.29	0.1
W9a	0.27	0.1
W7c	0.24	0.1
W9b	0.2	0.1
W5a	0.14	0.09
W5b	0.13	0.07

encouraged to reduce the vulnerability of the area. Box 1 shows our recommendations for the tree species to plant for each highly-vulnerable area and woodland type. We selected these alternative species to provide the specific values of functional traits for each location that could otherwise be lost after ash loss. Recommended species are listed in order of priority: the first species compensates for the trait most at risk in the location, and so on.

Changes in occurrence of traits and ecosystem service provision.

We plotted the change in occurrence of each trait separately to investigate which traits are most at risk from loss of ash, and whether there is geographic variation between them. The traits with the largest changes in trait values were seedbank type, mycorrhizal type and dispersal agent, with Ellenberg's light and nutrient indicators, litter decomposition rate, and type of appendages on the seed, also predicted to be strongly affected. Despite some variation in geographic distribution between traits, the reduction in trait similarity to ash was generally highest in the Yorkshire Wolds and some other lowland areas of England and Wales (Figure 4).

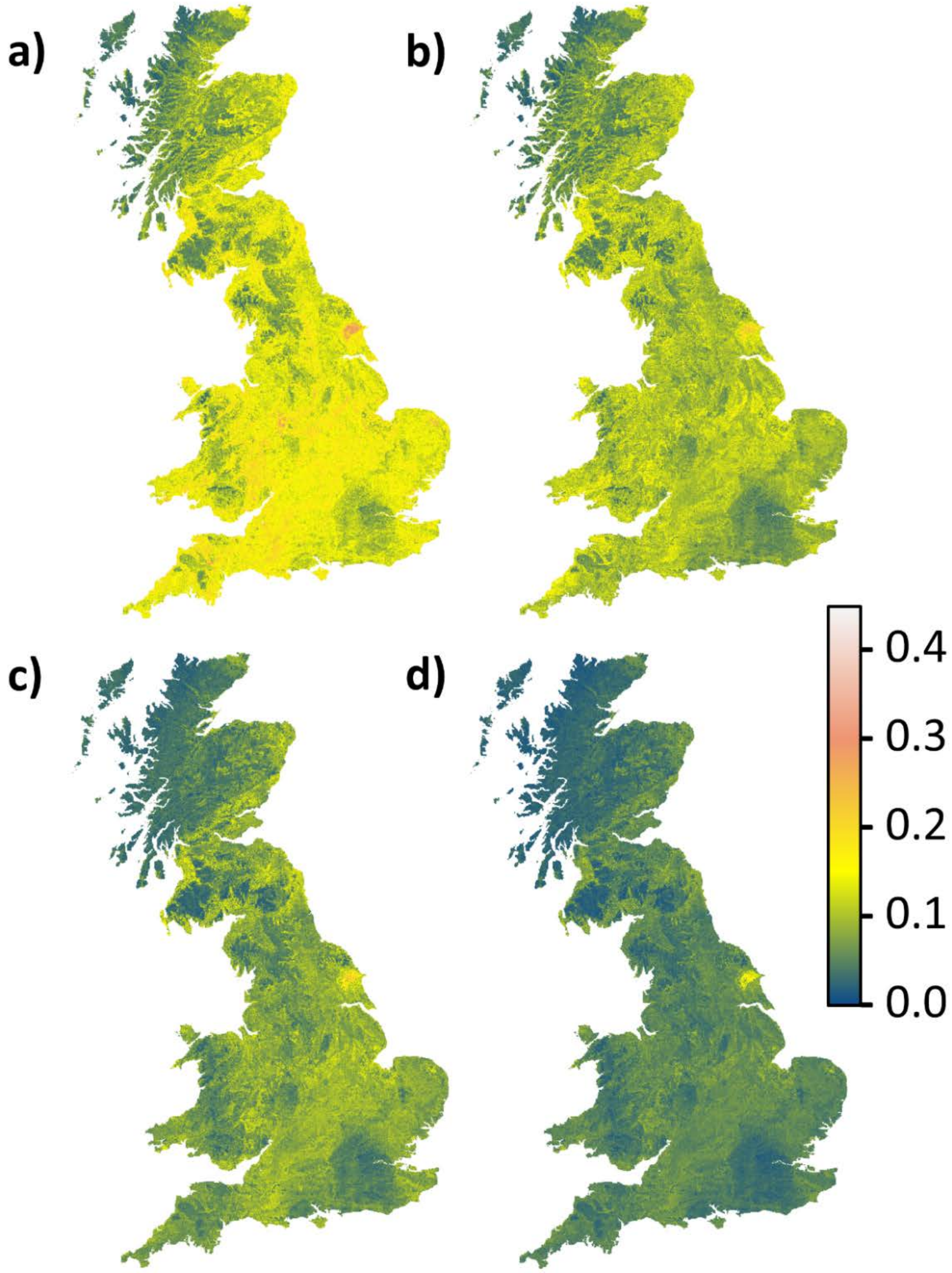

Figure 4. Vulnerability scores for four traits: **a)** litter decomposition rate; **b)** Ellenberg's light indicator; **c)** Ellenberg's moisture indicator, and; **d)** nitrogen fixing ability. The scores indicate the predicted change in the average trait values from the values provided by ash trees, with 0 indicating that the same trait values will continue to be available after the loss of ash trees, and 1 indicating that all trait values that are associated with ash could be lost. The four traits shown all had both high predicted loss and high weighting in the Analytic Hierarchy Process; they are expected to be important traits for the provision of key woodland ecosystem services, and the particular values of the traits ash provides are highly at risk in some areas. Despite differences in the degree of vulnerability, the geographic pattern of vulnerability is very similar between traits.

Box 1: Guidance for management and best replacement tree species to mitigate ash loss.

1. **Replace ash in vulnerable ecosystems with recommended tree species mixes, by planting or encouraging regeneration.**
   In many cases planting will be important to supplement natural regeneration. Older trees have higher ecological value, so planting should start as soon as possible after ash loss, especially in locations with very high densities of ash. This is particularly important in highly vulnerable areas and woodland types. See below for recommendations of species mixtures in different locations and woodland types.
2. **Replace lost ash trees outside of woodlands with suitable mixtures of trees.**
   Replant ash trees as they are lost from hedgerows *etc*. If you are in a vulnerable region, consider using recommended species (below). Ash trees outside of woodlands have a critical role in connecting patches of fragmented woodland across the countryside. Maintaining this connectivity after loss of many ash trees should be a key aim of management.
3. **Encourage compensatory growth and regeneration of other tree species.**
   Enhance natural regeneration and resilience of woodlands by managing pressures (such as herbivore damage, abandonment, pollution, invasive species and diseases). Management prescriptions will depend on specific threats to individual woodlands and might include thinning, herbivore control, action on invasive species, and promoting diversity within stands. More information and advice can be found in the UK Forestry Standard (UKFS), available at: www.forestry.gov.uk/ukfs

Recommended tree species: these are the most highly recommended tree species for the replacement of ash in regions most vulnerable to ash loss, and NVC woodland community types containing constant or frequent ash. Recommended species are those that would compensate best for the lost functional traits of ash in each area, and are listed in order of priority. Ideally all species listed would be included where possible.

Most vulnerable regions	**Recommendations for replacement species**
Yorkshire Wolds	*Populus tremula*; *Alnus glutinosa*; *Tilia cordata; Quercus petraea*
Cannock Chase	*Populus tremula; Alnus glutinosa*; *Acer campestre*
Fenland	*Populus tremula; Alnus glutinosa; Acer campestre*; *Quercus petraea*
Northern Norfolk Broads	*Prunus avium; Tilia cordata; Acer pseudoplatanus; Castanea sativa*
Anglesey	*Populus tremula; Alnus glutinosa; Acer campestre*; *Quercus petraea*
Western Wigtownshire	*Populus tremula*; *Alnus glutinosa*; *Quercus petraea*
West Ayrshire	*Populus tremula; Alnus glutinosa; Quercus petraea*
South Pembrokeshire	*Populus tremula; Alnus glutinosa; Castanea sativa*
Herefordshire	*Alnus glutinosa*; *Acer campestre*; *Quercus petraea*

NVC woodland sub-communities	
W5a	*Sorbus aucuparia*; *Rhamnus cathartica*; *Quercus robur*; *Betula pubescens*
W5b	*Sorbus aucuparia*; *Rhamnus cathartica*; *Alnus glutinosa*; *Quercus robur*
W7a	*Sorbus aucuparia*; *Betula pubescens*; *Acer pseudoplatanus*; *Quercus robur*
W7c	*Betula pubescens*; *Acer pseudoplatanus*; *Sorbus aucuparia*
W8a	*Populus tremula*; *Acer campestre*; *Sorbus aucuparia*
W8b	*Populus tremula*; *Sorbus aucuparia*; *Acer campestre*
W8c	*Alnus glutinosa*; *Populus tremula*; *Quercus petraea*
W8d	*Populus tremula*; *Acer campestre*, *Quercus petraea*
W8e	*Betula pubescens*; *Acer campestre*; *Quercus petraea*
W8f	*Acer pseudoplatanus*; *Acer campestre*; *Quercus petraea*
W8g	*Sorbus aucuparia*; *Prunus padus*; *Quercus petraea*
W9a	*Alnus glutinosa*; *Betula pubescens*; *Prunus padus*
W9b	*Prunus padus*; *Sorbus aucuparia*; *Populus tremula*
W10e	*Betula pubescens*; *Alnus glutinosa*; *Quercus petraea*
W12a	*Acer pseudoplatanus*; *Acer campestre*; *Quercus robur*

We saw similar geographic patterns when we plotted the potential changes in provision of each ecosystem service with no compensatory growth. All of the ecosystem services we investigated showed very similar distributions to the overall vulnerability map (Figure 2), with their greatest vulnerabilities in the Yorkshire Wolds. Flood protection, biodiversity and primary production appear to be slightly more vulnerable than the other ecosystem services (Table 3).

Table 3. Vulnerability of each ecosystem service. These scores were calculated using the AHP weightings for each ecosystem service in turn, rather than the overall weightings for all ecosystem services combined. Flood protection, biodiversity maintenance and primary production appear to be slightly more vulnerable to ash loss than the other ecosystem services. However, see discussion for note of caution on interpreting these results.

Ecosystem service	**Maximum vulnerability**	**Mean vulnerability**
Flood protection	0.57	0.15
Biodiversity	0.57	0.14
Primary production	0.57	0.14
Climate regulation	0.56	0.14
Nutrient cycling	0.53	0.14
Soil formation	0.52	0.14
Water quality	0.52	0.14
Pollination	0.52	0.12

Discussion

Widespread ash loss due to ash dieback (and, potentially, emerald ash borer) will undoubtedly cause changes to the ecological character of many British ecosystems. Our analyses suggest that the level of change could be very high in some situations; the vulnerability scores of 0.53 in the Yorkshire Wolds and 0.47 for W10e National Vegetation Classification (NVC) woodland community (assuming no compensatory growth by other species), indicate that there could be a high degree of change in the average trait values in certain ecosystems. These highly-vulnerable areas and woodland types share two characteristics: firstly, that a high proportion of the trees present are ash; and secondly that they have a low diversity of other tree species, limiting the degree to which these remaining trees can provide ash-like traits. However, our results also suggest that the degree of change could be reduced by certain actions. Compensatory growth of other tree species could play a particularly important role, and has the potential to approximately halve the reduction in overall trait similarity to ash, after ash death. We discuss possible effects of these changes on ecosystems and present three major management recommendations that have arisen from our results, with the aim of stabilising ecological properties of ecosystems after ash loss.

Effects on ecosystem services

The change in mean values of certain traits that are important to the provision of ecosystem services may be cause for concern in the worst-affected areas. For instance, litter decomposition rate, mycorrhizal type and Ellenberg's nutrient indicator are all thought to be important for flood protection and maintaining water quality; changes in mean values may alter the ability of ecosystems to provide these services in vulnerable areas such as the Yorkshire Wolds. This area has experienced recent severe flooding (East Riding of Yorkshire Council, 2013) and a possible reduction in this service due to ash loss could worsen this problem.

However, we advise care in interpreting the results for impact on ecosystem services (Table 3). Our present analysis shows how the values of traits that are particularly associated with ash may be lost, and these are not necessarily the values of the traits that are most effective for providing ecosystem services. Thus, we cannot say whether the provision of an ecosystem service is likely to increase or decrease in a particular area, only that it is likely to change as the average value of key traits for that service change. For instance, ash is an entirely wind-pollinated tree, so if it were rapidly replaced by insect pollinated trees the provision of pollination services from those areas may increase, although the overall ecosystem character would be less ash-like. However, in areas where ash makes up a large proportion of the trees present, it is likely that provision of most woodland ecosystem services, including flood protection, will be decreased, in at least the short to medium term.

A future development of our method could allow us to directly predict changes in ecosystem service provision. If trait values were scored according to which value of a trait is best for providing each ecosystem service, rather than scoring by similarity to ash, then our method could be used to predict how ecosystem services could be reduced or boosted by a change in community composition. Unfortunately, data on how different trait values may affect ecosystem services is currently very limited, and we were not able to carry out this analysis at this time.

Recommended tree species for replanting

Box 1 shows our recommendations for mixtures of tree species to plant**,** with species are listed in order of decreasing priority for the vulnerability of the traits that they replace; however, we stress that for the greatest ecological benefit, the recommended mixtures of trees should be used, not just the first priority species, as no single tree provides all of the important ash-like traits. The species recommended were selected from the species that already occur in each community or location, so we are confident that they have putatively compatible species' site requirements; where required, the ecological suitability of a species for any particular site can be checked using the Ecological Site Classification (Forest Research, 2017a; Pyatt, Ray, & Fletcher, 2001). However, ecological differences between species' silvicultural traits and shade tolerances may mean that long-term compositional stability will require skilled silvicultural intervention. It may be necessary to separate species at a fine scale, in both space and time, to ensure regeneration, survival and vigorous growth of trees in mixtures in the long term (Bauhus et al., 2017).

Epidemic pests and diseases are a serious concern for many British tree species. Elm species continue to be severely affected by Dutch Elm disease (*Ophiostoma novo-ulmi*; Brasier 1991); for this reason, we do not recommend *Ulmus glabra* or *procera* as a suitable replacement species, despite many of their trait values being similar to ash. The fungal-like disease *Phythophthora alni* (Brasier and Kirk, 2001) is now widespread in alders in Britain, although so far only around 20% of alder trees are affected (Forest Research, 2017b). We recommend *Alnus glutinosa* as a replacement tree in some cases, because it continues to be commonly planted in Britain in locations away from watercourses, where the risk of infection is lower. However, these cases highlight the severe impacts of concurrent outbreaks of disease in multiple species. The more diseases are present, the more difficult it is for an ecosystem to be resilient.

Our recommended species are predominantly native; we included four non-native species in our analyses that have been suggested for possible 'climate proofing'; *i.e.* to respond well to projected future climatic conditions (Mitchell, Bailey, et al., 2014) in the UK (*Acer platanoides*, *Acer pseudoplatanus*, *Castanea sativa* and *Pseudotsuga menziesii*). However, these did not generally have a high trait similarity to ash and only *A. pseudoplatanus* and *C. sativa*, which are already naturalised, appeared to be appropriate replacements for ash in any of the vulnerable areas or woodland types. Our analysis includes only a subset of British tree species, as there is a paucity of information available on traits or distributions even for the most common native species. However, we are confident that we cover an adequate breadth of species, especially those that co-occur commonly with ash. Rare species, by their nature, are likely to make small contributions to ecosystem functioning, so we believe we have been able to capture the dominant characteristics of ecosystems to produce our guidance.

Recommendation 1: Replace ash in vulnerable ecosystems with recommended tree species mixes, by planting or encouraging regeneration.

Box 1 shows our list of recommended species to encourage or replant, for different areas and woodland types, to reduce change in ecological characteristics after ash loss. The decision to replace ash on a site will be affected by a wide range of factors, and planting may not be appropriate in every case. However, if managers decide that replanting is required on a site, for instance if the density of ash in their woodland is high and there is little natural regeneration, we would encourage practitioners to use our recommended species mixtures. This will be particularly important in areas with high vulnerability, such as the Yorkshire Wolds and vulnerable woodland types.

Trees have their highest ecological value when they are mature; it is therefore desirable to start planting replacement trees as soon as possible. However, this must be balanced with the importance of maintaining ash trees in the landscape for as long as possible (Enderle et al., 2017; Mitchell, Bailey, et al., 2014; Pautasso et al., 2013) to help maintain populations of ash-associated species. In most situations, it will not be desirable to fell ash trees to enable replanting of alternative species, and replanting should take place as and when gaps start to develop.

Recommendation 2: Ash trees outside of woodlands should be replaced with a range of suitable tree species.

Our analysis suggests that ash outside of woodlands may make considerable contributions to the ecological characteristics of habitats outside of woodlands, and that there may be limited scope in many areas for remaining trees to compensate. Our predicted vulnerability to ash loss is much lower when only woodland trees are considered, in comparison to when all trees are considered together (including trees outside of woodlands) (Figures 2 and 3). We therefore recommend that our suggested mixtures of species (Box 1) should be used to replace ash outside of woodlands. Ash trees in Britain are frequently found as isolated trees and in linear features such as hedgerows and roadsides, and are believed to be the most common tree outside of woodlands (Brown & Fisher, 2009). In these positions, they are thought to play important roles improving connectivity across landscapes and between isolated woodland patches (Maskell et al., 2013; Mitchell, Beaton, et al., 2014). Maintaining this connectivity after loss of many ash trees should be a key aim of management.

Recommendation 3: Encourage compensatory growth and regeneration of other tree species.

The predicted vulnerability of ecosystems in our analysis was halved by allowing maximum levels of natural regeneration so that other tree species were able to fill the gaps left by ash trees. Encouraging regeneration of other tree species will therefore be a key way to reduce the ecological impact of ash dieback. Regeneration of many woody species in Britain has been in decline for several decades (Hopkins & Kirby, 2007; Kirby et al., 2005; Rackham, 2008) although silvicultural management, including herbivore control, can encourage regeneration by improving the health of other tree species, and enhancing woodland resilience to respond to major disturbances (Broome, Mitchell, & Harmer, 2014). The UK Forestry Standard (Forestry Commission, 2011) has further information on sustainable forestry management in the UK.

Comparison with previous analyses

Previous authors (most extensively, Broome et al., 2014 and Mitchell et al., 2016) have tackled the question of the most ecologically-appropriate species for replacement of ash in Britain. In this work, we have extended their work further, with the introduction of geographically explicit predictions of trait change. Our approach has the additional benefit of allowing us to include potential complementarity in the trait profiles of alternative species to identify optimal species mixtures, which was not possible in those previous analyses. This ensures that our recommended combinations of species provide the highest possible range of traits similar to ash, and allows us to analyse both the average degree of change of all traits together, and trait-by-trait analysis of change, across the geographic range.

Analytic Hierarchy Process

The use of the Analytic Hierarchy Process (AHP) to weight traits according to their importance for ecosystem services is a further innovation in our method, allowing us to prioritise the most ecologically meaningful traits to conserve. AHP allows us to weight each trait according to its importance for emergent ecosystem properties, such as ecosystem functions or services. Functional ecologists have long recognised the need to weight traits according to their functional importance in ecosystems, but the best way to do so has remained a stubborn question. We propose that using AHP to produce meaningful weights could be a significant advance for many different types of trait-based analysis.

Conclusions

Widespread ash death in Britain on the scale that has been predicted is likely to cause major changes to both woodland and non-woodland ecosystems. However, the degree of change that is likely to be experienced will be far lower if there is significant compensatory growth by other tree species in response to ash loss, and could be further reduced by the management actions recommended here. Our key guidance points can be found in Box 1, which is designed to be used directly as a guide for land managers and to accompany forestry best practice.

The approach we have used produces maps of vulnerability over a large scale that allows easy comparison between regions and scenarios. It also predicts exactly which functional traits are likely to be reduced in vulnerable areas, facilitating management decisions. Furthermore, the use of AHP is an advance that allows the weighting of traits according to their importance. These advantages give our approach considerable potential for application to general assessments of ecosystem functions and services. On the question of tree diseases, our method could easily be used to investigate the impacts of threats to other tree species, combined threats to multiple species, or as part of Pest Risk Assessment analyses. Extending this method to more scenarios could provide a major step forward in our understanding of the potential consequences of species loss.

Author contributions

LH collected data, performed analysis and wrote the first draft of the manuscript. All authors contributed substantially to the design of the study and manuscript revisions, and agreed on trait importance orders for the Analytic Hierarchy Process.

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Data accessibility

A complete database of the trait data used in the current study, including trait values and details of the original sources used for each species and all traits, is presented in Supplementary Material. Tree abundance distributions were taken from Hill *et al.* (2017). Woodland area data were taken from the National Forest Inventory Great Britain 2014: available from Forestry Commission at http://www.forestry.gov.uk/datadownload Last accessed 17 June 2016. All analyses were carried out using *R* version 3.3.2 (R Core Team, 2016).

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Supplementary material

The following supplementary material is available online:

- Detailed supplementary methods (Supplementary Methods)
- A complete database of the traits used, including trait values and details of the original sources (Spreadsheet of trait values and sources)
- The agreed orders of trait importance for AHP (Spreadsheet of trait importance orders and weights)
- The AHP output table (Supplementary Table 1)
- The yaml file containing complete pairwise comparisons (required for “ahp” package) (yaml file for AHP)