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Ash dieback risks an extinction cascade

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ABSTRACT

Large-scale decline in populations of European ash (*Fraxinus excelsior*) are occurring throughout Europe due to the invasive fungus *Hymenoscyphus fraxineus*. This has grave ecological implications not only for ash trees, but also for the biodiversity supported by, and in some cases solely dependent on ash. Here we used data on the tree-species associations of biodiversity in Sweden, to predict extinction risks for ash-associated organisms, and the potential for combinations of other tree species to sustain ash-associated biodiversity. Of the 483 ash-associated species identified, 11% are exclusive to ash, and a further 23% prefer mainly ash. Notably, many ash-associated species are shared with wych elm (*Ulmus glabra*) which is similarly threatened by an invasive fungus. Considering the level of host association and the species' conservation status, 115 species were deemed at high risk of regional extinction. Using a mathematical optimization model we found that up to nine additional tree species would be needed to sustain all non-obligate ash dependent/preferring species in the absence of ash and elm. We discuss mitigation and adaption options to reduce the potential for an extinction cascade and conserve ash-associated biodiversity, but all pose unique challenges.

1. Introduction

Biodiversity underpins the function of ecosystems and the delivery of goods and services upon which humanity relies (Cardinale et al., 2012). Despite this dependence, anthropogenic impacts on ecosystems via habitat loss and degradation, overexploitation of species, pollution of ecosystems and climate change are causing species loss at such a high intensity that it is now being equated with a sixth great extinction (Ceballos et al., 2015). Recent global assessments indicate that at least one million species are at risk of extinction, posing serious threats to human health, prosperity, and security (IPBES, 2019).

Invasive alien species are one of the five principal pressures directly driving global biodiversity loss (Maxwell et al., 2016). Increased globalization of trade and tourism have facilitated the long-distance movement of species into regions outside their historical distribution, and the number of alien species accumulating worldwide shows no signs of saturation (Prospero and Cleary, 2017; Seebens et al., 2017). Over the last 200 years Europe has witnessed an unprecedented increase in number of forest pathogen introductions, largely due to human-mediated international transportation and trade of plants and plant products (Brasier, 2008; Hulme, 2009; Santini et al., 2013).

Historically, only a small proportion of introduced pests and pathogens have caused widespread devastation of host tree species. However, when such events occur, and the populations of pests and pathogens become naturalized and subsequently invasive, large scale ecological impacts often result (Mack et al., 2000). These impacts can include changes to trophic interactions, forest composition, nutrient cycling, carbon storage and hydrology, the fragmentation and destruction of habitats, and altered ecosystems functioning at extensive spatial scales (Ellison et al., 2005; McNeely et al., 2001; Millennium Ecosystem Assessment, 2005; Moore, 2005). For example, in Western Australia, widespread devastation of a number of native woody hosts by invasive *Phytophthora cinnamomi* is thought to have caused major changes to both plant communities and associated fauna (Wills, 1992). American chestnut (*Castanea dentata*) was functionally extirpated in its native eastern North American range during the first half of the 20th century following the introduction of the chestnut blight fungus (*Cryphonectria parasitica*). The widespread loss of this keystone species from North American forests affected habitats for a plethora of species associated with chestnut, as well as impacting nutrient cycling and soil micro flora and fauna (Loo, 2009). Invasion by hemlock wooly adelgid (*Adelges tsugae*) in eastern North American has resulted in significant changes in avian communities – a direct result of the widespread infestation and subsequent tree loss in hemlock-dominated forests (Tingley et al., 2002). The more recent invasion of Emerald ash borer (EAB, *Agrilus planipennis*) to eastern North America has caused mass mortality of native eastern North American ash (*Fraxinus*) species and as a result, five of the six most prominent *Fraxinus* spp. are now

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critically endangered (IUCN Red List), and on the brink of functional extirpation. Studies suggest the widespread and rapid loss of ash can lead to ecosystem and regional scale impacts with alterations in biogeochemical and plant community composition (Flower et al., 2013; Klooster et al., 2014). This is of particular concern in riparian areas where the nutrient runoff from soils to adjacent aquatic ecosystems is affected (Nisbet et al., 2015). Across Europe, temperate broadleaved forests have been severely altered with the loss of nearly all mature elms due to two pandemics of Dutch Elm Disease. The first pandemic was caused by *Ophiostoma ulmi*, which was introduced also during the early 20th century. The second (and ongoing) pandemic is caused by the more virulent *Ophiostoma novo-ulmi* (Brasier et al., 2004) which has led to a number of elm-associated species becoming red-listed in the countries concerned. Because of the interconnectedness of species in ecosystems, it is largely assumed that secondary extinctions associated with these forest pest and disease epidemics may have occurred, however in general, there is a lack of data concerning cascade effects from invasive alien species.

A new forest disease epidemic is now spreading throughout Europe on native *Fraxinus* species, following the human-mediated introduction of the ascomycete fungus *Hymenoscyphus fraxineus* (Baral et al., 2014), presumbly on imported nursery stock of Asian *Fraxinus*. Wind-dispersed spores of *H. fraxineus* infect trees via their leaves and rachises during the summer. Subsequently, the fungus colonizes twigs and branches, disrupting nutrient and water transport, and leading to progressive dieback of the shoots, branches and crown and ultimately the tree's death (Cleary et al., 2013; Timmermann et al., 2011). The disease, commonly known as ash dieback, is now widespread throughout most of Europe and has dramatically reduced the host population size of European ash (*Fraxinus excelsior*) in most countries.

In Sweden, symptoms of ash dieback were first reported in 2001 (Barklund, 2005), and the disease has since had devastating consequences on the Swedish ash population. Despite the scarcity of ash in Sweden where its growing stock currently constitutes only 0.1% of the total growing stock (Nilsson et al., 2019), this tree species has regional importance in some areas of the country making up a large component of local broadleaved forest landscapes (Cleary et al., 2017), and has substantial cultural, economic and ecological importance. European ash (hereafer referred to as 'ash') is a *keystone species* and has a unique niche in the ecosystem because it provides critical habitat for many other species (Pautasso et al., 2013). Ash also has an important role in the ecosystem functioning of temperate broadleaved forests due its role in controlling fluxes of organic matter between trophic levels, and by influencing litter decomposition, nutrient cycling, hydrology, and interactions between other organisms and successional processes (Broome and Mitchell, 2017). Several studies have documented the capacity of ash to reduce levels of acidification in soil (Hagen-Thorn et al., 2004; Jacob et al., 2009; de Schrijver et al., 2012; Langenbruch et al., 2012), and to provide high litter quality and fast cycling of nutrients and carbon (Mitchell et al., 2014a), as well as high understory light availability that provide optimal conditions for regeneration (Emborg, 1998). The nutrient-rich bark also has a high pH, providing ideal microniches for many mosses, fungi and insects (Roberge et al., 2011), and epiphytic lichens (Thor et al., 2010; Jönsson and Thor, 2012).

Due to the large-scale decline of ash, in 2010 the species was added to the Swedish Red List with a vulnerable (VU) status (Gärdenfors, 2010). By 2015, the state of ash worsened and the species was reclassified as endangered (EN) (Artdatabanken, 2015); a consequence of disease intensification and increased tree mortality across the country. The ash dieback epidemic is a pressing conservation challenge which has implications not only for ash as a species, but also due to the risk that devastated populations can catalyze secondary (regional) extinctions among species dependent on ash for their habitat (Pautasso et al., 2013; Mitchell et al., 2014a; Mitchell et al., 2014b; Mitchell et al., 2017). Known as 'extinction cascades' (Dunne et al., 2002; Sanders et al., 2018), this process may have already begun, as indicated by the high proportion of ash-associated red-listed species in Sweden (Sundberg et al., 2019).

One obstacle to implementing forest management actions aimed at conserving local biodiversity associated with ash is our lack of understanding on the number of associated species that are threatened, their relative dependence on the host tree, and the disturbance threshold for species survival. Efforts to quantify ash-associated organisms have been made in the UK (Mitchell et al., 2014a, 2014b), but elsewhere, including Sweden, the few available studies have been limited to assessments of specific taxonomic groups (von Oheimb and Brunet, 2007; Jönsson and Thor, 2012; Brunet et al., 2014). The UK study provides a holistic approach to quantifying the ecological impact of ash dieback specifically in terms of the identification of associated biodiversity that is impacted by the tree disease. Here we build on this foundation to: *i)* examine the biodiversity associated with ash in Sweden and their potential risk of extinction, *ii)* determine the extent to which ash-associated species could be sustained via targeted management of other host tree species native to the region, and *iii)* discuss mitigation and adaption options to conserve ash-associated biodiversity in devastated landscapes. This knowledge can help to provide practical solutions for conserving biodiversity and reduce the vulnerability of ash-occurring forest systems to extinction cascades in temperate broadleaved forests during the chronic and post-epidemic phase of this forest disease outbreak.

2. Methods

2.1. Swedish Species Information Centre (SSIC) database retrieval

In order to predict the impact of ash dieback on biodiversity, we compiled data on species associated with ash for all taxonomic guilds from the Swedish Species Information Centre (SSIC) database. SSIC is a governmental organization whose main mission is to accumulate, analyze and disseminate information concerning species and habitats in Sweden. Among the key responsibilities of SSIC is to assess and evaluate the conservation status of species, which is disseminated in the Swedish Red List.

Data in the SSIC database are compiled from scientific articles, reports, and other published material. Additional data come from an observation system gathering citizen science: the Species Observation System http://www.artportalen.se/. These data sources are compiled by 14 expert committees comprising more than 100 members in total, as well as external species experts. The species database contains assessments of species attributes, hosts, habitat, ecological traits, Red List categories, legislation and directives. More than three million evaluations of more than 2000 parameters are included in the database, which is publicly accessible https://artfakta.se/. Further description of the methods and structure of the database is given in Sundberg et al. (2019). Data were complemented with data from Dahlberg and Stokland (2004) available from Swedish Species Information Centre.

2.2. Assessing species association, conservation status, and alternative hosts

Based on previous methods for species assessments (Mitchell et al., 2014a, 2014b), all species which in some way use or depend on ash to complete their lifecycle (hereafter referred to as "*ash-associated species*") were: *i)* assessed in terms of their association with other possible native tree species, *ii)* assigned a level of association to the host tree (obligate, highly-associated or generalist; see definitions below), and *iii)* assigned a conservation status according to the current Swedish Red List (last published in 2015).

2.2.1. Level of association

Species with no recorded host tree species other than ash were considered '*obligate*'. Species with a noted preference for ash, but which were also occasionally recorded on other host trees were considered '*highly-associated*', i.e. 25–100% of the population uses ash as a host tree. All other species utilizing ash and other tree species without any noted host preference were considered '*generalist*' species (defined as 5–25% of the population that uses ash as a host tree).

2.2.2. Conservation status

The conservation status of ash-associated species is in accordance with the Swedish Red List (Artdatabanken, 2015), which uses the same criteria as the International Union for Conservation of Nature (IUCN) for the purpose of creating an easy, understandable and commonly acknowledged system for classification of species' risk of extinction. The Red List includes the following categories: Regionally Extinct (RE), Critically endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least concern (LC), Not Evaluated (NE), Not Applicable (NA) and Data Deficient (DD) (Table S1) (Gärdenfors, 2014). In Sweden, approximately 21,600 of the 50,000 native multi-cellular species are assessed according to these criteria. Of those, 2029 are assigned to one of the "threatened" Red List categories: CR, EN or VU. Criteria for categorizing a species as CR, EN or VU includes population decline or a combination of very small populations, fragmentation of habitat or extreme population fluctuations (Table S2) (Gärdenfors, 2014).

2.2.3. Alternative hosts

Alternative hosts included living or dead, native or established trees from which ash-associated species were also recorded. These included *Acer platanoides*, *Alnus* spp., *Betula* spp., *Corylus avellana*, *Fagus sylvatica*, *Juniperus communis*, *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Prunus spp.*, *Quercus* spp., *Salix* spp., *Sorbus aucuparia*, *Ulmus* spp. and *Tilia* spp. All ash-associated species without obligate status were also assigned a level of association to each alternative host tree species as either: '*highly-associated*' if the tree has significant importance for the species (where 25–100% of the population uses the host tree species), or 'generalist' if the tree is merely utilized by the species (5–25% of the population uses it).

2.2.4. Species substrate utilization

The parts of the tree used by ash-associated species were assigned to one of two categories: 'wood' or 'non-wood' based on what is known about the species habitat requirements. 'Wood' included both bark and living and dead wood. When known, the species' habitat preference for either substrate was recorded. 'Non-wood' included leaves, flowers, and roots.

2.3. Extinction risk analysis

Predicting the impact of ash dieback on ash-associated organisms is a function of: *i*) the level of association an organism has with ash, and *ii*) its conservation status (Mitchell et al., 2014b). In order to prioritize which species could be at most risk of extinction, these two factors were combined into an Extinction Risk Analysis. We also considered that generalist species could be directly affected by large-scale population decline of ash if they have a high threatened conservation status, or vice versa. Ash-associated species were grouped into three Extinction Risk categories: High, Medium and Low. *High Extinction Risk* includes obligate species or those associated with only ash and elm (irrespective of conservation status due to the higher risk of extinction as both host trees are Red-listed species) and highly-associated species having a conservation status CR, EN or VU (Artdatabanken, 2015). *Medium Extinction Risk* includes highly-associated species but of 'lower conservation concern' (NT and LC categories) and 'threatened' generalist species. *Low Extinction Risk* includes generalist species with low conservation concern. Uncertain or non-evaluated species (categories DD, NA and NE) were not considered unless the species were obligate to ash or associated with only ash and elm. Extinct species (category RE), species with uncertain conservation status, or where conservation status is not applicable, such as non-native species, were not included in the analysis.

2.4. Modelling of alternative host trees for ash-associated species

To identify the minimum number of alternative host tree species that could retain all non-obligate ash-associated species in the absence of ash and elm, we used an optimization model originally developed for reserve selection, i.e. a maximal covering location problem commonly used by conservation planners for selecting or protecting sites based on the coverage of a species for suitable habitat (Church et al., 1996). The mathematical formulation of the problem in this study is as follows:

$$\text{Max } Z_1 = \sum_{j}^{J} y_j \tag{1}$$

Subject to:

$$\sum_{i=1}^{I} a_{ij} x_i \geq y_j \ \forall \ j \in J \tag{2}$$

$$\sum_{i=1}^{I} x_i \leq m \tag{3}$$

$$x_i = \{0, 1\} \tag{4}$$

$$y_j = \{0, 1\} \tag{5}$$

Z_1 = the number of ash-associated species covered by the set.
x_i = equals 1 if host tree species i is selected and equals 0 if not,
y_j = equals 1 if ash-associated species, j is covered by the selected tree species.
a_{ij} = equals 1 if ash-associated species, j is present in host tree species i otherwise a_{ij} equals 0.
m = the maximal number of host tree species that could be selected.

Eq. (1) attempts to maximize the number of different ash-associated species. Eq. (2) together with Eq. (5) ensures that $y_j = 1$ only if ash-associated species j is present in some of the selected tree species. Eq. (3) limits the total number of tree species that could be selected. Eqs. (4) and (5) ensure that x_i and y_j only could take the value of 1 or 0, i.e. either the species is selected (or covered) or not. The models were formulated within the Heureka PlanWise system using the ZIMPL optimization language (Koch, 2005) and solved using Gurobi 6.0 with integer programming using a traditional branch and bound algorithm. The approach considered all ash-associated species which are able to utilize host tree species other than ash and elm. The model was run repetitively for values on m (maximal number of host tree species that could be selected) from 1 to 9 which was the number of tree species needed to cover all ash-associated species ($n = 412$) for 14 tree species: *Quercus* spp. *Fagus sylvatica*, *Populus tremula*, *Acer platanoides*, *Betula* spp., *Tilia* spp. *Salix* spp., *Alnus* spp., *Sorbus aucuparia*, *Corylus avellana*, *Picea abies*, *Pinus sylvestris*, *Prunus* spp. and *Juniperus communis*.

3. Results

3.1. Ash-associated organisms

In total, 483 species are associated with ash in Sweden. Of all ash-associated species, 260 are invertebrates (211 beetles, 30 butterflies, 9 Diptera, 6 Hemiptera, 3 grasshoppers, and 1 snail), 87 are lichens, 71 are bryophytes and 65 are fungi. No birds, mammals or vascular plants are associated with ash in the SSIC database. Of the total number of ash-associated species, 52 are considered obligate, i.e. only utilizing ash as a substrate (4 fungi, 3 bryophytes, 43 invertebrates and 2 lichens). More than double the number of species ($n = 112$) were highly associated to ash and 19 of those (17%) were associated with both ash and elm (10

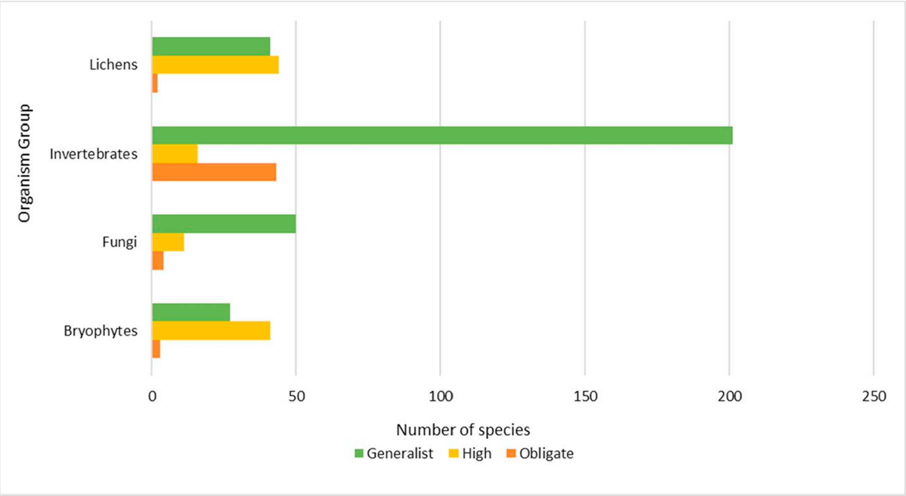

Fig. 1. Number of species in different organism groups and their different level of association (generalist, high, obligate) with *F. excelsior*.

bryophytes, 5 lichens, 3 fungi and 1 insect species). Generalists were represented by 319 species (Fig. 1).

3.2. Species utilization

Among all 483 ash-associated species, 90% (*n* = 437) use the wood of the tree. Of those wood dwelling species, 24% (*n* = 104) are exclusively found on living wood and 35% (*n* = 154) use only dead wood. Thirty-three percent (*n* = 144) of species can utilize both dead and living wood, whereas the remaining wood-dwelling species have no assigned preference in the SSIC database. Seven percent of ash-associated species (*n* = 36), almost exclusively insects, have a known preference for non-woody tissue.

3.3. Conservation status

Of all ash-associated species evaluated in Red-List categories (*n* = 460), 122 are 'threatened', whereas 333 are of 'lower conservation concern', and five species are regionally extinct (Table 1). The Extinction Risk Analysis, which prioritizes the threat to different ash-associated species, indicated that of the 462 applicable species, 115 are considered to be at High Extinction Risk, 111 species at Medium Extinction Risk and 236 species at Low Extinction Risk (Table 2). Species at large risk of extinction are those that are obligate to ash, or associated with only ash and elm (Table S3). These include a large proportion of Lepidoptera (e.g. *Caloptilia cuculipennella*), and Hemiptera (e.g. *Anthocoris amplicollis*), and a few Coleoptera (e.g. *Agrilus convexicollis*). Several lichens ranked as being at high extinction risk were not only associated with ash or elm. Among all taxonomic groups, several species of currently low conservation concern ranked high for extinction risk due to their obligate association with ash.

3.4. Alternative host trees

Among all other possible host trees utilized by ash-associated species (i.e. by generalists or highly associated species), *Ulmus* spp. and *Quercus* were found to host the largest number of species (*n* = 296 for both), followed by *F. sylvatica* (*n* = 275) and *P. tremula* (*n* = 273) (Fig. 2). However, many ash-associated species have a *preferred* alternative host to which they are considered 'highly-associated'. Among ash-associated organisms, the largest numbers were highly-associated with *Ulmus* spp. (*n* = 98), followed by *Quercus* spp. (*n* = 85), *F. sylvatica* (*n* = 83), and *P. tremula* (*n* = 73) (Fig. 2).

Using the optimization model formulated as a maximal covering location problem, we identified the minimum number of alternative host tree species required to sustain all ash-associated species in the absence of ash and elm (412 of the total 483 species; i.e. excluding species that are obligate to ash and species only able to utilize ash and elm). Of the 14 tree species included in the model, a minimum of nine would be sufficient to maintain the current non-obligate ash-associated biodiversity in the absence of both ash and elm; *A. platanoides*, *Betula* spp., *C. avellana*, *F. sylvatica*, *P. abies*, *P. sylvestris*, *P. tremula*, *S. aucuparia* and *Quercus* spp. (Fig. 3). Among these, *Quercus* spp., *Populus tremula*, *Acer platanoides* and *Fagus sylvatica* could together sustain 95% of the ash-associated biodiversity.

Table 1
Number of species in each organism group per level of association with *F. excelsior* and conservation status.

	Regionally extinct[a]	Threatened[b]	Lower conservation concern[c]
Bryophytes			
Obligate			3
High	1	5	32
Generalist		2	20
Fungi			
Obligate	1		1
High		5	5
Generalist		7	40
Invertebrates			
Obligate		5	34
High		4	12
Generalist	3	32	162
Lichens			
Obligate		2	
High		35	9
Generalist		25	15
Total[d]	5	122	333

[a] The last living individual in Sweden has without a doubt died.
[b] Red List categories Critically Endangered, Endangered and Vulnerable.
[c] Red List categories Nearly Threatened and Least Concern.
[d] Among the 23 species not included in this analysis, 12 were categorized as NA, 3 as NE and 8 as DD.

4. Discussion

We found that 11% of ash-associated species are obligate on ash and a further 23% are classified as highly-associated with ash on the basis that they prefer ash over other tree species. Since 2018, the number of highly associated species has increased due to an increase in the number of fungi evaluated – a reflection of the dynamic SSIC database,

Table 2
Number of species in Extinction Risk groups with respect to the impact of *F. excelsior* dieback[a]. High extinction Risk: threatened species obligate to *F. excelsior*, highly associated with *F. excelsior* or associated with ash and elm only. Medium Extinction Risk: species highly associated with *F. excelsior* but with low conservation concern, or threatened generalist species. Low Extinction Risk: generalist species with low conservation concern.

	Extinction risk			Total
	High	Medium	Low	
Bryophytes	19	25	19	63
Fungi	11	9	40	60
Invertebrates	48	43	162	253
Lichens	37	34	15	86
Total	115	111	236	462

[a] Among the 21 species not included in this analysis, 8 were categorized as NA, 1 as NE and 7 as DD. Five species were classified as RE. Note that species obligate to ash, or dependent on ash and elm only, are classified as High Extinction Risk, regardless of Red List Category.

though most of those species are of lower conservation concern. In this regard, the Swedish Red-List is currently being revised for publication in 2020, and includes changes to the red list categories for 15 species with a high preference for ash. Relative to the 2015 Swedish Red-list, on which this study was based, the status of nine species will be elevated to a higher risk category, including four from VU to RE, and six species will go down to a lower conservation status.

Based on both the species' level of association with the host tree and its known conservation status, approximately 24% ($n = 115$) of ash-associated species are considered to be at high risk of regional extinction; where 'regional' in this context is at the national level (Sweden). (Table S3). The extinction risk for ash-associated species was estimated to be high especially for lichens. For this taxonomic group, over 40% of species were classified as being at high extinction risk (Table 2). Earlier studies have also shown that the populations of epiphytic lichens have experienced significant reductions in species composition and richness as an indirect effect of ash dieback (Jönsson and Thor, 2012; Ellis et al., 2013; Broome et al., 2014; Lõhmus and Runnel, 2014). Lichens, as multi-species symbioses, are known to have narrow ecological amplitudes and many of the species are substrate obligates (Resl et al., 2018). The detailed causes of substrate specificity in lichens are still not known, but both carbohydrate sourcing and chemical environment (cation ratios and pH) may play a role (van Herk, 2001; Resl et al., 2018). However, ash dieback cannot be the only attributable factor affecting lichen extinction risk since several (mostly generalist) lichens already have a high threatened status (Table S3).

Bryophytes were another taxonomic group with a high proportion of species (30%) in the high extinction risk category (Table 2). Substrate diversity, along with the micro-habitat formed by stand structure (tree species diversity) is more important for bryophyte species diversity than spatial processes and topography (Chen et al., 2017). Compared to lichens and bryophytes, the proportion of species in the high extinction risk category was lower for fungi and insects, at approximately 20%. However, this proportion is still sufficiently high for biodiversity losses to be significant, as could the ecological impacts, due to the important functional roles these groups have in temperate forest ecosystems. If ash tree mortality continues, it is therefore highly probable that the resultant loss of resources and habitat will cause a corresponding population decline in a range of species with obligate and high-association with ash in the future. Among those, the threat is likely to be even more urgent to species which already have a high conservation concern (VU, EN or CR) due to other factors than ash decline. These species include e.g. the Spanish fly *Lytta vesicatoria* (CR), the false darkling beetle *Melandrya caraboides* (EN), the snout beetle *Rhycolus punctatus* (VU), and the lichens *Anthonia cinnabarina* (CR), *Bacidia auerswaldii* (CR) and *Calogaya lobulata* (CR).

However, conservation status is not the only important factor when predicting the risk of extinction. For example, several species such as the long horn beetle *Tetrops starkii,* the ash bud moths *Prays fraxinellus* or *Prays ruficeps,* or the dusky thorn *Ennomos fuscantaria* have a high extinction risk despite low conservation concern since they are obligate to ash. Thus, efforts may need to consider not only a species conservation status but also common but obligate species for which losing their sole host may ultimately imperil their survival. Other species identified here as having obligate associations with ash like the privet hawkmoth *Sphinx ligustri*, the feathered slender moth *Caloptilia cuculipennella*, the tortrix moth *Pseudargyrotoza conwagana*, and possibly the coronet moth *Craniophora ligustri*, are however able to utilize ornamental plants related to *Fraxinus* (Oleaceae), such as *Syringa* (lilac) and *Ligustrum* (privet). As such, urban parks and gardens may become important environments for their conservation. In the UK, privet has even been suggested to be utilized more widely in order to host organisms associated with ash (Broome et al., 2014).

Invasive alien species are largely contributing to global biodiversity loss. Although estimations of extinction cascades associated with invasive alien species are rare in the literature, evidence from the recent

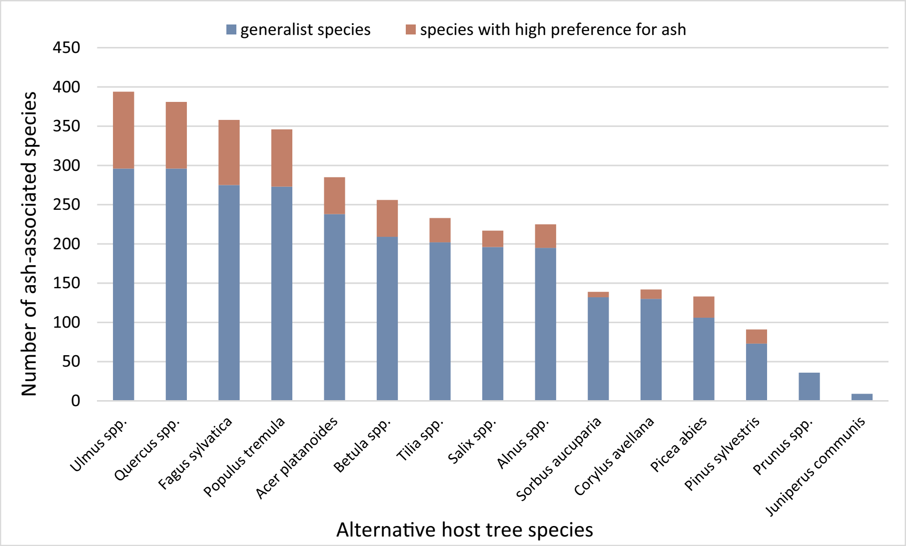

Fig. 2. Alternative tree hosts preferred by ash-associated generalist species and species with high preference for ash.

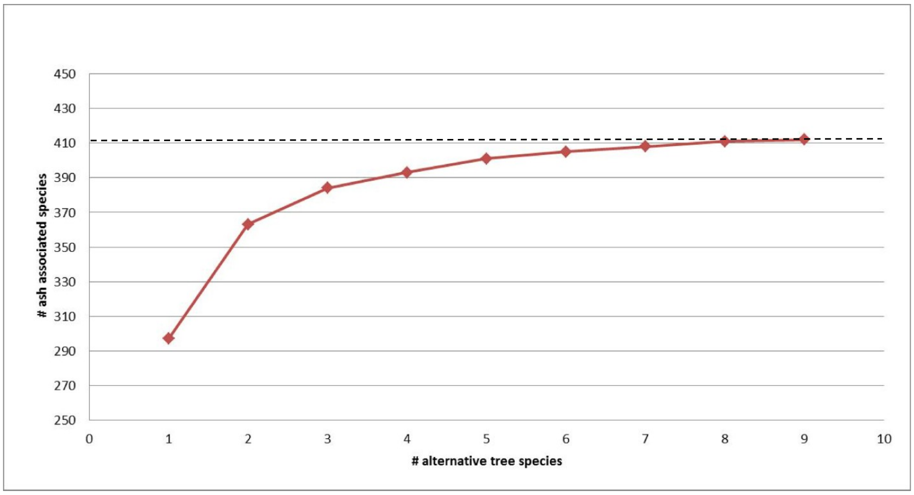

Fig. 3. An accumulation curve illustrating the number of alternative tree species required to support non-obligate ash-associated species other than those reliant solely on ash and elm (412 of the total 483 species). Tree species included in the model are *Quercus* spp. *Fagus sylvatica*, *Populus tremula, Acer platanoides*, *Betula* spp., *Tilia* spp. *Salix* spp., *Alnus* spp., *Sorbus aucuparia, Corylus avellana, Picea abies*, *Pinus sylvestris*, *Prunus* spp. and *Juniperus communis*. Dotted line, $n = 412$.

IPBES (2019) report suggest that the average abundance of native plants, animals and insects has fallen in most major ecosystems by at least 20% since 1900 because of invasive species (Tollefson, 2019). The dependency and interconnectedness of species negatively affected by the loss of whole tree populations has received too little attention in the past. Ash is notably a ‘keystone species’ and has critical importance for biodiversity and the functioning of temperate broadleaved ecosystems. We argue that ash dieback in Sweden poses the serious risk of instigating an extinction cascade. We make this case because of: *i)* the 52 species that are *obligate* (and therefore ash dependent), *ii)* the 112 species that are *highly associated* with ash, and *iii)* the 56 species belonging to either of these categories that are already threatened with extinction (two additional species are already regionally extinct). This study is a first attempt to identify target groups from which cascade effects could be quantified through more precise monitoring of species.

Currently, the possibilities to eradicate an established disease such as ash dieback from the landscape are limited. Fungicides are not an option for landscape scale forest management, and attempts to develop biological control of ash dieback have so far failed (Schlegel et al., 2016). Nevertheless, several options to minimize the ecological impact of ash dieback on associated biodiversity seem feasible.

Our study shows that ash has a high proportion of associated species using woody parts in relation to non-woody, due to a large proportion of bryophytes and lichens living on bark. This proportion is notably highest in ash compared to other trees species in Sweden (Sundberg et al., 2019). Among the obligate species, at least eight are able to utilize dead wood which emphasizes the importance of conserving woody substrate, including fallen standing trees, branches and stumps. In areas where declining trees do not constitute a safety risk, an important management goal to promote biodiversity should thus be to focus on retaining dying and dead trees for as long as possible (Mitchell et al., 2014b). The surplus of dead wood created by ash dieback-induced mortality may have a positive effect on associated biodiversity, but this effect will likely be short-lived (Heilmann-Clausen et al., 2013; Pautasso et al., 2013), and it neglects the significant proportion of ash-associated species (24%) that depend on living trees. Therefore, in areas where declining but still living trees do not constitute an immediate safety risk, the aim should be to retain them as long as possible, avoiding non-selective sanitary cuttings that risks also removing tolerant genotypes that could be utilized in breeding, and ensuring natural regeneration from the surviving trees.

If ash cannot be saved, but its decline only slowed, another option is to establish alternative tree species that can support the habitat requirements for ash-preferring and generalist species (Mitchell et al., 2016). We found that a large proportion of highly-associated species (17%) are limited to elm trees as their alternative host; this proportion is much larger than was associated with any other tree species paired to ash. A similar pattern of shared species between ash and elm has been shown in the UK (Broome et al., 2014; Sundberg et al., 2019). Unfortunately, elm is critically threatened due to Dutch elm disease spread by the vector beetle *Scolytus* sp. The populations of many species dually associated with ash and elm are also expected to decline, especially those that are associated with coarse bark on older trees (i.e. lichens and mosses) (Sundberg et al., 2019).

In the absence of both ash and elm, maximizing retention of ash-associated biodiversity using other tree species would promote alternative substrates for ash-associated species. In this study, nine tree species were identified as the minimum number needed to retain the maximal number of ash-associated species. Among these, *Quercus* spp., *P. tremula*, *A. pseudoplatanus* and *F. sylvatica,* together, support more than 95% of the ash-associated species. These broadleaves together account for less than 4% of the standing volume in Swedish forests (Nilsson et al., 2019). The most commercially important species in Sweden, *Pinus sylvestris* and *Picea abies*, together, hosted only four ash-associated species that were unable to use any other tree species in this analysis. Mitchell et al. (2014b, 2016) found that the tree species most resembling ash's ecological functions include *Acer campestre*, *Alnus glutinosa* and *Acer pseudoplatanus*. Currently *Acer* species constitute a minor component of the species composition of forests in northern Europe, and in Sweden *A. campestre* and *A. platanoides* together constitute only 0.1% of the growing stock on productive forest land (Fridman and Wulff, 2018) - but could be of great interest for biodiversity conservation in the future, and potentially also for production purposes (Hein et al., 2009). Due to its sometimes aggressive dispersal, *Acer pseudoplatanus* is avoided (Fries, 2015). *Acer* however is not the only alternative.

The use of multi-species tree mixtures as a tool in biodiversity conservation is challenged by the diverging biological requirements of species, poor adherence to economic forest management goals, but also by the legislation. In Sweden, the biologically valuable temperate broadleaved forest is required by law to remain dominated by temperate broadleaves. In other words, if such a forest is harvested, or otherwise lost, it must be regenerated with temperate broadleaved trees. When mature ash and elm are killed by alien invasive forest pathogens, light conditions might once again be favourable for regeneration of oak in temperate broadleaved forests (Brunet et al., 2014), which could serve as an ecological niche substitute only for some non-obligate ash-associated species. As many ash-associated species are highly dependent on several other broadleaves besides ash, the connectivity among temperate broadleaved stands, and stands currently dominated by ash, is crucial in order to facilitate migration of ash-associated species. Promotion of temperate broadleaves in general and the connectivity among temperate broadleaved stands, would also benefit the many currently threatened species associated with these tree species (Berg et al., 1994; Dahlberg and Stokland, 2004; Tikkanen et al., 2006) and the resilience of temperate broadleaved ecosystems (Loreau et al., 2001; Drever et al., 2006; Thompson et al., 2009).

Finally, breeding for disease resistance is considered to be a sustainable, long-term strategy, and perhaps the most desirable option, to reduce the risk of local extirpation of ash and its associated species. Studies from around Europe show a strong genetic basic for resistance in ash to *H. fraxineus* which is inheritable, but only a small percentage (1–5%) of the natural population shows disease tolerance (Stener, 2013; McKinney et al., 2014; Pliura et al., 2014). Since 2014, some small steps have been made to establish a breeding population of resistant ash in Sweden and to establish clonal archives for gene conservation (Cleary et al., 2017). However, the Swedish test populations are small and the work is largely curtailed by the lack of resources, responsive governance, and institutional accountability to prioritize resistance breeding to save this ecologically important tree species from further demise. Coordinated efforts and long-term planning are urgently needed to advance research and expedite operational breeding, using e.g. advanced phenotyping technologies (Villari et al., 2018) or genomics (Sollars et al., 2017), that will allow the deployment of resistant individuals and ash restoration across a diversity of landscapes. To avoid the regional extinction of the large number of threatened species associated to ash (especially those with *obligate* associations), support for genetic improvement of ash and restoration efforts at landscape and regional scales is urgently needed. Without active intervention and restoration with resistant genotypes, ash will eventually be replaced by other tree species, as natural regeneration of ash affected by ash dieback is inferior to other tree species (Lygis et al., 2014).

5. Conclusions

Nearly a decade after the first reporting of *H. fraxineus* to Sweden, ash became a Red-listed species and five years thereafter its status worsened to become endangered. The chronic situation of annual infections, disease intensification and mortality suggests a realistic scenario of ash being elevated to *critically* endangered status in the future. The ecological implications of the current and future scenario are grave due to the potential for an extinction cascade to occur, whereby a domino effect from the loss of ash will lead to secondary extinctions of other (obligate and highly-associated) species for which ash (and alternatively elm) serve as an important niche habitat. Experiences elsewhere stress the need to act fast to help avoid extinction (Martin et al., 2012). There is also a need for a more systematic environmental monitoring of ash decline impacts on associated biodiversity because at present, temporal stability probably exists only for a few limited species in local settings. Importantly, this study provides a basis from which targeted monitoring could be done to track the rate of decline in those species ranked as having high extinction risk due to their obligate or high association with ash (and elm), and those obligate species whose conservation status is currently near threatened (NT) or of low concern (LC), since anticipated further losses of ash trees will drive their status into threatened categories in the future. Understanding those critical 'rivet-like' thresholds (Dunne et al., 2002; Ehrlich and Ehrlich, 1981) at which species display extreme sensitivity to the removal of ash and for which losses could subsequently trigger an extinction cascade, is fundamental to implementing timely mitigation and adaptation actions. In addition, more efforts at landscape analysis (using remote sensing and laser scanning tools) is needed to monitor vegetation and help avoid fragmentation of affected species association with ash. The bureaucratic responsibility and allocation of resources for dealing with the negative effects of invasive species affecting biodiversity needs to be clarified to enable efficient implementation of conservation strategies. Although the low commercial interest in tree species such as ash places the issue low on the political agenda, a broader concern should be elevated to the value of *keystone* species in supporting a large number of species populations.

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CRediT authorship contribution statement

Tove Hultberg: Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Jonas Sandström:** Resources, Data curation, Writing - review & editing. **Adam Felton:** Writing - review & editing. **Karin Öhman:** Methodology, Formal analysis, Writing - review & editing. **Jonas Rönnberg:** Writing - review & editing. **Johanna Witzell:** Writing - review & editing. **Michelle Cleary:** Conceptualization, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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