Ecological impacts of ash dieback in Great Britain

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An ash I know stands, Yggdrasil by name,
a high tree, drenched with bright white mud;
from there come the dews that drop in the dales,
it always stands green over Destiny's well.

-The Elder Edda

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SUPPLEMENTARY MATERIAL

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A list of appendices and supplementary material relating to each chapter can be found on the chapter title pages.

Abstract

Ash dieback is a severe disease of ash trees (*Fraxinus* spp.), caused by the invasive fungus *Hymenoscyphus fraxineus*. In its native East Asia, *H. fraxineus* is a harmless endophyte, but since its accidental import into Europe in the early 1990s it has infected over 90% of ash trees in some areas, with long-term mortality sometimes exceeding 90%. The disease was discovered in Great Britain in 2012, and has since spread rapidly. This thesis investigates some of the possible impacts on biodiversity, ecosystem functioning, and society, and in doing so identifies ways to alleviate some impacts. Britain has only 13% tree cover (among the lowest in Europe), so may be particularly vulnerable to ash loss. Better understanding of the effects and how to minimise them is critical to deliver an evidence-based response.

First, we investigated impacts in woodlands by experimentally killing woodland ash trees by ring-barking. We found no short-term effect of ash loss on ground flora or earthworm communities, or on the regeneration or growth of other woody species. Observational evidence suggested that remaining canopy trees rapidly filled gaps left by ash, perhaps contributing to stability. Our woodlands appeared to be remarkably resilient to ash loss, although there may be long-term effects or impacts on other species that this experiment failed to observe.

To investigate broader-scale impacts, we required high-quality abundance maps for ash and other trees across Britain. Using species distribution modelling and random forest regression, we developed a protocol to produce abundance maps from readily available data. We tested the predictive power of the resulting maps using cross validation. Our maps are the best available for abundance of British tree species, and will be useful across a wide range of disciplines. We then used them to model ecosystem vulnerability to ash loss, based on the abundance of ash and other tree species, and their ecological trait similarity. We identified areas at risk of the largest impacts, and produced guidance for positive management actions to minimise ecological change.

Lastly, we investigated the financial impacts of ash dieback, estimating the total cost to Britain at £9.2 billion. This figure is many times larger than the value of lost trade if biosecurity were improved to prevent future invasions, questioning the validity of financial arguments against biosecurity. We also found that loss of ecosystem services accounted for less than a third of the total cost, suggesting that ecosystem service assessments may miss a large proportion of the true cost of biodiversity loss.

Overall, we found that some impacts may be less than expected, such as local effects on woodland ground flora, and others, such as the economic cost, may be much larger than expected. However, the resilience of ecosystems to a major shock such as loss of a common species, and actions to mitigate the impacts, depend on having a diversity of other trees present. The ash dieback outbreak highlights the importance of preventing other severe pests and diseases of trees from being introduced; something that has been increasing exponentially, largely due to international trade in trees. This thesis provides further firm evidence that there is an ecological and social imperative to halt this trend.

CHAPTER 1: INTRODUCTION

The making of an un-natural disaster

History and origin of the ash dieback epidemic

The spread of ash dieback across Europe and its arrival in Britain reads more like a detective story than an epidemiological case study. Sadly, it is also one which is likely to have severe and lasting impacts on many British ecosystems. In a case of unintended consequences, a combination of human activities and natural processes are thought to be behind what could be one of the worst exotic tree diseases that Britain has ever experienced.

Severe dieback of common or European ash (*Fraxinus excelsior* L.) was first noticed in Poland in the early 1990s (Pukacki & Przybył 2005; Kowalski 2006), but the causal agent, an alien ascomycete fungus, was not fully described until 2011 when it was named *Hymenoscyphus pseudoalbidus* by Queloz *et al.* (2011). This name was later changed to *Hymenoscyphus fraxineus* by Baral *et al.* (2014), in an attempt to reduce confusion arising from another synonym of the fungus, *Chalara fraxinea* (Kowalski 2006) – the correct name for the anamorph or asexual stage, as ascomycete fungi are generally given a separate binomial name for each of the sexual and asexual phases. A combination of factors, including this naming confusion, the presence of a range of variously pathogenic fungi on dying trees (Przybył 2002; Pukacki & Przybył 2005) and ash's natural tendency to die back

following very cold springs or hot summers (Hemery *et al.* 2010), led to the dieback initially being blamed on abiotic conditions or a combination of multiple disease agents (complex disease) (Gross *et al.* 2014), and so little was done to prevent the spread (Woodward & Boa 2013). By the time that *Chalara fraxinea* was identified as a novel fungal agent in Europe that was strongly associated with ash dieback (Kowalski 2006), the disease had already spread to at least 12 European countries, as distant as Finland and Romania (FRAXBACK 2012).

Even then, however, no action was taken by authorities (Woodward & Boa 2013). The picture was muddled as morphological research seemed to identify *Hymenoscyphus albidus*, a widespread, native, saprotrophic fungus, as the teleomorph (or sexual stage) of *Chalara fraxinea* (Kowalski & Holdenrieder 2009). This caused further confusion among researchers, as how could a native non-pathogenic fungus be responsible for such dramatic events? Eventually, genetic data revealed that the teleomorph of *C. fraxinea* was in fact a novel cryptic species, *Hymenoscyphus fraxineus*, and this is now known to be the cause of the dramatic dieback (Queloz *et al.* 2011). Further genetic analysis has since suggested that *H. fraxineus* probably originated as an introduction from East Asia, most likely through the ornamental tree trade (Zhao *et al.* 2012). By February 2012, however, *H. fraxineus* had been confirmed in Britain (Mitchell *et al.* 2014b), and is now present throughout almost the entire natural range of *F. excelsior* in Europe (Vasaitis & Enderle 2017).

Hymenoscyphus fraxineus progressed rapidly across Europe, at a rate of around 75 km per year (twice the rate of spread of chestnut blight in North America, one of the most devastating tree epidemics to date worldwide (Gross *et al.* 2014 and references therein).

The teleomorph produces vast numbers of infectious wind-borne spores, and modelling of prevailing winds and the locations of the British outbreaks has suggested that this was probably one route via which the pathogen entered Britain (Defra 2013b), although this finding has been contested (Chandelier *et al.* 2014). However, *H. fraxineus* was certainly also introduced to Britain on diseased imported ash seedlings (Defra 2013b), the trade in which was not restricted until after the discovery of ash dieback on newly-planted trees in Britain (UK Government 2012). Indeed, the extent of the symptoms shown by some of the newly-planted infected trees suggests that infected individuals were being imported and planted for several years prior to the discovery of ash dieback in Britain (Woodward & Boa 2013). This is believed to be the main route of entry into Britain (Sansford 2013); because these planted cases were distributed fairly evenly across Britain, it may have been important in speeding up the spread of the disease. As of July 2017, the disease had been recorded in the wider environment from 59.3% of 10 km squares in England, and 44.1% of 10 km squares across the whole of the UK (Figure 1) (Forestry Commission 2017a).

In Britain, the level of public interest in ash dieback, especially during the early stages of the outbreak, was notably higher than for the many other tree pests and diseases which threaten British trees (Pidgeon & Barnett 2013). It is an interesting question as to why the British media suddenly seemed to find this disease fascinating. Sadly, however, much public fear may be justified; in much of Europe, *Fraxinus* species are relatively uncommon forest trees which tend not to make up a major component of ecosystems (Beck *et al.* 2016), although their abundance has been increasing in many areas

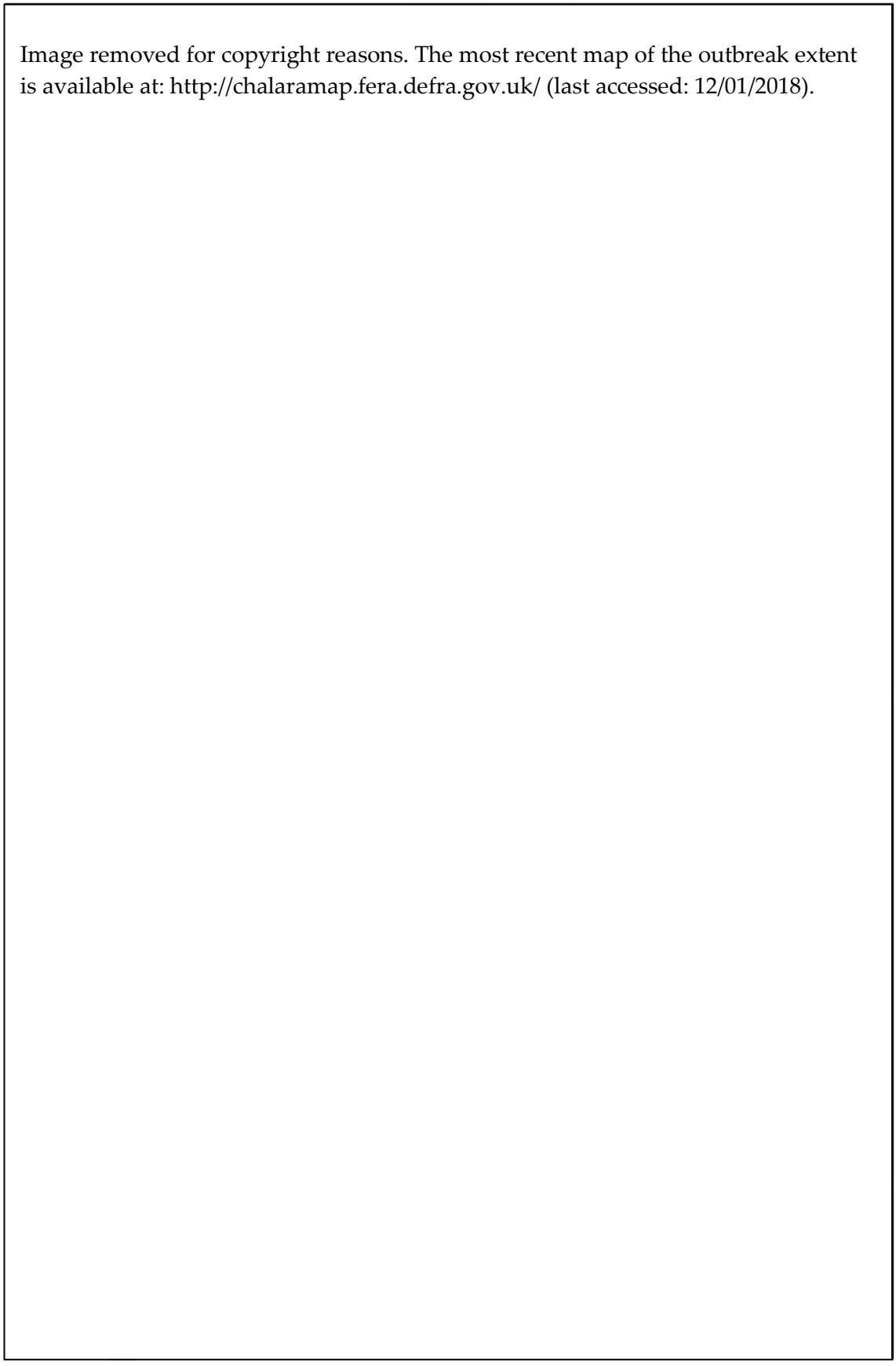

Figure 1. Forestry Commission: Confirmed ash dieback findings as of 3rd July 2017.

(Marigo *et al.* 2000; Hofmeister *et al.* 2004) – but in Britain, common ash is the third most abundant broadleaved woodland tree (Forestry Commission 2013), and the most common tree outside of woodlands (Brown & Fisher 2009; Maskell *et al.* 2013), with an estimated total of up to 185 million trees (Forestry Commission 2013; Maskell *et al.* 2013; The Tree Council 2015). Threats to ash could therefore lead to the loss of a major constituent of many British ecosystems, with serious consequences for biodiversity, people and forest economics in Britain.

Infection rates and mortality

Ash dieback is a chronic but generally lethal disease, which affects several species of ash (including *Fraxinus excelsior*) and all age classes (Kowalski 2006; Drenkhan & Hanso 2010;

Figure 2. The visible effects of ash dieback in the forests of Western Pomerania, Denmark, in 2010. Credit: Rørdrum (Wikimedia Commons)

Keßler *et al.* 2012; Gross *et al.* 2014; Kirisits & Schwanda 2015). Infection rates for *F. excelsior* in earlier-affected European countries have ranged between 80% in Latvia to almost 100% in some parts of Denmark (Figure 2) (FRAXBACK 2012), but it is difficult to predict what proportion of these infected trees will eventually die. There is evidence that young trees die faster, making regeneration unlikely (Kowalski & Holdenrieder 2009; Kirisits & Freinschlag 2012); but as yet there is no consensus on what the mortality rate will be for larger trees, or how long they may take to die. However, in Lithuania, (one of the earliest affected countries), mortality in the few remaining stands of *F. excelsior* has remained high, with 10% of the remaining trees dying every year (Hinsley & Pocock 2014), suggesting that rates of true long-term resistance are low. Similarly, monitoring plots in Switzerland have shown that each year between 2013 and 2017, half of the remaining asymptomatic ash trees have started to show symptoms (Queloz *et al.* 2017). Once ash dieback is established in a forest, control is beyond our current ability (Gross *et al.* 2014).

It is unlikely that the disease will be limited by climate; investigations into the physiological tolerances of *Hymenoscyphus fraxineus* have shown that it can tolerate the range of climatic conditions that are likely to be encountered in Britain (Kowalski & Bartnik 2010). The worst-case scenario for the eventual mortality rate of ash in Britain is considered to be more than 95% (Mitchell *et al.* 2014b) which is a similar level to that now predicted in several other countries (Enderle *et al.* 2017; Rozsypálek *et al.* 2017). Such levels of mortality would cause significant perturbations in many ecosystems, driving far-reaching impacts beyond the immediate loss of the trees.

Current research directions

The severity of the threat posed by ash dieback has spurred a dramatic increase in research into the disease, and into tree health more generally. In Britain, consortia and research networks were set up rapidly to investigate ways to tackle the disease. One of the largest of these was Nornex (http://nornex.org), a network of 11 institutions which aimed to produce rapid, high quality research into the genomics and pathology of *Hymenoscyphus fraxineus*, and the genetic basis for disease tolerance of a small number of ash trees (Downie 2016). All research produced by Nornex has been rapidly published online, on the website OpenAshDieback (http://oadb.tsl.ac.uk); the aim being to share ––– information with experts worldwide, especially data requiring complex analysis such as raw genetic data, and thus speed up the rate of progress on this time-critical issue. The consortium successfully sequenced the genome of *H. fraxineus* in 2014, and *Fraxinus excelsior* in 2017 (Sollars *et al.* 2017).

Research findings and experiences from across Europe have also been shared through the FRAXBACK EU Cost Action, which concluded in 2017 and resulted in a major report on the consequences of ash dieback and recommendations for management (Vasaitis & Enderle 2017). This report was the culmination of the research efforts of contributors from a variety of disciplines, from 26 European and five non-European countries, and provides a real opportunity to gain synergistic research benefits from collaboration. Ash dieback research has also been at the forefront of citizen science initiatives, with successful programmes such as Ash Tag, a smartphone app developed by researchers at the University of East Anglia to track the spread of the disease. This allowed the public to

report sick and dying ash trees (http://ashtag.org) and was very successful in monitoring the early stages of the outbreak in Britain.

Much research on ash dieback, however, has focussed on studying the pathogen and ways to produce resistant ash cultivars. Indeed, there have been several concurrent efforts to screen ash trees for resistance to *Hymenoscyphus fraxineus*, identify the genetic basis for resistance and fast-track a breeding programme to make resistant or tolerant ash commercially available as soon as possible (e.g. Clark 2014 (the Living Ash Project); Kjær *et al.* 2011; McKinney *et al.* 2011; and two Defra-funded research projects). This approach may secure the use of ash in silviculture and future planting, but it will not provide a "silver bullet" to prevent the potentially severe effects of ash dieback on ecosystems. Even given the huge collaborative effort, by the time resistant cultivars are commercially available on a large scale, much of the ecological damage may already have irreversibly occurred. Ash trees provide habitat not only for generalist forest organisms, but also for a large range of specialists for whom the loss of ash would represent complete habitat loss. If these at-risk species are unable to adapt and switch hosts, ash dieback could lead to a large number of population declines and possibly even extinctions of some species, such as possibly *Wadeana dendrographa*, a UK priority lichen species which is predominantly found on ash trees (Ellis *et al.* 2012). These severe impacts will occur concurrently with the loss of ash, and would not be automatically reversed by replanting ash in the future. The scale of replanting needed to repopulate Britain's landscape with ash is another challenge that will be difficult to overcome. Additionally, veteran trees are considered ecologically irreplaceable (Fay 2002; Vuidot *et al.* 2011; Lindenmayer *et al.* 2014) and their loss would not be offset by replanted saplings for many decades, if at all. Ash comprises 17% of

veteran trees in the wider countryside, with only oak more commonly represented (Maskell *et al.* 2013).

A long term concern for any replanting strategy is a second threat to *Fraxinus* species, the exotic bark beetle *Agrilus planipennis*, or the emerald ash borer. *A. planipennis* is native to Asia and eastern Russia, but was accidentally introduced to the USA where it has killed well over 100 million ash trees since 1990 (Donovan *et al.* 2013; Woodward & Boa 2013). Around its origin in southern Michigan, it is thought to have killed over 99% of ash trees with a diameter greater than 2.5 cm (Klooster *et al.* 2014); it has been suggested that the beetle represents the "worst-case scenario" of invasive forest pests (Herms & McCullough 2014). It was found near Moscow in 2008 (Baranchikov *et al.* 2008), and since then has spread as far as Russia's western border at a rate of 13 – 41 km per year (Valenta *et al.* 2017). Without strict vigilance, there is little to stop it spreading throughout Europe, and eventually to Britain (Orlova-Bienkowskaja 2014). Ash that is resistant to *Hymenoscyphus fraxineus* would nevertheless be vulnerable to *A. planipennis* (Sollars *et al.* 2017), and if this invasion does occur, an even bleaker outcome for ash and its associated biodiversity is likely – indeed, the possibility of extinction of common ash from large parts of Europe has even been suggested (Thomas 2016).

What are the likely effects of ash dieback on British ecosystems?

A different and complementary strategy to replanting is to use the time remaining before ash dieback has a profound impact on most British ash populations to investigate the future ecological impacts, and try to prepare for them. This has been the focus of a second

strand of ash dieback research and will be key to an evidence-based response. If certain organisms or communities are found to be at risk from ash dieback, management actions might be taken to protect them, such as planting suitable mixtures of alternative species to help maintain woodland communities (Mitchell *et al.* 2014b). Similarly, if certain regions or ecosystems are found to be particularly vulnerable to adverse effects of losing ash, limited resources may be targeted to these areas for monitoring and eventual replanting. Conservationists tend to work to preserve species which are already rare: the threats to ash present challenges on a totally different scale, so research into the wider ecological effects is critical.

A major report on the potential ecological impacts of ash dieback in the UK (Mitchell *et al.* 2014a) identified 1058 species which are associated with ash in the UK. Of these, 62 were highly ash-associated, and 44 were obligately associated (see Table 1).

Table 1. Number of species in different species groups by level of association with *Fraxinus excelsior* (table taken from Mitchell *et al.* 2014b).

	Level of association with *Fraxinus excelsior*					
Group	Obligate	High	Partial	Cosmopolitan	Uses	Total
Bird			7	5		12
Bryophyte		6	30	10	12	58
Fungi	11	19	38			68
Invertebrate	29	24	36	19	131	239
Lichen	4	13	231	294	4	546
Mammal			1	2	25	28
Vascular plant			78			78
Total	**44**	**62**	**421**	**330**	**172**	**1029**

Ash has an unusual ecology, allowing opportunities for ash specialists to evolve. Its seedlings are fast-growing, but it is also reasonably long-lived, reaching 180 years old or 300 in pollarded individuals (Grime *et al.* 1988). Its nutrient-rich litter degrades rapidly, leading to low soil carbon sequestration and unusually high nutrient turnover (references within Mitchell *et al.* 2014a). Its leaves allow a high level of light penetration below the canopy, and this allows a rich ground flora to develop (Grime *et al.* 1988; Dölle & Schmidt 2009). Its unusual alkaline bark is similar to that of elm species, and therefore supports a range of specialist species displaced by Dutch elm disease (Watson *et al.* 1988; Jönsson & Thor 2012).

The report by Mitchell *et al.* (2014b) on future impacts of ash dieback investigated the use of 22 alternative tree species by ash-associated species to establish whether alternative tree species would provide a suitable replacement habitat for ash-associated biodiversity. The authors found that no single species could provide a good overall substitute, with the best option, *Quercus petraea/robur*, supporting 69% of ash-associated species. However, the best host species, and the proportion of biodiversity supported, varied greatly between taxa. A separate study by Broome *et al.* (2014) also looked at utilisation by ash-associated species to recommend management approaches. However, they found that the lack of distribution data for ash-associated species was a major limitation of this approach, which also restricted Mitchell *et al.* to making general, and not geographically tailored, recommendations.

Mitchell *et al.* (2014b) also assessed the ecological similarity of alternative tree species to ash, summarising the differences between tree species in three ecosystem functions

(decomposition rate, leaf litter characteristics and soil chemistry). However, these results conflicted with the results from the species use profiles: they found that the most ecologically similar trees to ash were *Acer pseudoplatanus*, *Acer campestre* and *Alnus glutinosa* – entirely different from the recommendations from species use. These conflicting results present something of a challenge for interpretation, to scientists and conservation practitioners alike.

Mitchell *et al.* (2014b) also made predictions about the compositional changes that may occur in woodlands after ash dieback. In the majority of ash-containing woodlands in Scotland and northern England, ash comprises no more than 10% of the canopy, so gaps caused by ash dieback are likely to be filled relatively quickly by other trees in the canopy. However, in southern England, ash is usually a greater component in the canopy (more than 20%), so dieback may cause larger, more frequent gaps that would not be filled by canopy trees alone but would rely on the growth of saplings of other species.

Whether replacement of ash by other species in forests will actually occur in reality is uncertain. Other stresses such as climate change, other emergent pests and diseases, and damage from animals such as grey squirrels and deer, will also have an impact on recruitment and influence the eventual outcome for ecosystems (Gurnell 1996; Logan *et al.* 2003; Allen *et al.* 2010; Kirby *et al.* 2010). For instance, climate change is expected to bring new challenges for trees, causing drier summers and wetter winters with a higher likelihood of severe storms (Trenberth 2011), such as the October 2013 storms which are thought to have brought down 10 million trees across England (Forestry Commission 2014). These factors may place trees under greater stress, making them less able to respond to opportunities such as canopy gaps, thus potentially compromising the

recovery from ash dieback. Such factors emphasise the importance of well-considered management advice on how to respond to this outbreak, as a means to mitigate a further major perturbation to British woodlands which are already under significant strain.

All the above factors vary significantly from place to place within the UK. The ecosystem impacts of ash dieback are therefore likely to be highly spatially variable. Prediction and management of the putative impacts needs to take account of this; otherwise management guidance may be produced that is appropriate in some areas, and not in others.

Impacts of ash dieback on people

People, as well as woodland biodiversity, will feel multiple impacts from ash dieback. Ash in woodlands helps to provide essential ecosystem services, including climate regulation, flood protection and cultural services. In Britain's highly fragmented woodland ecosystem, ash trees outside of woodlands also provide important services including reducing air pollution alongside roads and reducing agricultural runoff in hedgerows (Rouquette & Holt (in prep.)). It is also used commercially as a productive timber tree, producing good quality, elastic timber used for making high-quality wood products such as tool handles and furniture (Pautasso *et al.* 2013). Ash is particularly useful for the growing wood fuel market, as it is one of the finest woods to burn and is marketable even when green (Worrell 2013). In recent years it has also been promoted for planting due to its resistance to squirrel damage, tolerance of pollution and nutrient enrichment, and its ecological value as a native (Little *et al.* 2009).

There are also significant health and cost implications of the prospect of large numbers of dead and dying ash trees across the country. These are likely to be particularly felt in transport infrastructure, such as roads and railways. Ash is one of the trees most commonly found alongside roads, due to both the characteristics that make it ideal for planting, and its own vigorous regeneration that has produced large numbers of self-seeded ashes along roads (Maskell *et al.* 2013; Kirby *et al.* 2014). Local authorities around Great Britain and bodies such as Highways England are expected to experience a huge surge in the amount of work required to keep roads safe and clear from fallen ash trees in the next decade (The Tree Council 2015). The cost implications of this are substantial; clearing a single dead roadside ash may require multiple chainsaw operators, a mobile platform, and a road closure, all of which can add up to over a thousand pounds. At a time of reduced public spending, these costs may be difficult for local authorities to absorb.

In Britain, very few people are killed by falling trees, and even with the expected increase in dead trees, direct deaths are likely to remain low. However, there may be significant indirect impacts on human health, arising from loss of ecosystem services. The presence of more trees in the environment is known to correlate with a wide variety of improved health outcomes for people, and conversely the loss of a large number of trees may contribute to poorer health. A 2013 study by Donovan *et al.* used the emerald ash borer outbreak in western North America as a natural experiment to investigate whether loss of trees led to poorer health among people in the outbreak zone. After accounting for confounding factors such as time and socioeconomic indicators, the authors found that the presence of emerald ash borer was associated with an additional 6.8 deaths per

100,000 population per year; over the entire outbreak, they estimated that there were an additional 6,113 deaths from lower respiratory conditions and 15,080 deaths from cardiovascular disease. We cannot extrapolate directly from this study to predict the health outcomes from ash dieback in Britain (although the scale of the outbreak and number of trees involved are similar) but even a fraction of that number of deaths would be a significant health impact and burden on communities and health services.

There is little evidence to suggest that the majority of local authorities and service providers have yet appreciated the scale of the potential impacts of ash dieback, or any major tree disease. Very few local and no national guidelines are in place for how authorities ought to react to the outbreak. For instance, is it cost effective for a local authority to replant trees alongside roads in order to continue to provide ecosystem service benefits, or should trees be removed without replacement to prevent a similar situation with a future outbreak? Research is urgently required to elucidate the cost and ecosystem service implications of the outbreak, to assist with strategic planning and mitigation.

Future outlook: the increase in invasive tree pests and diseases

The ash dieback outbreak does provide one potentially positive effect; it is a timely case study into the wider impacts of exotic tree diseases. Increased trade in plants across and between continents, together with the beginnings of climate change (Bentz *et al.* 2010) have driven a dramatic acceleration in the number of new tree pests and diseases

emerging worldwide, many with catastrophic effects on forest ecosystems (Brasier, 2008; Defra, 2012; Boyd *et al*. 2013). Future introductions of known and unknown organisms are also greatly feared for their likely ecological or economic impacts (Baker *et al.* 2008).

In Britain, many native trees other than ash are also threatened by introduced pests and diseases which are either already established in Britain or will soon become established if no action is taken (Brasier 2008). For example, oaks are affected by acute and chronic oak decline and oak processionary moth (Denman & Webber 2009; Tubby & Webber 2010), horse chestnut by bleeding canker and the horse chestnut leaf miner moth (Straw & Tilbury 2006; Webber *et al.* 2008), and many trees are threatened by invasive *Phytophthora* species (Brasier & Jung 2006). All of the best-case scenarios for the impacts of ash dieback in British ecosystems rely on other species compensating for the lack of ash, but the impacts of multiple diseases within forests could be much more severe, and prevent ecosystems from being resilient (Chapin 2009; Kirby *et al.* 2010; Boyd *et al.* 2013). If the legacy of ash dieback could be to kick-start responsible agencies into closing down pathways for invasion and preventing the spread of other diseases, it could mark a turning point in preventing a future environmental catastrophe.

Research Summary

The research presented in this thesis approaches the question of how ash dieback may affect ecosystems in Britain from a number of different directions. The four data chapters are summarised below:

Experimental simulation of ash dieback

So far, predictions of how British ecosystems will be affected by loss of ash have largely been based on ecological theory of how other species interact with ash (Charlton & Memmott 2013). However, experimental manipulations of woodlands to investigate the ecological consequences could have greater predictive power, and increase the ecological value of predictions. An experiment was set up in early 2014 where ash trees in plots in two woodlands were experimentally killed, to simulate the effects of ash dieback. Effects on the ground flora, regeneration of woody species, and earthworm communities (three key aspects of woodland ecosystems that have been predicted to be affected by ash loss) were monitored between 2014 and 2017. The aim of the experiment was to elucidate local impacts of ash dieback that have been predicted from theory but could not be observed in natural ecosystems until ash dieback has fully taken hold: if this can be achieved, advice can be produced for woodland managers to help mitigate specific effects in a timely manner.

Abundance distributions for tree species in Great Britain: a two-stage approach to modelling abundance using Species Distribution Modelling and Random Forest

Predictions of the impacts of ash dieback over the whole of Britain can only be made using good quality maps of the abundance of ash and other tree species. This was an unexpected knowledge gap; large amounts of presence-only data are readily available for tree species in Britain from databases such as the Distribution Database of the Botanical Society of the British Isles, but data on abundances is far rarer and not sufficient for an accurate national picture. However, information on abundance is far more valuable and

useful in more situations than presence-only data, and allows for far more sensible predictions to be made; most ecosystem functions of species will be strongly linked to the species' abundance within the ecosystem. It was therefore a major research aim to produce good-quality modelled abundance distributions of common British tree species that could then be used to inform geographical predictions of impacts and vulnerability.

Producing models that can predict abundance well, with good resolution over large areas, has long been an important aim in quantitative ecology. We present a two-stage approach to modelling abundance, combining two established techniques, that makes a useful contribution to the field. First, we produced ensemble species distribution models (SDMs) of trees in Britain, using a large amount of presence data and key environmental variables. Then we used Random Forest regression to predict abundance by linking the results of the SDMs to a much smaller amount of abundance data. This method performed well in predicting the abundance of 20 out of 25 tested British tree species, and produced maps of predicted tree abundance for the whole of Britain at 1 km resolution.

Maintaining ecosystem properties after loss of ash in Great Britain

Forests with a diverse tree species mix are likely to be more ecologically resilient to a disease that kills any single species, and more able to continue to provide forest habitat and ecosystem services (Chapin 2009). If we are to maximise future resilience of forest ecosystems, we need to start by identifying which areas of UK forest are currently least resilient so that they can be prioritised. Limited resources, such as replanting efforts, need to be targeted to the areas where they are most required; the same is true for tackling

other impacts on British woodlands which may exacerbate the effects of ash dieback, such as deer overabundance.

We mapped ecological vulnerability to ash loss in Britain, in terms of ability to maintain ash-associated ecosystem properties after widespread ash death. Our results indicate that in some areas of Britain, provision of ash-associated ecosystem properties could be reduced by over 50% if all ash is lost. Some woodland types, and trees outside woodlands, may be especially vulnerable to ash loss. We also use our predictions to make targeted recommendations for each highly vulnerable area and woodland type to reduce ecosystem vulnerability to ash loss, including recommending appropriate alternative species to encourage through management.

The financial impact of ash dieback in Great Britain

The ash dieback epidemic is likely to have significant cost implications for both the public and private sectors, and yet this consequence of tree diseases is generally poorly understood. Since by their nature the costs are spread between a large number of stakeholders and over a long timescale, they may not be considered as a whole and so the true cost could easily go unnoticed by policy makers and the public.

This chapter provides an estimate for the full cost of ash dieback outbreak to the British economy, to the best of our current knowledge. We estimate that the total cost will be £9.2 billion. The single highest contributor to the overall cost is health and safety interventions on roadside ash trees. Costs from this to individual local authorities may be very high, up to £357 million estimated for Devon, although the current level of awareness among local authorities is low; 88% have not yet attempted any surveys of roadside ash. Health

implications may also be significant, but it is not yet possible to estimate this effect. Overall, the socioeconomic impact of this single tree disease is extremely high, and will undoubtedly be worsened by interactions with other tree pests and diseases. This aspect of tree disease must be considered fully by policy makers deciding on reactive measures, plant health surveillance and biosecurity laws. It shows that more stringent regulations to reduce the likelihood of future introductions would be highly cost effective.

CHAPTER 2:
EXPERIMENTAL SIMULATION OF ASH DIEBACK

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Author Contributions

LH set up the experiment, collected and analysed data, and wrote the manuscript. All authors contributed to the design of the study and manuscript revisions.

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This article is in preparation to submit.

Supplementary materials

Supplementary figures for this chapter can be found in Appendix I.

Abstract

An experiment was set up to explore the effects of ash canopy loss on semi-natural ancient woodland ground flora and earthworm communities, simulating ash loss by *Hymenoscyphus fraxineus*. In early 2014, ash trees were killed by ring-barking and poisoning in plots in two Oxfordshire woodlands, Wytham Woods and Bagley Woods. In May 2015, earthworm communities were sampled in the plots, using mustard vermifuge. From 2014 to 2017 inclusive, biannual ground flora surveys were conducted.

No effect was found of ash death on ground flora community composition or diversity, or earthworm diversity or abundance. No compensatory growth by other tree species was observed using dendrometer band measurements; however, visual surveys of canopy cover suggested that remaining trees rapidly (within three years) began to grow into the gaps left by ash. This may have reduced the degree of environmental change experienced by ground-dwelling organisms, and could be a mechanism for resilience to some impacts of ash dieback in diverse woodlands.

Introduction

Ash trees in Britain and the ash dieback epidemic

The 2012 discovery of ash dieback in Great Britain caused significant alarm to ecologists, conservation professionals and the public alike (Pautasso *et al.* 2013; Woodward & Boa 2013). *Hymenoscyphus fraxineus*, the invasive fungal pathogen that causes ash dieback, is native to East Asia but was accidentally introduced into Europe in the 1990s (Kowalski

2006) where it has since spread rapidly and attacked all European ash (*Fraxinus*) species (Drenkhan & Hanso 2010; Kirisits *et al.* 2010; Gross *et al.* 2014). In Britain, common ash (*Fraxinus excelsior* L.) is the third most common broadleaved tree in Britain (Forestry Commission 2013) and is highly susceptible to the disease; perhaps as many as 95% of ash trees in Britain are predicted to die from ash dieback within the next few decades (Halmschlager & Kirisits 2008; Kjær *et al.* 2011; Pautasso *et al.* 2013) (although predictions of final mortality rates vary widely (FRAXBACK 2012)). However, the concern generated by the arrival of ash dieback was not only because of the death of the ash trees themselves, but because of the cascading effects that this may have on other woodland biodiversity (Pautasso *et al.* 2013; Mitchell *et al.* 2014b). Exotic tree pests and diseases are causing significant losses of forest biodiversity worldwide, and similar impacts have been predicted for ash dieback (Boyd *et al.* 2013).

Common ash in Britain is both extremely abundant and ecologically unusual, and as a result it supports a wide range of biodiversity in many habitats (Mitchell *et al.* 2014a, b; Littlewood *et al.* 2015). It supports woodland generalist species by virtue of being an important component of many British woodlands (Rodwell 1991; Forestry Commission 2013). It is also the most common tree species found outside of woodlands, meaning that it has a crucial role in maintaining connectivity of woodland ecosystems (Brown & Fisher 2009; Maskell *et al.* 2013). At 12%, Britain has one of the lowest percentages of woodland cover in Europe and highly fragmented woodlands (Hopkins & Kirby 2007; Mason 2007; "Global Forest Resources Assessment 2010: main report. *FAO, Rome.*" 2010); the corridors and stepping stones provided by ash between these fragments may be key for connecting fragmented populations of woodland biodiversity.

Ash also has a range of ecological traits that differentiate it quite strongly from other native tree species, and make it difficult to replace (Mitchell *et al.* 2014a, 2016). Ash woodlands allow a high level of light penetration to the woodland floor, encouraging high levels of floral biodiversity (Grime *et al.* 1988; Dölle & Schmidt 2009). The leaf litter is nutrient-rich with rapid decomposition, leading to unusually high nutrient turnover and low soil carbon sequestration (references within Mitchell *et al.* 2014a). Its bark is unusually alkaline, similar to elm species, so it has been able to support a range of specialist species displaced by Dutch elm disease (Thomas 2016). These and a range of other unusual traits have allowed opportunities for ash specialists to evolve; of the 953 species known to associate with ash in some way, 44 are thought to be obligately associated (Mitchell *et al.* 2014a, b). The knock-on effects of ash dieback on other biodiversity could therefore be significant, potentially causing population declines which may be severe in already rare species, and an overall reduction in biodiversity.

Effects of ash dieback on woodland ground flora and earthworm communities

It is not clear what the overall effects of ash dieback on woodland ground flora will be. On one hand, the rich ground flora commonly associated with ash may be adversely affected by death of trees and associated habitat modification (Mitchell *et al.* 2014a, b). On the other hand, much of the semi-natural ancient woodland in Britain, which has traditionally been managed by coppicing producing a very rich ground flora, has in recent decades been left to grow to a "high forest" state (Hopkins & Kirby 2007; Erenler *et al.* 2010). This situation, which tends to produce a closed canopy with low light penetration, is associated with a poorer floral diversity (Rackham 2008; Paillet *et al.* 2009).

It is possible that, in the short term at least, the loss of ash in some ancient woodland could lead to a more open forest structure (Heilmann-Clausen *et al.* 2013), which could benefit some rarer ground flora. Those woods which already have a relatively open structure could instead be affected by runaway growth of competitive, fast-growing species such as bramble or stinging nettle, which could smother richer ground flora communities and drive losses in biodiversity (Harmer *et al.* 2011).

The degree to which other tree species will regenerate after ash death is an important factor that will determine many longer-term impacts of ash dieback. Many forests in Britain and elsewhere are currently suffering impacts from high numbers of native and exotic deer compared to historical levels (Hopkins & Kirby 2007; Rackham 2008), which are severely limiting regeneration of the majority of tree species (Royo *et al.* 2010; Cook-Patton *et al.* 2014). Until the arrival of ash dieback, ash was considered the "tree of the future" in many woods, as it showed levels of natural regeneration far higher than other native species (Kerr 1995; Marigo *et al.* 2000; Butt *et al.* 2009), possibly due to the superior ability of ash to make use of increasing nitrogen levels in soils (Hofmeister *et al.* 2004). The recovery of forests from ash dieback will rely heavily on the regeneration ability of other tree species – but limited by deer overbrowsing together with rabbit and grey squirrel damage, regeneration may not approach pre-anthropocene rates in the majority of British forests (Rackham 2008).

Earthworms (Lumbricidae) are another important component of woodland ecosystems that may be affected by loss of ash trees. Earthworms are considered important ecosystem engineers, playing major roles in soil formation and quality, and nutrient turnover (Lee 1985; Feller *et al.* 2003; Blouin *et al.* 2013). This in turn can impact floral communities, other

soil organisms, and animals at higher trophic levels. They can themselves be affected, however, by their environment and the species present, as a high proportion of their food is made up of leaf litter (Reich *et al.* 2005; Cesarz *et al.* 2007; Curry & Schmidt 2007). Ash leaves, which are soft and high in nutrients, may be particularly palatable to earthworms, encouraging high abundance and diversity in the associated earthworm communities (Mitchell *et al.* 2014a). If earthworm populations are adversely affected by the loss of ash trees, this could in turn drive further impacts on other parts of woodland ecosystems.

Experimental ash dieback simulation

An experiment was set up in 2014 in two semi-natural ancient woodlands in Oxfordshire, Wytham Woods and Bagley Woods, in which ash trees were experimentally killed to simulate ash dieback and allow the effects of ash death on other aspects of the woodland ecosystem to be monitored. Wytham Woods (51° 46′ N, 001° 20′ W), roughly three miles to the north west of Oxford, is Oxford University's research woodland and one of the most researched areas of woodland in Europe. Bagley Woods (51° 43′ 5″ N, 1° 15′ 40″ W) lies two miles to the South of Oxford and is owned by St. John's College, Oxford. The experiment was run for three years after ash death, with surveys of ground flora carried out in May and July each year, and a survey of earthworm communities carried out in May 2015.

Predictions of how British ecosystems will be affected by loss of ash have largely been based on observations of which species interact trophically or coexist with ash (Charlton & Memmott 2013; Mitchell *et al.* 2014a, b). However, experimental manipulations of

woodlands to investigate the ecological consequences are necessary to increase the power and ecological value of predictions. This experiment, which is to the best of the authors' knowledge the first if its kind, aims to give advance warning of the possible effects of ash dieback on wider forest biodiversity and ecosystems, to allow the evidence-based design of management recommendations to help mitigate any major changes detected.

Methods

Site choice

39 plots of 25 by 25 metres were selected in areas of semi-natural ancient woodland within Wytham Woods (21 plots) and Bagley Woods (18 plots). All study plots were categorised as W8 *Fraxinus excelsior–Acer campestre–Mercurialis perennis* woodland, following the National Vegetation Classification (Rodwell 1991) but the two woods differed in the abundance of deer present. Wytham Woods have had an active program to reduce deer numbers since 1998, including deer fencing, which has produced a four-fold decrease in densities of all occurring deer species; Bagley Woods has some limited deer control but is unfenced and as such the impact of deer on the site is higher. Deer impact surveys carried out in June 2015 indicated a moderate impact of deer in Bagley and low impact in Wytham.

Plot locations

Wytham Woods contains an 18-hectare long-term monitoring plot, associated with the Smithsonian Institution Global Earth Observatories (SIGEO) programme. To reduce

uncontrolled factors and allow the treatment to be standardised, experimental plots were chosen to have similar tree species composition to the 18-hectare Smithsonian plot. Locations were selected using species composition records of the woodlands together with visual inspection. Plots were also sited well away from main paths, for safety considerations. The plots were arranged in blocks of three, with at least a 10 m buffer zone between them. In each block, one plot was assigned randomly to each of three treatment levels; high ash death (100%), medium ash death (50%) and a control (0% ash death).

Ash dieback simulation

Due to patchiness in the woodlands causing differing numbers and sizes of ash trees in each plot, simply killing a set percentage of trees would have produced highly variable levels of canopy openness. We therefore used basal area of ash killed as the actual treatment criterion, as this is very strongly correlated with crown area (Hemery *et al.* 2005) and therefore loss of canopy.

The basal area of ash killed in each treatment was based on the basal area of ash in the 18-hectare Smithsonian plot. The combined basal area of ash trees within the Smithsonian plot has been measured at 6.73 m^2 per hectare (Butt *et al.* 2009); this scales to an average of 0.42 m^2 combined basal area within each 25 x 25 m area. For the high ash death treatment, ash trees with a combined basal area of as near as possible to 0.42 m^2 were killed in each plot (leading to canopy loss of the same degree as would follow 100% ash death in the Smithsonian plot). For the medium ash death treatment, ash trees with approximately

0.21 m^2 combined basal area were killed in each plot. In some high ash death plots, not all ash trees were killed, as doing so would have opened the canopy beyond the desired maximum level and reduced the consistency of the treatment. However, on no occasion were other species of tree killed to make up the correct level of openness.

Ash trees were killed by a combination of ring-barking and poisoning with glyphosate. Ring-barking was carried out in January 2014; one or more strips of bark at least two centimetres wide were removed from around the entire girth of the tree close to the base of the stem, using a chainsaw for larger trees or a small stripping knife for small trees and saplings to prevent accidental felling. Ring-barking causes the death of the tree by disruption of the phloem, mimicking the effects of ash dieback. Ash trees were ring-barked in the order of smallest to largest, with a running total kept of the combined basal area ring-barked: when the required basal area for the plot had been reached, no more trees were killed. This imitates the behaviour of ash dieback, which characteristically kills small ash trees very quickly, but can take decades to kill larger trees. Not all trees were effectively killed by ring-barking. In May 2015, any ring-barked ash trees that were still alive (around 30%) were treated with glyphosate herbicide using "ecoplugs[1]", and all treated trees were visually confirmed to be dead in July 2015. Any regrowth from below the cut ring was removed each spring and summer.

[1]Ecoplugs are plastic plugs containing glyphosate herbicide that are hammered into holes drilled in tree trunks to kill them. Ecoplug MAX® is a registered trade mark of Monsanto Company.

Compensatory tree growth

Growth rates of other tree species in the experimental plots were monitored using dendrometer bands. These are permanent bands fitted around the trunk and held in place with a spring, allowing incremental growth to be accurately recorded using callipers (Butt *et al.* 2013). Four trees of species commonly found on the sites (*Acer pseudoplatanus*, *Betula pendula*, *Castanea sativa*, *Crataegus monogyna* and *Quercus* spp.) were fitted with dendrometer bands for each plot in April 2014. The bands were then checked and growth increments recorded in August 2014, January 2015, January 2016 and February 2017.

Floral surveys

Floral surveys were carried out in 10 x 10 m core plots at the centre of each treatment plot, to minimise the impact of edge effects of the treatment plot. Surveys were carried out once in May and once in July, from 2014 to 2017 inclusive. The survey procedure was the same as that used by Kirby & Thomas 2000 and was as follows: a line was laid across each of the diagonals of the plot and percentage vegetation cover was estimated by eye in three height categories: canopy cover (> 2.5 m high); shrub cover (0.5 – 2.5 m high) and ground cover (< 0.5 m high). Bramble cover in the plot was also visually estimated using a five-point scale (0%, 1-24%, 25-49%, 50-74%, >75%). The ground flora (vascular plants under two metres high, including seedlings of trees and shrubs) was then surveyed in thirteen 0.1 m^2 circlets, evenly spaced along the two diagonals of the core plot. The number of circlets a species occurs in gives a measure of species abundance. The entire core plot was

then slowly and systematically walked, and any further species that occurred were recorded as present.

Earthworm survey

A survey of the earthworm communities in each plot was carried out in May 2015. A 30 cm^2 quadrat was placed within the core plot, in a location chosen using random selection (constrained to avoid areas that might be unsuitable, such as large cracks in the soil). The earthworms present within the quadrat were then sampled, using vermifuge extraction with mustard (Sherlock 2012). Leaf litter was cleared to expose the soil surface, and any leaf litter- or surface-dwelling earthworms were collected. 40 g of hot mustard powder was then shaken into four litres of water, and immediately poured over the quadrat. This was done gradually to allow the mixture to permeate before more was added and to prevent the mustard from running onto the surrounding soil. All earthworms that emerged to escape the irritant within 30 minutes were collected. They were stored in ethanol in the field and then identified in the lab according to Sherlock (2012).

Canopy photos and analysis of light availability

Hemispherical canopy photographs were taken in September 2014, using a Nikon Coolpix995 digital camera and a hemispherical lens. Hemiview canopy photograph analysis software was used to quantify the canopy openness of each plot, using the metric Indirect Site Factor.

Statistical analysis

Ground flora community change in the plots was analysed using Constrained Correspondence Analysis (CCA) from *vegan* package in *R*. Models had the form: Community ~ Site + Treatment * Year, where the interaction term Treatment * Year is the variable of interest, as this tells us whether the ground flora communities of treatment plots diverged significantly from the control plots over time. Two analyses were run, using the same model form: the first used the ground flora community data with tree seedlings not included; the second included only tree species, to analyse regeneration of these species. Ground flora data from the May and July surveys were combined in each year, using the maximum abundance recorded at either survey for each species.

A linear mixed-effects model was run, using the *lme 4* package in *R*, to analyse change in Shannon-Wiener diversity of the ground flora over time in the different treatments. A random-intercepts-and-slopes form of model was used to allow for differences in the effect of treatment over time between blocks. Treatment (a factor with three levels; high ash death, medium ash death and control), year (factor with four levels; 2014, 2015, 2016 and 2017) and site (factor with two levels; Wytham and Bagley) were treated as fixed effects, and block as a random factor with 13 levels, with the model as follows: Diversity ~ Treatment * Year + Site + (1+Treatment|Block). A similar model was run to analyse changes in abundance of bramble over time in the high ash death treatment plots only. This model had the form: Abundance ~ Year + Site + (1+Block).

The Bray-Curtis dissimilarity index was also used to analyse changes between the ground flora communities in the different treatments over time, using the *R* package *vegan*. A dissimilarity matrix was calculated for each plot type (high ash death, medium ash death and control) and a principal components analysis of dissimilarity scores carried out to look for divergence between treatments over time.

Generalized linear mixed-effects models were used to analyse any differences in abundance and diversity of earthworms between the treatment and control plots. Both abundance and Shannon-Wiener diversity were analysed using the logged response variable to produce normally distributed residuals, with Block as a random effect: log Response ~ Treatment + Canopy Openness + Site + (1|Block).

For the analysis of compensatory tree growth, a linear mixed-effects model, with treatment, site and species (a factor with six levels) as fixed effects, and block as a random effect, was run. The response variable was the log of the incremental stem growth between 2014 and 2017, divided by the initial circumference. The model form was: logGrowth ~ Treatment + Species + Site + (1|Block). However, even when log transformed, the response was strongly non-normal as the values were bounded at zero. We therefore also analysed the same data using censored (Tobit) regression from the *VGLM* package, which is used to estimate linear relationships where there is "censoring" in the data, (i.e. data points above or below a particular value cannot be recorded). This model had the form: Growth ~ Treatment + Species + Site, tobit(Lower = 0). Finally, a linear model (ignoring Block) with the form logGrowth ~ Treatment * Species + Site was run to analyse the interaction between treatment and species, because a linear mixed-

effects model containing block and the interaction term was rank-deficient (unable to estimate all the effects of interest).

Canopy openness in the high ash death treatment plots was analysed using ANOVA, to identify changes to the canopy cover over time. The response variable was canopy cover (estimated by eye during the floral surveys), with year as the explanatory variable.

All statistical analysis was carried out using *R* version 3.4.1 (R Core Team 2016).

Results

Treatment: basal area ring-barked

The average basal area of ash ring-barked per plot was very close to the target basal area, for both sites and treatments (figure 3). For the high ash death treatment, the target basal area to ring-bark was 0.42 m^2 per plot, and the actual average basal areas achieved were 0.42 m^2 for Wytham and 0.4 m^2 for Bagley. For the medium ash death treatment, the target was 0.21 m^2 and the averages were 0.22 m^2 for Wytham and 0.23 m^2 for Bagley. The range of values for each plot was somewhat wider for Bagley than Wytham, due to the constraints of the sizes of ash trees that were present in the plots, but in general the standardization of the treatment was successful.

Analysis of ground flora

Constrained Correspondence Analysis showed that the ground flora communities differed significantly between the two sites (CCA, 199 permutations: Df = 1; F = 12.2; p = 0.005), and between different years (Df = 1; F = 3.48; p = 0.005), but that the term of

interest, the interaction of treatment by year, was not significant (Df = 2; F = 0.417; p = 1.0); i.e. there was no divergence between the vegetation communities of the control plots and the treatment plots over time (figure 4).

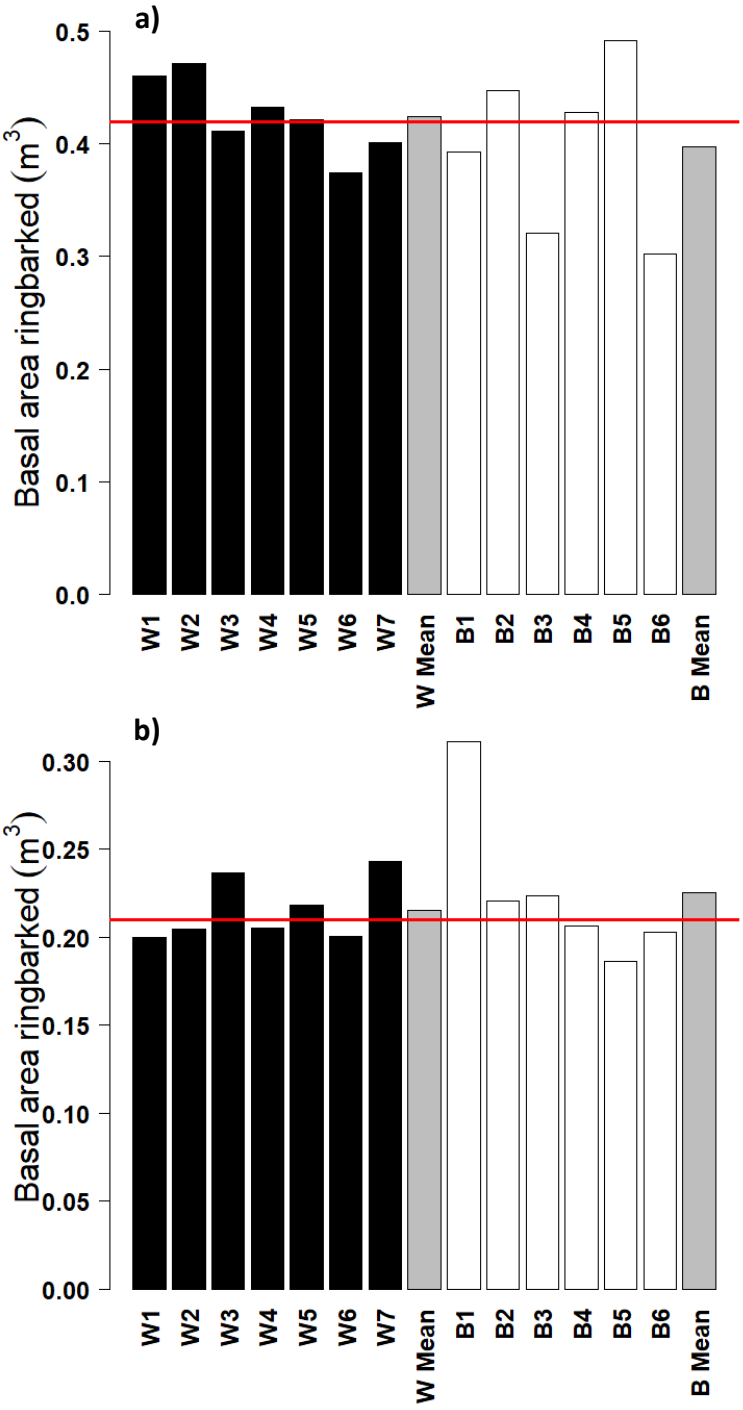

Figure 3: Standardisation of ring-barking treatment for **a)** high ash death treatment plots and **b)** medium ash death treatment plots. W1, W2 etc. and B1, B2 etc. refer to blocks of plots within Wytham (black bars) and Bagley Woods (white bars). Grey bars show the mean basal area of ash ring-barked per plot for each of the two woodlands. The red line shows the ideal basal area ring-barked for each of the two treatments.

Shannon-Wiener diversity index also showed no significant differences in ground flora communities between treatments over time (Linear mixed-effects model: Df = 6; Chi square = 0.176; p = 0.99) (supplementary figure 1), and bramble abundance in the high ash death plots did not differ significantly between years (Linear mixed-effects model: Df = 6; Chi square = 2.83; p = 0.83) (supplementary figure 2). Similarly, Bray-Curtis dissimilarity showed no divergence in vegetation communities between the treatment plots and control plots over time (see supplementary figure 3).

There was also no effect of treatment-by-year interaction on the tree seedling community (CCA, 199 permutations: Df = 6; F = 0.544; p = 1) (see supplementary figure 4), although year (Df = 3; F = 8.57; p = 0.005) site (Df = 1; F = 3.01; p = 0.005) and treatment (Df = 2; F = 1.45; p = 0.04) were all significant. Visual inspection of the data also confirmed that there was no significant difference in abundance of all tree seedlings between different treatments for any year (supplementary figure 5).

Compensatory growth by other tree species

Similarly, dendrometer band data showed no evidence of compensatory growth among tree species other than ash in the treatment plots. Both Linear mixed-effects modelling and censored (Tobit) regression agreed that treatment was non-significant (Linear mixed-effects model: Df = 2; Chi square = 1.86; p = 0.39; censored regression: Df = 2; Chi square = 0.83; p = 0.66). Some faster-growing tree species may be slightly more able to respond to changes in light levels than others. In particular, *Acer pseudoplatanus* seemed to be able to

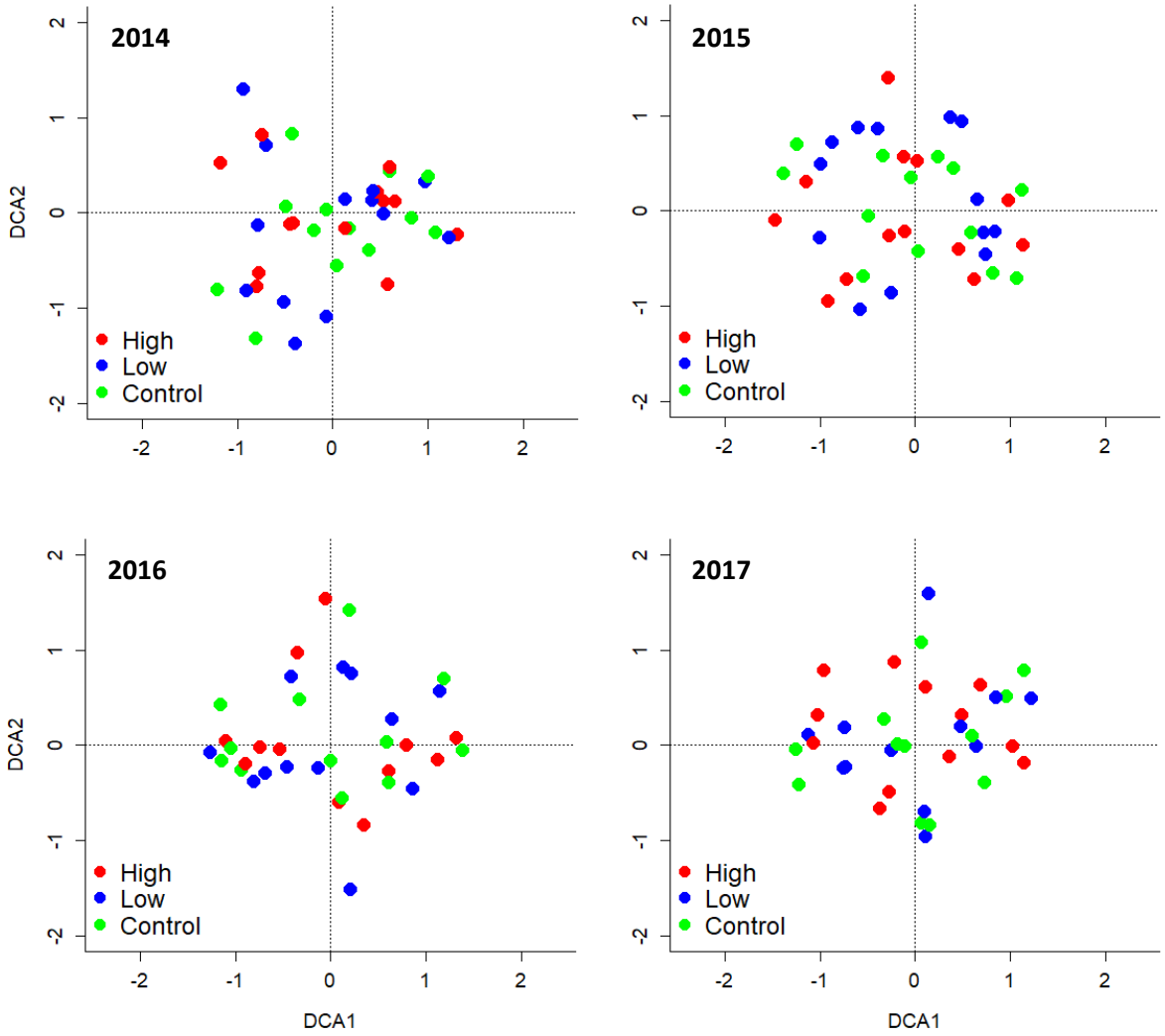

Figure 4. Detrended correspondence analysis (DCA) of effects of ash death treatments on ground flora communities over four years (not including tree seedlings; for effect on tree seedlings, see supplementary figure 4). DCA is shown here because it is a powerful tool for graphically displaying patterns in community data. However, no divergence was seen between treatments (high and low ash death and control) over time. Axes 1 and 2 are shown; no patterns were detected in any other axis combinations.

respond most rapidly to the increase in light levels and grow faster than other species (see supplementary figure 6). However, in our final linear model, the interaction term treatment by species was not significant (Df = 8; F = 1.29; p = 0.25), so there is not strong evidence to support this effect.

Earthworm communities

There was no significant effect of ash death on the abundance (linear mixed-effects model: Df = 2; Chi square = 3.05; p = 0.22) or Shannon-Wiener diversity (linear mixed-effects model: Df = 2; Chi square = 3.92; p = 0.14) of earthworms sampled in the plots (figure 5). Small, non-significant decreases in abundance were seen with high ash death treatment (est. = -0.14; 95% CI = -0.32, 0.06) (figure 5a and b), and similarly for diversity (est. = -0.20; 95% CI = -0.43, 0.04) (figure 5c).

In our initial linear model of earthworm abundance against treatment and canopy openness (ISF), a significant decrease in abundance was seen with higher canopy openness (Df = 1, p = 0.002, est. = -4.74) (figure 5d). However, when block was added as a random effect in our final GLMM (see methods), the significance of canopy openness became marginal (p = 0.091, est. = -2.69). There was no significant difference between sites for abundance or diversity of earthworms.

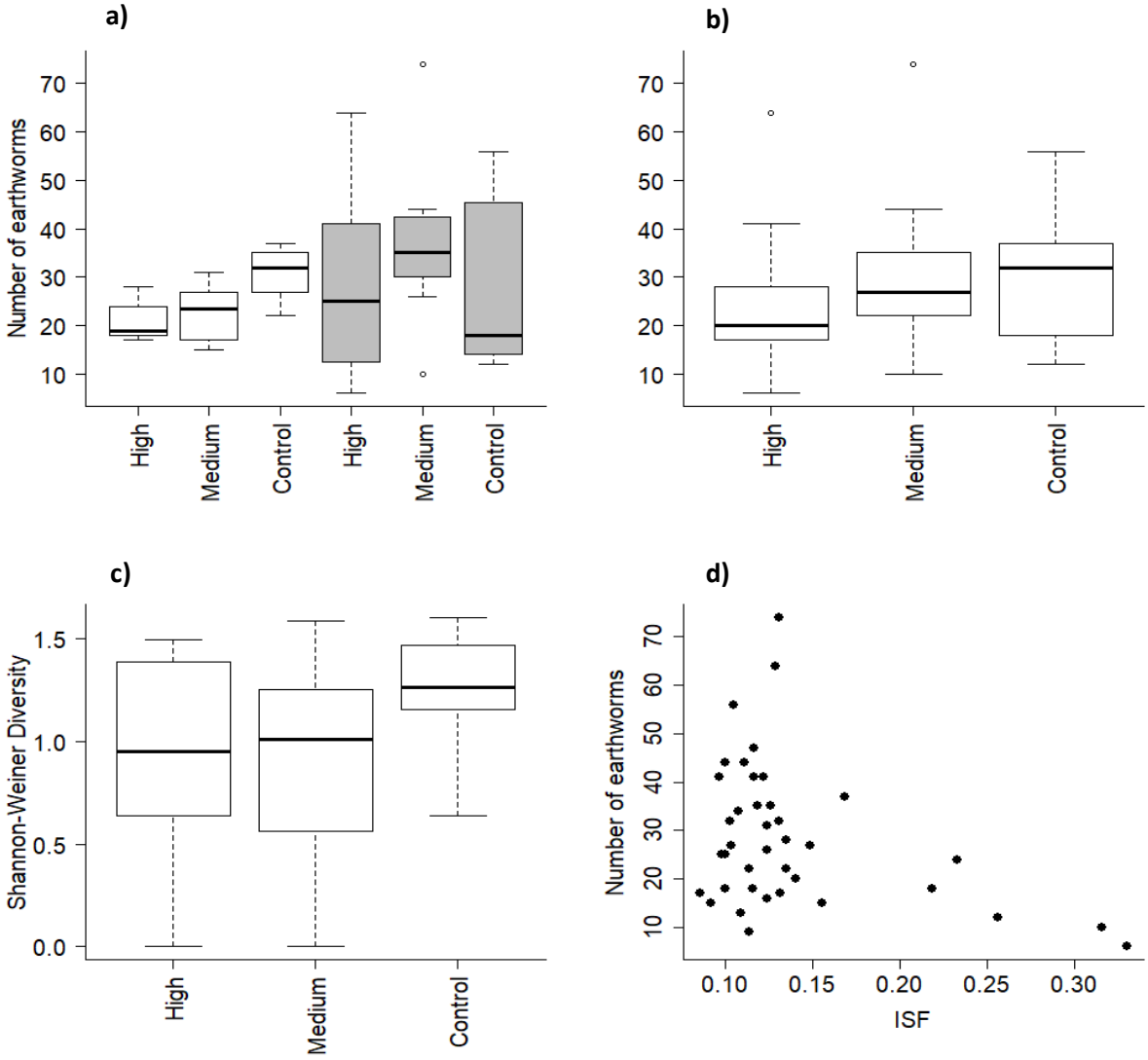

Figure 5: a) Earthworm abundance per sample in plots of different treatments (high or medium ash death treatments, or control). White bars are Bagley Woods, grey bars are Wytham Woods. **b)** Average earthworm abundance for each treatment across woods. Although the average abundance was highest in the control plots and lowest in the high ash death treatment plots, the differences between treatments were not significant. **c)** Earthworm diversity per sample in different treatments. Diversity was slightly higher in control plots, but this was not significant (p = 0.15) **d)** Earthworm abundance per plot against canopy openness (ISF). ISF was significant (p = 0.002, est. = -4.74) in an initial linear model of earthworm abundance against treatment and ISF, but when block was added as a random effect in a GLMM, ISF became only marginally significant (p = 0.091, est. = -2.69).

Canopy cover

No significant differences in canopy cover were found between years, for any of the treatment levels. Canopy cover in the high ash death treatment plots decreased slightly in 2015 and 2016, and increased slightly again in 2017 (figure 6), but these differences were not large enough to be significant.

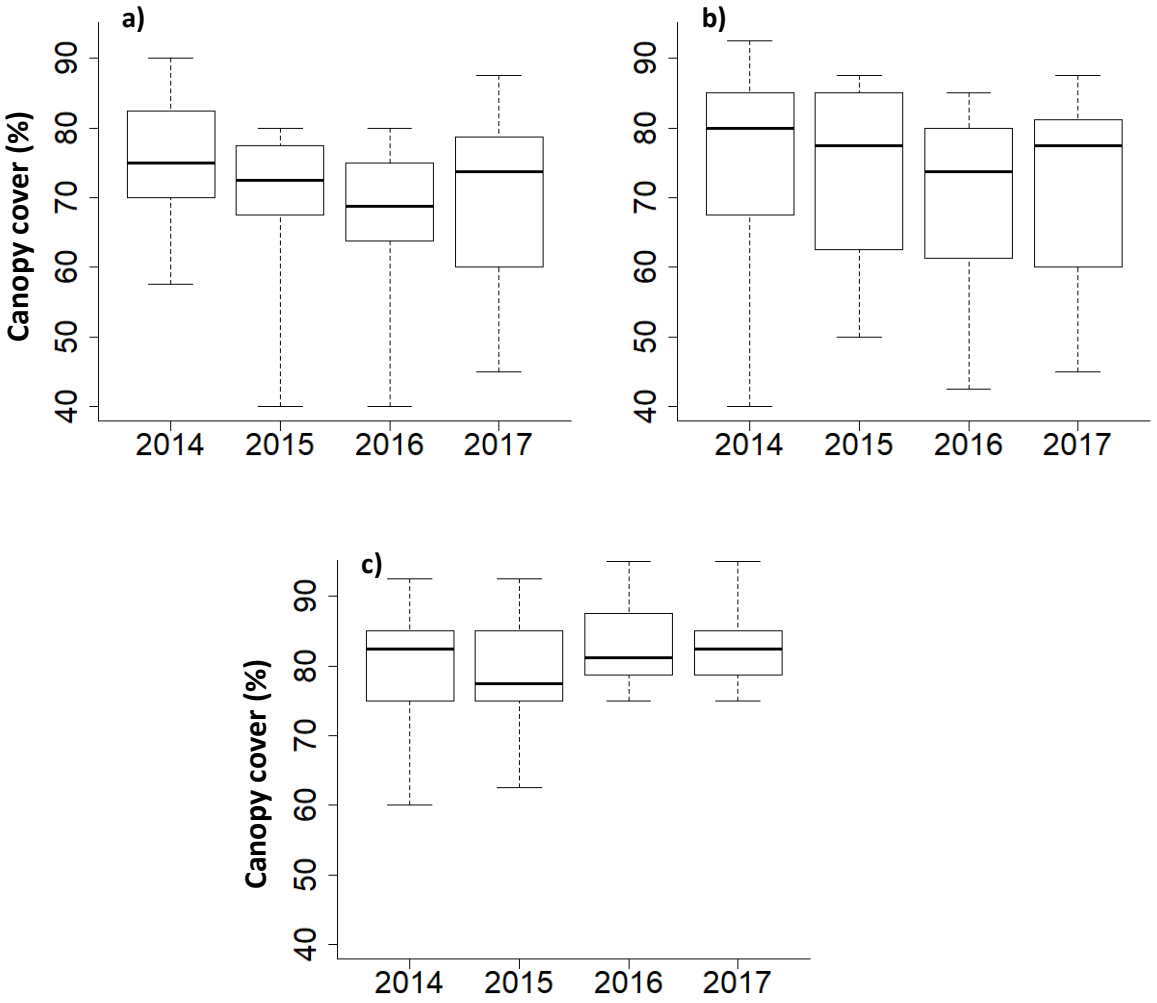

Figure 6: Canopy cover in the treatment plots over time: **a)** high ash death treatment plots, **b)** medium ash death treatment plots, **c)** control plots. No significant differences were seen over time within each plot type, although for both high and medium ash death plots, small decreases in cover were seen in 2015 and 2016 followed by recovery in 2017.

Discussion

Our experiment suggests that some components of woodland ecosystems may be more resilient to the effects of ash dieback than previously thought. Despite recording ground flora communities for four years after experimentally-induced ash death in our plots, we failed to detect any significant changes to ground flora communities or diversity. We also found no effect of ash death on bramble abundance, regeneration of tree species, increment growth of other trees or earthworm abundance or diversity.

There was, however, some weak evidence to suggest that compensatory growth of canopy trees occurred. Canopy cover was at its lowest two years after the loss of ash, and by three years the canopy gaps left by dead ash trees were already starting to be filled by the surrounding trees (figure 6). This may have reduced the degree of environmental change experienced by ground-dwelling organisms by, for instance, stabilising light levels. However, it is not clear to what degree this represents increased canopy growth or just plasticity of the existing canopy as in regrows each year. Woodland vascular plants and earthworms are both strongly affected by microclimate (Kirby 1990; Breshears *et al.* 1998; Eggleton *et al.* 2009; Palo *et al.* 2013), so this could be a mechanism for resilience to some impacts of ash dieback in diverse woodlands. Varying growth rates between different tree species present in the ecosystem may therefore be an important trait affecting the overall ecosystem resilience to ash loss, and it may be advantageous for woodland managers to promote fast-growing species such as *Acer pseudoplatanus* to help maintain canopy cover (supplementary figure 5) (see Chapter 3 for further exploration of how tree species traits may affect ecosystem resilience).

However, there are various alternative explanations for why we may have failed to detect effects, so the conclusion that semi-natural ancient woodlands may be more resilient than was feared can only be drawn tentatively. One potential alternative explanation is that the ecosystem effects of ash death may take longer to appear than the time frame of this experiment. Although changes to light levels and exposure can occur rapidly after loss of canopy cover, other changes may take many years to accumulate, particularly changes to soil chemistry or leaf litter composition. In the long term, we would expect topsoil to become more acidic following loss of ash, as ash litter is neutral to alkali and is uncommon in this regard (Mitchell *et al.* 2014b). However, high levels of buffering in soil systems mean that changes such as this may take years to emerge and progress down the soil profile (Ovington 1953; James & Riha 1985). Any effects of changing pH on ground flora or earthworms may therefore not have appeared within this timescale. Equally, any negative effects of deeper shade that may result from changes in tree species composition in the long-term, may be slow to occur (Dölle & Schmidt 2009).

A second possibility is that major impacts may be seen only when ash is present at a higher proportion than in our plots. Both woodlands in this experiment were diverse semi-natural ancient woodlands, and ash was killed in the plots at a density of 6.73 m^2 basal area per hectare. However, some areas of recent regeneration or ash plantation will have far higher ash densities than these, and it may be that large impacts to woodland ecosystems will only be seen above a certain threshold density of ash. This could be the case if light levels are a primary driver of ecological change; at high densities of ash, the compensatory growth seen in this experiment may not be sufficient to buffer the loss of ash. There are also likely to be greater impacts when dead ash trees start to fall naturally,

increasing the size of canopy gaps. This was only seen to a limited degree in the experimental plots by the end of the study period, and so may not yet have had a major impact. It is also possible that stronger effects will be seen when larger areas are affected, as our experiment was confined to small blocks and left the surrounding woodland untouched.

Additionally, this study only focussed on two components of woodland ecosystems; ground flora and earthworm communities. Other groups of organisms were not studied which may be more strongly affected by loss of ash, particularly lichens and insects which both have species that are thought to use ash obligately (Lõhmus & Runnel 2014; Mitchell *et al.* 2014a; Littlewood *et al.* 2015). Neither of these groups were investigated in this experiment due to the scale of the plots: 25 x 25 metres was considered too small a plot to have much relevance to highly mobile organisms such as flying insects, or highly patchy organisms such as lichens. However, species such as these, which feed or live exclusively on ash trees, are likely to be the most vulnerable to loss of ash, and unless they can change their life histories to utilise other trees, will not be helped by compensatory growth of other tree species.

Small, non-significant decreases in earthworm abundance and diversity were observed in high ash-death treatments, and marginally significant decreases in abundance were observed in plots with high canopy openness. Although our treatment was not significant in this experiment, we might expect that earthworms would be affected by changes in canopy cover and species composition in the longer term – indeed, even in this experiment, where earthworms were only sampled in a single year after ash death, plots with higher canopy openness were observed to have fewer earthworms. Earthworms'

primary food is leaf litter, and they are known to be strongly affected by the quality and quantity of leaf litter produced, and by differences in nutritional value of litter between tree species (Reich *et al.* 2005; Cesarz *et al.* 2007; Curry & Schmidt 2007; Palo *et al.* 2013). Earthworms are known to favour ash leaf litter because of its low toughness and high nutrient content, so a decrease in ash cover could plausibly cause a long-term decrease in earthworm abundance that was not seen in this short study period (Mitchell *et al.* 2014a).

This may be important because earthworms have a disproportionate effect on ecosystems and play key roles in nutrient cycling and soil production (Lee 1985; Feller *et al.* 2003; Blouin *et al.* 2013). Changes in nutrient cycling may themselves have knock-on effects on the abundance and composition of ground flora and other groups, so if changes to earthworm communities were to occur, this could contribute to long-term changes in the wider woodland ecosystem (Brown 1995; Partsch *et al.* 2006). Earthworms are also important contributors to woodland food webs, so this could have further impacts on higher trophic levels such as badgers (Brown 1995). We suggest that the effects of ash loss on earthworm communities would merit further investigation, especially as they were only sampled for a single year in this experiment. The mustard vermifuge method used (Sherlock 2012) has been shown to produce results consistent with hand-sorting (Lawrence & Bowers 2002), but earthworms are notoriously difficult to sample exhaustively across functional groups due to their wide range of behaviours and habitats and their close incorporation into soils. It may therefore be worthwhile to use additional earthworm sampling techniques for a more complete picture.

As well as having a short duration, this study was also limited in size for logistical reasons, comprising 13 blocks in two sites. Ecological experiments tend to give results

containing large amounts of random variation, or with many confounding factors that may mask real trends in small samples. In addition to this, woodlands are highly patchy, and very different floral communities can frequently be found within metres of each other. It is possible that more, and perhaps larger, plots would have smoothed out some of the "noise" and provided sufficient statistical power to find significant results. Observational studies are currently ongoing into the effects of ash dieback on ground flora in woodlands in the East of England, including Bradfield Woods in Suffolk – a highly diverse ancient coppice system currently suffering severe effects of ash dieback (Rob Fuller, *pers. comm.*). It will be interesting to see how these observations of the effects of ash dieback compare to the results of our experiment in future.

Our experiment was designed to mimic the effects of ash dieback as closely as possible (the reason for killing ash trees with ring-barking). Removing a strip of bark from around the entire base of the trunk kills trees by disrupting the phloem (similarly to ash dieback) and, initially, leaves standing dead trees. However, in the first year after ring-barking, it was clear that only around two thirds of the treated trees had died, with others in various conditions ranging from poor to indistinguishable from untreated trees. We therefore completed the treatment by poisoning the unaffected ash trees with glyphosate herbicide in spring 2015. All treated trees were visually confirmed to be dead in July 2015. This delay in the death of a proportion of treated ash trees may have contributed to the degree of resilience seen in other parts of the woodland community, perhaps giving other trees time to grow into gaps that developed gradually. However, this is in fact how ash dieback outbreaks tend to progress (Pliûra & Baliuckas 2007; Kjær *et al.* 2011; McKinney *et al.* 2011; Alsop 2015). Differences in inherent tolerance and microclimatic conditions mean that a

phased effect is most commonly seen, with some trees succumbing faster than others to infection. Young trees in particular are known to die more quickly than mature trees (Lygis *et al.* 2014) and this was mimicked intentionally in our experiment by killing smaller trees preferentially to make up our desired basal area of ash (see Methods). It is possible that this pattern of tree deaths may confer a level of resilience to woodland communities facing ash death, as we have seen, by reducing the degree of change that is felt at any one time.

Conclusions

The results of our experiment show that, at least in the short term and in woods with ash admixed in diverse tree communities, woodland ground flora and earthworm communities can show a surprising degree of resilience to ash loss. While this is undoubtedly good news for woodland biodiversity and land managers working to preserve it, it must not encourage complacency: tree diseases are certainly capable of driving wide-ranging changes to woodland ecology and communities and biodiversity loss. If ash dieback does not, under certain circumstances, lead to dramatic loss of some ash-associated communities, this is likely to be because of the ability of other tree species to compensate in part for the loss of ash, either by maintaining suitable woodland microclimates or directly providing habitat. Woodlands with a diverse mixture of tree species are known to have better outcomes for many stressors, ranging from invasive diseases to climate change. In the long term, it is therefore critical to respond to ash dieback not only by attempting to lessen the immediate effects, but also by protecting

other tree species and enhancing woodland diversity. With each species loss to an invasive pest or disease, woodlands become less resilient to future threats.

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CHAPTER 3:
ABUNDANCE DISTRIBUTIONS FOR TREE SPECIES IN GREAT BRITAIN: A TWO-STAGE APPROACH TO MODELLING ABUNDANCE USING SPECIES DISTRIBUTION MODELLING AND RANDOM FOREST.

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Author Contributions

LH collected data, performed modelling and analysis work and wrote the first draft of the manuscript. All authors contributed to the design of the study and manuscript revisions. MT additionally provided statistical advice on random forest regression, and SS provided data from the Countryside Survey.

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Supplementary materials

Supplementary figures and tables for this chapter can be found in Appendix II. The annotated R script and walkthrough for the method used can be found on the accompanying CD.

Abstract

High-quality abundance data is expensive and time consuming to collect and often highly limited in availability. Nonetheless, accurate, high-resolution abundance distributions are essential for many ecological applications ranging from species conservation to epidemiology. Producing models that can predict abundance well, with good resolution over large areas, has therefore been an important aim in ecology, but poses considerable challenges.

We present a two-stage approach to modelling abundance, combining two established techniques. First, we produce ensemble species distribution models (SDMs) of trees in Great Britain at a fine resolution, using much more common presence-absence data and key environmental variables. We then use Random Forest regression to predict abundance by linking the results of the SDMs to a much smaller amount of abundance data. We show that this method performs well in predicting the abundance of 20 out of 25 tested British tree species, a group that is generally considered challenging for modelling distributions due to the strong influence of human activities.

Maps of predicted tree abundance for the whole of Great Britain are provided at 1 km^2 resolution. Abundance maps have a far wider variety of applications than presence-only maps, and these maps should allow improvements to aspects of woodland management and conservation including analysis of habitats and ecosystem functioning, epidemiology and disease management, providing a useful contribution to the protection of British trees. We also provide complete R scripts to facilitate application of the approach to other scenarios.

Introduction

Robust information on the distribution and abundance of species is essential for many applications in ecology and conservation. Advances in Species Distribution Modelling have driven an explosion in the use of these and similar techniques, which are now widespread (Araújo & Guisan 2006). However, the most commonly desired output from these techniques, an estimate of the probability of species occurrence, is restricted in its uses. Furthermore, due to limitations in the quality of available data, the actual output of Species Distribution Models (SDMs) is often even less useful, producing only a relative, not absolute, likelihood of presence, and sometimes worse (Pearce & Boyce 2006; Guillera-Arroita *et al.* 2015). For many ecological questions, estimates of abundance would be far more valuable as they provide much more information about the state of populations and properties of ecosystems (Pearce & Ferrier 2001; Sagarin *et al.* 2006; Hui *et al.* 2009).

Predicting abundance distributions with accuracy is challenging. Even where presence-absence or presence-only data are easy to find, large amounts of abundance data are rarely available (Nielsen *et al.* 2005; Van Couwenberghe *et al.* 2013). Therefore, finding effective ways to model abundance is an important area of research in ecology. A variety of different approaches, including looking for a fundamental relationship between the area of occupancy and abundance (Gaston *et al.* 2000) and looking at how occupancy patterns change with different grain size (Hui *et al.* 2009) among others (Wenger &

Freeman 2008; Hwang & He 2011) have been attempted. However, none of these has produced consistently satisfactory results and each has significant theoretical or practical limitations.

Another approach has been to investigate relationships between likelihood of occurrence and abundance. This approach assumes that species abundance and occurrence are controlled by the same or related environmental factors (Brown 1984; Van Couwenberghe *et al.* 2013). Various studies have attempted to correlate the results of SDMs or related models with abundance data to produce models predicting abundance in unknown areas (Nielsen *et al.* 2005; Johnson & Seip 2008; Van Couwenberghe *et al.* 2013). However, wide variation in the relationships between species occurrence and abundance have been reported, with various studies showing weak relationships (Gaston *et al.* 2000; Nielsen *et al.* 2005; Van Couwenberghe *et al.* 2013). Another study by Pagel *et al.* (2014) used a hierarchical model to predict abundances in time and space using a combination of plentiful occurrence data and restricted abundance data. Their method produced unbiased results, but with very low precision in predictions, perhaps due to inflexibility in their models or not using environmental covariates. These studies have all suggested promise for a technique combining the use of large amounts of occurrence data with small amounts of abundance data, but none have yet performed well enough to be of use for many real-world applications.

We present a two-stage modelling approach for predicting abundance, where the results of SDMs produced using the R package biomod2 (Thuiller *et al.* 2016) are regressed against abundance data and additional predictors using Random Forest regression with the R packages caret and randomForest (Breiman 2001; Liaw & Wiener 2002; Kuhn *et al.*

2016). This approach performs well in almost all cases tested here and is flexible and simple to use. We argue that poor correlations between SDM results and abundance previously reported may be partly due to the use of less powerful or inappropriate modelling techniques in other studies. SDMs are first produced using, in our case, presence-absence data to produce a map of estimated probability of occupancy for the species of interest. Separate abundance data is then used to fit a Random Forest regression that predicts abundance from probability of occupancy. Additional predictors, which may be expected to influence abundance but not occupancy, can be included at this stage. We also include the SDM results of co-occurring species as covariates in the Random Forest regression, allowing biotic effects to be accounted for in the prediction of abundance and producing more realistic species responses.

We have used this approach to produce distribution maps showing the abundance of 20 common tree species in Great Britain. Available tree distribution data for Great Britain was surprisingly poor, presenting a knowledge gap for ecologists working on British woodlands, particularly in light of major threats such as emerging tree diseases (Boyd *et al.* 2013). Our distributions show total combined area covered by each species within each square kilometre (hectares per square kilometre) across Great Britain, and are a significant improvement on previously widely available distribution data. We envisage that such distribution maps could make an important contribution in a number of fields related to British forestry, from conservation planning to epidemiology.

Methods

We predicted abundance of tree species using a combination of two established techniques. First we used the R package biomod2 (Thuiller *et al.* 2016) to produce ensemble species distribution models (SDMs) of trees in Great Britain at 1 km^2 resolution. Then we used Random Forest regression, with caret (Kuhn *et al.* 2016) and randomForest (Liaw & Wiener 2002) packages in R, to link the results of these SDMs to a much smaller amount of abundance data, to predict abundance across Great Britain at the same resolution. Figure 7 shows a schematic overview of the methods.

Stage 1: Fitting species distribution models

From the Distribution Database of the Botanical Society of the British Isles (BSBI) (see Data Sources) we downloaded all records from Great Britain between 1950 and 2014 for 25 commonly found tree species: *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., *Populus tremula* L., *Prunus avium* L., *Prunus padus* L., *Pseudotsuga menziesii* Franco, *Quercus petraea* Lieblein, *Quercus robur* L., *Salix caprea* L., *Salix cinerea* L., *Sorbus aria* Crantz, *Taxus baccata* L., *Tilia cordata* Miller, *Ulmus glabra* Hudson and *Ulmus procera* Salisbury. We discarded records with location data less precise than tetrad level (2 km x 2 km), and simplified data with more precise locations to tetrad level. We chose tetrad resolution as a suitable compromise between having a high number of records to use and a small spatial scale, as using coarse scales can be

problematic when modelling species distributions (Guisan *et al.* 2007a; Dengler *et al.* 2009).

We then converted this presence-only data to presence-absence. We considered tetrads for which botanical surveys had been undertaken at least twice since 1950, and where at least 50 species of plants were recorded in each survey, to be "well-surveyed" (Groom 2013) (a map is provided in Supplementary Figure 7). Any well-surveyed tetrads that did not have records for the species of interest were reclassified as "absence" points for that species (i.e. locations where the species was likely to be either truly absent or at very low abundance and therefore playing little role in defining the dominant ecological characteristics of that tetrad). Accounting for the likelihood that common trees will have a higher detection probability than most species of plants, we kept this threshold low enough to prevent the exclusion of tetrads in species-poor areas, while being high enough to prevent the inclusion of too many poorly-surveyed tetrads (Groom 2013). This produced a total of 18,993 tetrads from across Great Britain that were considered well-surveyed and subsequently used as presence or absence points. Data manipulation was carried out using custom written scripts in Python (Python Software Foundation: Version 3.3.2).

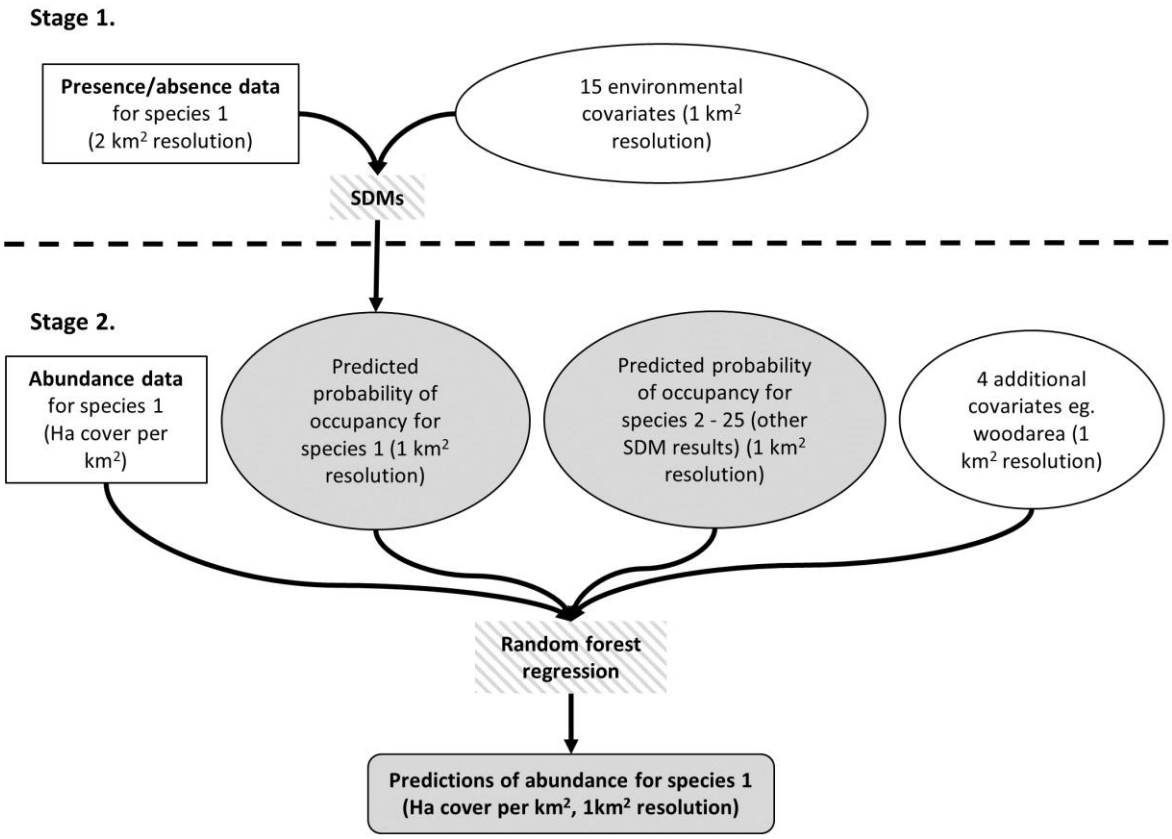

Figure 7. Schematic showing the outline of the two-stage method for predicting abundance distributions. The first stage uses SDMs to produce maps of predicted probability of occupancy, while the second stage takes these maps as inputs and uses Random Forest regression to produce maps of predicted abundance. Distribution data inputs are shown in square boxes, model covariates in round boxes, model outputs are shaded in solid grey and modelling processes in hashed grey.

We downloaded data on a variety of ecological variables across Great Britain from a variety of free sources (Table 2). See Data Sources for details. Pre-processing of layers was carried out in ArcGIS (Esri 2014) to ensure identical extent, cell size and coordinate system for use in species distribution modelling. All environmental covariates were used at 1 km resolution: vector datasets were rasterised to 1 km resolution.

We then fitted Species Distribution Models (SDMs) to these data. For reviews of these methods see Pearson & Dawson (2003b) and Elith & Leathwick (2009). SDMs use species records and environmental variables to fit models that describe the relationship of the

species' distribution to the environmental variables, which can then be used to predict the occupancy probability or related measures across a wider landscape (Thuiller 2003; Elith & Leathwick 2009). SDMs for all species were produced using the package biomod2 in R (R Core Team 2016; Thuiller *et al.* 2016).

We selected 15 environmental variables as covariates from the original set of 33 (see table 2). We removed one of each pair of variables with a pairwise Pearson's correlation coefficient higher than 0.7, while retaining variables that are known to be important determinants of plant growth (Prentice *et al.* 1992; Guisan *et al.* 2007b). The final selection

Table 2. Ecological variables downloaded and processed for Species Distribution Modelling. Details of data sources can be found in Data Sources.

Variable	Description	Unit	Source
bio1	Annual mean temperature	°C*10	Worldclim
bio2	Mean diurnal temperature range: mean of monthly (max temp – min temp)	°C*10	Worldclim
bio3	Isothermality (bio2/bio7 * 100)	°C*10	Worldclim
bio4	Temperature seasonality: standard deviation*100	°C*1000	Worldclim
bio5	Max temperature of warmest month	°C*10	Worldclim
bio6	Min temperature of warmest month	°C*10	Worldclim
bio7	Temperature annual range	°C*10	Worldclim
bio8	Mean temperature of wettest quarter	°C*10	Worldclim
bio9	Mean temperature of driest quarter	°C*10	Worldclim
bio10	Mean temperature of warmest quarter	°C*10	Worldclim
bio11	Mean temperature of coldest quarter	°C*10	Worldclim
bio12	Annual precipitation	mm	Worldclim

bio13	Precipitation of wettest month	mm	Worldclim
bio14	Precipitation of driest month	mm	Worldclim
bio15	Precipitation seasonality: coefficient of variation	cm	Worldclim
bio16	Precipitation of wettest quarter	mm	Worldclim
bio17	Precipitation of driest quarter	mm	Worldclim
bio18	Precipitation of warmest quarter	mm	Worldclim
bio19	Precipitation of coldest quarter	mm	Worldclim
altitude	Altitude	m*10	Worldclim
slope	Slope	%	Derived from Altitude using ArcGIS (Slope)
aspect	Aspect	Degrees	Derived from Altitude using ArcGIS (Slope)
directradiat	Direct radiation: incoming direct solar radiation	Watt hours m^{-2}	Derived from Altitude using ArcGIS (Solar Radiation Analysis)
directdurat	Direct duration: duration of direct solar radiation	Hours	Derived from Altitude using ArcGIS (Solar Radiation Analysis)
diffuseradiat	Diffuse radiation: incoming scattered solar radiation	Watt hours m^{-2}	Derived from Altitude using ArcGIS (Solar Radiation Analysis)
nfi	National Forest Inventory Great Britain 2014, forested areas	Nominal	Forestry Commission
soil	Soil type	Nominal	European Soil Database
soiltext	Dominant soil surface textural class	Nominal	European Soil Database
octop	Topsoil organic carbon content	Nominal	European Soil Database
awctop	Topsoil available water capacity	Nominal	European Soil Database
mintop	Topsoil minerology	Nominal	European Soil Database
ancient_es	Ancient woodlands in England, Scotland and Wales	Nominal	Natural England, Forestry Commission Scotland and National Resources Wales
land cover 07	UK Land cover map 2007 (1 km^2)	Nominal	Countryside Survey/CEH

was altitude, aspect, slope, direct incoming solar radiation, mean diurnal temperature range, temperature seasonality, annual precipitation, ancient woodland locations, topsoil available water capacity, topsoil minerology, topsoil organic carbon content, topsoil texture class, soil category, National Forest Inventory (NFI) forest type and land cover type (see Supplementary Table 1 for pairwise Pearson's correlations between selected variables). We ran six algorithms (GLM, GAM, Classification Tree Analysis (CTA), Generalised Boosting Models (GBM), Random Forest (RF) and Maximum Entropy (MaxEnt)) 15 times for each species using the 15 environmental covariates, producing a total of (25 species x 6 algorithms x 15 repeats) = 2250 models.

Each model run was carried out using a randomly chosen 70% of the presence-absence data (Thuiller 2003; Heikkinen *et al.* 2012); the remaining 30% were used for cross validation to assess the performance of each model using two model assessment criteria; area under the Receiver Operator Curve (ROC) and the True Skill Statistic (TSS) (Allouche *et al.* 2006). For each species, we selected the best-performing models (see Table 3) to build an ensemble distribution model (a mean of the raw model results, weighted by the model ROC scores), producing a single distribution map for each species that represents a robust estimate of a species' British distribution at 1 km^2 resolution (Thuiller *et al.* 2016). The model selection process was as follows. Firstly, we assessed ROC and TSS scores – for both metrics, a higher value indicates better model fit – and if there was a leading group of models whose ROC and TSS scores were a step higher than the remainder, this leading group was chosen. Often this leading group contained just the 15 Random Forest models. Otherwise, the top 20 models with the highest scores were selected. Secondly, we visually assessed the predicted responses of the species to each

environmental covariate for each of these models. Any models that contained biologically implausible responses were rejected, as were models where the responses or predicted occurrence maps disagreed greatly from the overall consensus, as these can lead to development of inappropriate ensemble models (Henrik Hannemann, *pers. comm*.). See the walkthrough of R code in Supporting Information for an example of how models were chosen and example response curves. After rejection of implausible models, the final number of models used to produce each ensemble ranged between 11 and 20. Ensemble models were therefore robust, biologically plausible, and had high predictive power for the majority of species (see Table 3).

Non-significant variables were not removed from the models because of the very large size of our datasets, and because the models were used to make predictions rather than to test hypotheses. Therefore final models may include terms that were not important to the outcome, but this should not have had a detrimental impact on the model fit. The numbers and types of models selected for each species are displayed in Table 3.

Stage 2: Modelling abundance using Random Forest regression

Abundance data for trees, in the form of hectares covered by a species per square kilometre (or percent cover), was obtained from the 2007 Countryside Survey and myForest (see Data Sources). The Countryside Survey is a large-scale survey in Great Britain measuring many aspects of landscapes and the countryside, including diversity and abundance of plant species. It uses a random stratified sampling procedure to capture a representative sample of all land cover types. By contrast, myForest is a service set up to help woodland owners map and manage their forests, which currently holds

data on over 45,000 Ha of woodlands across Great Britain, but does not contain any records outside of woodlands. For all tree species combined, 9800 randomly selected abundance data points from the Countryside Survey and 9453 abundance data points from myForest were used, making an average of 770 abundance data points per species (see Supplementary Table 3 for numbers of data points per species).

The two abundance datasets (Countryside Survey and myForest) were rescaled to express them as hectares covered per kilometre squared (percent cover), in order to make them comparable. For the myForest data, which was originally provided in the format percentage cover of each species within a woodland patch, this involved multiplying each percentage cover record by the proportion of woodland cover in the relevant kilometre square. For this, we used a shapefile downloaded from the National Forest Inventory (NFI), containing outlines of all woodlands over 0.5 hectares in Great Britain. For the Countryside Survey data, which was collected using a more complex methodology (details available in Barr *et al.* 1990) where linear features such as hedgerows were sampled separately from the rest of the landscape, more manipulation was required. The data was weighted by the length of linear features in the kilometre squared, to account for the fact that linear features are more likely to contain trees and the lengths of them are not equal across the country. The weighting was done using (linear plot percentage cover x percent of kilometre square covered by linear features) + (non-linear plot percentage cover x remaining area), with all required information taken from the Countryside Survey.

Tree cover data for England and Wales from Bluesky's National Canopy Map were made available by the Woodland Trust, to be used as a modelling covariate. Three layers from

this were used: the total tree cover, tree cover derived only from woodlands included in the NFI, and tree cover derived from trees outside woodlands. The National Canopy Map layers were used in England and Wales, while the more basic NFI layers were used in Scotland where complete tree cover data was not available. We also used the NFI dataset to calculate the proportion of each square taken up by broadleaved woodland edge, which was defined as any woodland within 50 m of non-woodland (Aune *et al.* 2005). All these layers were used as covariates in the Random Forest regression (below). We used R version 3.2.3 for all modelling and data processing (R Core Team 2016).

We used Random Forest regression to model the relationships between abundance, the probability of occupancy predicted by the SDMs, and our tree cover covariates which we expected would be important for modelling tree abundance (Breiman 2001). A separate Random Forest regression was implemented for each species. The SDM outputs for all species were included as variables for each species, so that the models would also capture interactions between species (such as competition). Potentially, this could also capture variation in other variables that are not included in that species' SDM but which correlate with the distribution of other species. Models had the form:

$$\text{Abundance}_{\text{focal sp.}} \sim \hat{P}_{\text{focal sp.}} + \hat{P}_{\text{sp. 2}} \ldots \hat{P}_{\text{sp. 25}} + C_A + C_W + C_O + C_E$$

where $\hat{P}$ is the predicted probability of occupancy from the relevant SDM, C_A is cover from all trees, C_W is cover from woodland trees only, C_O is cover from trees outside woodland only, and C_E is cover from woodland edge.

Models were run using the combined myForest and Countryside Survey data. We chose to use Random Forest regression because it is insensitive to data distribution and

therefore copes well with our data which has a high percentage of zeros. It can also take a large number of potentially collinear variables, and is robust to overfitting, making it extremely useful for prediction (Segal 2004; Prasad *et al.* 2006). We used these models to predict abundance of each species across the whole of Great Britain at 1 km^2 resolution. We used Root Mean Squared Error (RMSE) and Mean Absolute Error (MAE), produced by k-fold cross validation with 10 folds, to evaluate our models. These two commonly used evaluation metrics give interpretations of a model's average error when testing it against independent data, in this case, the 10% that was left out of each run (Chai & Draxler 2014).

Results

Species Distribution Modelling

All selected models had useful prediction capability (AUC > 0.7) (Boyce *et al.* 2002). In general, prediction accuracy of the selected models was good and they successfully predicted a large proportion of known presence or absence points. The selected models had ROC scores between 0.71 and 0.96 and TSS scores between 0.31 and 0.83 (Table 3). Ensemble models were built using 100% of the available data, so evaluations are not given for ensemble models as this would test the models on the same data they were generated with, resulting in unfair evaluation statistics. For the four species with the lowest predictive power (lowest TSS and ROC scores), (*Populus tremula*, *Prunus avium*, *Pseudotsuga menziesii* and *Tilia cordata*) (Table 3), we investigated further to ensure that all ecological factors known to be important to them were included in the model runs. However, no further improvements to the model fit were found. These were species that

tend to be either widespread but uncommon throughout their range (*P. tremula*, *P. avium*, *T. cordata*) or non-native trees whose distribution is largely controlled by human planting (*P. menziesii*) and as a result it is unlikely to be possible to generate high-scoring

Table 3. The number, type, and prediction accuracy of the individual models used to build ensemble distribution models for each tree species. Algorithms included were GAM (Generalised Additive Model), GBM (Generalised Boosted Regression), GLM (General Linear Model), RF (Random Forest) and MaxEnt (Maximum Entropy).

Species	Number of models used to build ensemble	Algorithms included	Mean ROC score	Mean TSS score
Acer campestre	20	GAM, RF, GBM	0.92	0.71
Acer platanoides	20	GLM, GAM, RF, GBM	0.76	0.44
Acer pseudoplatanus	20	GAM, RF, GBM	0.85	0.55
Alnus glutinosa	15	RF	0.80	0.46
Betula pendula	15	RF	0.79	0.46
Betula pubescens	15	RF	0.80	0.46
Carpinus betulus	20	RF, GBM, MaxEnt	0.78	0.40
Castanea sativa	15	RF	0.81	0.47
Corylus avellana	16	RF, GBM	0.86	0.46
Crataegus monogyna	20	GLM, GBM, RF, GBM	0.96	0.82
Fagus sylvatica	20	GAM, RF, GBM	0.81	0.48
Fraxinus excelsior	20	GLM, GAM, RF, GBM	0.92	0.83
Populus tremula	17	RF, GBM	0.71	0.31
Prunus avium	11	RF	0.75	0.36
Prunus padus	20	RF, GBM	0.80	0.48
Pseudotsuga menziesii	19	GAM, RF, GBM, MaxEnt	0.76	0.39
Quercus petraea	15	RF	0.82	0.49
Quercus robur	16	RF, GBM	0.90	0.64
Salix caprea	16	RF, GBM	0.79	0.42
Salix cinerea	16	RF, GBM	0.78	0.42
Sorbus aria	20	RF, GBM	0.84	0.53
Taxus baccata	20	GAM, RF, GBM	0.80	0.44
Tilia cordata	15	RF, GBM	0.76	0.36
Ulmus glabra	15	RF	0.79	0.43
Ulmus procera	15	RF	0.89	0.61

distribution models for these species (Guisan *et al.* 2007b). For 21 out of 25 species, however, SDMs produced high-quality ensemble models.

Abundance modelling

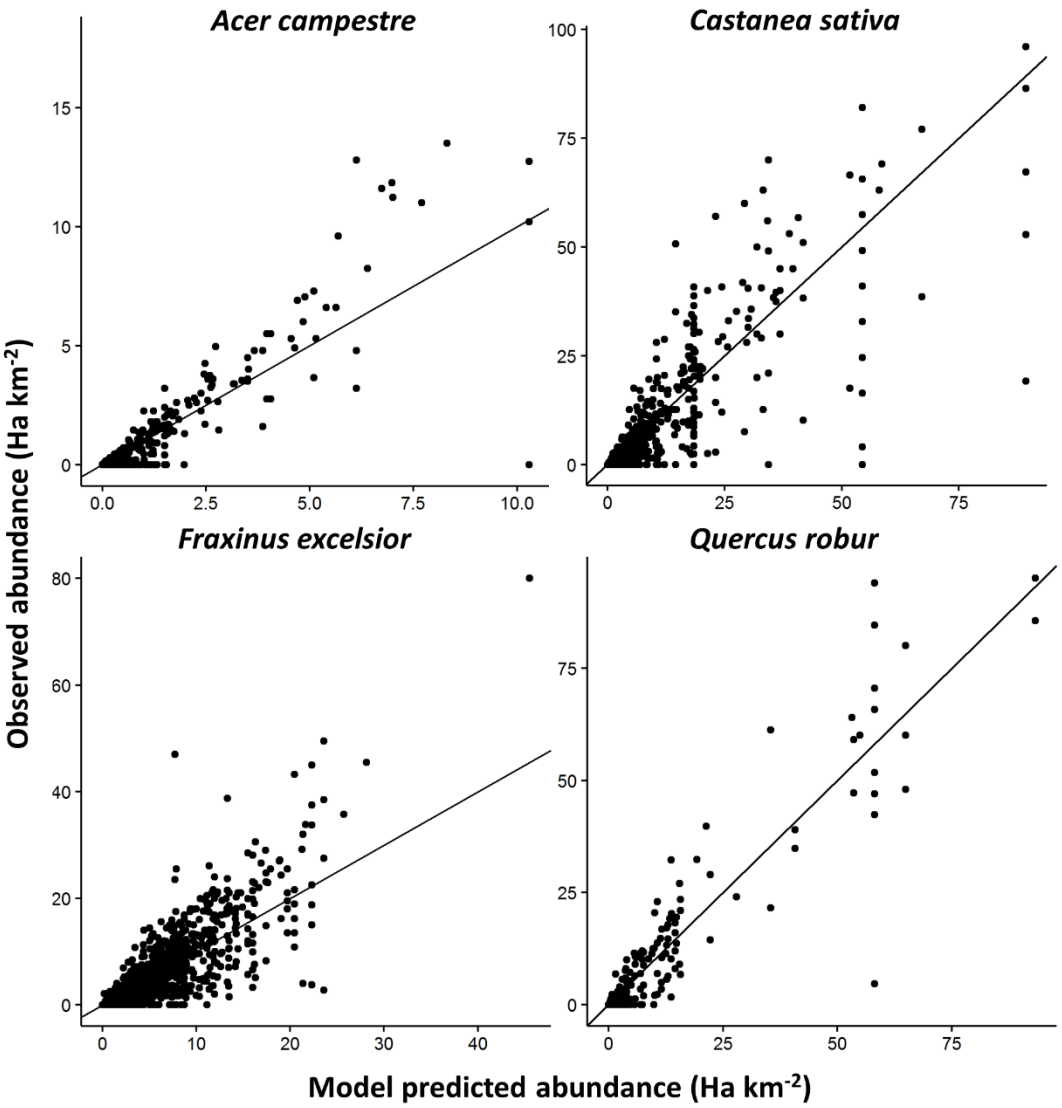

Figure 8. Observed abundance against abundance predicted by Random Forest regression, as used to assess model performance, shown for four tree species. The line on each graph is the 1:1 line showing perfect model fit.

In general, the Random Forest models were very successful in predicting the abundance of tree species. Figure 8 shows the predicted against observed abundance for four

representative species; graphs for all other species are shown in Supplementary figure 8. For the majority of species, the predictions of the models are similar to the observed values.

We produced Root Mean Square Error (RMSE) and Mean Absolute Error (MAE) scores using 10-fold cross validation to evaluate our models' performance. These two commonly used model evaluation metrics give interpretations of a model's average error when testing it against independent data (Chai & Draxler 2014). Table 4 shows RMSE and MAE scores for each species; the error scores are given in the same scale as the response variable, i.e. hectares covered per square kilometre (percent cover). All the models have RMSE scores under 10, and most are under 5. All MAE scores are under 5. The average prediction error for most of the models produced is therefore less than 5%.

For six species, *Acer platanoides*, *Populus tremula*, *Prunus padus*, *Sorbus aria*, *Ulmus glabra* and *Ulmus procera*, there were too few non-zero abundance data points to use 10-fold cross validation. We chose 50 positive data points as the cut off for using 10-fold cross validation, as this gives an average of five non-zero data points per fold. *Acer platanoides* had 42 positive abundance data points, so for this species we used 8-fold cross validation to maintain an average of five non-zero data points per fold. However, for the remaining five species we felt that there was not enough data available to produce reliable abundance models (see Table 4). These species were omitted and maps of predicted abundance of the remaining 20 species across Great Britain were produced (Figure 9 and downloadable from the Sylva Foundation website and Oxford University Research Archive (see Data Sources). Where adequate abundance data was available, however, Random Forest regression was able to improve the prediction of the species for which the

SDMs had a poorer fit. We were able to successfully model the abundance of *Prunus avium*, *Pseudotsuga menziesii* and *Tilia cordata* despite the SDM prediction accuracy for these species being poorer than the other species.

Table 4. Root Mean Square Error (RMSE) and Mean Absolute Error (MAE) scores for the Random Forest regression model for each species. The number of non-zero data points available for each species is also shown.

Species	RMSE	MAE	Number of non-zero data points
Acer campestre	1.44	0.35	315
Acer platanoides	1.27	0.19	42
Acer pseudoplatanus	4.01	1.40	634
Alnus glutinosa	2.40	0.66	195
Betula pendula	6.88	2.29	802
Betula pubescens	4.09	1.09	127
Carpinus betulus	3.79	1.05	320
Castanea sativa	9.56	3.58	501
Corylus avellana	4.47	1.47	935
Crataegus monogyna	1.10	0.23	339
Fagus sylvatica	8.45	2.91	918
Fraxinus excelsior	4.95	1.88	1629
Populus tremula	*NA*	*NA*	16
Prunus avium	1.98	0.56	401
Prunus padus	*NA*	*NA*	9
Pseudotsuga menziesii	7.66	1.96	193
Quercus petraea	5.99	1.84	209
Quercus robur	6.50	2.54	1867
Salix caprea	1.38	0.28	74
Salix cinerea	0.16	0.03	55
Sorbus aria	*NA*	*NA*	3
Taxus baccata	2.21	0.49	86
Tilia cordata	1.04	0.14	56
Ulmus glabra	*NA*	*NA*	22
Ulmus procera	*NA*	*NA*	27

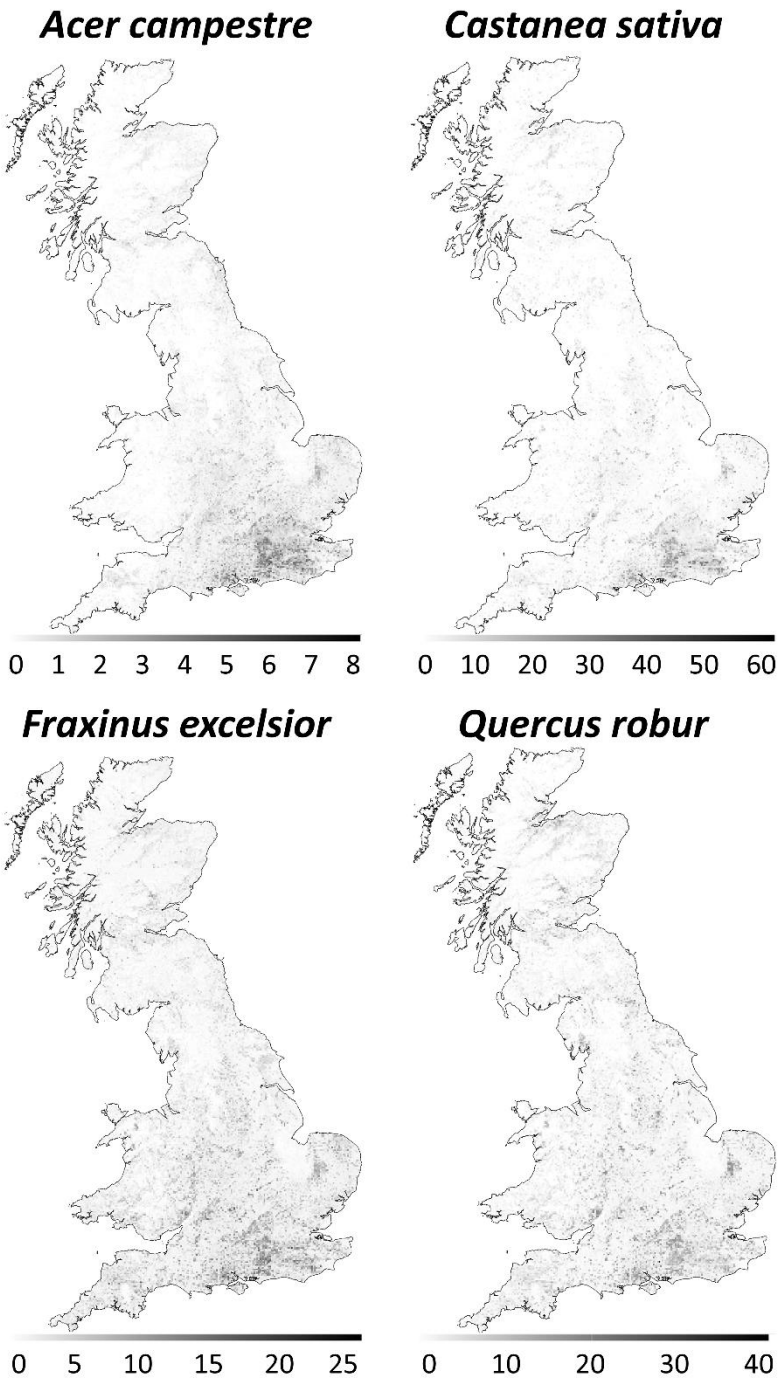

Figure 9. Maps of predicted abundance for four species, in hectares per km^2, or percent cover. Note the scale varies between species. Maps for all other successfully modelled species are available to download from Sylva Foundation website and Oxford University Research Archive (see Data Sources).

We also calculated R^2 scores for the models, and these are available in Supplementary Table 3. However, we recommend caution when interpreting these scores, as R^2 is not the most appropriate metric to use in this situation. R^2 is affected by the extent of the dependent variable (Gelman & Hill 2007), and as the maximum abundance varied greatly between species, this confounds comparison between our models. The high percentage of zeros in our datasets also produces difficulty in the interpretation of R^2. For instance, for *Acer campestre*, over 97% of the available abundance data points were zero. The model tended to predict very slightly higher than zero for these points (generally between zero and one percent cover), resulting in a low R^2 (0.523). However, the observed vs predicted graph (Figure 8) and the low RMSE and MAE scores (Table 4) for *Acer campestre* show that the model generally predicts very close to the true abundance, despite scatter in the data, and this is mirrored for most other species. For applications where the difference between zero and one or two percent cover is unimportant, these models can be used directly for predicting abundance; where it is more important, the predicted against observed graph can be used to select a cut off below which predicted abundance will be coerced to zero.

Discussion

The two-stage modelling approach produced good or excellent predictions of abundance for the majority of species across the whole of Great Britain, despite only being trained on a relatively small amount of abundance data. This is in contrast to several previous studies looking for relationships between SDM results and abundance, which have shown little or no relationship (Gaston *et al.* 2000; Nielsen *et al.* 2005; Johnson & Seip 2008).

However, to our knowledge no previous studies have used Random Forest regression to model this relationship, and doing so has a number of advantages. Most importantly perhaps is that it does not make any assumptions about the shape of the relationship. Previous studies have attempted to use the negative binomial and other theoretical distributions, but we argue that this is likely to be an oversimplification that may mask true relationships. The shape of such a relationship, which is likely to have several different drivers, may not follow a simple mathematical function, and is known to vary between species (Gaston *et al.* 2000; Nielsen *et al.* 2005; Harris 2015). The use of Random Forest regression allows for such variation, making it a much more powerful technique for this application (De'ath & Fabricius 2000; Prasad *et al.* 2006; Evans & Cushman 2009).

Our two-stage modelling approach has a number of other advantages. It can incorporate biotic effects, and include covariates that are expected to influence abundance separately from those expected to influence occupancy. It makes use of the large amount of presence or presence-absence data that is often available, rather than discarding it. It will work with any measure of abundance (number of individuals, percentage cover, biomass *etc*.) and has been shown to be effective over large spatial extents. It may be a particularly powerful approach where occurrence and abundance are not influenced by exactly the same factors (see Nielsen *et al.* 2005a). Although not tested here, this method also has the potential to be effective when used with the results of more problematic SDMs, such as those made using presence-only data, which can only predict a relative likelihood of occupancy (Araújo & Peterson 2012).

We can also make use of the covariate allocation of Random Forest to gain insights into underlying ecological processes within the community. For each species for which we

have modelled abundance, we can inspect which variables are having the strongest effects in the model (see Supplementary Table 2) (Breiman 2001). This means we can see which other species' SDM results are most strongly associated with the abundance of our species of interest, allowing us to identify possible biotic interactions such as competition. This does not allow us to distinguish causal relationships because of the possibility that hidden covariates could be at play; two species' SDM results could be correlated with each other not because of a biotic interaction, but because they are both influenced by an underlying factor. However, it does provide a qualitative estimate of biotic effects that could be an interesting starting point for further study. The inclusion of biotic effects may have the additional benefit of improving model performance for predicting abundance under new conditions, such as future climate scenarios (Araújo & Guisan 2006; Elith & Leathwick 2009; Anderson 2013; Harris 2015). Species distributions and abundances are predicted to be strongly influenced in future by both climatic changes and biotic effects, and to our knowledge this is the first technique for predicting abundance which is able to make some account of these biotic effects. However, the approach will not be able to incorporate changes to biotic effects with novel species assemblages, or other factors such as dispersal limitation, without further modification.

Not all species were successfully modelled using this technique. *Prunus padus*, *Populus tremula*, *Sorbus aria*, *Ulmus glabra* and *Ulmus procera* were all unsuccessful, in each case because very little abundance data was available for these species in our data sets. For example, our combined abundance data set contained only four non-zero data points for *Sorbus aria*, demonstrating the difficulty in acquiring abundance data even for such a well-studied system. However, various tree species which are generally considered to be

difficult to model – such as *Pseudotsuga menziesii*, a non-native species whose distribution is still largely controlled by planting, and *Tilia cordata*, which is thought to be both rare and widespread in Britain due to an unusual ecological history (Pigott 1991) – were successfully modelled by Random Forest regression, despite showing relatively poor SDM performance. Overall, the method performed well for the majority of species and seems to be generally effective across a range of species, provided that sufficient abundance data are available.

British trees exist in highly human-modified landscapes where their distributions have without exception been altered by human land use and preferences (Hopkins & Kirby 2007; Rackham 2008). This is a challenging scenario for modelling abundance; other studies which have tried to model abundance of vascular plant species have avoided trees for this reason (Van Couwenberghe *et al.* 2013). However despite this the models performed well for the majority of species. This suggests that the models may be flexible enough to work in a variety of contexts, and are likely to perform even better in less human-dominated landscapes. This flexibility is one of the major advantages of using Random Forest regression, and we expect it to offer broad application in modelling abundance of a wide range of species (Prasad *et al.* 2006). The next step for evaluating the method will be to compare its performance to other published methods for predicting abundance, which could be done by evaluating the relative performance of this and other methods with a variety of published datasets.

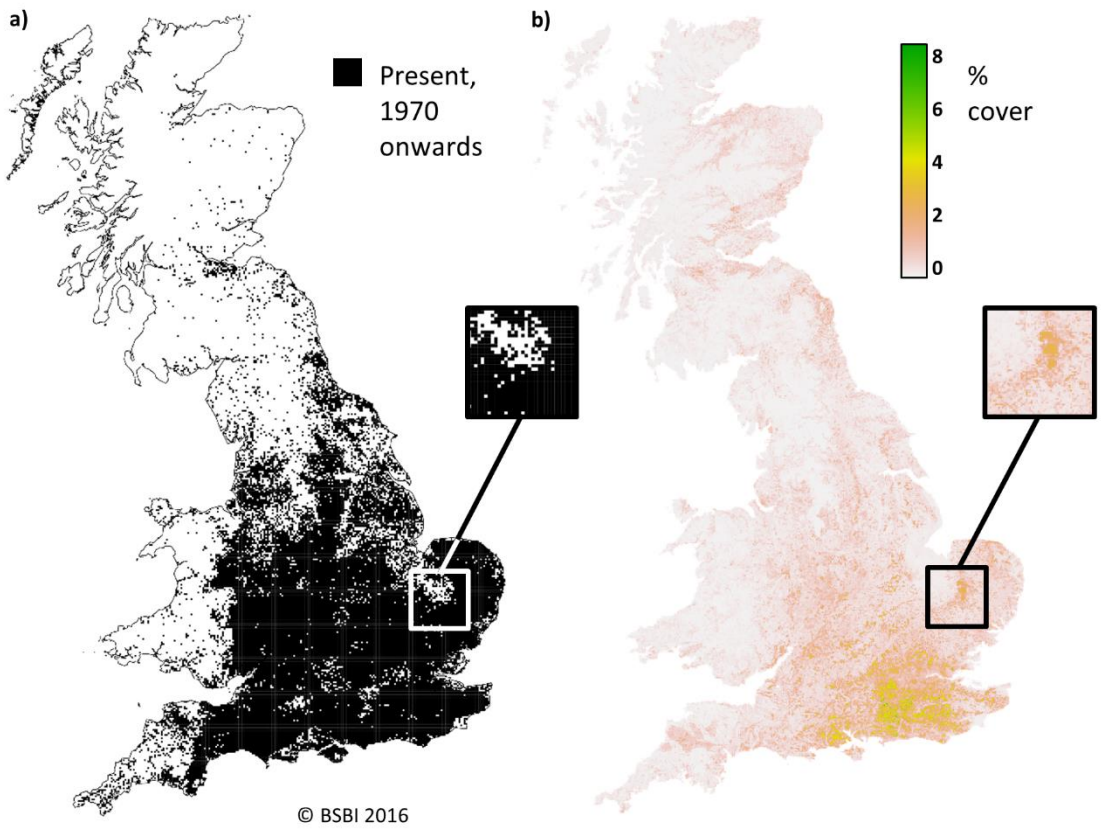

Figure 10. a) Presence records of *Acer campestre*, downloaded from the BSBI database (some of the best available distribution data at the country-wide level). The data is presence only on 2 x 2 km (tetrad) scale. Note that where presence is not recorded, it is impossible to say whether the species is truly absent. Compare with our modelled abundance distribution **(b)** showing modelled hectares covered by *A. campestre* per square kilometre for every 1 km square.

The abundance maps that we have produced are the best quality abundance distributions currently available for these species in Great Britain; previously, the best widely available distribution maps for trees in Great Britain were presence-only maps on 10 or 2 km square scales (see Figure 10). Our maps are modelled, not directly observed, and as is the case for modelling any highly noisy system, will not accurately predict abundance in every 1 km square; however, they are expected to capture overall patterns of distribution well. As more data, particularly abundance data and better quality environmental covariates, become available, our maps can continue to be improved. Abundance maps

have a far wider variety of applications than presence-only maps, and these maps will allow significant improvements to these applications. British woods face a range of threats, including invasive diseases such as ash dieback, under- or over-management leading to poor woodland quality, pollution and damage by deer (Rackham 2008). These improved maps should allow better planning and management of woodlands, analysis of habitats and ecosystem functioning, and epidemiology and disease management, and will be a useful contribution to the protection of British trees.

Conclusion

The two-stage method to predict abundance, using Random Forest regression to model the relationship between SDM outputs and abundance, is robust and easy to use producing good results for the majority of British tree species. Images and raster files of our abundance maps for the 20 successfully modelled tree species are available to download from the Sylva Foundation website and Oxford University Research Archive (see Data Sources). Both SDMs and Random Forest regression are well-established techniques, and using them together in this combination is a user-friendly way to produce good quality maps of predicted abundance. This opens the way for more abundance maps to be produced for a wider range of scenarios, which itself could drive improvements in a number of ecological research areas, from responses to climate change to epidemiology. To facilitate this, we provide annotated R code in the Supporting Information for the entire process, to act as a guide for those wishing to use this method themselves.

Data Sources

- Ancient Woodland shapefile data:
    - England: available from Natural England at http://www.gis.naturalengland.org.uk/pubs/gis/GIS_register.asp (accessed 17/06/2016).
    - Scotland: available from Forestry Commission Scotland at https://gateway.snh.gov.uk/natural-spaces/dataset.jsp?dsid=AWI (accessed 17/06/2016).
    - Wales: available from National Resources Wales at http://lle.wales.gov.uk/Catalogue/Item/AncientWoodlandInventory2011/?lang=en (accessed 17/06/2016).
- BSBI Distribution Database: available at http://bsbidb.org.uk/ (accessed 17/06/2016).
- Countryside Survey data: the data used is available to download from the Oxford University Research Archive, https://ora.ox.ac.uk/ "Merged abundance dataset from myForest and the Countryside Survey".
- Landcover Map 2007: available from Centre for Ecology and Hydrology at http://www.ceh.ac.uk/services/land-cover-map-2007 (accessed 17/06/2016).

- myForest: the data used is available to download from the Oxford University Research Archive, https://ora.ox.ac.uk/ "Merged abundance dataset from myForest and the Countryside Survey".

- National Canopy Map was made available for this study by kind permission of the Woodland Trust.

- National Forest Inventory Great Britain 2014: available from Forestry Commission at http://www.forestry.gov.uk/datadownload (accessed 17/06/2016).

- R scripts: see Supporting Information on accompanying CD.

- Raster and image files for the abundance maps produced for all species are available to download from the Sylva Foundation website, https://sylva.org.uk/ and Oxford University Research Archive, https://ora.ox.ac.uk/ "Predicted abundance maps for British Trees".

- Soil data from European Soil Database: available at http://esdac.jrc.ec.europa.eu/content/european-soil-database-v20-vector-and-attribute-data (accessed 17/06/2016).

- Worldclim: free global climate data, available at http://www.worldclim.org/ (accessed 17/06/2016).

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CHAPTER 4:
MAINTAINING ECOSYSTEM PROPERTIES AFTER LOSS OF ASH IN GREAT BRITAIN

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Author Contributions

LH collected data, performed modelling and analysis work 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. The manuscript has been read and approved by all authors.

Article Status

This article is in review at the journal Forestry.

Supplementary materials

Supplementary methods, a supplementary table and our recommendations for woodland managers (Supplementary Box 1) for this chapter can be found in Appendix III. A spreadsheet of trait values and sources, the overall vulnerability map in larger scale, a spreadsheet of trait importance orders and AHP weights and the *yaml* file used to perform the AHP can be found on the accompanying CD.

Abstract

Pests and diseases 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.

We present a method to locate the areas most ecologically vulnerable to loss of a major tree species (common ash), and identify the resultant loss of distinctive ecosystem properties. Our results indicate that in some areas of Britain, provision of ash-associated ecosystem properties could be reduced by over 50% if all ash is lost. Some 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. We produce guidance for management to reduce ecosystem vulnerability to ash loss, including appropriate alternative species to encourage through management.

Introduction

Trees are critical components of the majority of natural terrestrial ecosystems and provide supporting services essential for human survival, yet their long lifespans and slow rates of reproduction and migration make them uniquely vulnerable to modern pressures (Rackham 2008). In recent years, tree pests and diseases have emerged as one of the great challenges currently threatening ecosystems worldwide (Boyd *et al.* 2013; Ennos 2014;

Wingfield *et al.* 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; Pautasso *et al.* 2010; Cavers 2014).

The current threats to common ash (*Fraxinus excelsior* L.) in Great Britain are examples of such artificial processes. *Hymenoscyphus fraxineus* Baral *et al.*, or 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 (its introduction into Eastern Europe is estimated as the early 1990s), 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 (Halmschlager & Kirisits 2008; Kjær *et al.* 2011; Pautasso *et al.* 2013). A future severe threat comes from the recent introduction into Europe of *Agrilus planipennis* Fairmaire, the emerald ash borer (Straw *et al.* 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), and is likely to spread throughout Europe, including Britain, as there are no real barriers to its movement (Baranchikov *et al.* 2008; Straw *et al.* 2013; Thomas 2016).

In combination, these two threats are likely to lead to a rapid decline in population sizes of susceptible ash species across Europe (common ash, *Fraxinus excelsior*; narrow-leaved ash, *F. angustifolia* Vahl; and possibly flowering ash, *F. ornus* L. (Kirisits & Schwanda

2015)), 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 most of Europe, ash species are relatively uncommon forest trees which tend not to make up a major component of ecosystems (Beck *et al.* 2016), although their abundance has been increasing in many areas (Hofmeister *et al.* 2004). In Britain, 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 *et al.* 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 *et al.* 2014a). 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). Trade-offs may also exist between tolerance to ash dieback and emerald ash borer (Sollars *et al.* 2017). 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, and so it would be advantageous 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 *et al.* 2014b). 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 ecological 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 tree species – defined as experiencing the greatest degree of change in average trait values – and provides guidance for how to minimise the ecological change arising from ash loss that can be integrated with current practice. Changes in trait values in ecosystems are not the only important factors in designing management responses to disease outbreaks, 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. In this paper, we demonstrate the use of the method for the case of ash in Great Britain.

Methods

Our analysis is comprised of five steps which are summarised here and in figure 11. Further details are included 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 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.

The values of 36 ecological traits (see table 5) 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 *et al.* 2014c), 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.

Table 5. Ecological 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 Material.

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
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 (leaf area per leaf dry mass)
First flowering time	Leaf shape	Wood density

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 11. 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.

Step 2. Calculate average trait values across Great Britain, and how this may change with loss of ash: a) For different localities (every 1 km^2); 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' 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 all other tree species present increasing in proportion to their original abundance to fill the space left by the ash; 3) and 4) As the two scenarios above, 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). These scenarios (3 and 4) represent the change that may occur in woodland ecosystems only, with and without compensatory growth of other trees. We also carried out this analysis (with and without compensatory growth) for different woodland types, using species abundances from the National Vegetation Classification (NVC) floristic tables (Rodwell *et al.* 1991).

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, we included both litter decomposition rate and the type of appendages on a species' seeds in our analysis, but the 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 Material. 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. $a > b$, $b > c$, $c > a$). Our pairwise comparisons had

consistency indices ≤ 0.1, meaning that our comparisons are acceptably consistent (see Supplementary Material).

Our final weights were produced by averaging the weights produced for each ecosystem service. 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 11 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 which are most similar to ash for those traits; these species were recommended as replacement species; three or four species were required in each case to ensure that all five traits were provided for (see Box 1 in Supplementary Material). For the NVC communities, replacement species were only chosen from the subset of species that already occur in each NVC community. This avoided the recommendation of species that would drastically alter these communities or be unsuitable for the abiotic conditions present.

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. 12a). 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

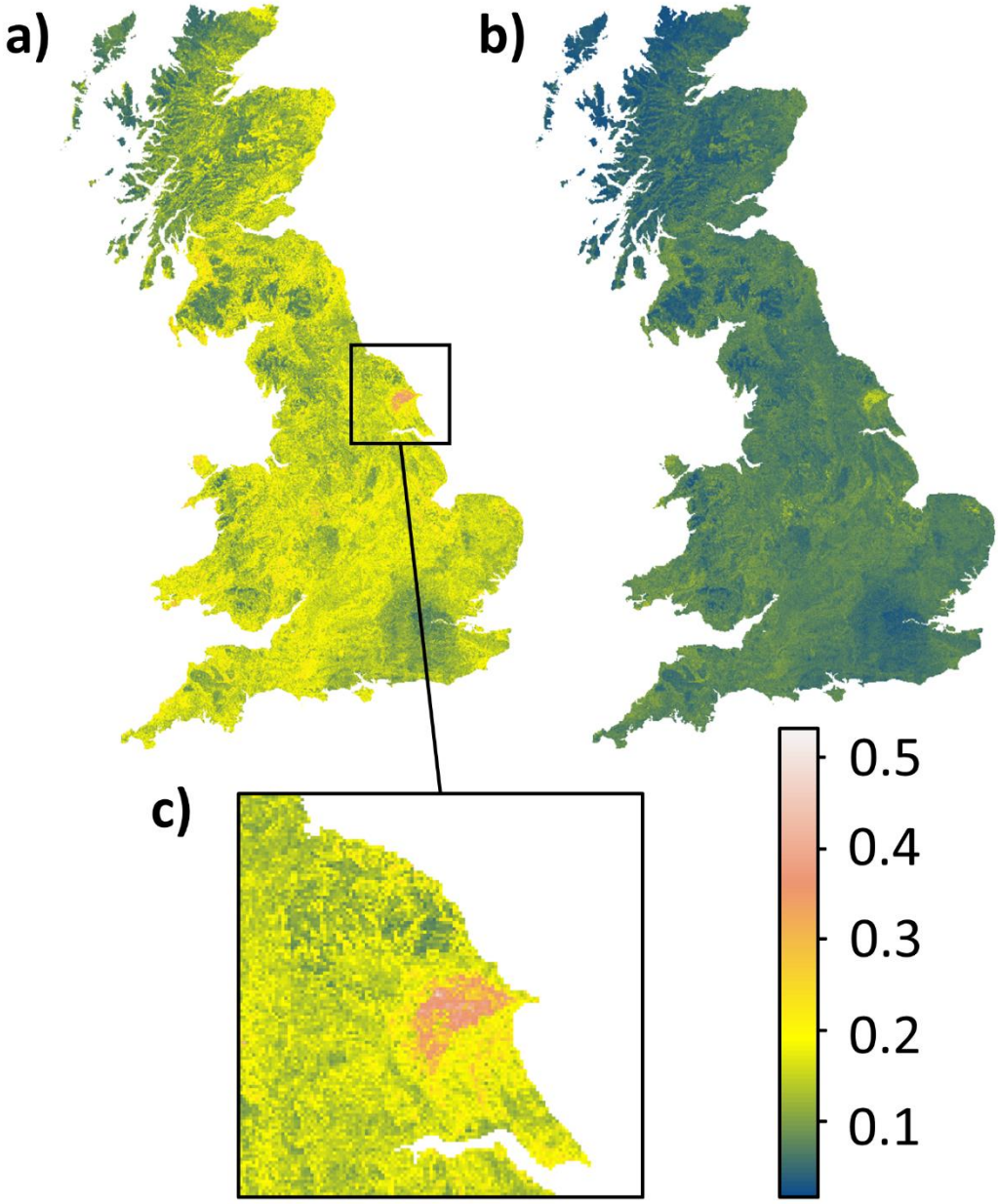

Figure 12. Vulnerability scores (reduction in average similarity to ash-like traits after 100% ash death) for two different scenarios: **a)** loss of all ash, no compensatory growth of other trees; **b)** loss of all ash, with compensatory growth of other tree species to completely fill the gaps left 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.

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 12c), with other smaller patches of high vulnerability occurring throughout much of Britain, in both lowland and upland areas (see Box 1). 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 fewer available species that may have similar traits to reduce ecosystem vulnerability.

In the second scenario (maximum compensation, Figure 12b), 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

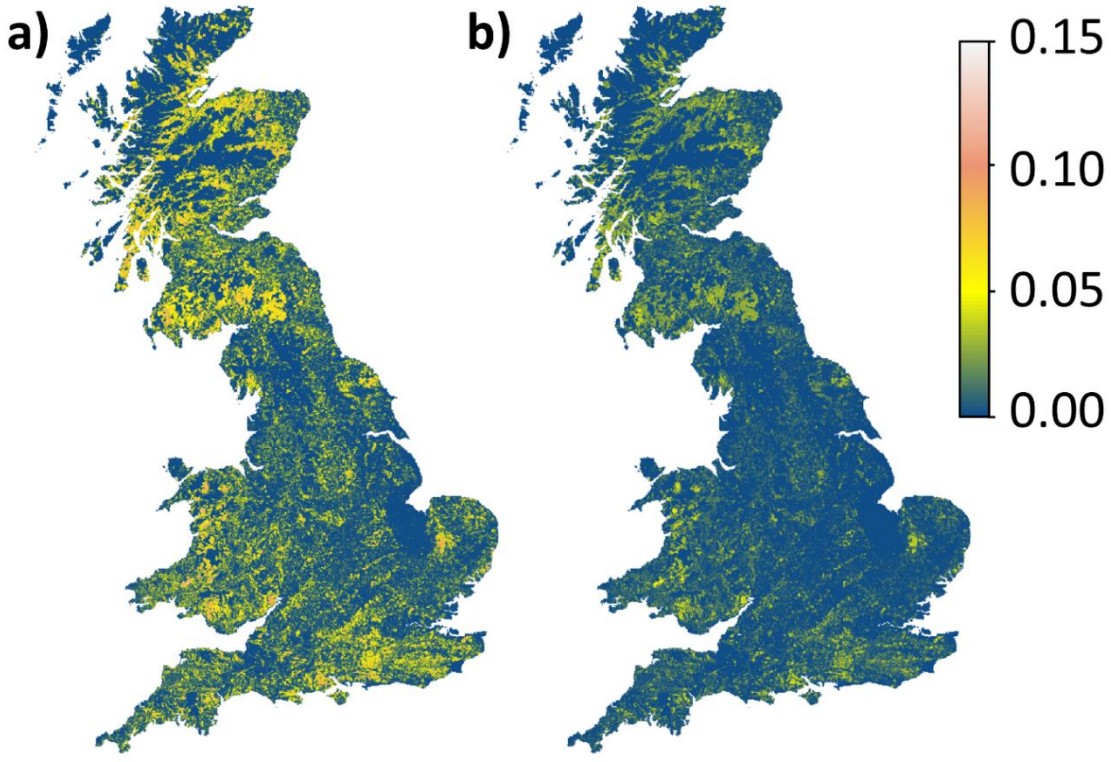

Figure 13. Vulnerability scores, for woodland trees only, for two scenarios: **a)** loss of all ash, no compensatory growth of other trees; **b)** loss of all ash, compensatory growth of other tree species to completely fill the gaps left by ash. Note that the colour scale is different from that used in Figure 12.

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 13a) 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 12). The maximum vulnerability for this scenario was 0.15 in parts of Scotland and Wales, and in England the south, north east and East Anglia. Compensatory growth also reduced vulnerability for woodlands-only (Figure 13b), 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 6). W10e contains only *Acer pseudoplatanus* and *Corylus avellana* as frequent tree species, in addition to ash. Neither of these species have highly similar traits to ash, which suggests that the loss of ash in W10e woodlands may produce more significant ecological changes than in other woodland types.

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

planted or encouraged to reduce the vulnerability of the area. The species recommended in each scenario are shown in Box 1 (Supplementary Material).

Table 6. 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 planting and regeneration for each community are shown in Box 1 (Supplementary Material).

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

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 14).

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 12), 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 7).

Table 7. 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

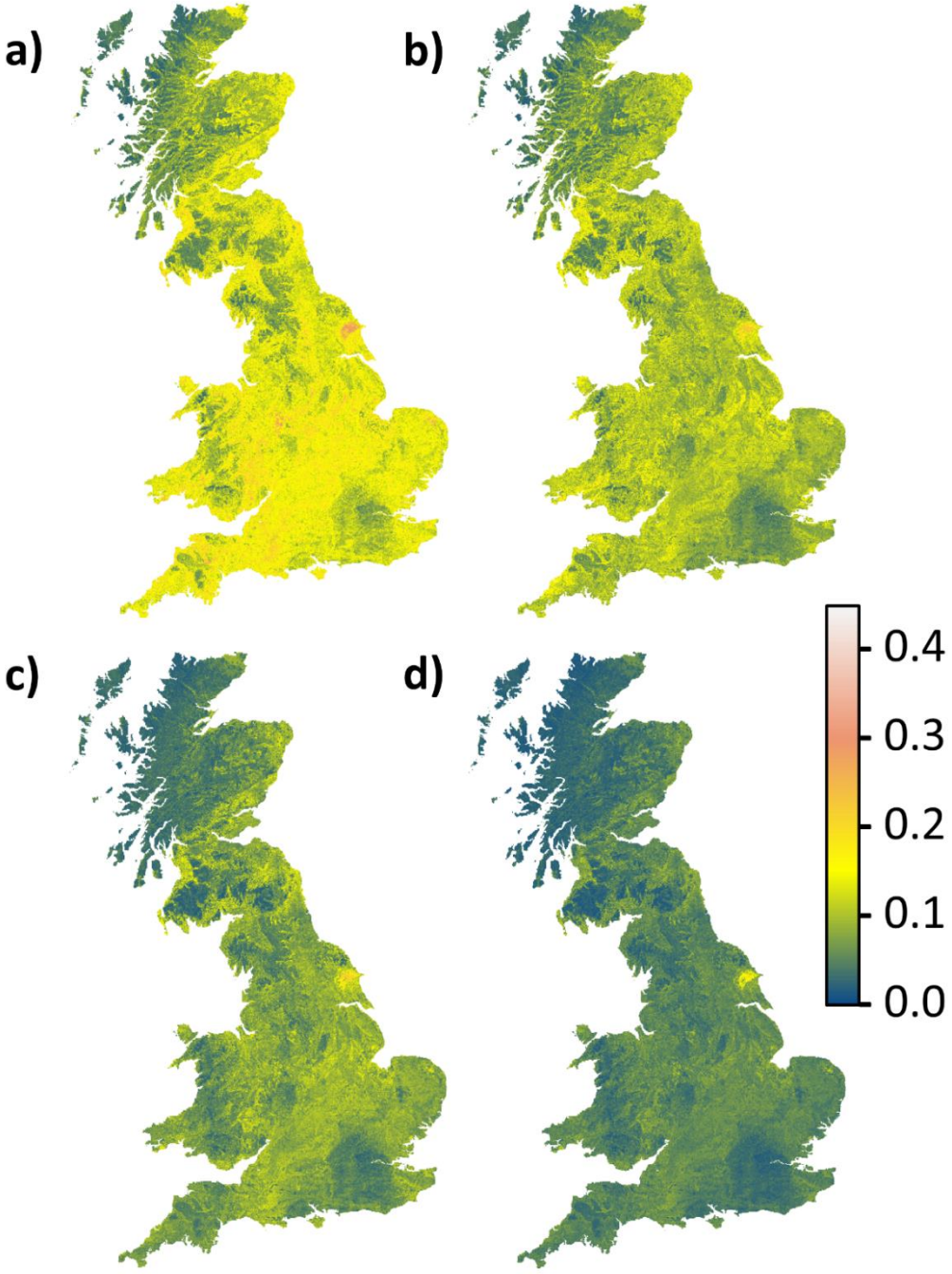

Figure 14. Vulnerability scores for four traits: **a)** litter decomposition rate; **b)** Ellenberg's light indicator; **c)** Ellenberg's moisture indicator, and; **d)** nitrogen fixing ability. The scores indicate the predicted change without compensatory growth in the average trait values from the 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 AHP weighting; 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.

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. These characteristics suggest that these communities may experience high degrees of ecological change.

However, our results also suggest that the degree of change could be reduced by certain actions. For instance, our analyses indicate that compensatory growth of other tree species could play a particularly important role, and has the potential to reduce, by around half, the reduction in overall trait similarity to ash, after ash death. We present three major management recommendations that have arisen from our results, with the aim of stabilising ecological properties after the loss of ash.

Recommendation 1: Plant or encourage regeneration of recommended mixtures of tree species to replace ash, especially in areas with high ash density.

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 mixtures of species to minimise the effects of ash loss on the ecological characteristics of the site. Trees have their highest ecological value when they are mature, and since replacement trees will take a considerable time to grow to maturity it is desirable to start planting replacement trees as soon as possible. This will be particularly important in areas with high vulnerability, such as the Yorkshire Wolds and vulnerable woodland types.

Box 1 (Supplementary Material) shows our recommendations for the tree species to plant for each highly-vulnerable area and woodland type, to provide the specific values of ecological traits that could otherwise be lost after ash loss. Recommended species are listed in order of priority: the first species compensates for the most vulnerable trait in the area, and so on. 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 most important ash-like traits. The species recommended for each NVC woodland community should be generally suitable for planting in the areas where that community occurs, as they were selected from the species that already occur

in each community. However, normal silvicultural considerations will remain important, especially the ecological suitability of a species for any particular site, which might be checked using the Ecological Site Classification (Pyatt *et al.* 2001; Forest Research 2017a) which provides advice on tree species that may grow well in particular geographical locations.

The trees we recommend are predominantly native species; 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 *et al.* 2014a) 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, came through as appropriate replacements for ash in any of the vulnerable areas or woodland types.

Epidemic pests and diseases are a serious concern for many British tree species, not only ash. For instance, 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* as a suitable replacement species, despite many of its trait values being similar to ash and therefore theoretically useful for compensation. 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. 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 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 2: Ash trees outside of woodlands should be replaced with a range of suitable tree species.

Ash death outside of woodlands could easily be dismissed by land managers as unimportant, and action not taken. However, this could lead to significant environmental consequences and loss of wider landscape connectivity. Ash trees 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. Maintaining this connectivity after loss of many ash trees should be a key aim of management.

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 12 and 13). This suggests that ash trees in Britain may be particularly important for their roles outside woodlands, supporting the conclusions of others (Maskell *et al.* 2013; Mitchell *et al.* 2014b). Our analyses also suggest that they 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.

Recommendation 3: Relieve concurrent pressures on woodlands.

It is important to recognise that high levels of compensatory growth by other tree species are not likely to occur naturally in many British woodlands. Regeneration of many woody species has been in decline in British woodlands for several decades (Côté *et al.* 2004; Kirby *et al.* 2005; Hopkins & Kirby 2007; Gill & Morgan 2010) and a well-documented range of pressures on woodland, including overgrazing by deer, damage by grey squirrels, atmospheric pollution and invasive species, may in fact make rapid compensation unlikely in the majority of woodlands (Rackham 2008). Many of these pressures can be relieved, to a certain degree, by good silvicultural practice, such as culling herbivores and removing invasive species. In areas with severe pressures on woodlands, this may be one of the most important ways to respond to ash dieback. Silvicultural management can improve the health of other tree species and the resilience of woodlands in general to respond to major disturbances now and in the future (Broome *et al.* 2014). Our predicted vulnerability was halved by allowing maximum levels of regeneration so that other tree species were able to fill the gaps left by ash trees. The UK Forestry Standard (Forestry Commission 2011) has further information on sustainable forestry management in the UK.

Comparison with similar papers

Previous authors (Broome *et al.* 2014; Mitchell *et al.* 2016) have tackled the question of the most ecologically-appropriate species for replacement of ash. Mitchell *et al.* 2016 firstly used Principal Components Analysis (PCA) to summarise the differences between species in three traits/ecosystem functions (decomposition rate, leaf litter characteristics and soil chemistry). They found that the most ecologically similar trees to ash were *A. pseudoplatanus*, *A. campestre* and *A. glutinosa*. However, they found that different species – namely *Q. petraea/robur*, *F. sylvatica* and *A. pseudoplatanus* – were most similar based on the number of ash-associated species supported by each tree. Mitchell *et al.* therefore concluded that there was no relationship between the ecosystem functions of the tree species and the biodiversity that they support. Lastly, they made a combined assessment of functioning and species use, to account for this apparent trade off, and recommended *A. pseudoplatanus*, *A. campestre* and *A. glutinosa* as the most suitable alternative species.

In this work, we have extended this approach somewhat further, with the introduction of geographically explicit predictions of trait change. As well as producing maps of the most vulnerable areas and guidance presenting locally-appropriate alternative trees, this approach allows us to include potential complementarity in the trait profiles of alternative species, to identify optimal species mixtures. Purely proposing the species with the highest overall trait similarity to ash (for instance, through using principle components analysis to identify the most similar species) could have inadvertently caused us to recommend species with greatly overlapping trait profiles, while leaving other key traits uncompensated for. However, by keeping all traits separate and then recommending mixtures of several species that each provide different key traits, we

ensured that our recommended combinations of species would provide the highest possible range of traits similar to ash. This also allowed us to analyse both the average degree of change of all traits together, and trait-by-trait analysis of change, across the geographic range. The use of the Analytic Hierarchy Process to weight traits according to their importance for ecosystem services was a further innovation in our method.

In our approach, we have not included species use as a criterion for selection of alternative trees. This is because the realised species use of any alternative tree will depend on the distributions of each ash-associated species, and very limited distribution data is available for the vast majority of the 955 species associated with ash trees. Broome *et al*. 2014 looked at utilisation by ash-associated species to recommend management approaches, and found that lack of distribution data for ash-associated species was a major difficulty for this approach. Mitchell *et al.* 2014 found no link between ecological traits and species use, but we might expect our analysis to provide a better proxy for species use as we used a greater range of traits in our analysis. Other studies have shown that it is possible to use plant traits to successfully predict emergent ecosystem properties such as ecosystem functioning and species use, especially when many traits are used (Wardle *et al.* 1998; Díaz *et al.* 2001; de Bello *et al.* 2010).

Despite the methodological differences, it is encouraging that there is some agreement between our results and those of Mitchell *et al.* (2016); in our results, we frequently recommend both species that these authors found to be most ecologically similar, and those with the highest number of ash-associated species. This finding is a suggestion that our analysis of traits may act sufficiently as a proxy for species use. However,

investigating whether this potential link proves to be true in this case will be an important next step to test the breadth of applications for our approach.

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 and Ellenberg's nutrient indicator are both 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. The finding that flood protection services may be altered in the Yorkshire Wolds may be of particular concern, as 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 lead to a worsening of this problem.

However, we advise care in interpreting the results for impact on ecosystem services (Table 7). 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 trees 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 will be decreased, at least in 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.

Limitations and next steps

As with all trait-based ecological research, this work is limited by issues around the use of plant traits that plague functional ecology. These are not new problems and have been discussed by many other authors, but several of the main caveats of trait-based functional ecology remain major obstacles (Weiher *et al.* 1999; Garnier & Navas 2012; Pérez-Harguindeguy *et al.* 2013). Researchers still tend to measure convenient traits, which are not necessarily the most important; for example, root traits remain neglected. Knowledge of how plant traits affect ecosystem properties and services remains poor. And, more fundamentally still, trait levels tend to be given as a single value, when often a range or standard deviation of possible values would be more valuable, reflecting phenotypic variation due to genetics, the environment and their interaction. Our approach makes use of functional traits to the best of our current ability, and we believe that we are able to

draw useful conclusions from our research, even with an incomplete picture of the full range of traits.

The use of the Analytic Hierarchy Process (AHP) for trait analysis in this paper also makes a positive contribution towards improving the use of traits, by allowing us to weight each trait according to its importance for emergent ecosystem properties, such as ecosystem functions or services. The best way to weight traits has so far been a stubborn question in functional ecology, and we believe that using AHP to produce meaningful weights is a useful step forward. However, we echo the calls of others to encourage research into the major caveats of trait-based research, to further increase the utility of such research and contribute to our understanding of ecosystems.

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 (Supplementary Material), which is designed to be used directly as a guide for land managers and to accompany forestry best practice.

The approach we have used complements work done by others on the theoretical outcomes of ash loss. Since it uses data with coverage of the whole of Britain, it has the advantage of producing maps of vulnerability over a large scale that allow easy

comparison between regions and scenarios (the map of overall vulnerability to ash loss with no compensatory growth is available at larger scale in the Supplementary Material). Our approach 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. We believe that extending this method to more scenarios could provide a major step forward in our understanding of the potential consequences of species loss.

Data Sources

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: raster files are available from the Oxford University Research Archive, "Predicted abundance maps for British Trees" https://ora.ox.ac.uk/objects/uuid:c381f783-7eaa-4be6-9788-c197c74b2953 (Last accessed 03 March 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).

Supplementary material

The following supplementary material is available on the accompanying CD:

- Larger-size version of the map of overall vulnerability to ash loss with no compensatory growth.
- Detailed supplementary methods
- A complete database of the traits used, including trait values and details of the original sources used for each species and all traits.
- The agreed orders of trait importance for AHP, the AHP output table, and the yaml file containing complete pairwise comparisons (required for "ahp" package).

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CHAPTER 5:
THE FINANCIAL IMPACT OF ASH DIEBACK IN GREAT BRITAIN

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Author Contributions

LH collected data, performed modelling and analysis work and wrote the first draft of the manuscript. GJ provided economic expertise and help with methods. All authors contributed to the design of the study, identification and estimation of cost factors, and manuscript revisions.

Article Status

This article is in preparation to submit.

Supplementary materials

The workbook used to calculate costs of ash dieback can be found on the accompanying CD.

Abstract

Invasive pests and diseases of trees are causing well-documented forest die-offs and associated biodiversity loss around the globe; however, they are also causing significant economic and social challenges. We estimate the financial cost to Great Britain of the invasive tree disease ash dieback to be approximately £9.2 billion, and argue that the scale of this cost has not previously been fully appreciated.

The single greatest contributor to the overall cost is safety interventions for roadside ash trees. Costs from this to individual local authorities may be very high, up to £357 million for Devon County Council. Health implications for people may also be significant, but it is not yet possible to quantify this effect. The cost of lost ecosystem services was found to be less than a third of the total cost, suggesting that economic assessments that focus exclusively on loss of ecosystem services may be dramatically underestimating true costs of biodiversity loss. A key output of this analysis is the accompanying workbook, which provides a framework for estimating costs arising from tree diseases, and allows users to vary uncertain factors to explore their effects on costs.

Overall, the socioeconomic impact of this single tree disease is extremely high, and will undoubtedly be worsened by interactions with other tree pests and diseases. We argue that policy interventions to reduce the likelihood of future invasions, such as more stringent biosecurity measures, restrictions of international trade in live trees, or the introduction of tariffs to truly represent the cost of introduced diseases, would be highly cost-effective and are urgently required.

Introduction

Invasive forest pests and diseases are causing high tree mortality in forest ecosystems around the globe (Wingfield *et al.* 2010; Boyd *et al.* 2013; Roy *et al.* 2014; Freer-Smith & Webber 2015). Accidentally introduced by people, through movement of ornamental plants, soil and timber, or driven by climate change, forest pests and diseases have become some of the most severe threats to forests (Brasier 2008; Bentz *et al.* 2010; Potter & Urquhart 2017). In Britain, one of the country's most common tree species, *Fraxinus excelsior* L. (common ash), is facing major decline due to the introduction of the fungus *Hymenoscyphus fraxineus* (Baral *et al.*, 2014), or ash dieback, from East Asia (Pautasso *et al.* 2013; Woodward & Boa 2013; Thomas 2016). There are thought to be between 155 and 185 million ash trees in Britain (Forestry Commission 2013; Maskell *et al.* 2013; The Tree Council 2015), of which 90% or more may eventually be killed by ash dieback (FRAXBACK 2012; Hinsley & Pocock 2014; Queloz *et al.* 2017). Any that are not killed by the fungus may soon face another threat; *Agrilus planipennis* (Fairmaire 1888), the emerald ash borer. This bark beetle, also native to East Asia, has devastated ash tree populations in North America and is currently present in Southern European Russia (EPPO 2017), having been found for the first time in Moscow in 2007 (Baranchikov *et al.* 2008; Straw *et al.* 2013). It is likely to reach Britain in the next few decades, where it is expected to attack trees that have survived ash dieback (Straw *et al.* 2013; Thomas 2016).

The ecological damage caused by events such as these is undoubtedly great, but major forest die-offs usually also have significant economic impacts, and this may be an under-

appreciated aspect of the problem (Kostichka & Cannon 1984; Kovacs *et al.* 2010; McKenney *et al.* 2012). Increased biosecurity measures, which could help reduce the numbers of invasive pests and diseases accidentally imported, are sometimes claimed to place too great a financial or administrative burden on industry to be put in place. However, the inevitable costs of allowing invasive diseases to take hold may be measured in billions of pounds and could represent a far larger cost to society than the cost of increased biosecurity. For example, the cost of the emerald ash borer to the US economy has been estimated to exceed $10 billion over the period 2009-2019 (Kovacs *et al.* 2010), just for treatment, removal and replanting of infested trees.

We present an estimate of the full cost to Great Britain of the ash dieback outbreak. To our knowledge, this is the first time it has been attempted to estimate the full cost of a tree disease to an entire country. There are many individual factors that contribute to the total cost. For ash trees, which are one of Britain's most common broadleaved trees, the costs from some of these factors are significant. Ash trees seed freely and have been preferentially planted alongside roads as a fast-growing and cosmopolitan tree that is resistant to problems such as squirrel damage and pollution (Maskell *et al.* 2013; Kirby *et al.* 2014; The Tree Council 2015). As a result, huge numbers of ash trees line Britain's roads, and now present a vast challenge to local authorities to make them safe (Worrell 2013; The Tree Council 2015). Other infrastructure, such as railway lines, will also be affected; for some major railway lines, the cost of felling or maintaining diseased ash trees may be as high as £1 million per mile (Neil Strong, *pers. comm.*). Other major costs will occur passively (rather than due to the cost of active management), such as the loss of ecosystem services that are provided by ash (Defra 2013b). Ash provides a wide range of

ecosystem services in Britain and, as a common tree, its loss is likely to lead to a marked reduction in many of these services. Some of these services, such as improvement of air and water quality, and carbon storage, are highly valuable to society (Rouquette & Holt in prep.; Defra 2013a).

We have included as many factors as possible into our analysis to produce a realistic estimate of the total cost of ash dieback, although some factors are inevitably impossible to estimate or can only be estimated with low confidence. Nonetheless, even when only accounting for a subset of factors, our estimates show that the ash dieback epidemic is likely to have significant cost implications for a range of stakeholders. We also show that some remedial actions, such as replanting roadside ash trees to help maintain levels of ecosystem services, could help to cap the overall cost. We therefore recommend specific policy areas where incentives, such as grants to replant lost trees, would be cost effective and beneficial.

The total cost to the country will inevitably, however, be high, as there are no methods currently available to control the ash dieback epidemic meaningfully since it became established. Substantial investment in biosecurity measures, to reduce the rate of arrival of future significant pests and diseases, may be cost effective in the long term in preventing such inevitable costs of pest and disease invasions.

Methods

Overview

Through discussion between authors, we identified as many factors as possible that have contributed or will contribute to the total cost of ash dieback. We then consulted 35 forestry, arboriculture and conservation professionals and experts (see Acknowledgements) to develop a comprehensive list of cost factors (table 8).

The proportion of ash trees in Britain that will be killed by ash dieback is still uncertain. Ash dieback kills young ash trees rapidly, but older ash trees can decline for decades before finally succumbing, making it difficult to predict final mortality rates even for countries where ash dieback has been present since the 1990s (Pautasso *et al.* 2013; Vasaitis & Enderle 2017). To produce our estimate, we used a final mortality rate for ash trees of 90%, which is supported by the most recent evidence from earlier infected countries (Vasaitis & Enderle 2017). We also estimated higher and lower bounds for each cost, based on mortality rates of 100% and 50%. This encompasses a slightly larger range than the reported final mortality rates from mainland European countries (Enderle *et al.* 2017; Kjær *et al.* 2017; Rozsypálek *et al.* 2017) and so provides suitable best- and worst-case scenarios.

We identified the stakeholders who might incur a cost for each factor, and estimated the costs of each using a predicted rate of ash loss of 90% and a bounding range of possible rates from 50% to 100% (Vasaitis & Enderle 2017). All costs were estimated conservatively, where there were choices to be made that affected cost. A next step for our estimate will be to conduct a sensitivity analysis to vary uncertain cost factors and analyse

their effects on the overall cost. The estimation of each factor is described in turn below; more details of the cost calculations can be found in the accompanying workbook, which

Table 8: Complete list of cost factors considered in our analysis. For each factor, we defined the cost type and the sectors who might incur the primary cost.

Cost factor	Sectors primarily affected	Cost type
Safety felling of roadside ash	Public, private (business/personal)	Damage
Safety felling of lineside ash	Public	Damage
Safety felling of urban ash	Public, private (business/personal)	Damage
Safety felling of ash on rights of way	Private (business/personal)	Damage
Replanting in woods over 0.5 ha	Public, private (business/personal)	Replacement
Replanting in small woods (< 0.5 ha)	Private (business/personal)	Replacement
Replanting hedgerows	Private (business/personal)	Replacement
Replanting roadside ash	Public	Replacement
Replanting urban ash	Public	Replacement
Replanting individual ash trees	Private (business/personal)	Replacement
Loss of profits from commercial forestry	Private (business)	Lost value
Loss of profits from nurseries	Private (business)	Lost value
Loss of profits from international trade in young ash	Private (business)	Lost value
Publicly-funded research projects	Public	Damage
Publicly-funded surveys	Public	Damage
Loss of woodland ecosystem services	Public	Lost value
Loss of non-woodland ecosystem services	Public	Lost value
Grant aid for removing ash trees under statutory plant health notices and restocking	Public	Damage
Public liability insurance increases for councils	Public	Damage
Loss of profits from downstream ash products	Private (business)	Lost value
Cost of hiring additional treeworkers and administrative staff	Public	Damage
Reductions in property prices	Private (personal)	Lost value
Reductions in revenue from countryside visits and tourism	Private (business)	Damage

also allows a user to explore the effects of different ash mortality rates and components of the cost on overall costs (see supplementary materials).

Total cost

We summed each of the constituent cost factors to calculate the total cost of ash dieback to Britain. We also calculated the total cost to each sector (public, business and individual). Finally, we split the costs according to the type of cost of each factor (table 8): damage cost (a cost incurred by repercussions from a direct environmental impact, such as need to fell dead trees); replacement cost (the amount required to replace an asset, such as replanting trees); or lost value (reduction in the value of an asset, such as reduced ecosystem service provision).

Factors for which cost has been estimated

Safety felling of roadside ash. *Confidence: Medium.* Using freedom of information (FOI) requests to all 207 local authorities in Britain (English unitary authorities, county councils, metropolitan boroughs, London boroughs, Scottish unitary authorities, Welsh principal areas and the Isles of Scilly) we collected information on the numbers of ash trees in each local authority (LA) area that could pose a threat to roads should they fail. Most LAs had no information on this, but 24 had data on at least publicly-owned roadside ash trees and 11 had estimates of the entire stock of roadside ash trees within their boundary.

We used the data gathered from the FOI requests to estimate the numbers of roadside ash trees in all LAs. Numbers of roadside ash trees in each LA were estimated using a linear model of number of roadside ash trees against amount of ash in linear features in each

LA. Amount of ash in linear features in each LA was derived from a dataset of the estimated amount of ash per kilometre of linear features across Britain, at 1 km^2 scale (Maskell *et al.* 2013), developed from results of the 2008 Countryside Survey (Carey *et al.* 2008). Models were also run with terms for the length of different types of roads per LA (figures for 2017 from the Department of Transport, see Data Sources), but the model fit was not improved so road lengths were dropped. The number of ash trees and amount of ash in linear features were both logged (after adding one to every value to eliminate zeros) to improve linearity and produce homoscedastic residuals. We knew the true intercept to be zero, as a small number of local authorities have no ash trees, so we set the intercept to zero which did not distort the relationship across non-zero values. The final model used was:

log(number of roadside ash trees + 1) ~ 0 + log(amount of ash in linear features + 1)

where 0 represents an intercept constrained to be zero.

The cost of felling a single "average" roadside ash tree was estimated at £800, following advice from a number of foresters from Kent, Norfolk and Oxford County Councils, and Nicholson's Nursery in Oxfordshire (see Acknowledgements for details). This accounts approximately for the size distribution of roadside ash trees (noting that some trees will require no or very little work), the need for road closures and mobile elevated work platforms in some cases, and additional site costs for difficult access, such as working outside standard working hours. Inevitably, this figure is a simplification of the range of possible costs; however, it was agreed by a range of professionals (above) and no data is currently available to refine this estimate.

We calculated the annual and total cost to each local authority for safety felling of roadside ash. We assumed that ash trees will become unsafe and die gradually and asynchronously over the next decade at a rate of 10% of the original number per year, leading to repeated costs of returning to the same stretches of road. This assumption is supported by the experiences of foresters in mainland Europe and the observed mortality pattern of ash dieback to date (Vasaitis & Enderle 2017). We used this to estimate net present value using the recommended discount rate of 3.5% (HM Treasury 2003). We also assumed that councils will follow current Forestry Commission advice of only felling trees when they become a threat to health and safety. Data from our FOI requests suggested (with low confidence) that 36% of roadside trees may be in public ownership, so we also split the total cost between sectors using these proportions.

Safety felling of lineside ash. *Confidence: High*. We used estimates made in 2011 by Network Rail of the numbers of lineside ash trees across the entire rail network in Britain (The Tree Council 2015, Jon Stokes, *pers. comm*.). There are thought to be 500,000 ash trees above 15 cm diameter alongside railway tracks. We assumed that the cost of handling an average lineside ash tree would be higher than for an average roadside ash, at £1,000 (Jon Stokes, *pers. comm*.).

Safety felling of urban ash. *Confidence: Medium*. The report "Trees in Towns II" (Britt & Johnston 2008) estimated that ash comprises on average 4.1% of trees in British towns, or 3.6 million ash trees. Our FOI requests suggested that 64% of these are likely to be privately owned (a similar figure was reached in the 1993 report "Action for London's trees" (The Tree Council 2015, appendix 2) which estimated that 69% were in private ownership).

To avoid double-counting, we removed from our estimate the number of urban ash trees that can also be considered as roadside trees. Our FOI requests suggested that 30% of urban trees are found alongside roads, so we removed this percentage from the estimate of total urban ash trees. The cost per "average" ash tree was again estimated at £800, following discussion with arboriculturists at Nicholson's Nursery in Oxfordshire, and Oxford and Norfolk County Councils, although this may be an underestimate if many trees are situated in areas of high risk, such as adjacent to schools or hospitals.

Safety felling of ash on rights of way. *Confidence: Low.* We used figures for approximate lengths of rights of way from Christie & Matthews 2003 (England), McCraw & Davison 2000 (Scotland) and Natural Resources Wales (Wales) (total: 237,079 km) (see Data Sources for details). We calculated the average number of ash trees outside woodlands per km^2 using the lower estimate of 27.2 million ash trees outside woodlands in Britain from The Tree Council 2015, and then used this to estimate the average number of ash trees per kilometre of footpath (below). This will be a conservative estimate, in the absence of better data, as it does not account for footpaths passing through woods or alongside hedges.

Through discussion with foresters, we estimated the cost of clearing and leaving *in situ* a single average-sized ash tree at £20 (Nigel Fisher, *pers. comm.*). This was based on a rate of roughly 3.5 trees per hour for a team of two chainsaw operators, each paid £200 per day, working 6 hours per day (to allow for the distance between trees).

To calculate the total cost, we made two assumptions. Firstly, we estimated that any ash trees within 25 m either side of a footpath could be of potential concern, as mature ash

trees commonly reach 25 m tall or higher. This allowed us to use the average density of ash trees in the countryside to estimate the total number of ash trees that might be found within 25 m of a right of way, along the entire length of countryside rights of way in Britain. Secondly, we assumed that only trees that actually fall onto a footpath are likely to be cleared, and estimated that this might be 10% of the trees that die. The total cost was therefore calculated as the cost of clearing 10% of the ash trees estimated to occur within 25 m either side of a right of way, multiplied by the ash mortality rate of 90%.

Replanting costs. With advice from foresters from Nicholson's Nursery in Oxfordshire, we estimated representative costs for replanting dead ash trees with alternative species in different situations, including breakdowns of the components of the cost. We used these to approximately estimate replanting costs in different situations, below. We assumed that the costs of saplings would be the same regardless of whether they were alternative species or, potentially in future, resistant ash cultivars (Jo Clarke, *pers. comm*.).

Replanting in woods over 0.5 ha. *Confidence: Low.* Ash represents approximately 5.4% of all trees in British woods (or 11.1% of broadleaves) (figures from the National Forest Inventory (NFI), Forestry Commission 2013), but not all of these are likely to be replanted; many will be left as gaps or to regenerate naturally, especially where ash is at a low density or in neglected woodlands. The report "Chalara in ash trees" (Defra 2013a) estimated that 20-30% of "ashy woodlands" are under active management, and that in total this represents 1-2% of total British woodland. We assumed, therefore, that up to 1.5% of British woodland may eventually be replanted in response to ash dieback.

We used the number and average size of British woodlands (both from the report "UK Indicators of Sustainable Forestry" (Forestry Commission 2002)) to estimate approximately the area of ash that is likely to be replanted, and the number of felling licences that might be required. We then used a standard stocking density of 2500 per hectare (from the UK Forestry Standard, Forestry Commission 2011) to estimate the cost of replanting this area. We also used data on woodland area-by-ownership classes from the National Inventory of Woodland and Trees (Forestry Commission 2003) to split the cost between sectors.

We accounted for revenue from extracted ash biomass as part of the total cost, following the method used in Worrell (2013). There are currently 22 million tonnes of ash stock in Britain (Forestry Commission 2013), of which 73.9% is over 25 years old (i.e. large enough to be harvested and sold). We assumed ash would be sold for firewood, at a price of £35 per m^3 (Worrell 2013, Colin finlay, *pers. comm.*) (a stable price compared with the current as there is unlikely to be a large enough spike in production to severely flood the market), and that 60% of felled ash might be recovered as some is likely to be badly affected by disease and therefore not marketable.

Replanting in small woods (< 0.5 ha). *Confidence: Low.* We assumed the same proportion of small woods (20%) are under active management. However, labour costs will be somewhat higher in smaller woodlands due to small and awkwardly shaped areas. The Tree Council (2015) report estimates there to be 25.5 million ash trees in small woods, covering 38,510 ha. We estimated the cost of replanting 20% of this area, using standard stocking densities. We also accounted for revenue from extracted ash biomass in the same way as for larger woods.

Replanting hedgerows. *Confidence: Low.* The Tree Council (2015) report estimates there to be 19,700,000 ash trees in ash-dominated hedgerows. Hedgerow trees provide a wide range of ecosystem services and maintenance costs are low (Rouquette & Holt in prep.); we therefore estimated the cost of replanting all hedgerow ash trees, using the standard stocking density. We assumed no revenue from ash biomass, as most hedgerow replanting will be on a very small scale and, as such, any sales of biomass would be also.

Replanting roadside ash. *Confidence: Low.* The cost of replanting roadside ash will vary greatly depending on whether a road is rural or urban. For this reason, we subtracted the number of roadside ash trees that are in urban areas from the total number estimated by our modelling of roadside ash numbers (and instead included these under replanting urban ash).

Roadside trees are highly cost effective in terms of their ecosystem service provision (Rouquette & Holt in prep.), so we have assumed that all roadside ash will be replanted. However, as road closures are expensive, we have assumed that most replanting will happen at the same time as the removal of dead ash, to minimise costs, so we have not included the cost of road closures in this estimate. As with woods, we have accounted for revenue from 60% of felled ash being sold for biomass.

Replanting urban ash. *Confidence: High*. The London Assembly (2011) estimated that the average cost for planting a single urban tree was £110. Urban ash trees have very high ecosystem service value (Rouquette & Holt in prep.), so we assumed the majority will be replanted, and none sold for biomass as production is likely to be in small quantities over

a prolonged period. We used the full estimate of numbers of urban ash trees (3,600,000) from Trees in Towns II to estimate the cost (see replanting roadside ash).

Replanting individual ash trees. *Confidence: Low*. The Tree Council (2015) estimated there are 2,300,000 individual ash trees in the countryside in Britain. These have high ecosystem service value, so we have assumed that they will be replanted. We also assumed none will be sold for biomass (see replanting urban ash).

Loss of profits from commercial forestry. *Confidence: Low*. We calculated the total ash biomass managed for timber (pre-ash dieback) from the amount of ash biomass currently estimated to be in British woods over 0.5 ha (33,829,000 m^3 (Forestry Commission 2013)) and the percentage of this thought to be managed for profit (20-30% (Defra 2013a)). Following the method in Worrell (2013), we estimated the difference between the amount of biomass that is likely to be harvested due to ash dieback and the amount that could have been harvested, if all stock could be utilised. We calculated this as the difference between 60% of ash that is managed for timber being recovered (due to loss of value of diseased wood, as in the replanting sections above) and 100% being harvested.

Loss of profits from nurseries. *Confidence: Medium*. A report from the Horticultural Trades Association in 2012, which undertook a survey of ash growers in Britain, estimated the total value of lost ash stock in nurseries be £2-2.5 million (Defra 2013a). We used the lower estimate and assumed that all stock held in nurseries was destroyed in 2012, as was legally required. We assumed no further losses, as nurseries are likely to have switched immediately to producing other species.

Publicly-funded research projects. *Confidence: High*. We searched the research grant award archives of Defra, NERC and BBSRC using the keywords "ash dieback", "*Chalara*" and "*Hymenoscyphus*" to find the values of all government and research council-funded research programmes that have focussed on ash dieback since its arrival into Britain. Forestry Commission and Forest Research grants are included under Defra grants. We only included research projects that focussed exclusively on ash; for instance, we did not include research into novel phytopathogenic fungicides, although this research may have applications relating to ash dieback in future. For comparison with projects aimed at reducing harmful disease introductions, we also searched the same archives for all projects in the last decade relating to the keywords "tree disease", "tree health" and "biosecurity".

Publicly-funded surveys. *Confidence: Medium*. An initial rapid survey in 2012 to find the extent of ash dieback across Britain was headed by the Forestry Commission, with help from the MOD, Highways Agency, Network Rail, the National Trust and the Woodland Trust among others. This was largely completed in 10 days of intense effort. Complete records of people who took part across the full range of organisations are not available, due to the scale and short notice of the operation. However, at least 2,500 people from the Forestry Commission were employed in the survey. The average rate of pay for the Forestry Commission employees who took part was roughly £800 (Forestry Commission, *pers. comm*.). There have also been annual surveys since 2012 of 25% of the remaining uninfected squares, carried out by the Forestry Commission. These are estimated to have cost £155,000 to summer 2017 (Forestry Commission, *pers. comm*.).

Forestry is a devolved issue, and additional annual surveys have been carried out by Natural Resources Wales at a cost of £6,000-£10,000 p.a. (Andrew Wight, *pers. comm*.). Some local authorities have also carried out their own surveys of ash trees; the only such survey whose cost is currently known is a survey of roadside ash in Norfolk, which cost £60,000 in 2017 (Norfolk County Council, *pers. comm*.). Future surveys, both national and local, will undoubtedly be carried out, but it is not possible to estimate the number, scale or cost of these at present.

Loss of woodland ecosystem services. *Confidence: Low*. The total non-commercial (social and environmental) benefits of woodland and urban ash trees have been tentatively estimated at £150 million per annum (Willis *et al.* 2003; Defra 2013a). This figure includes landscape, recreation, biodiversity and carbon sequestration. Ash trees are likely to die gradually over a period of at least 10 years, and in many situations, other tree species will grow to replace them. However, replacement by other tree species will take time; larger trees provide a greater amount of ecosystem services, so we conservatively assume that there will be 10 years of lost ecosystem services value from ash trees. We estimated net present value using the recommended discount rate of 3.5%.

This is the most frequently used data on the ecosystem service value of urban and woodland ash trees, but as the authors of the original report state, it is likely to be a significant underestimate. This is due to factors that were not included, such as improvement to air quality, and other factors that cannot be estimated.

Loss of non-woodland ecosystem services. *Confidence: Low*. The ecosystem service benefits of a single non-woodland ash tree, accounting for maintenance costs, have been

estimated at £56 per annum for urban ash trees and £8.85 per annum for roadside ash trees (Rouquette & Holt in prep.). We used estimated numbers of urban ash trees and non-urban roadside ash trees from Britt & Johnston (2008) and our modelling results. We assumed 10 years of lost ecosystem service provision (as for loss of woodland ecosystem services) and estimated net present value using the recommended discount rate of 3.5%.

This estimate will again be an underestimate due to inestimable factors, and because we cannot currently include values for other types of non-woodland ash trees, such as hedgerow or parkland trees.

Factors for which total cost has not been estimated

Grant aid for removing ash trees under statutory plant health notices and restocking. Decisions on whether to provide grant aid for removal of infected recently-planted ash trees and subsequent restocking are devolved, and so differed between the constituent countries of Great Britain.

In England, no statutory plant health notices (SPHNs) were served for ash dieback but grant aid was made available for a short time for removal of infected recently-planted ash trees, and for a longer time for restocking. In Wales, no SPHNs were issued and, to date, grants have not been made available, although this may be considered for the future. In Scotland, there were initially a number of SPHNs and these were supported by government grants. However, records of the figures awarded in England and Scotland are only readily available grouped together with grants for removal of Rhododendron

and larch infected with *Phythophthora ramorum*, and we have not been able to split out the value of grants relating to ash dieback.

Additionally, government grants for removal and restocking are intended to cover up to half of the cost of the work required. We have estimated the full costs for removal and replanting a realistic proportion of ash trees across the whole of Great Britain, so it would be difficult to avoid double-counting if we included the value of grant aid in the overall cost. We have therefore not attempted to estimate the cost of grant aid awards relating to ash dieback.

Public liability insurance increases for councils. We contacted several providers of public liability insurance for councils (Zurich Municipal, Norris and Fisher, BHIB, AON) to ask about the impact that ash dieback might have on insurance premiums for councils. However, none of the providers responded to our requests. Ash dieback is likely to lead to increased risk of damage to people and property from falling trees, which may in turn drive higher insurance premiums. However, these increased premiums may simply reflect and counterbalance some of the costs already mentioned, so there is a risk of double-counting if insurance premium increases were included.

Loss of profits from international trade in young ash. The "Chalara Management Plan" (Defra 2013b) estimated the annual value of trading young ash trees to UK importers at up to £300,000. The import of ash to Britain was banned in late October 2012 (just prior to the main planting season), following the initial discovery of ash dieback in a nursery in Buckinghamshire in March 2012. However, in many cases nurseries will have been able to rapidly switch to alternative species to protect profits. In the absence of contradictory

evidence, we have therefore conservatively assumed that there were no lost profits from international trade in young ash. There may in fact have been a small cost associated with this, but it is likely to be less than £300,000, which is already a very small proportion of our total cost.

Other factors that were not estimated. Some of the possible costs that we identified will depend very strongly on unpredictable behaviours of people or are otherwise not currently possible to estimate. These factors are: loss of profits from downstream ash products; the cost of hiring additional treeworkers and administrative staff; reductions in property prices; reductions in revenue from countryside visits and tourism. We include these factors as "known unknowns", but make no attempt to estimate their values. However, these costs are likely to be small compared to others, so will make little difference to the estimation of the total cost.

Results

Total cost of ash dieback.

The total cost to Great Britain of all components of the ash dieback outbreak is estimated at £9.2 billion, using ash mortality of 90% (table 9). The higher and lower bounds of the total estimated cost are £10.1 billion for a mortality rate of 100%, and £5.4 billion for a mortality of 50% (figure 15).

Of the total estimated cost, £5.6 billion will be felt by the public sphere (table 9). Costs can also be split out as damage costs, replacement costs and lost values. Categorising the cost components in this way reveals an estimated £5 billion of damage costs, £1.1 billion of replacement costs and £3 billion of lost value (figure 15, and see accompanying workbook for details).

Table 9: The estimated total cost of ash dieback with a mortality rate of 90%, and the cost of each component split between the public and private sectors. See accompanying excel workbook for more details of individual costs, calculations and data sources.

Cost factor:	Cost to:					
Name	Public	Private			Total cost	Confidence rating
		Business	Personal	Both/either		
Safety felling (roadside)	£977,819,567			£1,738,345,896	£2,716,165,463	Medium
Safety felling (lineside)	£450,000,000				£450,000,000	High
Safety felling (urban)	£653,184,000			£1,161,216,000	£1,814,400,000	Medium
Safety felling (rights of way)				£239,333	£239,333	Low
Replanting (large woods)	£178,136,067	£69,934,900	£191,771,174		£439,842,141	Low
Replanting (small woods)				£145,230,021	£145,230,021	Low
Replanting (hedgerows)				£146,804,400	£146,804,400	Low
Replanting (roadside)	£13,305,127				£13,305,127	Low
Replanting (urban)	£356,400,000				£356,400,000	High
Replanting (individual)				£17,139,600	£17,139,600	Low
Loss of profits (forestry)		£72,932,209			£72,932,209	Low
Loss of profits (nurseries)		£2,000,000			£2,000,000	Medium
Publicly-funded research	£6,672,757				£6,672,757	High
Publicly-funded surveys	£21,501,000				£21,501,000	Medium
Woodland ES loss	£1,162,037,679				£1,162,037,679	Low
Non-woodland ES loss	£1,788,209,404				£1,788,209,404	Low
Human mortality	Unknown				Unknown	Low
Total:	**£5,607,265,600**	**£144,867,110**	**£191,771,174**	**£3,208,975,249**	**Grand total: £9,152,879,133**	

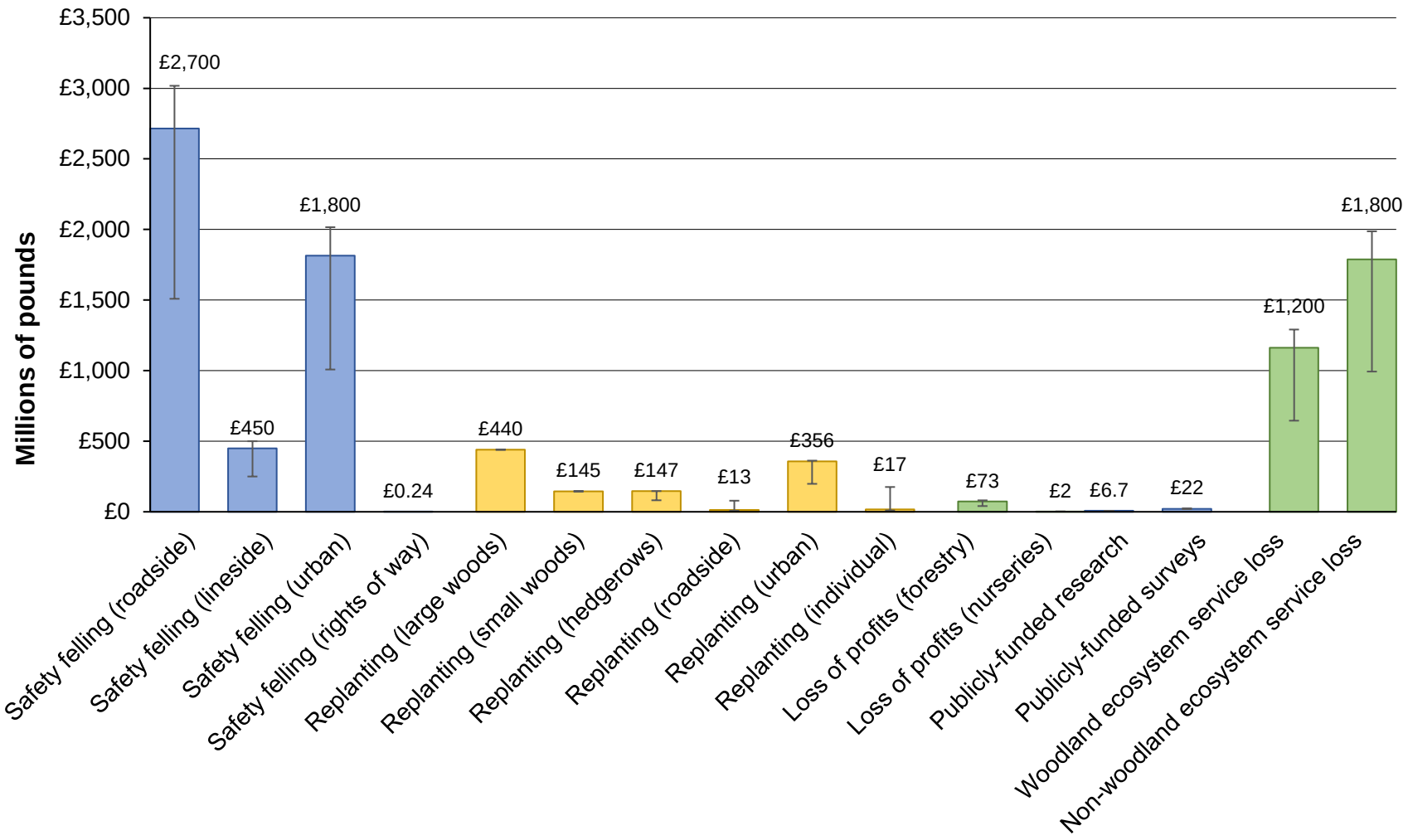

Figure 15: Components of the total cost of ash dieback in Britain. Damage costs are in blue, replacement costs in yellow, and lost values in green. The estimate for each is the cost calculated using 90% ash mortality rate; bars show costs for best- and worst-case mortality rate scenarios (50% and 100%).

Safety felling of roadside ash.

The linear model estimates that there are roughly 4,380,000 roadside ash trees in Britain (95% confidence intervals: 1,200,000; 16,290,000). Our estimate is supported by an independent estimate from the Highways Agency in 2014, which estimated there to be 4 million roadside ash trees that could threaten road safety. At an average cost of £800 per ash tree to fell or maintain an infected roadside ash, this gives a total predicted cost of roughly £2.7 billion to maintain the safety of Britain's road network. This makes safety felling of roadside ash the single largest component of the total cost of ash dieback.

£1.7 billion of the total cost of roadside ash is predicted to be the responsibility of the private sector, with the remaining £1 billion borne by the public sector. However, conversations with several county councils (Oxfordshire, Norfolk, Kent) suggests that in

Table 10. The 10 local authorities with the highest predicted annual cost of safety felling of roadside ash trees. Each authority's published annual revenue forecast is shown, along with the percentage of the annual revenue that is represented by the cost of maintaining roadside ash safety.

Local authority	Predicted annual cost of maintaining roadside ash safety (£ millions)	Local authority annual revenue 2017-18 (£ millions)	% of annual revenue
Devon CC	£35.70	£684.75	5.2
North Yorks CC	£28.90	£615.60	4.7
Lincolnshire CC	£18.20	£437.12	4.1
Cornwall CC	£17.20	£579.90	3.0
Norfolk CC	£14.80	£1,382.9	1.1
Suffolk CC	£10.70	£480.00	2.2
Essex CC	£9.42	£913.00	1.0
Cumbria CC	£9.05	£374.00	2.4
Staffordshire CC	£8.76	£470.41	1.9
Somerset CC	£8.65	£316.43	2.7

many cases, costs are unlikely to be recouped when local authorities have to fell trees on private land, so it is likely that the proportion of the cost borne by the public sector will be higher. The predicted total annual cost of maintaining roadside ash safety within a county may be a significant proportion of a council's gross annual income: up to 5.2% in the case of Devon County Council (table 10).

Discussion

Total cost and overview

Our analyses suggest that the ash dieback outbreak will have a very large financial cost to Great Britain, of approximately £9.2 billion (table 9 and figure 15). We believe this is the first time it has been possible to estimate the total cost of a tree disease to a country; our shockingly high estimate may indicate that the scale of the cost of tree diseases has not been previously appreciated. We have estimated costs conservatively, and as comprehensively as possible, although there are still large uncertainties associated with the estimate. However, even the predicted cost for our best-case scenario, for a very low level of ash mortality of 50%, is extremely high (£5.4 billion).

Potential costs as high as this would justify large investments to reduce the overall cost; however, many components, such as felling ash to maintain road safety, are unavoidable at this stage in the outbreak. We advocate strongly that the most cost-effective future strategy for tree diseases will be investment focussing on prevention of similar outbreaks.

Damage costs, and health and safety

The highest costs associated with ash dieback are damage costs, estimated at £5 billion (figure 15). The cost of felling dead and diseased ash trees alongside roads, estimated at £2.7 billion, is the largest single cost factor in our analysis (table 9 and figure 15), and is likely to be largely non-negotiable; local authorities have a duty of care to maintain the safety of roadside trees (Health and Safety Executive 2014). The majority of roadside ash trees (around 64%) are found on private land, where the legal responsibility for maintenance falls to the landowner. However, discussion with several local authorities suggests that often, council-employed tree workers are urgently required to fell trees on private land when they become hazardous, and the cost of this is frequently not recovered from the landowner. In reality, most of the £2.7 billion bill is likely to be met by local authorities.

Devon County Council has the highest predicted total annual cost of maintaining roadside ash trees, of £35.7 million. This is well over 100 times the average total annual tree budget for local authorities in 2003/04 of £271,000 (Britt & Johnston 2008), and amounts to over 5% of the county council's gross annual income (table 10). Other rural local authorities face similar levels of cost increase (table 10). This will be a significant additional strain for local authorities that are already under strong financial pressure. It is likely that some local authorities may require additional funding to respond adequately, or will be forced to divert funds from other services, with potentially severe social impacts. Costs to other public and quasi-public bodies, such as Network Rail, are also expected to be high. Indeed, the surprising scale of these costs indicates that the financial impacts of tree diseases has been underappreciated in the policy response, and highlights

a need for a clear funding strategy to support the public sphere in responding appropriately.

This is further demonstrated by the poor response from most councils to our Freedom of Information requests: in total, only 11 out of 207 local authorities (5%) could provide us with detailed information on the numbers of roadside ash trees within their boundaries, and 183 local authorities (88%) claimed to have no information at all on their roadside ash trees. This lack of knowledge is indicative that the potential costs of new ecosystem disservices (negative effects of ecosystems on people and human societies, such as trees falling into roads (Lyytimäki & Sipilä 2009)) resulting from ash dieback are not being widely considered, and risks leaving councils entirely unprepared.

Ecosystem service loss, and cost-effective investment to maintain services

The lost value of ecosystem services is estimated to be £2.9 billion for woodland and non-woodland ash combined (see figure 15). This estimate is large, but interestingly makes up less than a third of our total cost estimate of £9.2 billion. This is an important finding; most existing economic assessments of biodiversity, such as the Natural Capital framework, concentrate overwhelmingly on the lost value of ecosystem services. In doing so, these analyses risk severely underestimating the true cost of loss of species. Our analysis has demonstrated that the process of losing species can itself generate very large costs associated with the creation of ecosystem disservices. Ecosystem service assessments must consider the creation of such disservices, even if they are transitory like hazardous trees. Without this, underestimates produced by current assessments may promote actions that prove to be detrimental.

Replacement costs for replanting lost ash trees are the smallest cost type in our study (£1.1 billion) (figure 15). However, our analysis shows that replanting lost trees will represent an important investment for Britain, helping to cap the levels of ecosystem service loss. We assumed in our analysis that non-woodland trees will be replanted, as active management of non-woodland trees is generally thought to be cost effective when compared to the value of services that they provide (Rouquette & Holt in prep.). If, however, non-woodland trees are not replanted, the cost of lost ecosystem services could be far higher than our estimate. Older trees provide far higher levels of services (Fay 2002; Lindenmayer *et al.* 2014), so we estimated the loss of ecosystem services from ash dieback as 10 years of the estimated annual value of services from ash, to allow time for planted alternative trees to grow and start to provide similar levels of services (although some ecosystem functions can only be performed by veteran trees, see Lindenmayer *et al.* 2014). However, if no alternative trees are planted, it is likely to take many more years for natural regeneration to replace ash and the services it once provided, so the cost of lost ecosystem services could easily double or treble from what are already very high levels.

A simplified benefit-cost analysis demonstrates the potential value of replanting lost non-woodland trees to maintain ecosystem service levels. If we assume that by failing to replant, ecosystem services from these trees would be lost for 30 years rather than 10, we can estimate the cost of lost ecosystem services without replanting to be c. £4 billion. By contrast, the predicted cost of replanting all non-woodland ash trees is £534 million, and the predicted lost value from non-woodland ash, assuming 10 years of lost ecosystem services, is £1.8 billion. Roughly £0.5 billion of replanting could therefore reduce ecosystem service losses by c. £2.2 billion, giving a benefit to cost ratio of 4.5:1. Evidently,

replanting could in the long term be one of the most effective investments for capping costs, and produce very substantial savings.

However, a disjuncture between the beneficiaries of such investments, and the individuals or organisations responsible for making the investment, could create difficulties. The benefits of ecosystem services are public goods, and may not provide the necessary compensation to those people who will be responsible for much of the replanting. To a landowner, the maintenance of ecosystem services may not be a great enough incentive to spend money on replanting, which could potentially be prohibitively expensive at the scale of the individual. Similarly, local authorities faced with a large bill for replanting ash trees may opt to save money in the short term by not replanting, even if this leads to a long-term reduction in ecosystem service provision. This is a clear case where incentives from central government, in the form of grant aid to landowners for replanting after ash dieback, or grants to councils for replanting roadside trees, will be critical in shaping behaviour, and could lead to direct public benefit. Such interventions would also be expected to provide future public savings from, for example, improved air quality and flood protection.

Ash dieback research in Britain

The cost of government-funded research into ash dieback, at £6.7 million between 2012 and 2017, is small by comparison to the major costs but strategically important. An aim of government in funding research is to offset other costs and mitigate harmful impacts, such as the impacts on biodiversity. However, it is important for the future to consider critically whether the post-establishment stage of an outbreak is the best point upon

which to focus intensive research efforts. Many of the costs in our analysis, and broader impacts described by other authors, became unavoidable as soon as the disease was established in Britain.

Research can be extremely cost effective in finding novel solutions to problems, and the massive research effort into ash dieback has produced some fascinating and useful results. However, a more cost-effective strategy may be to fund research into preventing future disease outbreaks; not just for monetary reasons, but also from environmental and social perspectives. This is the frontier where we have the most to lose or gain, and where research has the potential to provide the greatest positive impacts (Brasier 2008; Potter & Urquhart 2017). Despite this, we could only find records for government awards totalling £2.8 million for research on reducing tree disease invasions, in the last decade. This is less than half of the value of the grants awarded reactively to study ash dieback after its establishment in Britain.

Many other known significant pests and diseases have yet to reach Britain, and could have a devastating impact if or when they do. These include *Xylella fastidiosa* (Wells *et al.*, 1987) and *Phytophthora cinnamomi* (Rands), both devastating diseases with very wide host ranges, and emerald ash borer, a severe pest of ash trees which would be likely to kill any ash trees that survive the ash dieback epidemic and push costs to the top of our range of estimates. Both preventative and responsive research are clearly important, but research into prevention has been neglected by comparison, and there is a strong argument that this balance should be redressed.

Effects of ash dieback on human health

The human costs of ash dieback are expected to go beyond monetary factors; public health could also be significantly impacted. Donovan *et al.* (2013) investigated an increase in human deaths that occurred after the emerald ash borer (EAB) epidemic in North America. They developed models to describe the increase in mortality rates from cardiovascular and lower respiratory conditions in North American counties affected by EAB, and found that both causes of death were significantly increased in counties with high rates of tree loss. After accounting for confounding factors such as socioeconomic indicators, they found that the presence of EAB in a county was associated with 6.8 additional deaths per year from lower respiratory disease, and 16.7 additional deaths per year from cardiovascular disease, per 100,000 adults. This amounted to 15,080 extra deaths from cardiovascular disease, and 6,113 extra deaths from respiratory disease, over a five-year period.

Donovan *et al*.'s model cannot be used directly to predict an increase in mortality in Britain following the ash dieback epidemic, because many underlying factors, such as the present health of the population, current pollution levels, human population densities and so on, may differ. However, in certain key respects the outbreaks are quite similar: both outbreaks may affect over 100 million trees, and the percentage of total canopy that ash comprises is similar or higher in British towns (min: Virginia, 1.5%; max: New York, 7.9% - c.f. min: London, 3.5%; max: Glasgow, 12.7% (data from Donovan *et al.* (2013) and responses to our FOIs). Ash dieback should therefore be expected to contribute to thousands of premature deaths in Great Britain, representing a significant human cost. This would remain true even if the effect seen is an order of magnitude smaller than that

of EAB in North America. An increase in these health conditions would also constitute an increased load on the National Health Service, with associated cost, as well as further economic losses from lost work hours and other knock-on effects that are impossible to quantify at this stage.

Incalculable costs and uncertainties

It was not possible to estimate every contributing factor to the overall cost of ash dieback in this analysis (see Methods). Some costs are incalculable, and others depend strongly on unpredictable human behaviour; these factors are likely to have a cost, but we are unable to estimate it currently. However, we are confident that we have estimated the largest and most important costs, so factors for which we have not estimated cost are unlikely to have a major impact on the overall estimate.

Perhaps more importantly, some of the components of the cost are likely to be significant underestimates, most notably the estimates for loss of ecosystem services. The two major sources for the estimated values of ecosystem services, from both woodland and non-woodland ash trees, both stressed that not all aspects of value from ash trees could be included, and that many of their own categories were likely to be severe underestimates (Rouquette & Holt in prep.; Defra 2013a).

Despite our efforts to develop a comprehensive list of possible costs, there may also be further costs that we have not considered at all. We are reasonably confident, however, that the analysis includes all major cost factors, after consultation with a wide range of experts (see Acknowledgements). Furthermore, additional costs would only strengthen the case for investment in prevention of tree diseases, and would in no way change our

conclusions. We believe that this is the most complete analysis of the total financial cost of a tree disease to date, and the first time that it has been possible to attempt such an analysis.

Range of ash mortality rates

Our range of predicted costs, from best-case to worst-case, is very wide (£5.4 – 10.1 billion). This is largely due to the high degree of uncertainty surrounding final mortality rates from ash dieback. We used final mortality rates of 50% and 100% for our best- and worst-case scenarios, as these fully encompass the range of the most recent published mortality rates (Vasaitis & Enderle 2017).

Recent reports have suggested that higher mortality rates of 90% or more are the most commonly seen across Europe (Vasaitis & Enderle 2017). An analysis of genetic markers associated with tolerance of ash dieback has suggested that, in Britain, 25% of ash trees may suffer less than 25% crown damage (Sollars *et al.* 2017). However, canopy damage does not equate to final mortality rate, firstly because it does not account for gradual decline over many years (Harper *et al.* 2016), and secondly because it cannot accurately predict the development of root collar rots, the most severe symptom of ash dieback that is increasingly responsible for much mortality from ash dieback (Enderle *et al.* 2013; Marçais *et al.* 2017). We therefore chose to use a final mortality rate of 90% for ash trees in Britain. This is our best estimate from the currently available evidence; many of the highest mortality rates and fastest rates of spread have been recorded from regions with high humidity (such as Britain), as this facilitates both sporulation of *Hymenoscyphus fraxineus* and development of root collar rots (Keßler *et al.* 2012; Heinze *et al.* 2017).

Additionally, early modelling work assessing the likely rate of spread in Britain has already proved to be optimistic, with the disease appearing to spread faster than expected (Defra 2013b; Forestry Commission 2017; M. Castle and R. Cox, unpublished (2013)). Finally, the majority of ash trees that survive are likely to be in poor condition, and in many cases this will provoke felling of surviving ash trees, either for safety reasons or to protect profits. Discussion with local authorities suggests that it is now common to fell ash trees that reach 50% crown dieback, rather than waiting for them to die entirely, which will also help to push costs towards the higher end of our range. To the best of our current knowledge, 90% mortality (used to produce our estimate) is a reasonable prediction for what might occur in Britain. However, the accompanying excel workbook can be used to explore the cost implications of different mortality rates, as well as differential estimates of other cost factors.

International trade in live ash and the need for improved international biosecurity

The value to British businesses of international trade in ash seedlings and saplings (prior to the 2012 movement ban) has been estimated at £300,000 per annum (Defra 2013b). This cost is modest compared to others; nevertheless we did not include it in our analysis, because it is likely that the majority of businesses were able to switch rapidly to other species (see Methods). £300,000 can therefore be considered as a worst-case scenario for the lost international trade in live ash, and we expect that the true cost will have been significantly lower. The loss of profits from trade represent no more than 0.003% of the total cost of the ash dieback epidemic to Britain.

International trade in live trees is known to be a major route by which tree diseases are transported between continents to new naïve hosts, and is thought to be the largest factor behind the recent dramatic growth in pest and disease invasions (Brasier 2008; Roy *et al.* 2014; Freer-Smith & Webber 2015; Potter & Urquhart 2017). Indeed, *Hymenoscyphus fraxineus* is thought to have been introduced into Europe in the early 1990s via trade in ornamental plants into Poland from its native range, the Far East (Kowalski 2006; Pautasso *et al.* 2013; Gross *et al.* 2014). Once present in Europe, *H. fraxineus* is believed to have spread naturally via wind-borne spores across almost the whole of Europe, including Britain (Gilligan *et al.* 2013) (although imports of infected ash material from the continent undoubtedly speeded up the process in Britain (Woodward & Boa 2013)).

However, many tree pests and diseases do not have such effective long-distance dispersal abilities, and there are growing calls for restrictions on international trade in live trees and soil into Britain, which could be extremely powerful in preventing new diseases' arrival thanks to Britain's geographic separation (Brasier 2008; Roques 2010; Boyd *et al.* 2013; Roy *et al.* 2014). Current UK phytosanitary protection relies on restricting movements of known threats, via the use of Pest Risk Analyses; however, diseases and pests will only be categorised as high risk once they have already caused damaging outbreaks, and as such this method is inadequate protection on its own. Indeed, *H. fraxineus* was itself an unknown pathogen when it was introduced into Europe, and therefore could not have been prevented by even the best-executed Pest Risk Analysis. As the number of outbreaks of invasive tree pests and diseases continues to rise, there is a clear and pressing need to consider regulating high-risk routes of introduction, such as

international trade in live plants, rather than individual organisms (Brasier 2008; Roy *et al.* 2014).

Such proposed regulations, however, challenge much traditional thinking in international trade policy. The World Trade Organisation (WTO), of which 164 nations, including the EU trade bloc, are members, exists to promote and facilitate free trade between member states. The WTO accepts the necessity for regulations of biological imports under certain circumstances (notably to protect the value of agriculture from invasive disease imports through the Sanitary and Phytosanitary Measures Agreement), but states that protective measures must not be allowed to constitute "disguised restriction on international trade" (WTO 2009, Articles 2.1 and 2.3). In practice, the WTO has often classified restrictions on potentially risky material as trade-limiting or protectionist – especially where environmental, rather than agricultural, protection has been the goal – and countries have been required to remove such restrictions (Perrings *et al.* 2005; Maye *et al.* 2012). This political environment has made it difficult or impossible for member states to impose scientifically-sound precautionary restrictions based on high-risk introduction routes, rather than the reactionary restrictions based on specific known organisms (Brasier 2008; MacLeod *et al.* 2010).

The result of this is that unintended consequences of introductions remain externalities to the trade in live plants: costs that are not reflected in the market price, which can encourage market behaviour that may be harmful (Perrings *et al.* 2005). However, to function for public benefit, trade agreements must be able to recognise the harms, as well as the benefits, that may arise from trade, and accommodate these appropriately. If the WTO seeks to promote the benefits of free trade, it must also respond to cases of market

failure where the economic arguments against free trade are strong. In the past, this logic has been applied successfully to introduction risks for economically important crop plants, but it has generally been poorly applied to environmental protection such as tree diseases, in part due to the lack of evidence of economic impact (MacLeod *et al.* 2010; Williams *et al.* 2010; Maye *et al.* 2012; Boyd *et al.* 2013). The current reactive measures on plant health, such as banning imports of known harmful organisms, have been shown to be ineffective (MacLeod *et al.* 2010; Roques 2010; Roy *et al.* 2014). Biosecurity inspections at borders, which by necessity can only inspect a tiny proportion of imports, and by definition can only catch symptomatic infections, are insufficient (Brasier 2008; Roques 2010). The harm that is caused by high volume trade in live plants and soil around the world has become clear, and increasingly, the weight of evidence suggests that controlling this trade to reduce the incidence of pest and disease outbreaks would have worldwide environmental and economic benefits (Drew *et al.* 2010; Williams *et al.* 2010; Roy *et al.* 2014; Freer-Smith & Webber 2015; Potter & Urquhart 2017).

On the specific case of ash dieback in Britain, our analysis has clearly shown that the economic impact of the epidemic dwarfs the cost of hypothetically restricting trade in live ash trees. For ash dieback, prevention of its introduction into Europe would probably have been the only way to prevent its arrival in Britain, emphasising again the need for a global response to disease introductions. However, other invasive pests and diseases with poorer dispersal may be prevented from spreading naturally from mainland Europe to Britain, thanks to the natural barrier of the Channel. For severe diseases where this is the case, the cost of preventing outbreaks is likely to be orders of magnitude smaller than the cost of letting them arrive. Ash is one of Britain's most common tree species, and one of

the most commonly planted, so we would expect that both the overall costs estimated here and the value of international trade would be similar for other common species. Indeed, as more tree species are decimated by disease outbreaks, the remaining trees become more valuable, so the costs of further losses of trees would most likely be even higher (Boyd *et al.* 2013). We are therefore confident that our analysis provides strong evidence that restricting non-essential trade in live plants to prevent future imports of pests and diseases, either by strictly regulating imports or by imposing tariffs, would be highly cost-effective.

Conclusion

Despite the uncertainty in our estimate, this analysis makes one point extremely clear: that ash dieback and other high-impact tree diseases have the potential to cause very significant economic impacts, that may far outweigh the value of trade in live plants. Many severe tree pests and diseases, including the emerald ash borer beetle, the bacterium *Xylella fastidiosa* (which can kill 359 species of European plants) and many others, are at risk of spreading to Britain in the short to medium term, primarily through trade (Fera 2017). Many of these, if they do arrive, will threaten an economic impact as large as, if not larger, than ash dieback. Most biodiversity valuation methods, including the Natural Capital framework, focus exclusively on the lost value of ecosystem services – however, in this analysis, ecosystem services made up less than a third of the total cost. Clearly, there are many other components of the true cost that these analyses may fail to consider, leading to a falsely low impression of the value of protecting ecosystems, and

potentially informing policy actions wrongly. The cost of creating new ecosystem disservices can be very high.

The costs of restricting trade and improving border biosecurity have often been used to justify not imposing greater biosecurity measures for plants. However, this argument must be urgently reviewed in the light of evidence for the high economic impact of invasive tree pests and diseases. More tree pests and diseases have arrived in Britain in the last 40 years than in all of previous recorded history – human influences, especially trade, are increasing the rate of introductions at a far higher rate than the natural background (Brasier 2008; Boyd *et al.* 2013; Freer-Smith & Webber 2015). The need to prevent the arrival of pests and diseases has long been recognised in agriculture, but pests and diseases of natural ecosystems have yet to be given equivalence. In Britain, we find ourselves at a unique moment: when the evidence for the importance of restricting imports of plants is emerging just at the moment when British trade laws are set to be re-written following Brexit, providing an opportunity for evidence-based change in policy.

Ash dieback is just one example of where a disease introduction will have cascading impacts far beyond those that were initially predicted. Britain's current phytosanitary controls for live plants rely on banning known pests and diseases, and are outdated and insufficient (Brasier 2008; Potter & Urquhart 2017). Unless drastic changes to border biosecurity are implemented, many more introductions will follow – and with each species loss, the remaining tree species will become more valuable, and more threatened. Declining biodiversity in ecosystems causes reduced resilience to future shocks, including future diseases and climate change, while essential ecosystem services are provided by fewer and fewer trees (Boyd *et al.* 2013; Freer-Smith & Webber 2015). A new vision of a

healthier future for Britain's woodlands urgently requires a unified and evidence-based approach to tacking introductions of invasive pests and diseases.

Great Britain benefits from geography in relation to disease outbreaks of many kinds. As an island, many pests and diseases cannot cross from mainland Europe without human assistance, and this provides a real opportunity to tackle the routes of introduction and dramatically reduce outbreaks (Brasier 2008). However, in countries around the world, the numbers of outbreaks of invasive tree diseases are increasing, and the economic, as well as ecological, impacts of this are making themselves felt. Increasingly, evidence suggests that reducing international trade in live trees to reduce pest and disease outbreaks would have global environmental and economic benefits (Brasier 2008; Drew *et al.* 2010; Roy *et al.* 2014; Freer-Smith & Webber 2015; Potter & Urquhart 2017), and the research presented here provides further weight to these conclusions.

Data sources

- Ash density in linear features and individual countryside trees was produced by Maskell *et al.* 2013 using data from the Countryside Survey 2008 (Carey *et al.* 2008). Spatial layers are available at: https://data.gov.uk/harvest/gemini-object/1bc985ef-969d-4e54-acd0-92f0143976af (last accessed (18/09/2017)

- Road lengths data was downloaded from the Road Network Size and Condition collection, produced by the Department of Transport. Available at: https://www.gov.uk/government/collections/road-network-size-and-condition (last accessed 18/09/2017)

- Approximate lengths of footpaths from: Christie & Matthews 2003 (England); McCraw & Davison 2000 (Scotland); "Public rights of way in Wales" page of the Natural Resources Wales website (Wales), available at: https://naturalresources.wales/days-out/recreation-and-access-policy-advice-and-guidance/managing-access/public-rights-of-way/?lang=en (last accessed 18/09/2017)

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CHAPTER 6:
GENERAL DISCUSSION

There is no question that ash dieback, and tree diseases more generally, will leave lasting impacts in Britain – ecologically, financially and socially. Of course, this is not the first time in recent history that Britain has felt the effects of a serious disease in a widespread tree species; the impact of Dutch elm disease, which was introduced in the 1960s, can still be seen clearly in the British landscape (Harwood *et al.* 2011; de Bruin *et al.* 2013). The effects of loss of ash may be even more severe than Dutch elm disease – there were thought to be 30 million elm trees in Britain (Brasier 1996), compared to 155 to 185 million ash trees (Forestry Commission 2013; Maskell *et al.* 2013; The Tree Council 2015). Nevertheless, it appears that some ecosystems may be more resilient to the effects of ash loss than was originally feared, and may have the capacity to buffer some of the inevitable changes (Chapter 2). This gives us a positive opportunity: to use good management to improve overall outcomes for people and other organisms.

Using modern ecological modelling techniques and the wealth of ecological data available in Britain, we have attempted to provide advice that could lessen some of the impacts of ash loss. We have mapped the most severely hit areas (in terms of the degree of ecological change) and produced region and ecosystem-specific guidance to land managers, in an attempt to improve outcomes practically for natural ecosystems and associated biodiversity. We have offered regionally-specific guidance on appropriate species for replanting, and have highlighted the importance of good forestry practice in allowing ecosystems to respond to major shocks like ash dieback. We estimate that if our

guidelines were to be followed, they could substantially reduce the degree of overall ecological change that results from ash dieback.

However, the resilience of ecosystems to shocks and our ability to help their resilience with management could in future be compromised by additional pests and diseases. If unchecked, these have the potential to make Britain's woodland ecosystems increasingly depauperate and vulnerable through their synergistic effects (Brasier 2008; Rackham 2008; Boyd *et al.* 2013; Freer-Smith & Webber 2015). Ash dieback and Dutch elm disease show how this has already started to occur. Ash trees are thought to provide habitat for certain threatened lichen species that were once found on elms, owing to both species having unusual alkaline bark (Watson *et al.* 1988; Thor *et al.* 2010). If the ash population is critically reduced, this could lead to the loss of not only ash specialist species, but also elm specialists that have adapted to use ash as refugia; thus, the ecosystem's resilience to Dutch elm disease will be reduced by the loss of ash (Jönsson & Thor 2012).

On the economic side, tree diseases can also be extraordinarily expensive – far more so than the potential cost of regulating international trade in trees (Chapter 5). The financial cost of ash dieback is likely to have extensive impacts on local authorities, private landowners and a range of other stakeholders, many of whom may not even yet be aware of the scale of the problem. Although cost has been considered as a major motivation for preventing the spread of crop diseases, it is not often fully appreciated as an important issue relating to tree diseases (MacLeod *et al.* 2010; Maye *et al.* 2012).

The 2016 vote for Britain to leave the European Union provides a unique opportunity to change our trajectory of ever-increasing pest and disease introductions (Boyd *et al.* 2013;

Freer-Smith & Webber 2015). New restrictions or tariffs on trade in plants and improvements in border biosecurity could have widespread benefits by preventing severe outbreaks like ash dieback in the future (Perrings *et al.* 2005; Maye *et al.* 2012; Roy *et al.* 2014). It may generate less media attention than the immediate crises that occur when invasive pests and diseases are discovered in new areas (Pidgeon & Barnett 2013), but it is in prevention that the greatest benefits stand to be gained, as control is often impossible once invasive diseases become established (Mack *et al.* 2000; Brasier 2008).

We will now discuss a brief synthesis of each chapter in this thesis in turn, followed by general conclusions from all chapters.

Experimental simulation of ash dieback

This experiment aimed to elucidate some of the specific and local effects of losing ash in semi-natural ancient woodlands. We recorded ground flora communities and the regeneration of woody species for three years after ash death, and earthworm communities for one year. However, we found no short-term effects on any of these of loss of ash, even at the highest level of ash death.

This interesting result gives hope that some woods, including semi-natural ancient woodlands which tend to have high biodiversity and social value, may be resilient to the effects of ash dieback – at least where the current abundance of ash is not overwhelming. Over the course of the experiment, the canopy gaps caused by loss of ash were seen to begin to close quickly, helping to restore understory shade levels and minimise short-term change for the ground flora.

However, much uncertainty remains as to the long-term impacts on biodiversity. Impacts from soil changes, for instance, are likely to occur over longer time scales than this experiment as a result of high levels of buffering within soil systems (Ovington 1953; James & Riha 1985); and a long-term reduction in light levels, as tree species with lower canopy light transference take over from ash, may also cause a reduction in floral biodiversity (Dölle & Schmidt 2009; Mitchell *et al.* 2014b). Indeed, rather than key aspects of woodland ecosystems being genuinely unaffected by a profound change in the nature of woodlands, it seems more likely that we may be seeing time lags occurring and that effects will emerge later on.

Additionally, the scale of this experiment was not suitable for investigating impacts on insects or lichens, two groups which have been predicted to be particularly severely hit by ash dieback (Broome *et al.* 2014; Mitchell *et al.* 2014a). Both of these types of organisms would have required far greater experimental areas to study effectively. Many insects are highly mobile, and so our experiment, with small patches where ash was killed surrounded by large areas where it was not, would not have constituted an effective treatment for insects which could easily move in and out of the experimental treatment blocks. Lichens, on the other hand, tend to be extremely patchily distributed, and so would also have needed far larger experimental areas to see effects beyond random noise. Woodland ground flora is also patchy (although generally less extreme), so it may be that more experimental plots or larger areas would have given this experiment greater statistical power to be able to tease out genuine ecological changes.

We did not investigate the effect of ash death on woodland ecosystem functions or services, and this would be a key extension of this experiment. For instance, how much

CO_2 was released from the death and decomposition of ash trees, and to what extent was the observed low degree of growth by competitors able to compensate for this loss? Measurement of these and more ecosystem functions would provide a rare opportunity to improve our understanding of the effects of tree species loss on people and general ecosystem characteristics.

Nonetheless, the woods in our experiment showed higher resilience than we anticipated; this appears to have been based on other tree species being able to respond and fill in the gaps left by ash. It will be interesting to see in the future how the results of our experiment compare with observations of woods that are affected by ash dieback.

Modelling abundance distributions of common British tree species

Researchers in Britain are very fortunate to have access to a large amount of freely available environmental data, including detailed species distribution records such as those in the BSBI Distribution Database, and this has been instrumental in allowing us to make useful predictions of the impacts of ash dieback. Despite this, we were initially missing a key piece of information for our predictions: how does the abundance of tree species vary across Britain?

This was an important question to answer, not only because the areas with the most ash trees might be expected to feel the most severe effects of ash dieback, but also because the effects of their loss and the most beneficial management interventions will vary with the abundance of other species too (see Chapter 4). The number of trees that will remain after ash loss and whether they are ecologically similar or very different to ash will help to

determine the actual impacts of ash loss, both on biodiversity and the ecological identity of ecosystems (Broome *et al.* 2014). Many other questions, on subjects ranging from species dynamics to epidemiology, are best answered using abundance distributions – they contain far more information and so are much more useful than simple presence-only maps of species records, or even modelled presence-absence maps (Pearce & Ferrier 2001; Sagarin *et al.* 2006; Hui *et al.* 2009).

We developed maps of abundance of common tree species in Britain using a combination of two established techniques (species distribution modelling and random forest regression), and found the combination to be highly effective. Data on species abundances tends to be very limited; this method was able to link presence-only data, of which a large amount is available for species observations in Britain, with key environmental variables and a much smaller amount of abundance data, to produce predicted maps of abundance. The use of random forest regression to do this allowed for any shape of relationship between the two types of data, and this lack of assumptions may have been critical in the effectiveness of the method. It also allowed us to incorporate the effects of abundance of other species on the target species, and to separately apply covariates that are expected to influence abundance and those expected to influence occupancy.

Modelling good quality abundance distributions has been a challenging technical question in quantitative ecology for many years (see Gaston *et al.* 2000; Wenger & Freeman 2008; Hwang & He 2011), and our analysis has made a useful contribution to this field. The technique worked well for a group, trees, that is traditionally considered challenging to model due to major human influences on tree distributions (Van

Couwenberghe *et al.* 2013), and produced maps of an acceptable quality for use in our analysis of the impacts of ash dieback (Chapter 4).

Modelling ecosystem vulnerability to ash loss

We mapped the areas of Britain most vulnerable to ecological change as a result of losing ash, based on the abundance of ash and the identities, abundance and ecological traits of the other tree species present. The aims were to identify the areas and woodland types at risk of the largest impacts, and produce guidance for specific management actions for each of these areas. An important discovery from this work was that the ecological impacts may not be most severe in the areas of highest ash abundance. Rather, we found that the proportion of trees that were ash, and the identity of other tree species present, were both important factors affecting the impact. This highlights how the synecological significance of a species can be more important than its raw abundance in measuring impacts of species loss.

Using our maps of overall impacts and individual trait loss, we produced a range of targeted management recommendations for each highly vulnerable area and woodland type. This advice should aid land managers in reducing the level of ecological change that occurs with ash death, helping to protect ecosystem characteristics and associated biodiversity. We were able to produce such guidance to reduce the levels of ecological change because of the availability of a wide range of largely native alternative tree species, which help to improve resilience to environmental change (Chapin 2009; Boyd *et al.* 2013).

The novelty in this approach lies in directly assessing the change in available trait values in a geographically-explicit manner. This allowed us to see patterns of impacts and develop management advice separately for different areas with different community compositions, as well as nationally where this was appropriate. We used as many ecological traits in our analysis as we could find (36), and used an Analytic Hierarchy Process (AHP) to weight traits according to their importance for ecosystem services. How to weight traits appropriately has long been an unanswered question in functional ecology, and we believe that using AHP to produce meaningful weights is a useful step forward. We also hope that by using a large number of traits in our analysis, we may have captured relationships between tree species traits and their associated biodiversity; investigating this potential link will be an important next step to test the breadth of possible applications for this approach.

This method for mapping ecosystem vulnerability to species loss has a range of potential applications beyond ash dieback. The approach could be broadened to include the impacts of other tree pests and diseases, as the effects of loss of multiple tree species in the same area are likely to be more severe. Future adaptations of this approach could be used to directly include the effects on associated biodiversity and to highlight geographic areas where particular species may be at risk from cascading effects of species loss, or even to include effects of additions of invasive plant species.

The financial impact of ash dieback in Great Britain

Finally, we investigated the financial impact of ash dieback, which we believe to be an underappreciated issue for tree diseases, and strategically key to influencing policy. A theme that emerged from the previous chapters was the importance of preventing more introductions of pests and diseases, because with each species loss, ecosystems become progressively less able to respond to future shocks (Chapin 2009; Boyd *et al.* 2013). Improved biosecurity for trees has been rejected politically in the past, largely due to trade agreements which seek to protect business from loss of trade, as the costs of regulating trade are considered to be too high (Perrings *et al.* 2005; Maye *et al.* 2012). Ash dieback provides us with an ideal opportunity to test the validity of this argument, or to see whether market failure is occurring.

The answer we reached was a shockingly high estimate for the cost for losing ash trees: £9.2 billion in Great Britain. Significant costs to the public sphere, business, public goods and human health will all result from ash dieback, and by extension other major tree diseases. The results of allowing tree diseases to become established are many times higher than the potential lost trade that may result from tighter regulation (see Chapter 5). There may be additional costs of improved biosecurity that have not been included in our analysis, but clearly the high cost of tree diseases would make even large investments in biosecurity or restrictions to trade in live plants cost-effective, if they were to reduce the chance of future invasions.

The identification of different costs and the stakeholders they will affect allowed us to identify reciprocal relationships between costs, and opportunities to keep costs to their

minimum. Replanting non-woodland ash trees would help maintain levels of ecosystem services and prevent further large losses of the value of the countryside, and would be highly cost-effective in the long-term (Rouquette and Holt in prep.). We also identified areas where strategical policy responses will be key, such as providing grants to landowners and local authorities to help them to replant lost trees for public benefit.

Additionally, we were surprised to find that the loss of ecosystem services represented only a third of the total cost in our analysis; the greatest costs came from safety implications. This suggests that the Natural Capital Framework, and other purely ecosystem service-based models, may be missing the majority of real-world impacts that biodiversity loss has on people (Turner & Daily 2008; Silvertown 2015). The unintended consequences of profound ecological change can be to introduce new ecosystem disservices, such as in this case the high cost to local authorities of maintaining a safe tree stock. If this is not explicitly taken into consideration by ecosystem assessments, valuations of species may give a highly inaccurate picture of the effects of change, potentially encouraging damaging behaviour or policy approaches.

General conclusions

With just one or two species threatened by highly damaging diseases, there are actions we can take to minimise the harm and help ecosystems to cope and recover (Chapter 4; Schröter *et al.* 2005; Pautasso *et al.* 2013a; Broome *et al.* 2014; Mitchell *et al.* 2014b). This is in part possible because of the excellent environmental data available in Britain which allows ecological modelling to be carried out, with wide-ranging benefits. This thesis

helps to develop some further resources – abundance maps – and uses these to develop practical management advice that may reduce the harm done to ecosystems from ash dieback. These outputs are respectively published and in review, and should help to produce practical improvements on the ground.

However, opportunities such as these will become harder to achieve in future if the current trajectory of ever-increasing pest and disease invasions continues (Loo 2009; Boyd *et al.* 2013; Woodward & Boa 2013). Already we find that some of the most useful species when it comes to replacing ash with ecologically similar trees (elm, alder) are problematic to recommend due to their own problems with invasive diseases (Chapter 4; Harwood *et al.* 2011; Sieber 2014; Alsop 2015).

It is no longer possible to look at a single invasive disease in isolation (Brasier 2008; Woodward & Boa 2013). Ash dieback is a perfect illustration of this; the available evidence strongly suggests that a proportion of ash trees will survive the disease (Mckinney *et al.* 2014; Alsop 2015; Lobo *et al.* 2015; Rosenvald *et al.* 2015), and this has led some commentators to suggest that the threat from ash dieback has been overstated, or even that we should celebrate the potential short-term benefits for saprophytic organisms (Heilmann-Clausen *et al.* 2013). However, survivors of ash dieback are not expected to survive attack by the emerald ash borer, which could, if current projections are borne out, reach Britain in the next few decades (Baranchikov *et al.* 2008; Valenta *et al.* 2017). A far bleaker future outcome for ash and its associated biodiversity is therefore likely when considering ash dieback and emerald ash borer together (Thomas 2016). The cost analysis provides the final evidence that preventing future tree pests and diseases is no longer just an ecological imperative, but also a political one. If our estimation of the total cost of ash

dieback proves to be remotely accurate, then the economic argument for supporting large-scale international trade in trees to protect the interest of business would appear to be entirely false.

There remain, of course, many questions to be answered on the impacts of ash dieback in Britain, and further afield. What will be the long-term effects on common and rare associated biodiversity? What will be the social and broader human impacts of losing a sizeable proportion of the tree cover? (Britain already has one of the lowest tree cover percentages in Europe ("Global Forest Resources Assessment 2010: main report. *FAO, Rome.*" 2010)). What will the effects of ash loss be on landscape connectivity and carbon storage (Reay 2013; Mitchell *et al.* 2014a)? Exactly how might the ash dieback outbreak interact with future introduced diseases, or other crises such as climate change? These are all important questions connected to issues that people and ecosystems face immediately as a result of ash dieback. But the long-term problem of invasive tree pests and diseases is one of those rare scientific problems with a clear solution: regulating international trade in plants and soil, the largest pathway for such introductions (Brasier 2008; Roy *et al.* 2014; Freer-Smith & Webber 2015; Potter & Urquhart 2017). The ash dieback epidemic, if nothing else, has served to make that abundantly clear (Pautasso *et al.* 2013; Woodward & Boa 2013). The challenge now, is to persuade politicians to act.

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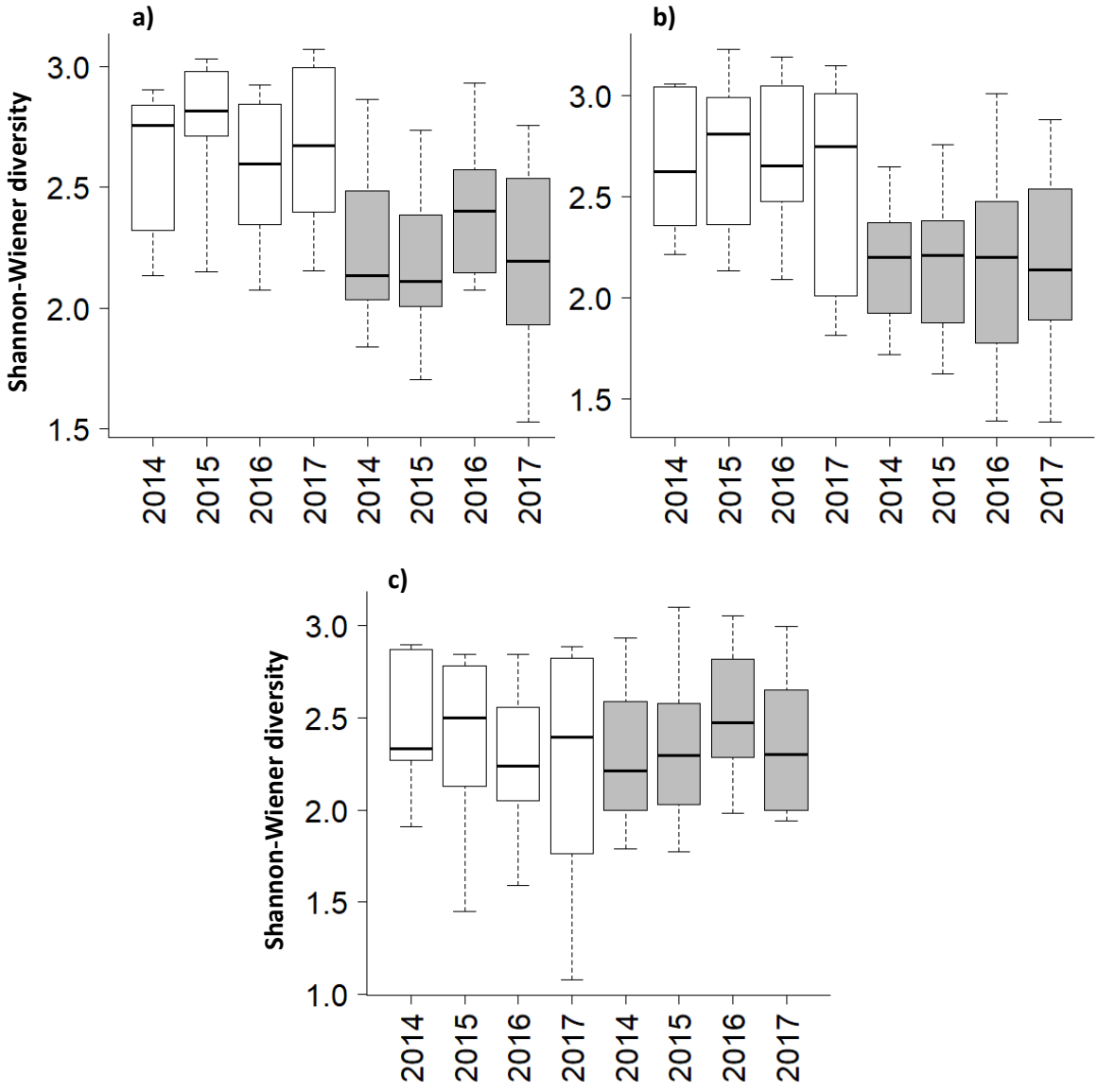
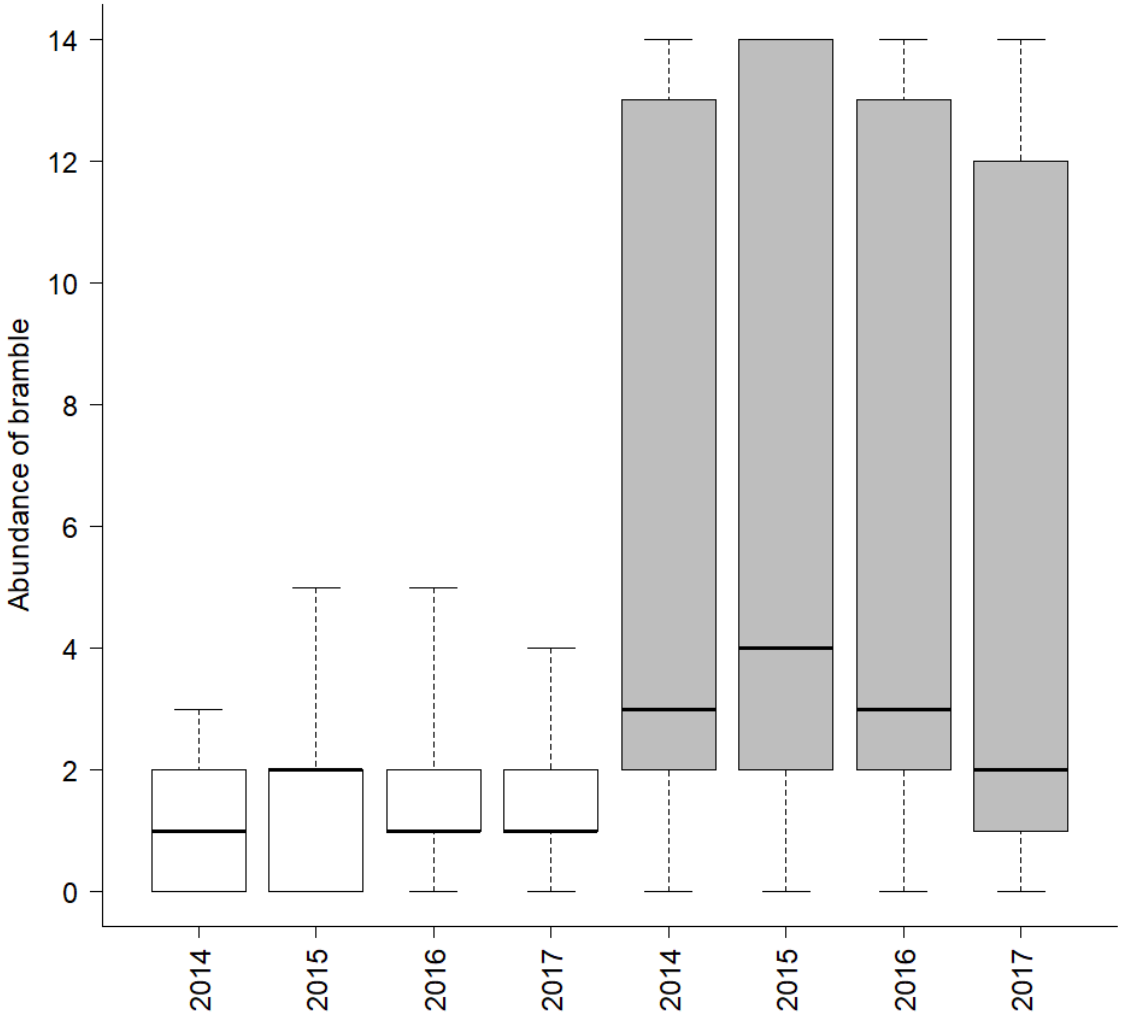
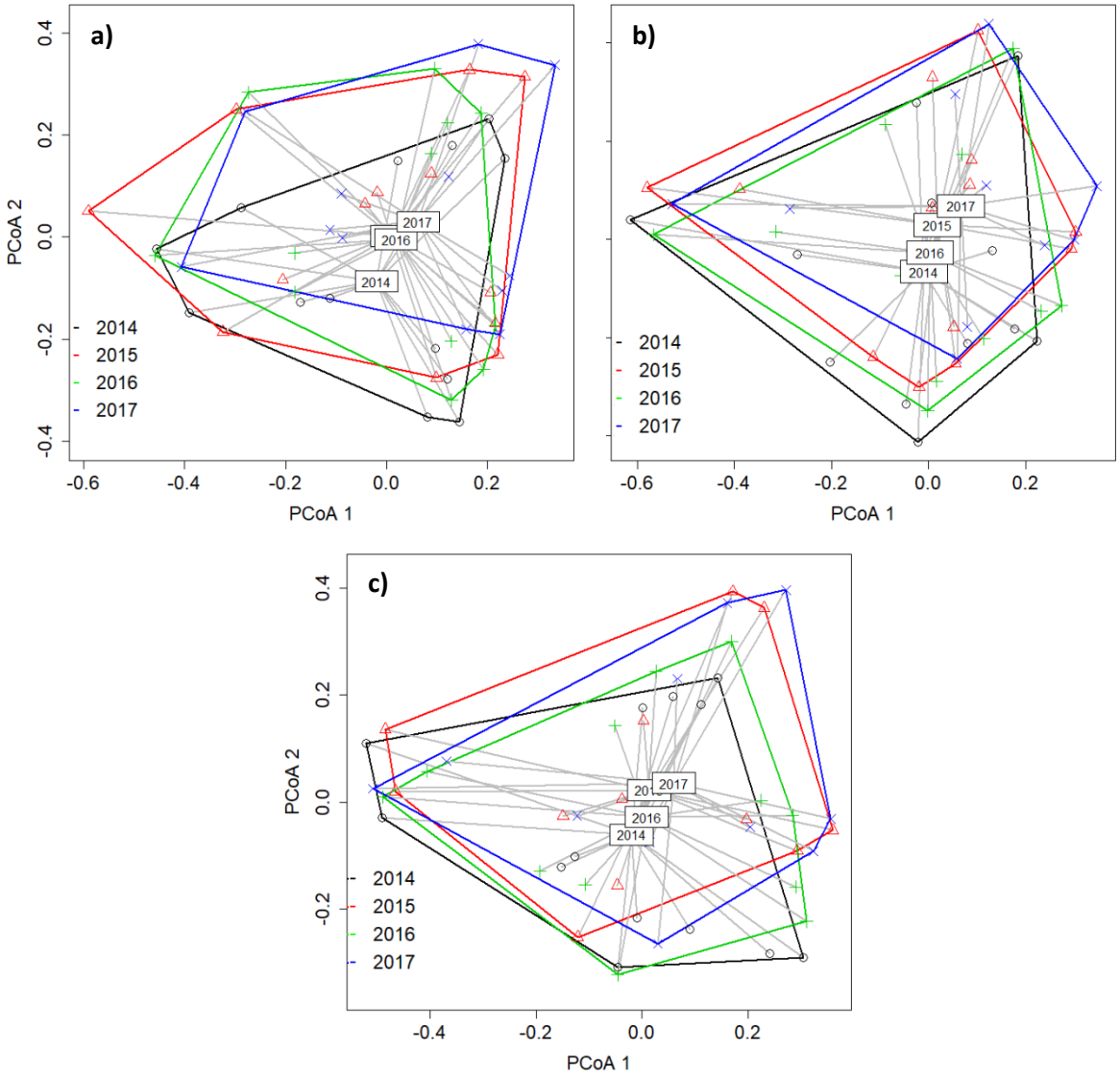
APPENDIX I:
SUPPLEMENTARY FIGURES FOR CHAPTER 2



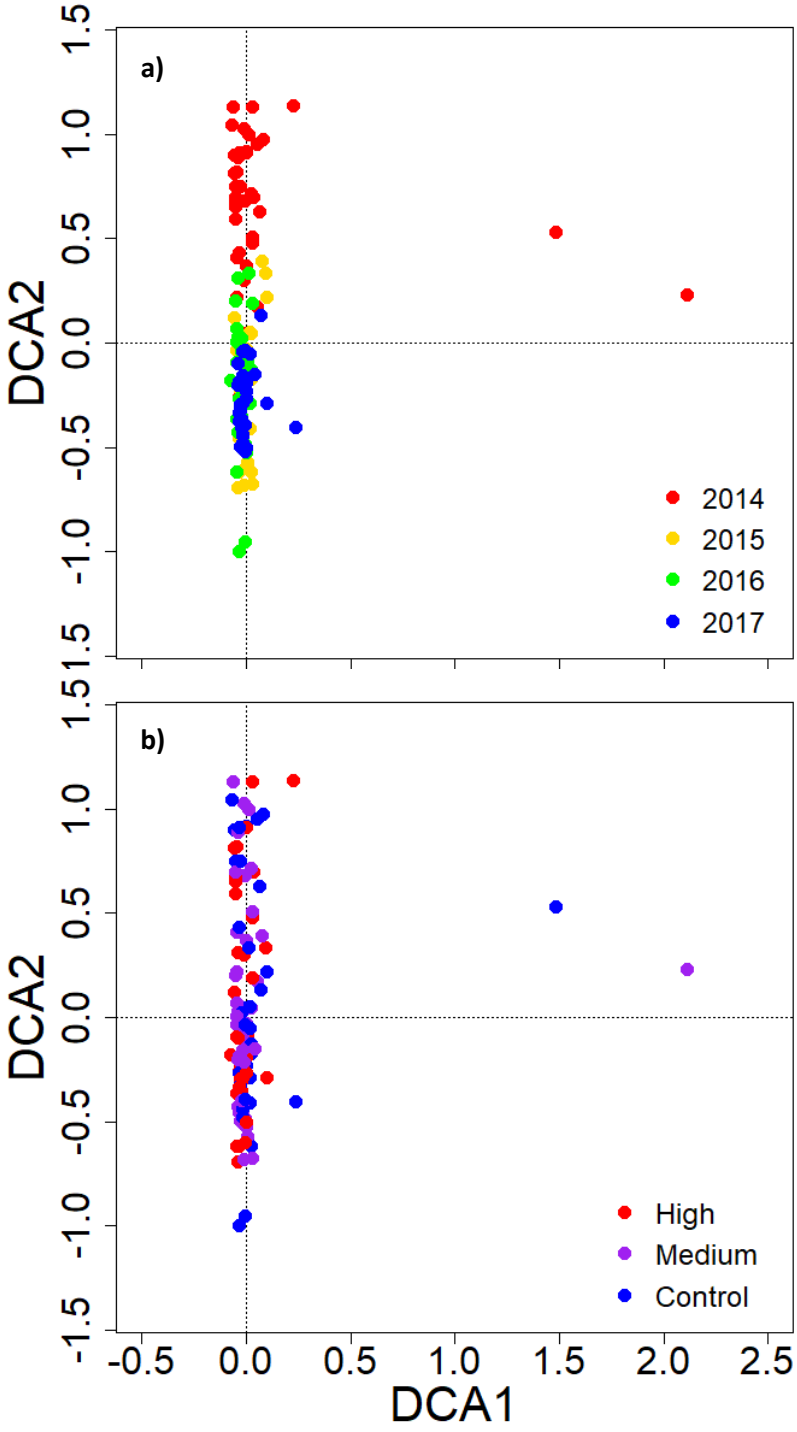
Supplementary figure 1. Shannon-Weiner diversity of ground flora communities (showing mean, upper and lower quartiles, and range. Plots in Bagley (white bars) and Wytham (grey bars) woods are shown between 2014 and 2017. **a)** shows high ash death treatment plots, **b)** medium ash death treatment plots, and **c)** control plots. No significant differences in diversity were found over time within any of the treatments.



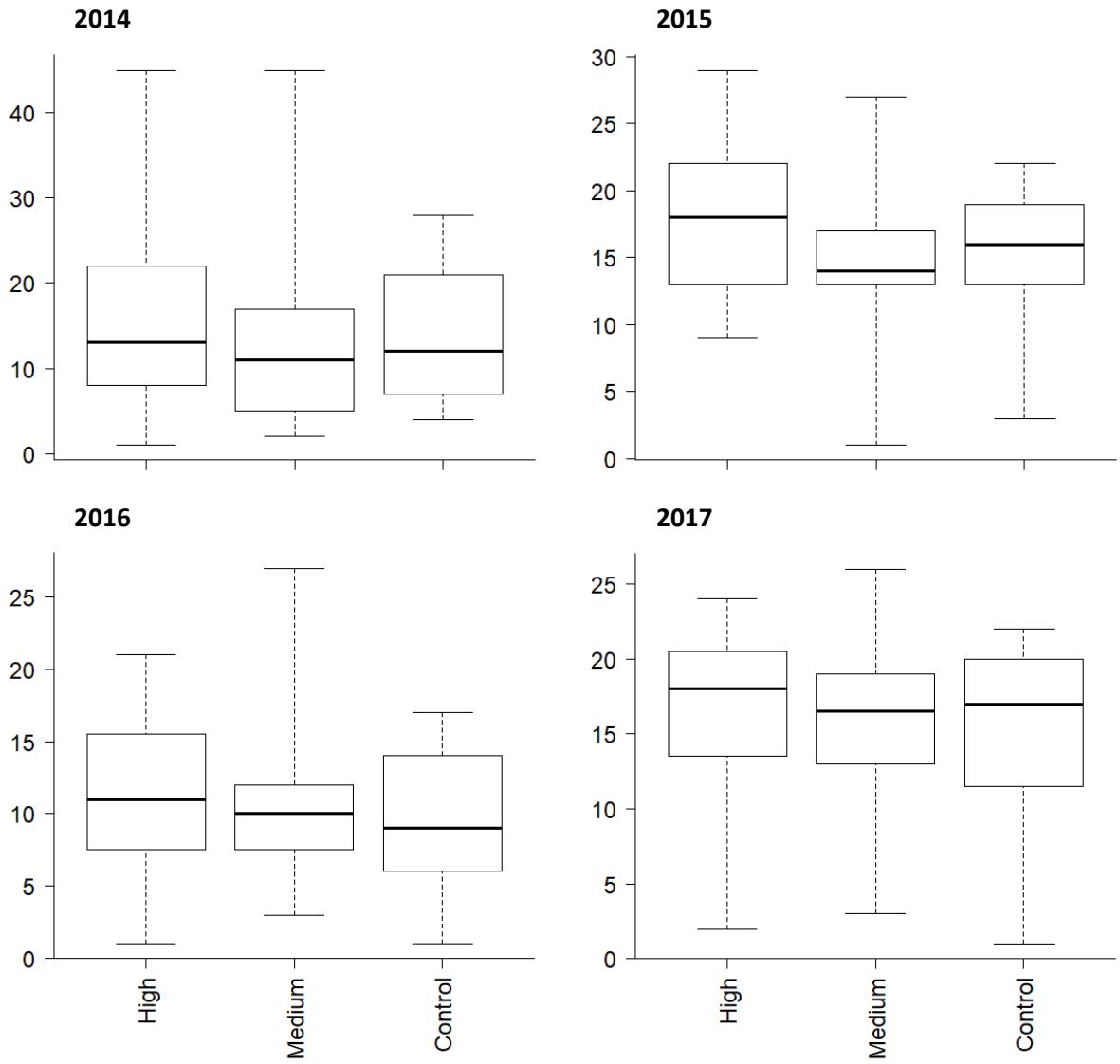
Supplementary figure 2. Bramble abundance in high ash death treatment plots in Bagley (white bars) and Wytham (grey bars) woods, between 2014 and 2017 (showing mean, upper and lower quartiles, and range). Abundance was measured on a 14 point scale within sample plots (see Methods). There was no significant effect of year on the abundance of bramble in plots in Wytham or Bagley.



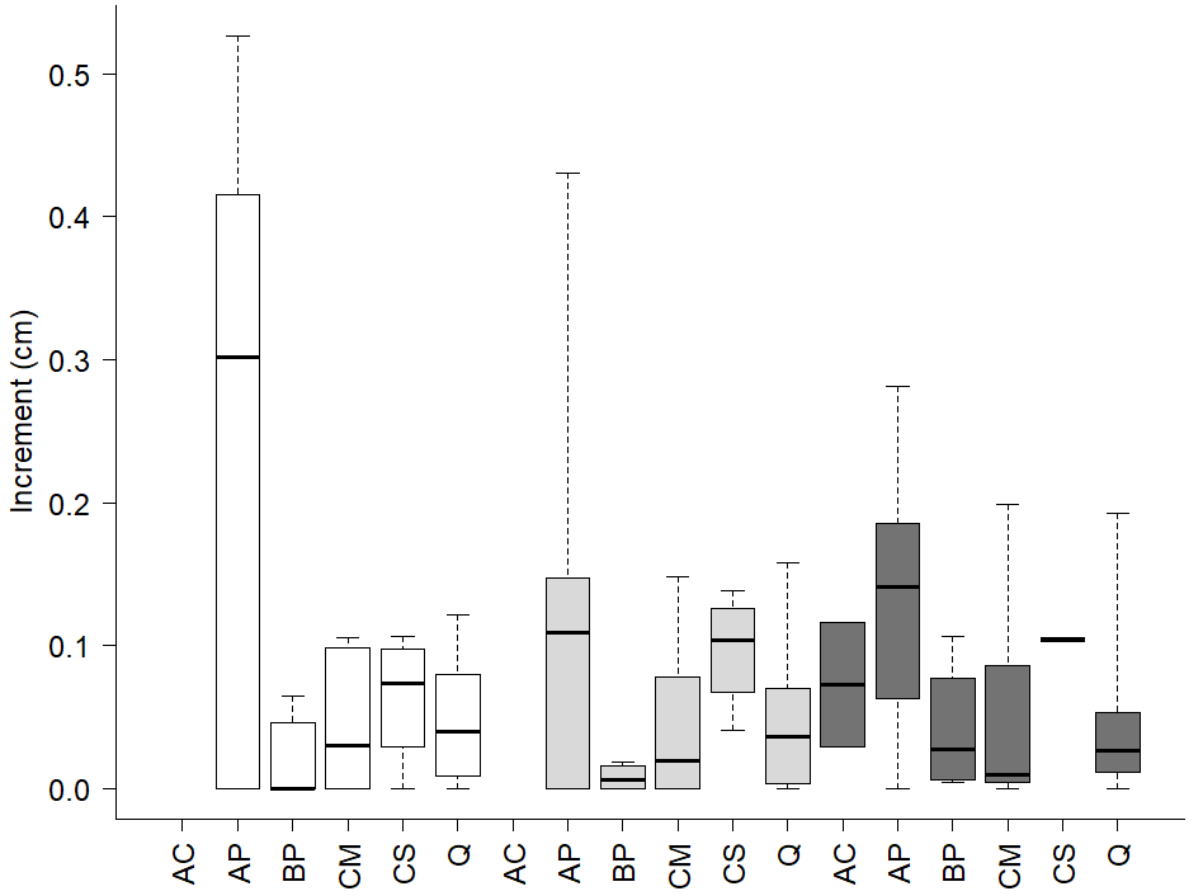
Supplementary figure 3. Principal components analysis of Bray-Curtis dissimilarity indices for ground flora communities, showing no differentiation between years for each treatment type: **a)** high ash death; **b)** medium ash death; and **c)** control. Treatment appears to have had no effect on similarity of communities, as there is a similar degree of overlap between years for the treatment plots as for the control plots.



Supplementary figure 4. Detrended correspondence analysis (DCA) of tree seedling communities in the experimental plots, coloured by **a)** year and **b)** treatment. There is a clear divergence of seedling communities between years, and just a very slight divergence by treatment: these observations are supported by the results of a constrained correspondence analysis (CCA) which found that year and treatment were both significant factors (year: $p = 0.005$; treatment: $p = 0.04$). However, no significant effect was found for the interaction of treatment and year ($p = 1.0$), suggesting that time affected the communities in all plots similarly and no additional effect was seen in the treatment plots.



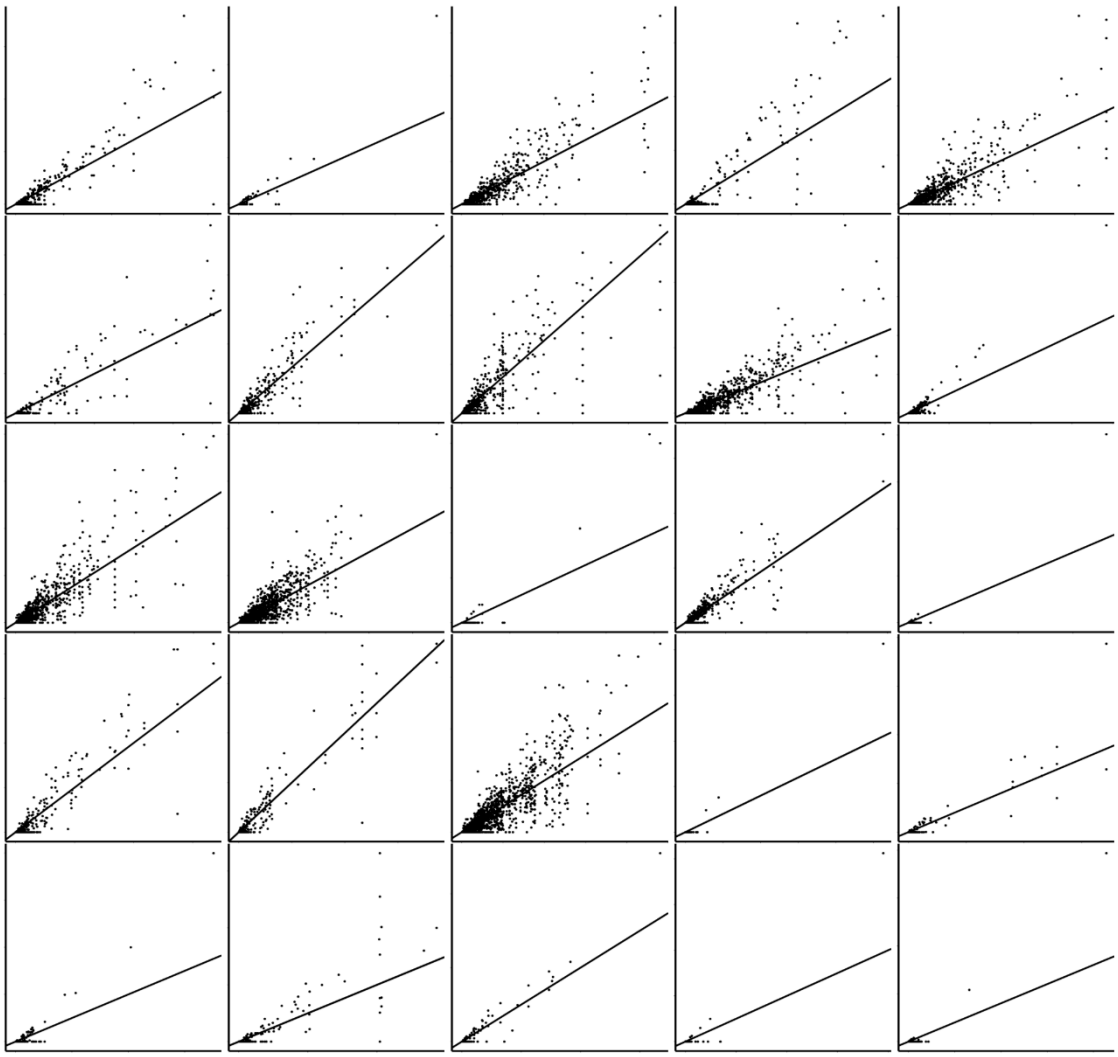
Supplementary figure 5. Abundance of tree seedlings of all species combined in different treatment plots in different years (showing mean, upper and lower quartiles, and range). No significant difference in abundance was seen between treatments for any year.



Supplementary figure 6. Increment (stem circumference growth) of non-ash tree species, over the entire study period (showing mean, upper and lower quartiles, and range). White bars are high ash death treatment plots, light grey are medium ash death treatment plots, and dark grey are controls. No significant difference was found for growth in any species between treatments. Species codes: AC = *Acer campestre*; AP = *Acer pseudoplatanus*; BP = *Betula pendula*; CM = *Crataegus monogyna*; CS = *Castanea sativa*; Q = *Quercus* spp.

APPENDIX II:
SUPPLEMENTARY INFORMATION FOR CHAPTER 3

Supplementary figure 7. Map of well-surveyed tetrads (black) that were used to convert presence-only data into presence-absence data. 18,993 tetrads were found to have been surveyed at least twice since 1950, with at least 50 species of plants recorded in each survey. These tetrads were considered to be well surveyed enough that if a tree species had not been recorded in one, it was considered very likely to be either truly absent or present at very low abundance with low ecological importance in the tetrad, and was therefore classified as an "absence".



Supplementary figure 8. Observed abundance against abundance predicted by Random Forest regression, as used to assess model performance. The line on each graph is the 1:1 line showing perfect model fit. From top left, species are: *Acer campestre*, *Acer platanoides*, *Acer pseudoplatanus*, *Alnus glutinosa*, *Betula pendula*, *Betula pubescens*, *Carpinus betulus*, *Castanea sativa*, *Corylus avellana*, *Crataegus monogyna*, *Fagus sylvatica*, *Fraxinus excelsior*, *Populus tremula*, *Prunus avium*, *Prunus padus*, *Pseudotsuga menziesii*, *Quercus petraea*, *Quercus robur*, *Sorbus aria*, *Salix caprea*, *Salix cinerea*, *Taxus baccata*, *Tilia cordata*, *Ulmus glabra,* and *Ulmus procera.*

Supplementary table 1. Pearson's pairwise correlations for the numeric variables used in species distribution modelling. The cut off for correlation coefficient used for variable selection was 0.7.

	Altitude	Aspect	Slope	Direct incoming solar radiation	Mean diurnal temperature range	Temperature seasonality	Annual precipitation	Topsoil available water capacity	Topsoil minerology	Topsoil organic carbon content	Topsoil texture class
Altitude	1	0.015396	0.518652	0.591347	-0.20693	-0.03162	0.621356	0.231888	0.000805	0.303198	0.428471
Aspect	0.015396	1	-0.02016	0.062394	-0.05345	-0.0269	0.062306	0.014767	0.019412	0.035133	0.041259
Slope	0.518652	-0.02016	1	0.224245	-0.08178	0.00709	0.331202	0.104236	-0.01246	0.154548	0.180757
Direct incoming solar radiation	0.591347	0.062394	0.224245	1	-0.30348	-0.17634	0.627365	0.225541	0.055276	0.231702	0.407135
Mean diurnal temperature range	-0.20693	-0.05345	-0.08178	-0.30348	1	0.620974	-0.57396	-0.0862	0.068989	-0.26488	-0.27498
Temperature seasonality	-0.03162	-0.0269	0.00709	-0.17634	0.620974	1	-0.37328	-0.13755	0.054918	-0.21352	-0.27218
Annual precipitation	0.621356	0.062306	0.331202	0.627365	-0.57396	-0.37328	1	0.27932	0.039224	0.36968	0.506227
Topsoil available water capacity	0.231888	0.014767	0.104236	0.225541	-0.0862	-0.13755	0.27932	1	0.152653	0.305173	0.590749
Topsoil minerology	0.000805	0.019412	-0.01246	0.055276	0.068989	0.054918	0.039224	0.152653	1	0.142262	0.298536
Topsoil organic carbon content	0.303198	0.035133	0.154548	0.231702	-0.26488	-0.21352	0.36968	0.305173	0.142262	1	0.386809
Topsoil texture class	0.428471	0.041259	0.180757	0.407135	-0.27498	-0.27218	0.506227	0.590749	0.298536	0.386809	1

Supplementary table 2. Table showing the most important variables in the random forest regressions of abundance for each species. Full variance importance plots for each species are available from the authors on request.

Species	**Most important variable in abundance model**
Acer campestre	Cover of trees in NFI
Acer platanoides	Probability of occupancy of *Crataegus monogyna*
Acer pseudoplatanus	Cover of trees in NFI
Alnus glutinosa	Probability of occupancy of *Crataegus monogyna*
Betula pendula	Cover of all trees
Betula pubescens	Cover of trees outside of NFI
Carpinus betulus	Cover of all trees
Castanea sativa	Cover of trees in NFI
Corylus avellana	Cover of trees in NFI
Crataegus monogyna	Probability of occupancy of *Betula pendula*
Fagus sylvatica	Cover of all trees
Fraxinus excelsior	Cover of trees in NFI
Prunus avium	Probability of occupancy of *Prunus padus*
Pseudotsuga menziesii	Cover of trees in NFI
Quercus petraea	Cover of trees outside of NFI
Quercus robur	Cover of trees in NFI
Salix caprea	Probability of occupancy of *Fagus sylvatica*
Salix cinerea	Probability of occupancy of *Corylus avellana*
Taxus baccata	Cover of trees in NFI
Tilia cordata	Probability of occupancy of *Fagus sylvatica*

Supplementary table 3. Additional information about abundance models. R^2 scores are shown for each species, along with RMSE (Root Mean Squared Error) and MAE (Mean Absolute Error) scores. For information about interpreting R^2 scores see main text. Number of abundance data points per species and number of non-zero abundance data points per species are also shown.

Species	R^2	RMSE	MAE	Number of data points per species	Number of non-zero data points
Acer campestre	0.523	1.44	0.35	679	315
Acer platanoides	0.207	1.27	0.19	444	42
Acer pseudoplatanus	0.426	4.01	1.40	906	634
Alnus glutinosa	0.271	2.40	0.66	484	195
Betula pendula	0.450	6.88	2.29	1261	802
Betula pubescens	0.596	4.09	1.09	501	127
Carpinus betulus	0.690	3.79	1.05	755	320
Castanea sativa	0.764	9.56	3.58	982	501
Corylus avellana	0.344	4.47	1.47	1282	935
Crataegus monogyna	0.049	1.10	0.23	413	339
Fagus sylvatica	0.496	8.45	2.91	1388	918
Fraxinus excelsior	0.397	4.95	1.88	1986	1629
Populus tremula	0.126	*NA*	*NA*	400	16
Prunus avium	0.589	1.98	0.56	886	401
Prunus padus	0.004	*NA*	*NA*	394	9
Pseudotsuga menziesii	0.596	7.66	1.96	600	193
Quercus petraea	0.841	5.99	1.84	584	209
Quercus robur	0.462	6.50	2.54	2303	1867
Salix caprea	0.644	1.38	0.28	445	74
Salix cinerea	0.081	0.16	0.03	392	55
Sorbus aria	0.055	*NA*	*NA*	392	3
Taxus baccata	0.372	2.21	0.49	518	86
Tilia cordata	0.442	1.04	0.14	461	56
Ulmus glabra	0.037	*NA*	*NA*	394	22
Ulmus procera	0.013	*NA*	*NA*	393	27

APPENDIX III:
SUPPLEMENTARY INFORMATION FOR CHAPTER 4

Supplementary methods

Methods overview

Our analysis is comprised of five main steps:

1. Compile data on (i) tree abundance distributions and (ii) tree species trait values.

2. Combine the two datasets in step 1 to calculate the average trait values in the ecosystem, and how they will change with loss of ash:

    a) For different localities (every 1 km^2).

    b) For different woodland types.

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

4. Calculate "vulnerability", based on the projected degree of change in the average trait values, weighted by the importance of each trait.

5. Identify recommendations for alternative tree species, with the aim of enhancing compensation for ash-like trait values after loss of ash.

We consider each step in more detail below. Figure 1 (Chapter 4) also shows a simplified worked example, going through each step to calculate vulnerability for a single square kilometre.

Step 1. Compiling data: tree distributions and trait levels.

Modelled abundance distributions of 20 common British tree and shrub species at 1 km^2 resolution were obtained from Hill *et al.*, 2017. The units of abundance were hectares of cover per km^2. The species modelled 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* (Matt.) Liebl., *Quercus robur* L., *Salix caprea* L., *Salix cinerea* L., *Taxus baccata* L. and *Tilia cordata* Miller. We chose to use the same species for this analysis as used by Mitchell *et al.,* 2014, as these trees had previously been identified as potential replacements for ash by silviculturists and are all found commonly in Britain.

The values of 36 ecological traits were obtained for each of the above species (and additionally for a further six species, *Populus tremulaI* L., *Prunus padus* L., *Rhamnus cathartica* L., *Sorbus aria* Crantz, *Sorbus aucuparia* L. and *Ulmus glabra* Huds., that occur regularly alongside ash in NVC communities). We included all traits for which we could find information for all species, and we took particular care to include, as far as possible, traits that are considered to be functionally important such as seed mass and specific leaf area (Weiher *et al.* 1999; Westoby & Wright 2006). We used a variety of databases (Ecoflora("Ecoflora: Ecological Flora of the British Isles" 2017), AshEcol (Mitchell *et al.* 2014c), the TRY Plant Database (Kattge *et al.* 2011), and Wageningen University and Research Tree Database(Goudzwaard 2017); see Data Sources and Trait Values and Sources table (Supplementary Material) for a complete list) and a wider literature search to fill gaps in coverage to maximise the number of useable traits, as our analysis does not

permit missing values. Wherever possible, published and peer-reviewed sources were used. However, for a small number of trait values, such sources were not available and it was necessary to use 'grey' literature. These instances represent a small minority of values and allow us to retain more traits and reduce the amount of data that are discarded. A summary of the traits used is given in Table 1 (main document). All trait values used and the sources for each are available in the Trait Values and Sources table (Supplementary Material). Where multiple sources were available for a single trait, the mean of their values was used.

Step 2a). Calculating average trait values across Great Britain, and how this may change with loss of ash.

This is the core of the analysis, and is an equivalent process to the averaging approach described by Hooper & Vitousek 1998 and Byrnes *et al.* (2014) for assessing overall levels of traits that occur in ecosystems. It summarises multiple traits into a single index, and calculates how this index will change with changes to the community composition (such as loss of ash).

The stages are as follows: i) For each trait, the range of trait values among all species is 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 is calculated for each 1 km^2, by multiplying the standardised trait values of each species by that species' abundance, and summing across species. iii) The average standardised trait value is then recalculated for each 1 km^2, without ash; this indicates how much the trait values present

may change after the loss of ash (i.e. how much less similar to ash the ecosystem may become). Each of these stages is now explained in more detail below.

i) Standardising traits. Nominal traits, such as pollination syndrome, were standardised by assigning 1 to any species with the same character as ash, and 0 to any species with a different character. Ordinal traits, such as bark pH, were standardised as follows: 1 was again assigned to species with the same trait value as ash and 0 to species with the most different trait value, but any species with intermediate trait values were given evenly-spaced intermediate scores (*e.g.* for bark pH, the trait values "alkaline", "neutral" and "acidic" were assigned the scores 1, 0.5 and 0 because ash has alkaline bark). Continuous traits, such as height, were standardised by subtracting the trait level of ash from each other trait level, making each difference absolute (to remove negative differences), and dividing each by the largest difference. This was then subtracted from 1 so that species with the same trait value as ash receive a score of 1 and the most dissimilar species receives a score of 0, with intermediate species falling on a continuous scale between 1 and 0.

ii) Calculating average trait values. Maps of abundance of each species, as a proportion of the total tree cover in each 1 km^2, were derived from the current abundance distributions in Hill *et al.* 2017, using the raster package in R. These proportional abundance maps were then multiplied by the standardised trait values for every trait-by-species combination, producing 36 map layers of trait values per species, and a total of 720 layers for all species combined. We summed across species for every trait to calculate the average value of each trait. Because the traits had been standardised according their similarity to ash, this gave the similarity of the average trait value in each km^2 to ash.

iii) We then recalculated the proportional abundance of each species to represent four different 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 all other tree species present increasing in proportion to their original abundance to fill the space left by the ash; 3) and 4) As the two scenarios above, 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). These scenarios (3 and 4) represent the change that may occur in woodland ecosystems only, with and without compensatory growth of other trees. For each of these scenarios, we recalculated the average values for every trait, to see how much less similar to ash the average trait values may become following ash loss.

The proportional change in average trait values between the current scenario and the four future scenarios was then calculated (*i.e.* future average trait value/current average trait value), for every 1 km^2 across Britain. This produced a score of vulnerability for each trait: higher values indicate greater loss of traits associated with ash, with a maximum value of 1 if the average trait value becomes completely dissimilar to ash after ash death.

Step 2b). Calculating average trait values for different NVC (National Vegetation Classification) woodland communities

We used the NVC floristic tables (Rodwell *et al.* 1991) to identify woodland sub-communities that contain ash as a constant or frequent species (15 woodland types). For each constant or frequent tree species in each community, we used the midpoint of the range of abundances indicated to produce representative relative abundance figures for species composition of each woodland type, and then repeated the procedure to calculate

average trait values (above) using these relative abundances. We did not produce relative abundance figures for occasional or scarce woody species, because these species only occur in a minority of woods of a certain NVC designation; we recognise that a scarce tree species may help to compensate for loss of ash where it is present, but to assume it could generally compensate for ash in an NVC community would be inappropriate for the majority of cases where that species does not occur.

Step 3. Weighting traits by importance: the Analytic Hierarchy Process.

Traits are unlikely to have equal contributions to emergent ecosystem properties, such as ecosystem services: for example, we included both litter decomposition rate and the type of appendages on a species' seeds in our analysis, but the litter decomposition rate is likely to have a far greater impact on most ecosystem services. We therefore used an Analytic Hierarchy Process (AHP) (Saaty 2008) to produce weights for all traits based on their relative importance for woodland ecosystem services. For detailed explanations of how to use AHP, see Saaty 2008 and Glur 2017.

The use of AHP is an important step in our method because it allows us to quantify the differences in importance between the traits, and produces weights that we can use to calculate our final vulnerability scores, in which the most important traits contribute the most strongly. We considered eight key woodland ecosystem services (climate regulation, primary production, nutrient cycling, soil formation, water cycling, flood protection, pollination services and supporting biodiversity). These were selected from a list of woodland ecosystem services defined by Watts *et al.* 2015; we included all ecosystem

services that our suite of traits could reasonably be expected to influence (we did not include cultural services that are unlikely to be adequately explained by species traits).

We used the *R* package "ahp" (Glur 2017) to carry out the AHP. As the simplest starting point, we chose to weight all our ecosystem services equally, to avoid arbitrarily assigning more importance to one service over another (but alternative weightings can easily be incorporated in any future analyses). Then, we compared all 36 traits in a pairwise manner in terms of their importance to each ecosystem service. We used a standard AHP scoring system, where 1 means that traits *a* and *b* are equally important, 3 means that *a* is slightly more important than *b*, 5 means that *a* is more important than *b*, 7 means that *a* is much more important than *b*, and 9 means that *a* is absolutely more important than *b*. We used our knowledge of woodland ecosystems and best judgement to agree scores between us (all authors). 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 files Trait Weights table and yaml file for ahp. 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. $a > b$, $b > c$, $c > a$). Our pairwise comparisons had consistency indices ≤ 0.1, meaning that our comparisons are acceptably consistent (see AHP output table in Supplementary Material).

We produced our final weights by averaging the weights produced for each ecosystem service. Finally, we used these to weight each trait by importance; we multiplied the

average trait values for each trait (produced in step 2) by its weight, before averaging across traits. This produced overall average trait levels weighted by importance of traits, for both the initial ecosystem and each of the four future scenarios.

Step 4. Calculating vulnerability scores.

Our final vulnerability scores are the proportional change in average trait values between the current scenario and the four future scenarios (see Figure 12 and 13, Chapter 4). 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 11 (Chapter 4) 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.

Step 5. Identifying planting recommendations.

We also produced vulnerability scores 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, we took the five traits with the highest vulnerability scores. We then identified the tree species which are most similar to ash for those traits from our compiled trait database. These species are our

recommendations for replacement species; three or four species were required in each case to ensure that all five traits were provided for (see Box 1).

For the NVC communities, we chose replacement species only from the subset of species that already occur in each NVC community. This avoided the recommendation of species that would drastically alter these communities or be unsuitable for the abiotic conditions present. We included occasional and scarce species in this selection to provide a wide-enough pool of species for effective compensation. Similarly, only trees that were known to occur in a particular geographic area were recommended for that area.

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

1. **Plant or encourage regeneration of recommended mixtures of tree species, especially in areas with high ash density.**
   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, 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. **Improve condition of woodlands to improve resilience to shocks.**
   Manage pressures – such as overgrazing, abandonment, squirrel damage, pollution, invasive species, and diseases – to enhance natural regeneration and resilience. 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 ecological 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*

Supplementary table 4. The AHP output table showing weights for each trait-by-ecosystem service pair, total weights for each trait and the consistency index for each ecosystem service.

	Weight	LitterDecomp	Deciduous	L	Nfix	LDMC	SLA	FTRAIT	Height	R	growth	NTRAIT
Weight traits	88.9%	6.1%	4.7%	4.6%	4.6%	4.3%	4.3%	4.2%	4.0%	3.8%	3.7%	3.7%
Biodiversity	11.1%	0.8%	0.8%	0.8%	0.3%	0.4%	0.4%	0.4%	0.1%	0.4%	0.1%	0.4%
Nutrient cycling	11.1%	1.0%	1.0%	0.5%	1.0%	0.6%	0.5%	0.5%	0.1%	0.5%	0.5%	1.0%
Pollination	11.1%	0.1%	0.1%	0.5%	0.1%	0.1%	0.1%	0.1%	0.5%	0.1%	0.1%	0.1%
Primary production	11.1%	0.6%	0.1%	0.9%	0.9%	0.6%	0.6%	0.3%	0.9%	0.3%	0.9%	0.9%
Soil formation	11.1%	1.0%	0.5%	0.5%	1.0%	1.0%	1.0%	0.5%	0.1%	0.5%	0.1%	0.5%
Water quality	11.1%	1.0%	1.0%	0.2%	0.2%	0.5%	0.5%	1.0%	1.0%	1.4%	0.1%	0.2%
Flood prevention	11.1%	1.0%	1.0%	0.5%	0.2%	0.5%	0.5%	1.0%	0.5%	0.2%	1.0%	0.2%
Climate regulation	11.1%	0.6%	0.2%	0.6%	1.0%	0.6%	0.6%	0.3%	1.0%	0.3%	1.0%	0.3%

WoodDens	Longevity	Mycc	Psyn	BarkpH	Larea	InfType	FlReward	shadeTol	FirstFl	FlPeriod	AnSeed	germRate	resprou
3.6%	3.2%	2.7%	2.4%	2.1%	2.1%	2.0%	2.0%	1.9%	1.8%	1.7%	1.6%	1.4%	1.4%
0.1%	0.8%	0.1%	0.8%	0.8%	0.1%	0.4%	0.4%	0.1%	0.3%	0.1%	0.4%	0.1%	0.1%
0.3%	0.1%	0.5%	0.1%	0.5%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%
0.1%	0.1%	0.1%	1.2%	0.1%	0.1%	1.2%	1.2%	0.5%	1.2%	1.2%	0.5%	0.1%	0.1%
0.9%	0.9%	0.2%	0.1%	0.1%	0.1%	0.1%	0.1%	0.4%	0.1%	0.1%	0.1%	0.4%	0.4%
0.3%	0.1%	0.5%	0.1%	0.1%	0.5%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%
0.1%	0.1%	0.5%	0.1%	0.2%	0.5%	0.1%	0.1%	0.2%	0.1%	0.1%	0.1%	0.1%	0.1%
1.0%	0.1%	0.5%	0.1%	0.2%	0.5%	0.1%	0.1%	0.2%	0.1%	0.1%	0.1%	0.1%	0.2%
1.0%	1.0%	0.2%	0.1%	0.1%	0.2%	0.1%	0.1%	0.4%	0.1%	0.1%	0.1%	0.4%	0.4%

LLife	SMass	FirstSeed	LShape	DispSize	Seedbank	DispAgent	FType	GermTime	DispersalTime	Appendages	Inconsistency
1.3%	1.3%	1.3%	1.3%	1.1%	1.0%	0.8%	0.8%	0.8%	0.8%	0.6%	0.0%
0.1%	0.3%	0.1%	0.1%	0.1%	0.1%	0.3%	0.3%	0.1%	0.1%	0.0%	9.5%
0.3%	0.3%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	4.6%
0.1%	0.1%	0.5%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	1.6%
0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	9.0%
0.3%	0.3%	0.1%	0.2%	0.3%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	8.7%
0.2%	0.1%	0.1%	0.2%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	2.4%
0.2%	0.1%	0.1%	0.5%	0.1%	0.2%	0.1%	0.1%	0.1%	0.1%	0.1%	1.7%
0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	❗ 10.4%